Cultural eutrophication, anoxia, and ecosystem recovery in Meretta Lake, High Arctic Canada

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Abstract

We studied the effects of four decades of cultural eutrophication on Meretta Lake, in the Canadian High Arctic, through a multiproxy analysis of its sediments, including sedimentary pigments, metal concentrations, stable isotope ratios, chironomids, and diatoms. While Meretta Lake's biota clearly responded to nutrient inputs, the manner in which the changes differed from those expected in temperate lakes underlined the profound effects in Arctic lakes of extended ice and snow cover on light penetration, mixing, and interactions with the atmosphere. Hypolimnetic anoxia developed rapidly in Meretta Lake in response to sewage enrichment and was accompanied by the appearance of photosynthetic sulfur bacteria. Benthic communities responded rapidly to sewage inputs, but phytoplankton biomass did not increase until eutrophication was accompanied by climate warming, further reinforcing the importance of ice cover in controlling biotic processes in high Arctic lakes. With climate-mediated ice cover reductions in Meretta Lake, the response to eutrophication began to more closely resemble temperate processes. Recent trajectories indicate that slightly more than a decade after the cessation of sewage inputs, Meretta Lake is recovering toward pre-enrichment conditions.

Cultural eutrophication, the fertilization of lakes due to anthropogenic nutrient inputs, has affected lakes on a global scale. While relatively common in lower-latitude ecosystems, cultural eutrophication has been limited in scope in the polar regions as a result of the generally lesser effects of human activities at high latitudes. However, as growth and development continue around the Arctic, the freshwaters of the region will be increasingly subject to human-induced eutrophication (Schindler and Smol 2006). Increased nutrient influx to lakes—and therefore higher trophic status—is also among the predicted effects of climate warming in Arctic aquatic ecosystems independent of point-source pollution (Prowse et al. 2006). Some degree of eutrophication is therefore probable in most Arctic lakes in the future, and understanding the effects of these trophic increases is a critical element of predicting future limnological change across the Arctic.

Eutrophication has pervasive effects on aquatic ecosystems, including increased algal biomass, oxygen depletion, the development of potentially toxic algal blooms, and the degradation of potable water supplies (Smith and Schindler 2009). While different from the ecological effects in temperate ecosystems, dramatic responses of Arctic phytoplankton to anthropogenic fertilization have been observed (Schindler et al. 1974; Holmgren 1984; Welch et al. 1989).

However, several characteristics that distinguish Arctic lakes from their temperate counterparts have important implications for eutrophication-related processes, including the duration of thick ice cover and its control of light penetration and plankton dynamics, and the disproportionate importance of benthic communities in lake food webs (Sierszen et al. 2003; Smol and Douglas 2007). While the benthos often dominates production in polar lakes (Vincent and Laybourn-Parry 2008), the response of these communities to eutrophication is poorly understood relative to that of the plankton (Vadeboncoeur et al. 2003). A better understanding of the effects of eutrophication in Arctic aquatic ecosystems is therefore clearly required.

While there have been few comprehensive studies of Arctic limnology, Meretta Lake was examined during the International Biological Programme (IBP) of the 1970s. The limnological interest in Meretta Lake was, and still is, driven by the inputs of human sewage that it received for nearly four decades and the attendant rare opportunity to study eutrophication in a high Arctic lake. Past studies of Meretta Lake have included those on general limnology and the effects of eutrophication (Schindler et al. 1974), phytoplankton ecology (Kalff and Welch 1974; Kalff et al. 1975), bacterial dynamics (Morgan and Kalff 1972), rates of photosynthesis and respiration (Welch 1974), and diatom paleolimnology (Douglas and Smol 2000; Miche-

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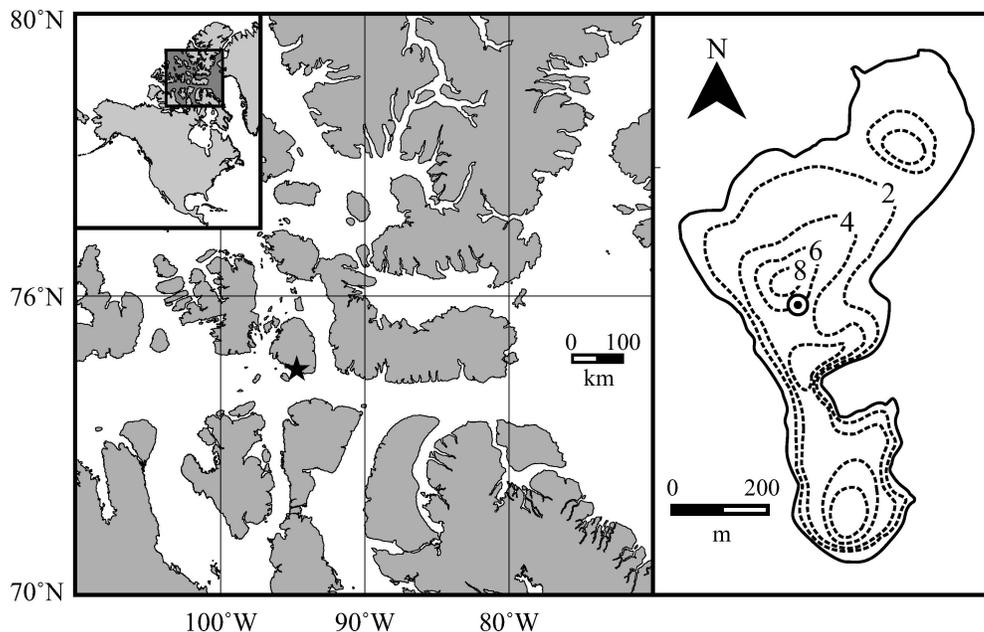* Corresponding author: dermot.antoniades@cen.ulaval.ca

Fig. 1.   Location map of Meretta Lake and Cornwallis Island in the Canadian High Arctic. Bathymetric data are from Schindler et al. (1974). The star represents the location of Resolute Bay, and the circle in the right panel represents the coring site.

lutti et al. 2002). Although few studies exist from Arctic sites that chronicle long-term limnological responses to cultural eutrophication (Douglas and Smol 2000; Michelutti et al. 2007), paleolimnology is ideally suited to reconstructing past changes in such lakes (Smol 2008) and, thereby, to providing insight into both past variability and future limnological trajectories in polar freshwaters.

Our objective was to investigate long-term limnological change in Meretta Lake through a multiproxy analysis of phytoplankton, phytobenthos, and benthic invertebrates in the sedimentary record. To this end, we examined photosynthetic pigments, metal concentrations, stable isotopes of carbon (C) and nitrogen (N), organic matter (OM) content, subfossil chironomids, and diatoms in a ^{210}Pb-dated sediment core to develop a comprehensive picture of the effects of eutrophication due to sewage inputs in Meretta Lake and to detect possible limnological records of recovery.

Methods

Site description—Meretta Lake (74°42′N, 94°59′W) is a 0.26-km² lake located in the hamlet of Resolute Bay (Qausuittuq), Nunavut, on Cornwallis Island in the Canadian High Arctic (Fig. 1). Resolute Bay has a polar desert climate, with a mean annual temperature (MAT) of −16.4°C and mean annual precipitation of 150 mm (Environment Canada 2010). A weather station was established in Resolute Bay during the summer of 1947, and an air base was constructed in 1949. Between 1949 and 1998, sewage from the base at Resolute Bay was released untreated into the environment, with Meretta Lake as its ultimate destination (Masemann 1971; Douglas and Smol 2000). Until 1979, the sewage was discharged from two

outlets and traveled 1.6 km through a series of streams and small ponds before reaching Meretta Lake. As a result of diminishing use, one outlet was dismantled in 1979, whereupon the sewage entered Meretta Lake via a more direct route through a stream (Schindler et al. 1974; Douglas and Smol 2000).

Sample collection—We cored Meretta Lake on 08 June 2008 using an Aquatic Research Instruments gravity corer with a polycarbonate coring tube of 69-mm internal diameter. The 12.5-cm core was taken through 2.2 m of ice at 74°41.71′N, 94°59.66′W at a depth of 5 m. The core was transported whole, cold and in the dark, to the laboratory, where it was immediately split lengthwise and sectioned at 0.25-cm intervals.

Pigment analysis—All sample preparation for pigments was performed in the dark or under green light to minimize degradation. Prior to analysis, sediments were freeze-dried for 24 h. Samples of approximately 0.1 g dry weight (g dry wt) were weighed and extracted for high-performance liquid chromatography (HPLC) pigment analysis by addition of 2 mL 100% acetone, placed under argon, and left for 24 h in a freezer. These samples were then cleared by centrifugation and filtered into vials through 2-μm polytetrafluoroethylene filters. Argon was again added to the vials, and the extracts were immediately injected into a Varian ProStar HPLC system equipped with a Symmetry C8 column (3.5-μm pore size), a photodiode array, and a programmable fluorescence detector. The solvent protocol followed Zapata et al. (2000), but with a modified flow rate of 0.7 mL m^{-1} and a total run time of 34 min. Carotenoids and bacteriochlorophylls were detected by diode-array spectroscopy (350–750 nm) set to a slit width of 2 nm,

while all other chlorophylls were detected by fluorescence (excitation 440 nm; emission 650 nm). Absorbance chromatograms were obtained at 450 nm for carotenoids and at 476 nm for bacteriochlorophylls. Pigments were identified and quantified using standards from Sigma Chemical: chlorophylls *a* (Chl *a*) and *b*, β,β-carotene; and DHI Water and Environment: chlorophyll *c2*, diadinoxanthin, echinenone, fucoxanthin, lutein, and zeaxanthin. For bacteriochlorophyll *e* (BChl *e*), isorenieratene, and β-isorenieratene, identification and quantification was done by comparison with published spectra, retention times, and extinction coefficients (Hurley and Watras 1991; Borrego et al. 1999). Concentrations of unidentified carotenoids were calculated using the extinction coefficient for β,β-carotene, while those of chlorophyll degradation products were calculated using our calibration coefficients for their respective undegraded chlorophylls. Sediment Chl *a* was also inferred using visible reflectance spectroscopy with a Foss Near Infrared Systems Model 6500 series Rapid Content Analyzer (Tidestone Technologies), following the methods described by Michelutti et al. (2010). Sedimentary pigment concentrations are expressed relative to the OM content of sediment (i.e., mg g^{-1} OM^{-1}).

Isotopes, sedimentary OM, and metals—For elemental and isotopic analysis of N and C, sediments were freeze-dried and acid-fumigated to remove carbonates. Between 5 and 20 mg of freeze-dried sediments were weighed into small tin boats and flash combusted at $1800°C$ in an elemental analyzer (EA 1110, CE Instruments). The resulting gases were carried via helium and separated into N_2 and CO_2 and were carried into an isotope ratio mass spectrometer (DeltaPlus Advantage, ThermoFinnigan) for isotope analysis via a Conflo interface (Conflo III). Stable isotope values are reported in δ notation using parts per thousand units (‰) and are defined as $\delta = [(R_{sample}/R_{standard}) - 1] \times 1000$. We determined that acid fumigation did not affect the isotopic composition of N in sediments. Replicate samples were run, and an average precision of 0.14‰ was achieved for $\delta^{13}C$ ($n = 5$) and of 0.25‰ for $\delta^{15}N$ ($n = 5$). C : N ratios were calculated as the atomic ratio of organic C to total N.

For metals analysis, weighed samples of $\sim$ 0.5–1 g dry wt were pulverized with a ceramic mortar and pestle, subjected to an aqua regia digestion, and analyzed at SGS Minerals Services in Lakefield, Ontario, Canada, using inductively coupled plasma mass spectrometry and inductively coupled plasma optical emission spectrometry. Quality assurance and quality control were performed by running certified reference materials, internal standards, blanks, and duplicates with every batch of 20 samples. All metal concentrations are expressed as ratios to titanium (Ti) to account for changes in background sedimentation and diagenesis.

Microfossils—Standard methods were used for subfossil chironomid analyses (Walker 2001). This included washing a sediment subsample through a 100-μm mesh, with retained sieve residue being washed into a glass Petri dish and sifted for subfossil invertebrate remains using stereomicroscopes at 10–40× magnification. Subfossil remains

were collected using fine forceps and were then mounted on glass microscope slides using Entellan® mounting medium. Other Dipteran remains (Ceratopogonidae, Simuliidae, Chaoboridae, Culicidae) were searched for but were not found in sediment subsamples. Diatom samples were prepared by oxidation of OM with 30% H_2O_2, mounted on glass slides using Naphrax® mounting medium, and counted under oil immersion at 1000× magnification. Diatom absolute abundances were calculated using microspheres, after the method of Battarbee and Kneen (1982), and are expressed as valves per gram of OM.

Chronology—The sediment chronology was generated from ^{210}Pb activities measured by gamma spectrometry in the Centre d'études nordiques (CEN)–Université Laval dating laboratory. The age–depth model was created using the constant rate of supply (CRS) model (Appleby 2001).

Statistical analysis—One-way ANOVA was used to determine whether the mean values of proxy indicators differed significantly between the pre-enrichment, anoxic, and oxic periods. We also ran a series of multivariate analyses using standardized principal components analysis (PCA). We analyzed the following subsets of our data set: pigments (Chl *a*, pheophytin *a*, β,β-carotene, BChl *e*, isorenieratene, fucoxanthin, diatoxanthin and diadinoxanthin, lutein, alloxanthin, echinenone, and zeaxanthin); metals (aluminum [Al], calcium [Ca], cadmium [Cd], cobalt [Co], iron [Fe], potassium [K], magnesium [Mg], manganese [Mn], molybdenum [Mo], sodium [Na], lead [Pb], silicon [Si], Ti, thallium [Tl], and zinc [Zn]); chironomids (*Limnophyes*, *Micropsectra insignilobus*, *Nanocladius*, *Sergentia*, *Pseudodiamesa*, *Tanytarsus pallidicornis*, and undifferentiated Tanytarsina); and C and N variables (percent organic C, C : N, $\delta^{13}C$, and $\delta^{15}N$). These data sets were subsequently combined and run in a single standardized PCA in order to explore overall patterns of proxy indicator variation. To examine similarities between trends of Meretta Lake sedimentary Pb and Resolute Bay annual precipitation, we took averages for consecutive 5-yr periods to account for differences in the temporal resolution of the two data series and used simple linear regression to determine the strength of the relationship.

Results

Chronology—^{210}Pb activities were low throughout the Meretta Lake core, a feature characteristic of high Arctic lakes. Supported ^{210}Pb was calculated as the average activity of the three lowest core intervals. Unsupported ^{210}Pb declined sharply with depth in the sediments, and the CRS model indicated that the period of sewage inputs in Meretta Lake (i.e., after 1949) was contained in the upper 5.25 cm of the core (Fig. 2). As a result of the low overall ^{210}Pb activities the chronology was sensitive to background influences beyond the last $\sim$ 50 yr. Sedimentation was slightly more rapid in the sediments affected by sewage inputs, consistent with increased biomass and OM content due to lake fertilization.
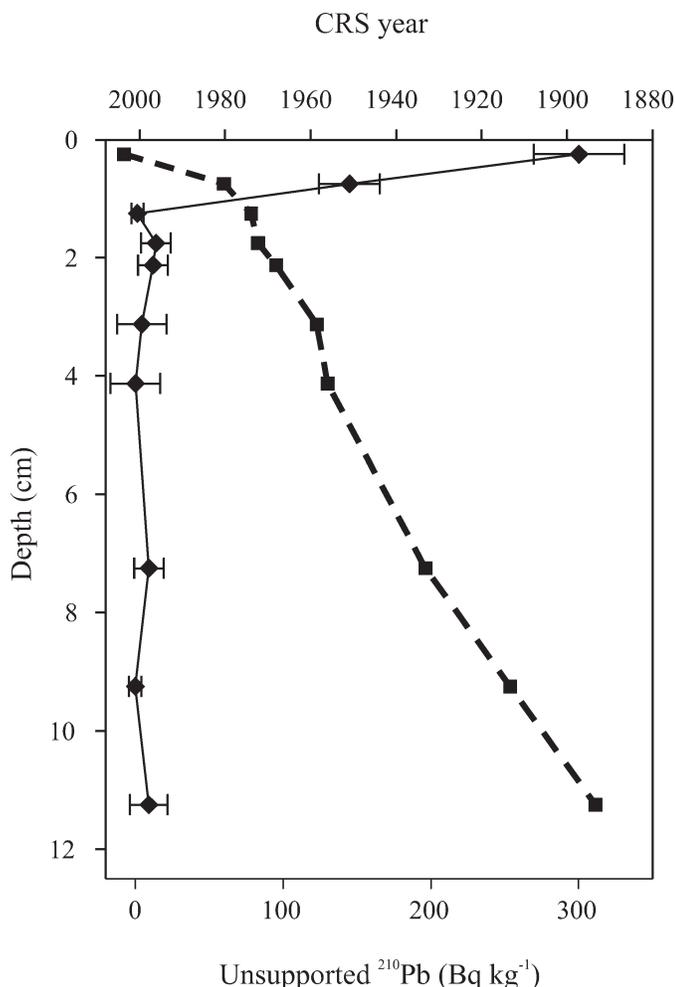
CRS year

Fig. 2. Measured unsupported ^{210}Pb activities (diamonds) and CRS model ages (squares).

Pigment analysis—HPLC analysis (Fig. 3) indicated three distinct stages in pigment composition: (1) low concentrations of all pigments from the base of the core to ~ 1949 (i.e., 12.5–5.25 cm); (2) a large increase in bacterial pigments (i.e., BChl *e* and isorenieratene) and a moderate rise in phytoplankton pigments between ~ 1949 and ~ 1972 (i.e., 5.0–1.25 cm); and (3) the disappearance of bacterial pigments and a sharp rise of phytoplankton pigments from ~ 1973 to 2008 (i.e., the upper 1.25 cm). Visible reflectance spectroscopy Chl *a* concentrations were highly correlated with HPLC Chl *a* ($r = 0.90$, df = 31, $p < 0.001$; Fig. 3). Although concentrations of most pigments declined in the surface sediments, we are hesitant to infer a trend based on a single data point.

Metals—Metal concentrations generally followed one of two distinct trends (Fig. 4). The first group, including Cd, Co, and Tl, had slowly changing, low values before ~ 1949, rose rapidly thereafter, and then declined after ~ 1970. These metals were correlated with BChl *e* ($r = 0.81$, 0.69, and 0.72, respectively; df = 27, $p < 0.001$). The second group changed slightly after ~ 1949, and this change was followed by pronounced shifts after ~ 1970. Metals

including Al, Na, Pb, and Zn increased at these horizons, while Ca and Mg decreased (Fig. 4). The trends of many of these metals then reversed in the uppermost sediments (Fig. 4). Fe concentrations were distinct, with decreases after ~ 1949 and recovery to pre-enrichment levels beginning ~ 1970. There was a significant negative relationship between Fe and BChl *e* ($r = 0.72$, df = 27, $p < 0.001$). Mn concentrations were low and generally declined throughout the core, while Fe : Mn ratios were stable until a rise after ~ 1970, followed by a decrease in the surface sediment (Fig. 4).

Total organic C (TOC), C : N, δ^{13}C and δ^{15}N—There was little variation in percent TOC, with slight increases toward the core surface (Fig. 5). Atomic C : N ratios varied from 47.7 at the base of the core to 10.8 in the surface sediments, with relatively stable values until ~ 1965 and sharp decreases thereafter (Fig. 5). There was no significant change in mean C : N between the periods of ~ 1880–1949 and 1949–1972, but there was a significant decrease ($F_{18} = 29.8$, $p < 0.001$) between the periods 1949–1972 and ~ 1973–present. Mean pre-enrichment δ^{13}C was -5.0‰ ± 1.3‰, with a gradual shift toward more negative δ^{13}C ratios after ~ 1957 and a pronounced shift of a further ~ 10‰ after ~ 1972. One-way ANOVA indicated significant differences ($F_{18} = 131.6$, $p < 0.001$) between the means of samples from ~ 1880–1957, ~ 1957–1972, and ~ 1973–present. δ^{15}N had a pre-enrichment mean of 9.2‰ ± 0.2‰, subtle changes toward lower values after ~ 1949, and a more pronounced shift after ~ 1972 to a surface minimum of 5.9‰. ANOVA indicated significant ($F_{18} = 49.4$, $p < 0.001$) differences between sample groupings ~ 1880–1949, ~ 1949–1972, and ~ 1973–present.

Microfossils—Chironomid head capsules were absent prior to ~ 1960. Densities increased gradually after this time, varying between 2.5 and 23.4 capsules g dry wt^{-1} until the surface sediments, where they increased to 116 capsules g dry wt^{-1} (Fig. 6). Taxa identified in the sediments included Tanytarsina, *Micropsectra*, *Limnophyes*, *Pseudodiamesa*, *Nanocladius*, and *Sergentia* (Fig. 6). The identified diatom taxa were exclusively benthic, and the slight species changes mirrored those recorded in previous studies from this lake by Douglas and Smol (2000) and Michelutti et al. (2002). Diatoms were sparse prior to ~ 1956 (i.e., $< 10^6$ valves g OM^{-1}; Fig. 3). Concentrations rose to a peak in ~ 1973 and declined thereafter.

Multivariate analysis—PCA revealed similar structures in the shifts of all proxy indicator groups. The first two PCA axes explained 71% of the variation in the combined data set (Fig. 7), compared with 75% (chironomids), 85% (metals), 86% (pigments), and 91% (C and N variables) for each proxy group considered alone. The first axis of all analyses was controlled by the large shifts in the upper 2 cm (Fig. 7) and was most strongly associated with Al, Pb, Ti, *Sergentia*, *Pseudodiamesa*, Tanytarsina, TOC, and all major phytoplankton pigments (positive correlation) and with δ^{13}C, δ^{15}N, Ca, Mg (negative correlation). The second
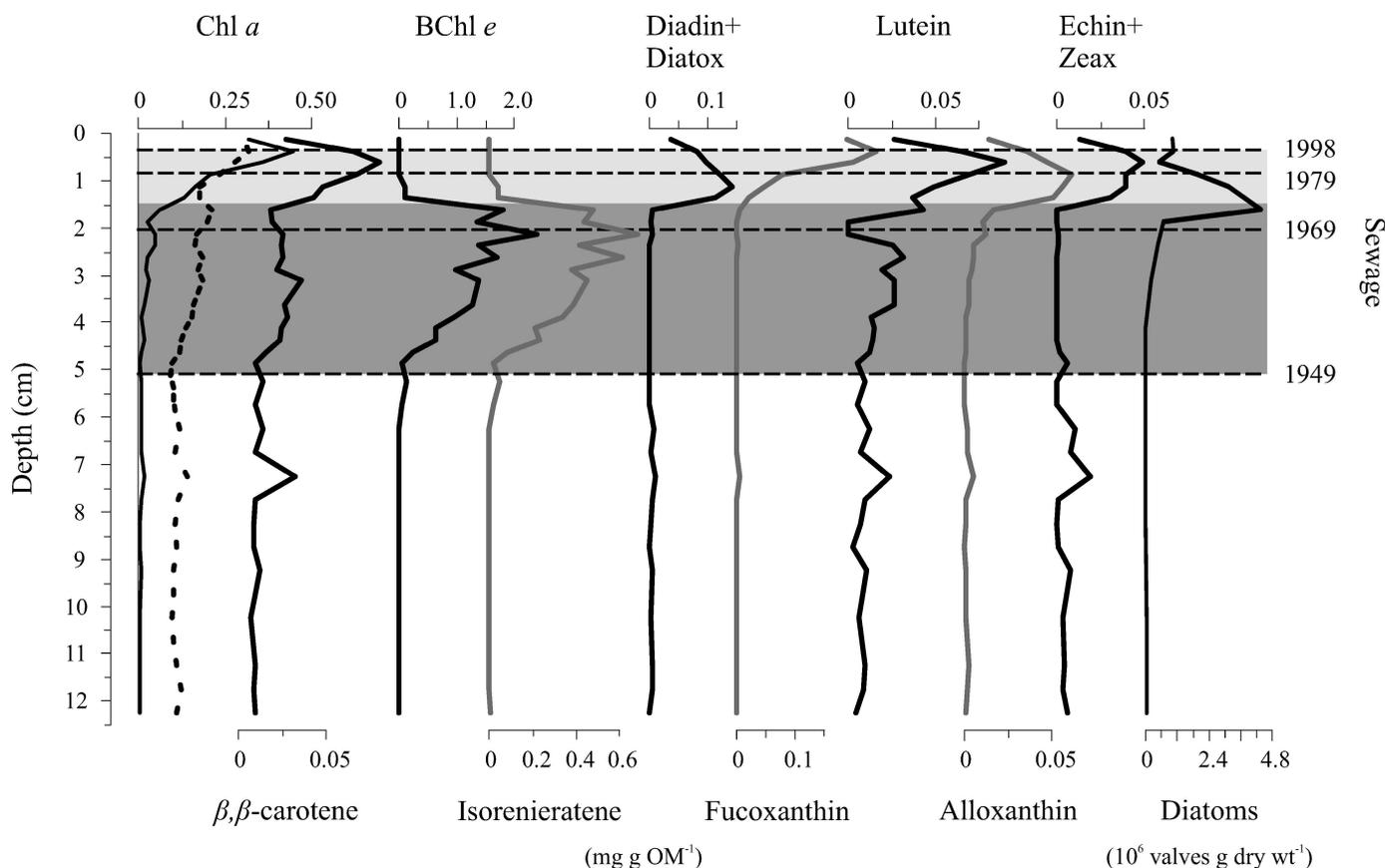
Fig. 3. HPLC pigment indicators of algal and bacterial photosynthetic biomass. Pigments represent overall productivity (Chl *a*, *β,β*-carotene); photosynthetic green sulfur bacteria (BChl *e*; isorenieratene); chromophyte algae (fucoxanthin, diatoxanthin + diadinoxanthin); chlorophytes (lutein); cryptophytes (alloxanthin); and cyanobacteria (echinenone + zeaxanthin). Note the different x-axis scales. The dashed plot for Chl *a* represents visible reflectance spectroscopy measured concentrations. All pigment values are expressed as mg g OM^{-1}. The shaded area represents the period of sewage inputs, and the dark gray section represents the inferred period of sewage-induced anoxia.

axis in each PCA was related to changes that occurred under anoxic conditions (Fig. 7). The variables with the strongest positive relationship to the anoxic period were isorenieratene, BChl *e*, pheophytin *a*, Cd, Tl, *Limnophyes*, and *Micropsectra*, while Mo was negatively correlated to these shifts.

Discussion

Our paleolimnological data reveal the profound nature of the changes in Meretta Lake caused by cultural eutrophication, with markedly different responses in benthic vs. planktonic communities. The switching of the pigment assemblage from algal to bacterial domination closely followed anthropogenic enrichment and was a strong indicator of oxygen depletion. The reduction and cessation of sewage inputs led to recovery in Meretta Lake; current trajectories indicate that while to some degree the lake is returning to pre-enrichment conditions, it is also being affected by recent climate warming.

Pre-anthropogenic variability—All evidence indicates that Meretta Lake was a typical oligotrophic high Arctic

lake prior to anthropogenic nutrient and organic C enrichment, and only minor stratigraphic changes were recorded in the sediments prior to the onset of sewage inputs in 1949. Its oligotrophic status was reflected by low pigment concentrations (Fig. 3) and C isotope ratios that indicated minimal fractionation by biotic activity (Fig. 5). Sedimented OM was likely influenced by the input of vascular plant material, as indicated by high C:N ratios (Meyers 2009). The extremely low concentrations of diatoms and the absence of chironomids (Figs. 3, 6) likely resulted from the combined effects of prolonged ice cover and low nutrients on diatoms (Smol and Douglas 2007) as well as a combination of lack of food due to low productivity and insufficient degree-days or extremely cold water that hampered the completion of chironomid life cycles. In-lake processes before 1949 were therefore dominated by low nutrient levels, cold temperatures, prolonged ice cover, and short growing seasons.

Sewage effects and oxygen depletion—Cultural eutrophication and the development of hypolimnetic anoxia with increased organic loading and the associated biological oxygen demand (BOD) were clearly reflected in the
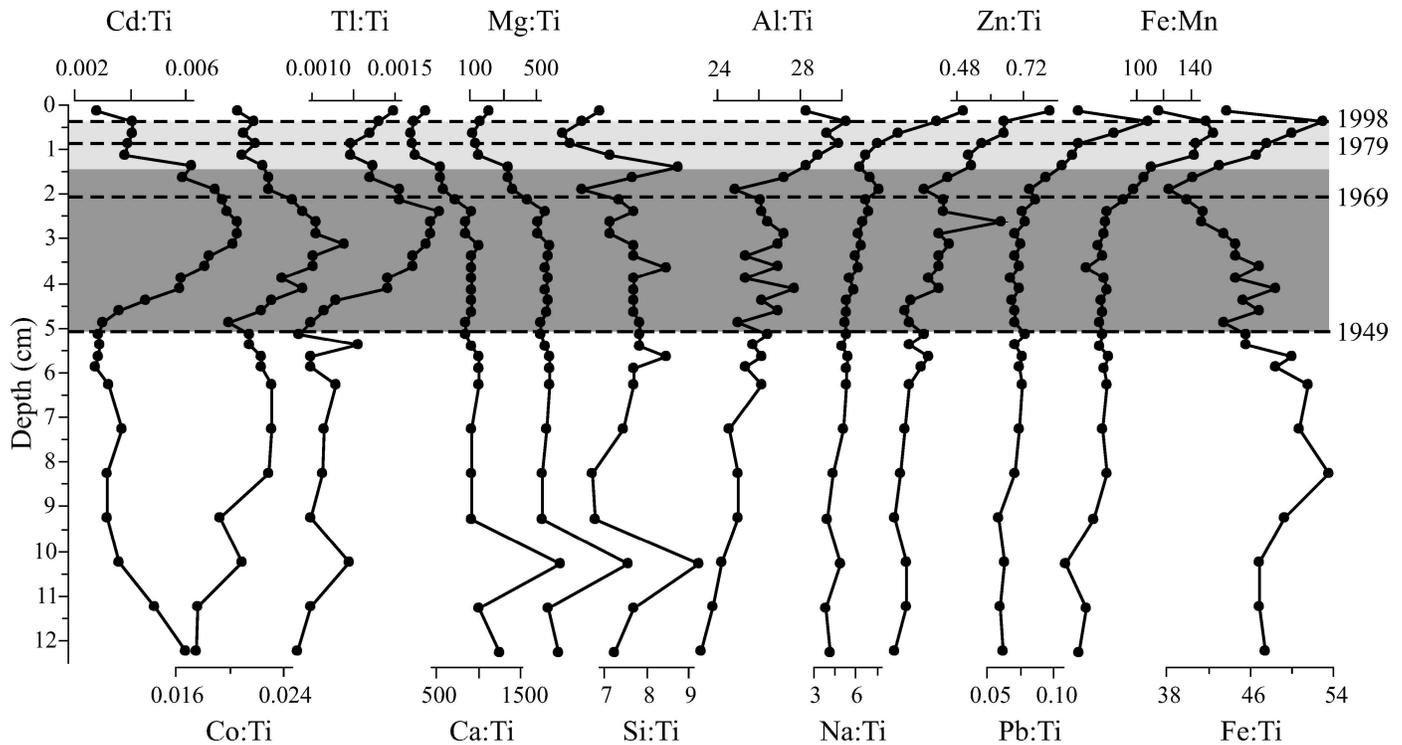
Fig. 4.   Metal concentrations in Meretta Lake sediments. Concentrations are expressed as ratios to Ti to account for changes in background sedimentation and diagenesis. The shaded area represents the period of sewage inputs, and the dark gray section represents the inferred period of sewage-induced anoxia.
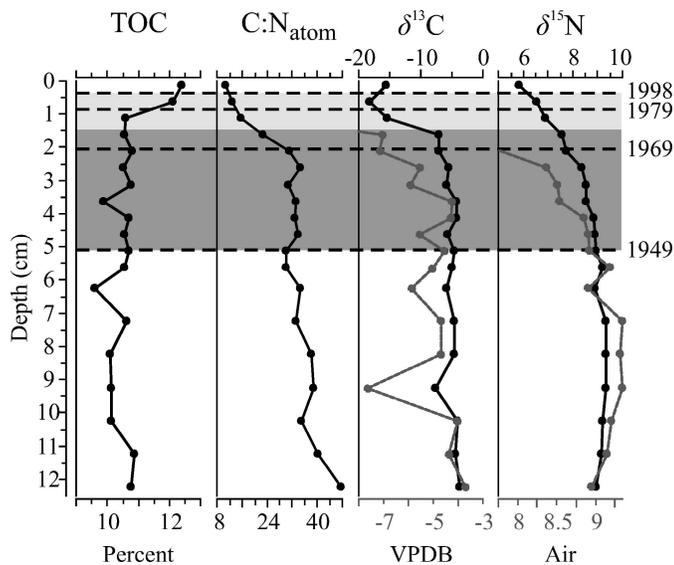

Fig. 5.   TOC, atomic C : N ratio, and stable isotope ratios. Isotopes are expressed in parts per thousand deviation from the standards Peedee belemnite (PDB), and air for ^{13}C and ^{15}N, respectively. Black lines are measured values, while the gray δ^{13}C and δ^{15}N lines have exaggerated x-axis scales to accentuate the changes between 2 and 5 cm. The shaded area represents the period of sewage inputs, and the dark gray section represents the inferred period of sewage-induced anoxia.

sedimentary record shortly after the onset of sewage inputs in 1949. Like other polar lakes, Meretta Lake is susceptible to oxygen depletion as a result of its ice cover, which lasts for 10 or more months per year (Schindler et al. 1974), and the development of sustained anoxia occurred during a time of relatively low temperatures (MAT; Fig. 8) that implied persistent, stable ice cover. The effects of anoxic conditions on proxy indicators at this time were clearly reflected by shifts in PCA axis 2 scores (Fig. 7). Anoxic conditions in Meretta Lake after 1949 were indicated by the rise of BChl *e* and isorenieratene (Fig. 3), pigments characteristic of obligately anaerobic brown strains of photosynthetic green sulfur bacteria (PGSB) from the genus *Chlorobium* (Overmann 2006). These bacteria are restricted to anoxic environments in the presence of sulfide, and although they are more commonly found in stratified waters, they are capable of reaching extremely high benthic densities in fine layers (van Gemerden and Mas 1995). Moreover, these bacteria are capable of photosynthesis at extremely low irradiances (Overmann 2006), similar to those that would have occurred in Meretta Lake during much of the year as a result of the thick ice and snow cover. Anoxia in Meretta Lake was reported to prevent copepod eggs from hatching, even while climatic conditions permitted their success in nearby lakes (Roff 1972). In our study, the continuing absence of chironomids during this period may also indicate the impairment of reproductive cycles by anoxic conditions, in addition to low temperatures.

The deduction of hypolimnetic anoxia is also supported by the geochemical data, with a decline in Fe concentra-
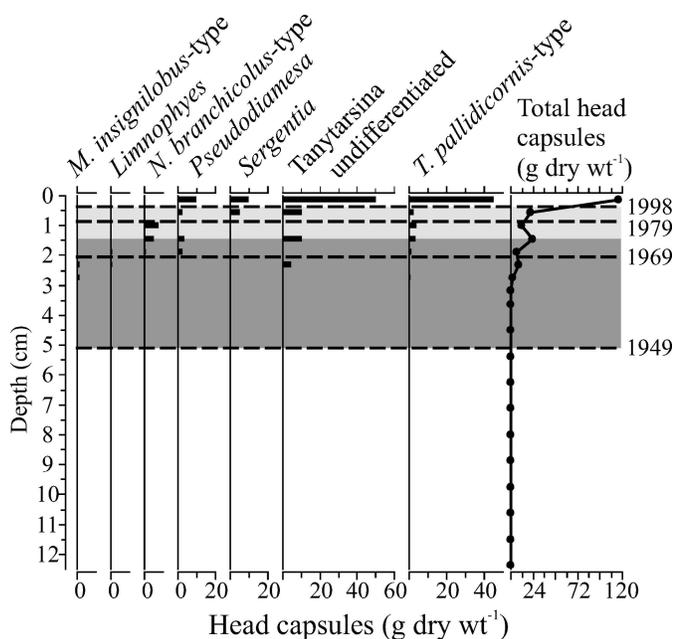
Fig. 6.   Chironomid absolute abundances. All concentrations are specimens per gram dry weight (g dry wt). The shaded area represents the period of sewage inputs, and the dark gray section represents the inferred period of sewage-induced anoxia.

tions beginning in $\sim$ 1949. Fe solubility increases under strongly reducing conditions, and its depletion in Meretta Lake during the anoxic period (Fig. 8B) is consistent with diffusion from sediments into the overlying water (Balistrieri et al. 1992). Bioaccumulative metals characteristic of sewage inputs further demonstrated the effects of effluent on Meretta Lake's chemistry (Fig. 4). Although there are no industrial sources of Cd or Tl near Meretta Lake, concentrations of toxic metals have been shown to increase in other Arctic lakes receiving sewage. Elevated blood concentrations of toxic metals have been measured in Inuit communities, and the source of such metals in affected lake sediments was inferred to be human ingestion through food and cigarettes (Benedetti et al. 1992; Hermanson and Brozowksi 2005). Sedimentary processes may also play an important role in determining the concentration of these metals. Cd is typically known to co-precipitate with sulfides produced by anaerobic sulfate-reducing bacteria (Gobeil et al. 1997), while augmented Tl deposition to sediments has been observed in anoxic conditions (Laforte et al. 2005). The elevated concentrations of Cd and Tl during the sewage-affected period in Meretta Lake, and their correlation with BChl e (Fig. 8A), may therefore be related to inputs from sewage, changes in depositional and diagenetic processes under anoxia, or a combination of these factors.

Fe : Mn ratios are also often used as an indicator of hypolimnetic anoxia, although numerous post-depositional processes control their final concentration in sediments. These processes may result in poor correlation between Fe : Mn and other indicators of anoxia, and changes in Fe : Mn must therefore be interpreted with caution (Engstrom and Wright 1984). In Meretta Lake, Fe : Mn was largely unchanged during the period of inferred anoxia

(Fig. 4), and Fe and Fe : Mn were strongly correlated (r = 0.90, df = 30, p < 0.001). Such positive correlations between Fe and Fe : Mn indicate that Fe : Mn patterns are controlled by supply rather than by redox conditions (Engstrom and Wright 1984). The importance of supply in determining Meretta Lake Fe : Mn is supported by both the lack of change during the anoxic period and its increase with the warmer temperatures that imply enhanced delivery from the catchment. Other metals were also unchanged or increased only slightly during the anoxic period (Fig. 4), indicating that sewage inputs and redox effects did not exert primary control on their concentrations.

Although shifts to higher sedimentary $\delta^{15}N$ are often seen in response to higher productivity in phosphorus (P)-limited ecosystems (Meyers 2009), the opposite occurred in Meretta Lake. Several factors may account for this discrepancy. Little fractionation from N sources occurs under N-limited conditions (Meyers 2009), and the continued addition of nutrients with the very low N : P ratio measured in sewage from Resolute Bay (i.e., 1.63; Schindler et al. 1974) would almost certainly lead to N-limitation. Reductions in Meretta Lake $\delta^{15}N$ may therefore simply reflect a lowering of the signature of available N, similar to $\delta^{15}N$ measured elsewhere in sewage discharges (Tucker et al. 1999). N-fixing organisms also produce OM with low $\delta^{15}N$ signatures (Meyers 2009), and given the ability of photosynthetic sulfur bacteria to fix N (Hallenbeck 1987), their rise in Meretta Lake may have also contributed to the $\delta^{15}N$ shift toward atmospheric values. Benthic N-fixing cyanobacteria are also common in lakes throughout the Arctic (Vincent and Laybourn-Parry 2008); they would likely have been stimulated by the low N : P enrichment of Meretta Lake.

During the entire period between $\sim$ 1949 and $\sim$ 1972, Meretta Lake $\delta^{13}C$ was far above values characteristic of phytoplankton or land plants (Meyers 2009). However, PGSB use the reverse tricarboxylic cycle in C fixation and produce OM that is, on average, only 4‰ depleted from their C source (Sinninghe Damsté and Schouten 2006). The Meretta Lake sedimentary $\delta^{13}C$ signature is therefore consistent with the fixation of C from bicarbonate by PGSB. The decrease in $\delta^{13}C$ values from $\sim$ 1957 through the $\sim$ 1970s likely reflects the moderate increase in phytoplankton productivity indicated by pigment concentrations (Figs. 3, 5).

Evidence of eutrophication effects in phytoplankton was subtle during the period from $\sim$ 1949 to 1972, with only modest biomass increases recorded by algal pigments (Fig. 3). Estimates indicate that the benthic contribution represented about two thirds of primary production in Meretta Lake, and in Arctic lakes elsewhere it exceeded 80% (Kalff and Welch 1974; Vadeboncoeur et al. 2003). In Meretta Lake, the most striking response to eutrophication was in the benthos, and planktonic diatoms were absent. Although shifts from benthic to planktonic production have been observed with eutrophication (Vadeboncoeur et al. 2003), no such trend was observed in our study. Eutrophication caused species shifts within the benthic diatom communities of Meretta and other Arctic lakes, but planktonic diatom taxa failed to appear (Douglas and Smol
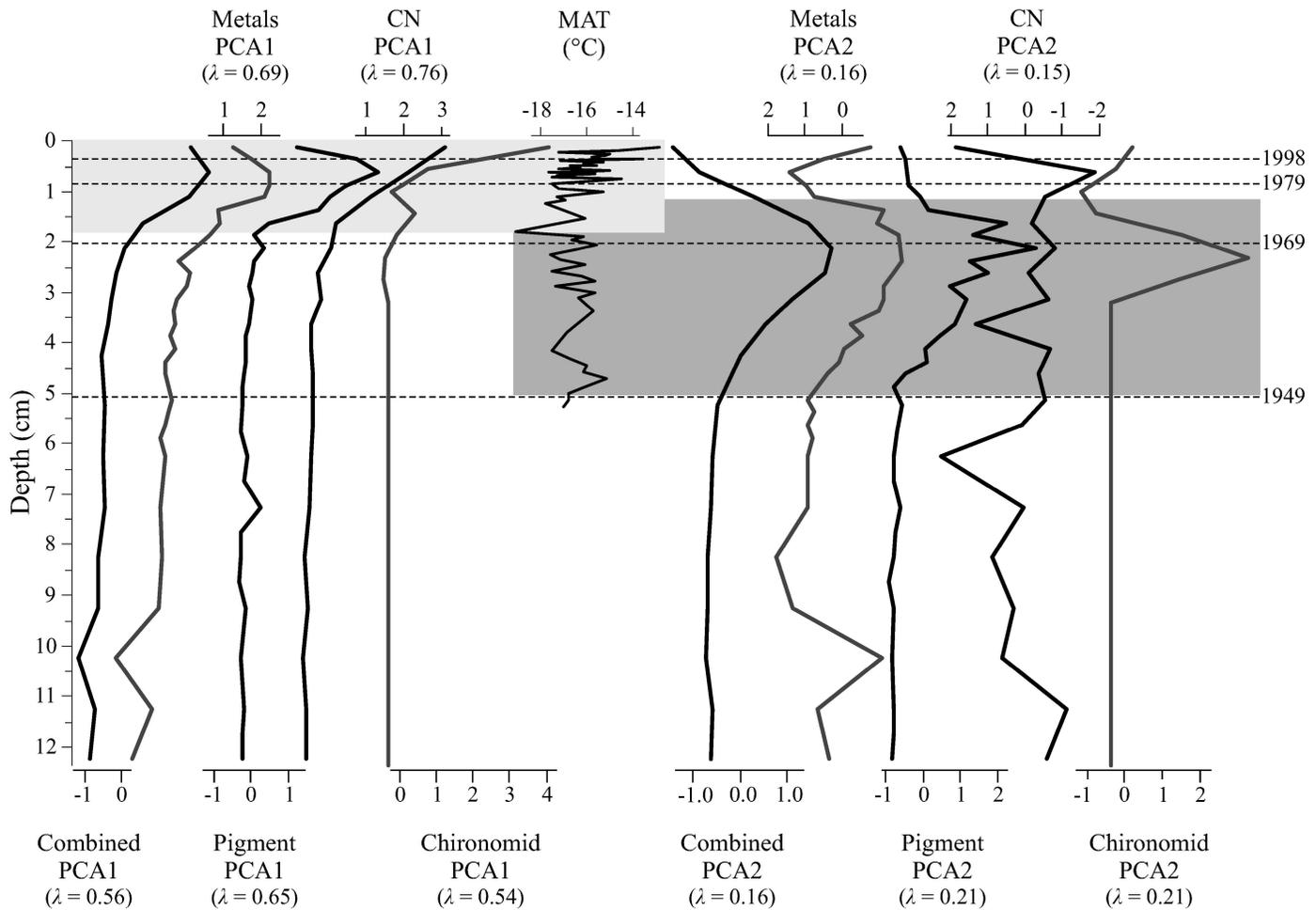
Fig. 7.   PCA axis 1 and 2 scores for the combined data set and each proxy indicator group. MAT = Resolute Bay mean annual temperature. The shaded areas represent the periods of change in axis scores, with axis 1 shifts related to climate-mediated catchment variables and axis 2 shifts due to anoxia-related effects.

2000; Michelutti et al. 2007). Many of the pigments recorded in Meretta Lake sediments may also be derived from the phytobenthos as well as the phytoplankton. This illustrates the effects—distinct from temperate ecosystems—of the control of ice and snow cover on the light, nutrient, and mixing properties of high Arctic lakes (Smol and Douglas 2007) and the limited ability of phytoplankton to respond to nutrient enrichment in these systems. Moreover, pollution by heavy metals, including Cd, has been shown to inhibit photosynthesis, with far stronger effects on photosystem II than on photosystem I (Clijsters and Van Assche 1985). While PGSB lack photosystem II (van Gemerden and Mas 1995) and clearly responded to sewage inputs to Meretta Lake, the inhibition by Cd of algal and cyanobacterial photosynthesis involving photosystem I may have further reduced the capacity of the phytoplankton to respond to nutrient increases. The coincidence between the period in Meretta Lake characterized by anoxic conditions and muted phytoplankton response and relatively cold, stable climate (MAT; Fig. 7) was reflected by flat PCA axis 1 profiles during this time, indicating a link between PCA axis 1 and climate. The relatively cold conditions imply the persistence of ice cover;

this thick ice both prevented the development of significant phytoplankton due to reduced entrainment of nutrient-rich bottom waters into the upper water column (where light conditions were more suitable for algal photosynthesis) and favored sustained anoxia by impeding oxygen exchange with the atmosphere and its turbulent mixing through the water column.

Sewage lagoons and the onset of recovery—In 1969, berms were constructed that formed sewage lagoons along the path of sewage flow into Meretta Lake. The solid sludge was removed from these lagoons once per year and taken to a dump (Masemann 1971; Douglas and Smol 2000). Although this was initially thought to have minimal effects on nutrient retention (Masemann 1971), the abrupt crash of *Chlorobium* populations in the sedimentary record indicates reduced organic loading to Meretta Lake and profound changes in its oxygen dynamics shortly thereafter (Fig. 8A). Given the toxicity of even minute oxygen concentrations to PGSB (Overmann 2006), two hypotheses may explain these changes. The reduced organic load may have reduced the BOD sufficiently that the hypolimnion moved from anoxia to the hypoxic conditions observed
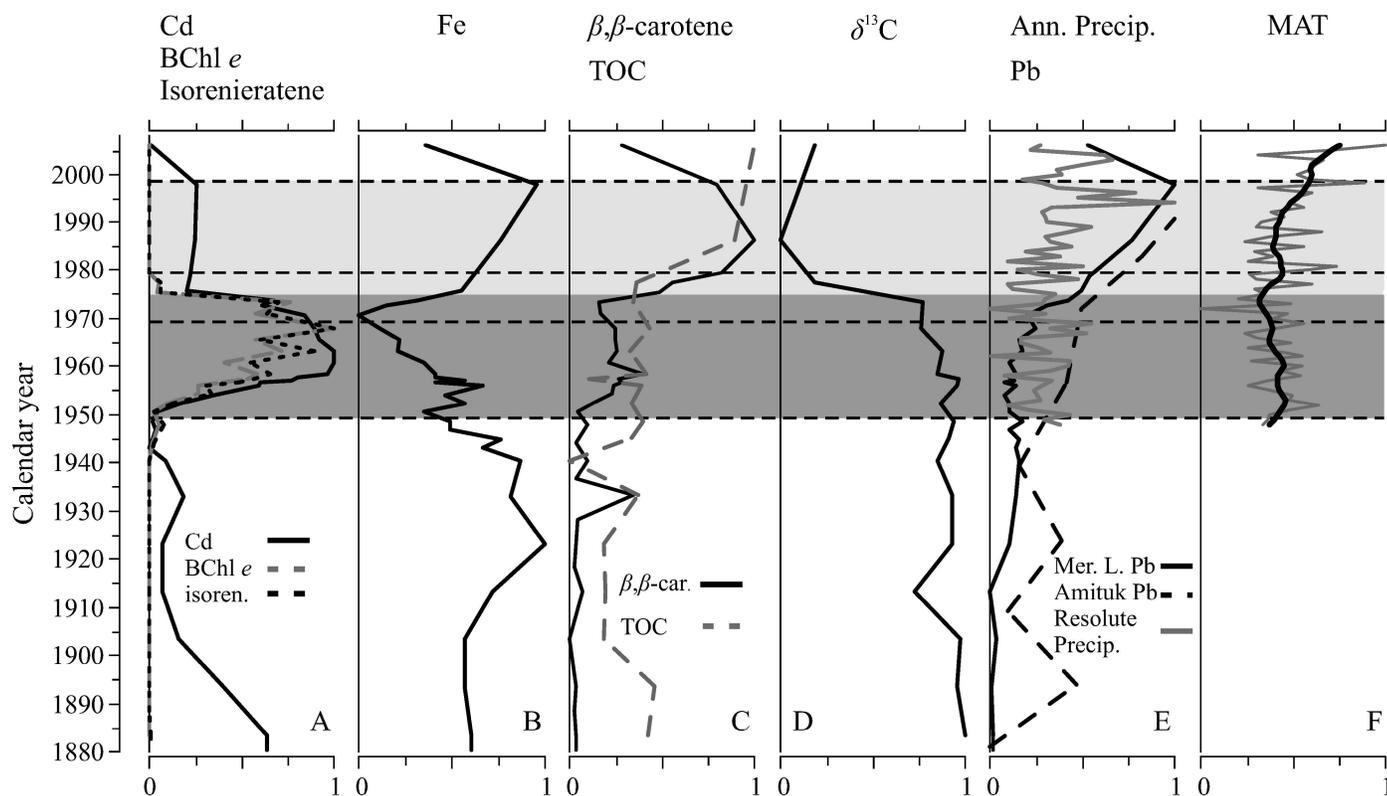
Fig. 8. Synthesis of standardized Meretta Lake stratigraphic data. The shaded area represents the period of sewage inputs, and the dark gray section represents the inferred period of sewage-induced anoxia. All values represent Meretta Lake sediment values, except as noted. (A) BChl, isoren. = isorenieratene; (B) Fe; (C) β-car. = β,β-carotene; (D) $\delta^{13}C$; (E) Meretta Lake (Mer. L.) sediment Pb (solid black line); Amituk Lake sediment Pb (dashed black line; data from Outridge et al. [2002]); Ann. Precip. = Resolute Bay total annual precipitation (gray line; data from Environment Canada); (F) MAT = Resolute Bay mean annual temperature (gray line) and locally weighted smoothing curve (black line).

during the IBP. Alternately, the warming trend that began in ~ 1975 (Figs. 7, 8) may have reduced ice cover duration and increased turbulence enough that oxygen was mixed throughout the water column and anoxic habitats were lost. A similar disappearance of PGSB was noted in a lake following catchment deforestation; the cause was inferred to be reduced anoxia due to greater wind-induced mixing (Scully et al. 2000). In either case, increased oxygenation in the early 1970s permitted algal colonization of previously inaccessible habitats, and a striking rise in algal biomass ensued (Fig. 3), accompanied by shifts in PCA axis scores of all proxy groups across this horizon (Fig. 7). Chromophyte algae rose in importance (i.e., fucoxanthin, diatoxanthin and diadinoxanthin, diatom valves), and the concurrent rise of cyanobacteria (echinenone and zeaxanthin), chlorophytes (lutein), and cryptophytes (alloxanthin) was also evident. Although Peridineae were prevalent during the IBP (Schindler et al. 1974; Kalff et al. 1975), peridinin was not identified in the sediments, likely as a result of its lability (Leavitt and Hodgson 2001). The increase in phytoplankton productivity resulted in significant shifts of C:N and $\delta^{13}C$ between the anoxic and oxic periods (Fig. 5) to values characteristic of algal OM (Meyers 2009). Despite the demise of photosynthetic bacteria, the rise of cyanobacteria in Meretta Lake was indicated by increasing cyanobacterial pigments, while

$\delta^{15}N$ decreased toward atmospheric values, as would be expected with increasing abundances of N-fixing cyanobacteria (Meyers and Teranes 2001). Meanwhile, the pronounced change in $\delta^{13}C$ was consistent with a shift from OM from bacterial production (discussed above) to the much greater fractionation inherent in phytoplankton photosynthesis (i.e., ~ 20‰ from their C source; Meyers and Teranes 2001).

The concentrations of sewage-related metals (i.e., Cd, Co, Tl) also decreased dramatically after ~ 1970 (Fig. 4). Reductions in solubility associated with increased oxygen led to greater Fe retention in the sediments and a concomitant rise in Fe concentrations (Fig. 8B). Increasing Pb concentrations did not appear to be related to sewage inputs (Fig. 4). ^{210}Pb deposition and precipitation are correlated in North America (Preiss et al. 1996), and Outridge et al. (2002) suggested that Pb deposition in the Arctic is controlled by limited atmospheric scavenging due to low precipitation. This hypothesis is supported by a near-significant relationship between Resolute Bay annual precipitation and Meretta Lake sedimentary Pb ($r = 0.57$, df = 10, $p = 0.07$) and by the general similarity of the Pb trend in Meretta Lake to that observed in Amituk Lake, 52 km to the northeast (Outridge et al. 2002) (Fig. 8E).

Chironomids were absent or near-absent until significant ($p = 0.05$) increases occurred after ~ 1973. The stepwise

appearance of several taxa (*Micropsectra insignilobus*, *Limnophyes*, *Nanocladius*, *Sergentia*) implied continuing gradual environmental change in Meretta Lake after an ecological threshold was crossed that permitted chironomid colonization. The species assemblage was composed mainly of psychrophilic taxa (Brodersen and Anderson 2002; Porinchu et al. 2009), which is indicative of the continued cold water temperatures and prolonged ice cover in Meretta Lake. Despite slight increases in response to higher production, continuing low concentrations at this time indicated that the primary control on chironomid abundances in Meretta Lake was climate. Our data also show the advantages of bacterial pigments over chironomids for tracking anoxia in cold northern ecosystems. Temperature and trophic optima in chironomid taxa are correlated (Brodersen and Anderson 2002), and chironomid taxa with the capacity to withstand anoxic conditions (e.g., *Chironomus*, *Procladius*) are also more temperate taxa that are unlikely to be found in lakes with cold water and prolonged ice cover. These taxa therefore cannot be used to infer periods of oxygen depletion in Arctic ecosystems, and paleolimnological analysis using bacterial pigments to track anoxia in colder regions may provide a more suitable approach.

Post-sewage recovery and the effects of climate change—Schindler et al. (1974) predicted that as a result of the limited flux of N and P from the sediments to the water column, Meretta Lake would quickly return to natural conditions with the cessation of sewage. Sewage inputs declined through the 1970s, culminating in the dismantling of one of two sewage outputs in 1979 (Douglas and Smol 2000). Sewage inputs ceased completely in 1998, and the low sedimentation rate implies that this period is contained entirely in the surface 0.25 cm. Despite the limited number of data points in the core following sewage declines, changes in several proxy indicators suggesting rapid recovery are nonetheless observable. Production began to decline toward pre-enrichment levels and dropped sharply after 1998, as indicated by biomass decreases in all major phytoplankton groups as well as diatom concentrations (Fig. 3). After the dismantling of the utilidor, Cd and Co dropped to their lowest concentrations since the beginning of anthropogenic enrichment, although Tl increased. The concentrations of metals controlled by deposition from the catchment (i.e., Al, Na, Zn; Fig. 4) increased along with rises in mean annual temperature and precipitation (Fig. 8). The trends of some other metals reversed in the upper sediments, but given the lack of a clear, direct link between either of these metals and sewage, the cause remains uncertain. There was no indication of any return to anoxic conditions.

The recovery of Meretta Lake from cultural eutrophication may be obscured by the effects of recent climate change, which are similar to those of increased nutrient inputs, and include greater productivity and community diversity (Smol et al. 2005). Despite a more widespread circumpolar trend toward biotic change beginning between the mid-19th and early 20th centuries (Smol et al. 2005), the effects of recent warming were not evident in the largely ice-covered lakes of the Resolute area until the 1980s (Michelutti et al. 2003), coincident with the period of declining sewage inputs to Meretta Lake. Moreover, the highest mean annual temperatures recorded at Resolute occurred after the dismantling of the utilidor in 1998 (Fig. 8F). Mean total P from samples taken in Meretta Lake from 1969 to 1980 (48.0 μg L^{-1}, standard deviation [SD] = 18.1 μg L^{-1}, n = 4) was over four times that measured between 1992 and 2009 (10.7 μg L^{-1}, SD = 9.1 μg L^{-1}, n = 25) (Douglas and Smol unpubl.). As a consequence, while Meretta Lake was recovering from point-source cultural eutrophication, it was also being increasingly affected by climate warming, thereby complicating the interpretation of paleolimnological indicators during the recent past. In particular, the greatly increased abundances of chironomids in the surface sediment indicate that the longer ice-free seasons and warmer temperatures may have played a greater role than trophic status in controlling past chironomid abundances.

Our study indicates that eutrophication can have profound effects on Arctic lakes. While dramatic, these effects were distinct from those observed in temperate sites, largely as a result of the extent and duration of ice cover, the resulting suppression of phytoplankton, and the importance of the benthos in primary production. However, given the accelerated warming and ice cover declines projected throughout the Arctic during the next century, the differences between ecozones may become less pronounced. With the greater nutrient inputs to many polar lakes that are expected to accompany warmer climates, the trajectories observed in our study will provide insights into eutrophication processes in the Arctic. In both eutrophication and subsequent recovery, therefore, Meretta Lake will continue to be a valuable reference site for understanding the response of Arctic aquatic ecosystems to trophic change.

References

APPLEBY, P. G. 2001. Chronostratigraphic techniques in recent sediments, p. 171–203. *In* W. M. Last and J. P. Smol [eds.], Tracking environmental change using lake sediments. Volume 1: Basin analysis, coring, and chronological techniques. Kluwer.

BALISTRIERI, L. S., J. W. MURRAY, AND B. PAUL. 1992. The cycling of iron and manganese in the water column of Lake Sammamish, Washington. Limnol. Oceanogr. **37:** 510–528, doi:10.4319/lo.1992.37.3.0510

BATTARBEE, R. W., AND M. J. KNEEN. 1982. The use of electronically counted microspheres in absolute diatom analysis. Limnol. Oceanogr. **27:** 184–188, doi:10.4319/lo.1982.27.1.0184

BENEDETTI, J. L., F. TURCOTTE, M. LEFEBVRE, F. THERRIEN, AND J. P. WEBER. 1992. Blood and urinary cadmium levels in Inuit living in Kuujjuaq, Canada. Sci. Total Environ. **127:** 167–172, doi:10.1016/0048-9697(92)90475-8

BORREGO, C. M., J. B. ARELLANO, C. A. ABELLA, T. GILLBRO, AND J. GARCIA-GIL. 1999. The molar extinction coefficient of bacteriochlorophyll e and the pigment stoichiometry in *Chlorobium phaeobacteroides*. Photosynth. Res. **60:** 257–264, doi:10.1023/A:1006230820007

BRODERSEN, K. P., AND N. J. ANDERSON. 2002. Distribution of chironomids (Diptera) in low Arctic West Greenland lakes: Trophic conditions, temperature and environmental reconstruction. Freshw. Biol. **47:** 1137–1157, doi:10.1046/j.1365-2427.2002.00831.x

CLIJSTERS, H., AND F. VAN ASSCHE. 1985. Inhibition of photosynthesis by heavy metals. Photosynth. Res. **7:** 31–40, doi:10.1007/BF00032920

DOUGLAS, M. S. V., AND J. P. SMOL. 2000. Eutrophication and recovery in the High Arctic: Meretta Lake (Cornwallis Island, Nunavut, Canada) revisited. Hydrobiologia **431:** 193–204, doi:10.1023/A:1004000530997

ENGSTROM, D. R., AND H. E. WRIGHT, JR. 1984. Chemical stratigraphy of lake sediments as a record of environmental change, p. 11–67. *In* E. Y. Haworth and J. W. G. Lund [eds.], Lake sediments and environmental history. Univ. of Minnesota Press.

ENVIRONMENT CANADA. 2010. Canadian Climate Normals 1971–2000 [Internet]. [Accessed 2010 April 26]. Available from http://climat.meteo.gc.ca/climate_normals/index_e.html

GOBEIL, C., R. W. MACDONALD, AND B. SUNDBY. 1997. Diagenetic separation of cadmium and manganese in suboxic continental margin sediments. Geochim. Cosmochim. Acta **61:** 4647–4654, doi:10.1016/S0016-7037(97)00255-X

HALLENBECK, P. C. 1987. Molecular aspects of nitrogen fixation by photosynthetic prokaryotes. Crit. Rev. Microbiol. **14:** 1–48, doi:10.3109/10408418709104434

HERMANSON, M. H., AND J. R. BROZOWSKI. 2005. History of Inuit community exposure to lead, cadmium, and mercury in sewage lake sediments. Environ. Health Perspect. **113:** 1308–1312, doi:10.1289/ehp.7985

HOLMGREN, S. K. 1984. Experimental lake fertilization in the Kuokkel area, northern Sweden: Phytoplankton biomass and algal composition in natural and fertilized subarctic lakes. Int. Rev. Gesamte Hydrobiol. **69:** 781–817, doi:10.1002/iroh.19840690603

HURLEY, J. P., AND C. J. WATRAS. 1991. Identification of bacteriochlorophylls in lakes via reverse-phase HPLC. Limnol. Oceanogr. **36:** 307–315, doi:10.4319/lo.1991.36.2.0307

KALFF, J., H. J. KLING, S. K. HOLMGREN, AND H. E. WELCH. 1975. Phytoplankton, phytoplankton growth and biomass cycles in an unpolluted and in a polluted polar lake. Verh. Int. Verein. Limnol. **19:** 487–495.

———, AND H. E. WELCH. 1974. Phytoplankton production in Char Lake, a natural polar lake, and in Meretta Lake, a polluted polar lake, Cornwallis Island, Northwest Territories. Can. J. Fish. Aquat. Sci. **31:** 621–636.

LAFORTE, L., A. TESSIER, C. GOBEIL, AND R. CARIGNAN. 2005. Thallium diagenesis in lacustrine sediments. Geochim. Cosmochim. Acta **69:** 5295–5306, doi:10.1016/j.gca.2005.06.006

LEAVITT, P. R., AND D. A. HODGSON. 2001. Sedimentary pigments, p. 295–325. *In* J. P. Smol, H. J. B. Birks, and W. M. Last [eds.], Tracking environmental change using lake sediments. Volume 3: Terrestrial, algal and siliceous indicators. Kluwer.

MASEMANN, V. 1971. Phosphorus budget of an Arctic lake. M.A.Sc. thesis. Univ. of Toronto.

MEYERS, P. A. 2009. Organic geochemical proxies, p. 659–662. *In* V. Gornitz [ed.], Encyclopedia of paleoclimatology and ancient environments. Springer-Verlag.

———, AND J. L. TERANES. 2001. Sediment organic matter, p. 239–269. *In* W. M. Last and J. P. Smol [eds.], Tracking environmental change using lake sediments. Volume 2: Physical and geochemical methods. Kluwer.

MICHELUTTI, N., J. M. BLAIS, B. F. CUMMING, A. M. PATERSON, K. RÜHLAND, A. P. WOLFE, AND J. P. SMOL. 2010. Do spectrally inferred determinations of chlorophyll a reflect trends in lake trophic status? J. Paleolimnol. **43:** 205–217, doi:10.1007/s10933-009-9325-8

———, M. S. V. DOUGLAS, AND J. P. SMOL. 2002. Tracking recent recovery from eutrophication in a high Arctic lake (Meretta Lake, Cornwallis Island, Nunavut, Canada) using fossil diatom assemblages. J. Paleolimnol. **28:** 377–381, doi:10.1023/A:1021654516828

———, ———, AND ———. 2003. Diatom response to recent climatic change in a high Arctic lake (Char Lake, Cornwallis Island, Nunavut). Global Planet. Change **38:** 257–271, doi:10.1016/S0921-8181(02)00260-6

———, M. H. HERMANSON, J. P. SMOL, P. J. DILLON, AND M. S. V. DOUGLAS. 2007. Delayed response of diatom assemblages to sewage inputs in an Arctic lake. Aquat. Sci. **69:** 523–533, doi:10.1007/s00027-007-0928-8

MORGAN, K. C., AND J. KALFF. 1972. Bacterial dynamics in two high-Arctic lakes. Freshw. Biol. **2:** 217–228, doi:10.1111/j.1365-2427.1972.tb00050.x

OUTRIDGE, P. M., M. H. HERMANSON, AND W. L. LOCKHART. 2002. Regional variations in atmospheric deposition and sources of anthropogenic lead in lake sediments across the Canadian Arctic. Geochim. Cosmochim. Acta **66:** 3521–3531, doi:10.1016/S0016-7037(02)00955-9

OVERMANN, J. 2006. The Family Chlorobiaceae, p. 359–378. *In* M. Dworkin, S. Falkow, E. Rosenberg, K.-H. Schleifer, and E. Stackebrandt [eds.], The Prokaryotes. Springer.

PORINCHU, D., N. ROLLAND, AND K. MOSER. 2009. Development of a chironomid-based air temperature inference model for the central Canadian Arctic. J. Paleolimnol. **41:** 349–368, doi:10.1007/s10933-008-9233-3

PREISS, N., M.-A. MÉLIÈRES, AND M. POURCHET. 1996. A compilation of data on lead 210 concentration in surface air and fluxes at the air-surface and water-sediment interfaces. J. Geophys. Res. **101:** 28847–28862, doi:10.1029/96JD01836

PROWSE, T. D., F. J. WRONA, J. D. REIST, J. J. GIBSON, J. E. HOBBIE, L. M. J. LÉVESQUE, AND W. F. VINCENT. 2006. Climate change effects on hydroecology of Arctic freshwater ecosystems. Ambio **35:** 347–358, doi:10.1579/0044-7447(2006)35[347:CCEOHO]2.0.CO;2

ROFF, J. C. 1972. Aspects of the reproductive biology of the planktonic copepod *Limnocalanus macrurus* Sars, 1863. Crustaceana **22:** 155–160, doi:10.1163/156854072X00417

SCHINDLER, D. W., J. KALFF, H. E. WELCH, G. J. BRUNSKILL, H. KLING, AND N. KRITSCH. 1974. Eutrophication in the High Arctic—Meretta Lake, Cornwallis Island (75° N lat.). J. Fish. Res. Board Can. **31:** 647–662.

———, AND J. P. SMOL. 2006. Cumulative effects of climate warming and other human activities on freshwaters of Arctic and Subarctic North America. Ambio **35:** 160–168, doi:10.1579/0044-7447(2006)35[160:CEOCWA]2.0.CO;2

Scully, N. M., P. R. Leavitt, and S. R. Carpenter. 2000. Century-long effects of forest harvest on the physical structure and autotrophic community of a small temperate lake. Can. J. Fish. Aquat. Sci. **57:** 50–59, doi:10.1139/cjfas-57-S2-50

Sierszen, M. E., M. E. McDonald, and D. A. Jensen. 2003. Benthos as the basis for Arctic lake food webs. Aquat. Ecol. **37:** 437–445, doi:10.1023/B:AECO.0000007042.09767.dd

Sinninghe Damsté, J. S., and S. Schouten. 2006. Biological markers for anoxia in the photic zone of the water column, p. 127–163. *In* J. K. Volkman [ed.], Marine organic matter: Biomarkers, isotopes and DNA. Volume 2: Reactions and processes. Springer-Verlag.

Smith, V. H., and D. W. Schindler. 2009. Eutrophication science: Where do we go from here? Trends Ecol. Evol. **24:** 201–207, doi:10.1016/j.tree.2008.11.009

Smol, J. P. 2008. Pollution of lakes and rivers: A paleoenvironmental perspective. Blackwell.

———, and M. S. V. Douglas. 2007. From controversy to consensus: Making the case for recent climatic change in the Arctic using lake sediments. Front. Ecol. Environ. **5:** 466–474, doi:10.1890/060162

———, and others. 2005. Climate-driven regime shifts in the biological communities of Arctic lakes. Proc. Natl. Acad. Sci. USA **102:** 4397–4402, doi:10.1073/pnas.0500245102

Tucker, J., N. Sheats, A. E. Giblin, C. S. Hopkinson, and J. P. Montoya. 1999. Using stable isotopes to trace sewage-derived material through Boston Harbor and Massachusetts Bay. Mar. Environ. Res. **48:** 353–375, doi:10.1016/S0141-1136(99)00069-0

Vadeboncoeur, Y., E. Jeppesen, M. J. Vander Zanden, H.-H. Schierup, K. Christoffersen, and D. M. Lodge. 2003. From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. Limnol. Oceanogr. **48:** 1408–1418, doi:10.4319/lo.2003.48.4.1408

Van Gemerden, H., and J. Mas. 1995. Ecology of phototrophic sulfur bacteria, p. 49–85. *In* R. R. Blankenship, M. T. Madigan, and C. E. Bauer [eds.], Anoxygenic photosynthetic bacteria. Kluwer.

Vincent, W. F., and J. Laybourn-Parry [Eds.]. 2008. Polar lakes and rivers—Limnology of Arctic and Antarctic aquatic ecosystems. Oxford Univ. Press.

Walker, I. R. 2001. Midges: Chironomidae and related diptera, p. 43–66. *In* J. P. Smol, H. J. B. Birks, and W. M. Last [eds.], Tracking environmental change using lake sediments. Volume 4: Zoological indicators. Kluwer.

Welch, H. E. 1974. Metabolic rates of Arctic lakes. Limnol. Oceanogr. **19:** 65–73, doi:10.4319/lo.1974.19.1.0065

———, J. A. Legault, and H. J. Kling. 1989. Phytoplankton, nutrients, and primary production in fertilized and natural lakes at Saqvaqjuac, NWT. Can. J. Fish. Aquat. Sci. **46:** 90–107, doi:10.1139/f89-013

Zapata, M., F. Rodriguez, and J. L. Garrido. 2000. Separation of chlorophylls and carotenoids from marine phytoplankton: A new HPLC method using a reversed phase C8 column and pyridine containing mobile phases. Mar. Ecol. Prog. Ser. **195:** 29–45, doi:10.3354/meps195029