LIMNOLOGY
and
OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 00, 2016, 00–00

doi: 10.1002/lno.10459

Climate warming and changes in *Cyclotella sensu lato* in the Laurentian Great Lakes

Euan D. Reavie,[1]* Gerald V. Sgro,[2] Lisa R. Estepp,[1] Andrew J. Bramburger,[1] Victoria L. Shaw Chraïbi,[3] Robert W. Pillsbury,[4] Meijun Cai,[1] Craig A. Stow,[5] Alice Dove[6]
[1]Natural Resources Research Institute, University of Minnesota Duluth, Duluth, Minnesota
[2]John Carroll University, University Heights, Ohio
[3]Tarleton State University, Stephenville, Texas
[4]University of Wisconsin Oshkosh, Oshkosh, Wisconsin
[5]National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan
[6]Water Quality Monitoring and Surveillance Division, Environment and Climate Change Canada, Burlington, Ontario, Canada

Abstract

We present the first evidence of biological change in all of the pelagic Laurentian Great Lakes associated with recent climatic warming. We hypothesized that measured changes in lake temperature, and the resulting physical changes to water columns, were affecting diatom communities in the Great Lakes. A paleolimnological analysis of 10 sediment cores collected from deep locations throughout the Great Lakes basin indicates a recent (30–50 yr) reorganization of the diatom community to one characterized by elevated abundances of several species from the group *Cyclotella sensu lato*, coinciding with rising atmospheric and water temperatures. These *Cyclotella* increases are a probable mechanistic result of new physical regimes such as changing stratification depths and longer ice-free periods, and possibly water quality shifts. Efforts to understand the mechanisms of these changes are ongoing, but this compositional reorganization in primary producers could have important implications to Great Lakes food webs.

As atmospheric warming continues, seasonal exposure of lake water columns to sunlight lengthens and ice periods become shorter and less intense. The frequency and duration of stratification events may be expected to increase, as has been observed in Lake Superior (Austin and Colman 2008). Changes to the biota of the Laurentian Great Lakes due to warming are likely occurring. The Great Lakes comprise almost 90% of the surface water resources of North America, so it is imperative to understand the effect of climate shifts on general biology and food webs.

Studies of species shifts driven by climate have largely focused on larger flora and fauna (Smol 2012) and usually track how a species alters its phenology or shifts its range. For instance, as a region becomes warmer and wetter, some plants and animals will thrive while other species populations will fragment, shrink and be driven to extinction. Some species adjust to climate change by moving outside their historical geographic boundaries. For phytoplankton, a climate-driven shift tends to mean a change in the dominant flora and reduction or extirpation of previously dominant taxa. It has been recognized in paleorecords from freshwater aquatic systems that phytoplankton, particularly diatoms, exhibit the greatest modification due to recent climate change, followed by invertebrates such as cladocerans and chironomids (Rühland et al. 2014). For instance, diatoms in a dated sediment core from Lake of the Woods, northwestern Ontario, were compared to instrumental records (Rühland et al. 2008) and *Cyclotella sensu lato* taxa increased concurrently with a lengthening ice-free period (by almost 30 d in the past 40 yr) and increasing water temperature, providing evidence that warming played a role in diatom community re-organization. Also, a decline in wind speeds over the past 50 yr was significantly correlated with the increasing relative abundance of *Cyclotella*. Atmospheric warming and associated changes in lake thermal properties were the most plausible explanation for the increase in cyclotelloid taxa. Similarly, Sorvari et al. (2002) noted that deep, thermally stratifying lakes experienced a pronounced increase in small cyclotelloid species. Many similar examples exist (Rühland et al. 2015), providing a weight of evidence that warming is playing an important role in these changes.

---

*Correspondence: ereavie@d.umn.edu

There are two prevailing, possibly simultaneous, mechanistic hypotheses for the changes in phytoplankton composition:

1. Physical changes. Longer periods of surface water warming each year, combined with changes to average wind speeds, affects stratification regimes. A longer ice-free period would allow summer populations to persist longer, potentially contributing to greater numbers of smaller, summer taxa that are better adapted to decreased mixing intensity (Winder et al. 2009). Beall et al. (2016) observed increased growth of smaller-sized cells during ice-free conditions in Lake Erie.
2. Chemical changes. Changes in diatom assemblages are well-known to be driven by nutrients. Nitrate levels in all of the Great Lakes have increased over the last century due to atmospheric inputs created by agricultural fertilizer and industrial emissions (Sterner et al. 2007; Dobiesz et al. 2010; Dove and Chapra 2015), leading us to evaluate whether recent increases in varieties of the diatom *Cyclotella comensis* may be related to this chemical shift (Shaw Chraïbi et al. 2014). Studies have been undertaken to decipher nitrogen-*Cyclotella* relationships in the presence of multiple driving variables including thermal structure (Saros et al. 2012), but a weight-of-evidence synthesis suggests nitrogen deposition is far less correlated to paleolimnological changes in *Cyclotella* than atmospheric warming (Rühland et al. 2015). Mechanistically, chemical and physical changes are not easily separated, such as enhanced stratification leading to greater sequestration of nutrients in the hypolimnion.

The recent, apparently climate-driven reorganization of Lake Superior's phytoplankton (Shaw Chraïbi et al. 2014) indicated that warming can reengineer the biology of large lakes. It was unknown whether similar changes are occurring throughout the Great Lakes basin. We hypothesize that recent climate change is having a widespread effect on Great Lakes biology beyond that observed for Lake Superior. Researchers have observed increasing water temperatures and decreasing ice extent (Mason et al. 2016) and duration (Assel et al. 2003) in all of the lakes. A concordant biological response has not been confirmed.

Further, no consideration has been given to the implications of a climate-driven change in planktonic primary producers in the Great Lakes. In this paper, we summarize new findings that indicate that the apparent diatom-climate signal, i.e., an increase in *Cyclotella sensu lato* that has been recognized in several worldwide lakes, is occurring in Great Lakes sediment cores. While it was expected that the multi-stressor Great Lakes environment would make it difficult to confirm specific drivers of diatom abundance, we hypothesized that climate-based drivers would be more strongly related to the recent changes in *Cyclotella* than environmental variables that are also changing (water levels, nutrient deposition, and water chemistry). We synthesize the possible and likely mechanisms of this recent shift and discuss the potential implications of this change on food webs, including areas of research that would support future management of this changing aquatic system.

Materials and methods

Water quality and physical data

Environmental data were compiled to evaluate relationships with diatom occurrence in modern and fossil records (Reavie et al. 2014*b*). Water quality data were collected and analyzed as part of the United States Environmental Protection Agency's (USEPA) Great Lakes pelagic, synoptic spring and summer surveillance monitoring from standard stations throughout the Great Lakes, and here we used those data from 2007 to 2011 to relate to corresponding phytoplankton collections. Water quality of samples was analyzed in situ (e.g., temperature) or in the laboratory (nutrients). Summer water column temperature measurements were used to calculate epilimnion thicknesses using scripts developed in R. The depth of maximum water density change (calculated from temperature) in a given profile was used as the estimate of thermocline depth. Sampling and analytical procedures of water quality are described in the USEPA's procedures (USEPA 2010). Daily surface water temperature data for each Great Lake were obtained from the public archives of National Oceanic and Atmospheric Administration's (NOAA) Coastwatch Great Lakes Surface Environmental Analysis which is generated daily based on satellite sensors on polar orbiting satellites (NOAA 2015). Measurements represent average lake surface temperatures of visible surface water.

Sediment core sampling

Sediment cores were collected at 10 locations throughout the Great Lakes (Fig. 1): three cores representing Lake Superior, two cores from Lakes Huron, Erie, and Ontario, and one core from Lake Michigan. Some cores were collected from the USEPA's research vessel *Lake Guardian* using an Ocean Instruments model 750 box corer (30 cm × 30 cm × 90 cm), from which two 6.5-cm internal diameter cylindrical cores were subsampled. Other cores were collected from the research vessels *Lake Guardian* or *Blue Heron* with an Ocean Instruments model MC-400 multi-corer (9.4 cm diameter). For each location one core was extruded at fine intervals (as fine as 0.25 cm in upper intervals to 1 cm intervals at the bottom of the core) depending on estimated accumulation rates and need for temporal resolution. This core was used for ^{210}Pb dating and diatom analysis. Isotopic dating to develop temporal records for each core follows methods described by Shaw Chraïbi et al. (2014). All cores had exponential ^{210}Pb profiles indicating typical isotopic decay with time, and errors associated with dates ranged from ± 1–2 yr in the most recent three decades to ± 10–20 yr around ca. 1850. The western Lake Erie core dating included supplementary ^{137}Cs analysis to pinpoint the 1963 peak resulting from weapons testing (Appleby 2001).

Fig. 1. Map of sediment core locations throughout the Laurentian Great Lakes (SU = Superior, MI = Michigan, HU = Huron, ER = Erie, ON = Ontario). Locations within each lake are characterized as north (N), south (S), east (E) or west (W), and a core was also collected near Isle Royale in Lake Superior.

Diatom processing

Diatom frustules were cleaned of organic material by digestion in acidic solution to allow identification of diatom species. Diatom samples were rinsed eight times and slides were prepared using the Battarbee et al. (2001) method. Diatoms were identified and enumerated at 1000–1250 X magnification with oil immersion. At least 500 diatom valves were counted per slide. The valve sizes (length, width, diameter, and/or depth) of the first 10 encountered valves of each taxon were measured to determine average valve dimensions in each sediment interval (Reavie et al. 2010) for subsequent biovolume calculations. Diatom taxonomy and enumeration techniques were based on USEPA photographic records and plates, and several diatom iconographs (see Shaw Chraïbi et al. 2014 for details).

To evaluate historical changes in whole diatom assemblages, non-metric multidimensional scaling (NMDS; implemented in R using the vegan package; R Development Core Team 2015; Oksanen et al. 2016) analyses were performed on the sedimentary diatom data from each lake. Relative abundance data were analyzed and sample assemblages were assessed using ordination to trace historical changes relative to the dominant diatom species. Only taxa that comprised at least 5% relative cell abundance in one or more samples were included in NMDS analyses.

Based on existing literature, we compiled a subset of phytoplanktonic diatom taxa known to be changing in response to recent warming in stratifying lakes, namely species in the group *Cyclotella sensu lato*. Our intent was to examine climate-related changes, but eventually each lake will have a detailed paleolimnological treatment (e.g., Shaw Chraïbi et al. 2014). These selected taxa were summarized based on their historical changes (increasing or decreasing over time), their seasonal occurrence and responses along temperature and nutrient gradients. Upon plotting the data vs. time, the obvious, recent increases in the relative abundance of *Cyclotella* across all cores prompted a changepoint analysis (implemented in R; Killick and Eckley 2014) to determine the time of greatest change in mean relative abundance. For seasonal water temperature and chemical responses we used public data provided by Reavie et al. (2014*b*), who examined whether species abundances significantly increased or decreased along water quality gradients.

We used a basic synchrony analysis (Magnuson et al. 1990*a*) to determine whether *Cyclotella sensu lato* was changing similarly across the Great Lakes. Synchrony in *Cyclotella* relative abundance among the 10 cores was measured by calculating the Pearson correlation coefficients among stratigraphic time series from all possible core pairs. All stratigraphic series were first Z-transformed to standardize variances. The sample dates varied in each stratigraphic time series, so for correlation analysis *Cyclotella* values were harmonized by linear extrapolation. For instance, if a 1980 sample in core A had no matching 1980 sample in core B, a linear extrapolation of core B's 1978 and 1985 sample data was used to estimate a corresponding *Cyclotella* relative abundance value.

Historical data collection

Several long-term datasets were acquired so that we could relate fossil records of *Cyclotella* with past environmental conditions.

Nutrients

We acquired historical measurements of offshore Great Lakes total phosphorus (TP) and nitrates + nitrites ($NO_3 + NO_2$) as collected by Environment and Climate Change Canada and compiled by Dove and Chapra (2015).

Air temperature

Historical monthly minimum, maximum and mean air temperature data from 1900 to present were summarized for each of the Great Lakes by averaging the monthly minimum, maximum and mean data of meteorological stations assigned to each lake. Meteorological stations were selected per Hunter et al. (2015) as being within the Great Lakes basin boundary, including a 50 km outer buffer. Daily temperature data were downloaded from NOAA's National Climatic Data Center (NCDC 2016), and from Environment and Climate Change Canada (2016). Mean temperature at each station was computed as the monthly average of daily data. The monthly minimum and maximum temperatures were the lowest and highest daily temperatures in each month.

Chemical deposition

Atmospheric deposition monitoring stations within 100 km distance of each Great Lakes shoreline were selected to calculate loading. Annual wet deposition loadings of ammonium, nitrate, inorganic nitrogen, and chloride were downloaded from National Atmospheric Deposition Program (NADP 2015) and USEPA Clean Air Status and Trends Network (CASTNET 2015) stations from 1979 to 2014. For a given year, the number of stations for a lake ranged from 1 to 16. The chemical loadings for each lake were calculated by using distance weighted averages.

Ice cover

Monthly (December to May) % ice cover maps from 1973 to 2013 were obtained from GLAHF (2016). The GIS maps showing ice cover were analyzed in ArcMap using the zonation tool, then divided by the total lake area to obtain percent cover for each month. We present the maximum monthly % cover value for each year, noting that these data are highly correlated with ice duration data (not presented; 89–95% variance explained in the lakes).

Water level

Annual average water levels from 1860 to 2014 were downloaded from USEPA (2015).

For each core the stratigraphic relative abundance of *Cyclotella* was related to these historical environmental data by linking ^{210}Pb dates for diatom samples (stratigraphic dates) to sample dates for monitoring data. Stratigraphic dates did not have precise matching dates in the monitoring data, so simulated environmental data were calculated by assuming a linear interpolation of the environmental data between each pair of temporally adjacent collection dates (i.e., before and after the stratigraphic date). The value for each environmental variable was estimated when the stratigraphic date intersected the linear function. Environmental data were compiled and related to *Cyclotella* data using Spearman correlation coefficients. Although most of the environmental variables had normal distributions, the *Cyclotella* data were highly skewed, so a Spearman analysis was deemed appropriate. The records for surface water temperature and epilimnion thickness were too recent (1995–2014) to adequately perform historical correlations with the diatom fossil data.

Results

Compiled surface temperature data since 1995 illustrate the increase in Great Lakes water temperatures that has occurred in the last two decades (Fig. 2). Changes were significant in all lakes for regressions performed on annual winter minima, but not for summer maxima. Positive, annual mean slopes were significant for Superior, Huron, and Ontario. During the same period, Lakes Superior, Erie, and Ontario experienced a thickening epilimnion while Lake Michigan's thermocline shallowed. No significant change in Lake Huron's thermocline depth was observed.

It is beyond the scope of this report to fully describe the complexities of diatom shifts in each of the Great Lakes, but some of the key assemblage compositional changes are illustrated by NMDS (Fig. 3). With the exception of Lake Huron (which showed a top-to-bottom migration), species assemblages migrated from right to left along the primary NMDS axis. This long-term shift in assemblages generally reflected a change from a pre- or early-impact state (which varied by lake) to a modern assemblage better represented by *Cyclotella sensu lato* taxa. In many cases, the middle of the long-term transition included temporary shifts to assemblages dominated by *Aulacoseira* (e.g., *Aulacoseira islandica* [AULISLA] in Ontario and Michigan) or eutrophic *Stephanodiscus* (e.g., *Stephanodiscus minutulus* [STEMINUT] and *Fragilaria capucina* [FRACAPU] in Lake Erie's central basin). Within-lake variations in assemblage reorganization were also observed, such as the greater shift to *Cyclotella* dominance in the Lake Huron's northern core compared to the southern core. In addition to the increase in *Cyclotella*, some lakes have concurrent modern increases in species, such as *Fragilaria crotonensis* (FRACROT) in Lake Ontario and Lake Michigan, and *A. islandica* in central Lake Erie. Overall, the distance of modern sample scores from the cluster of *Cyclotella* taxa scores reflects the relative importance of *Cyclotella* in modern assemblages; e.g., very important in Lake Superior and Lake Ontario, much less so in western Lake Erie and southern Lake Huron.

Sedimentary analysis from all Great Lakes sediment cores indicated an increasing relative abundance in *Cyclotella sensu lato* in recent decades (Fig. 4), indicating consistency in reorganization of the diatom assemblages at all locations. The changepoints marking the greatest difference in pre- and post-increase in *Cyclotella* relative abundance indicate that

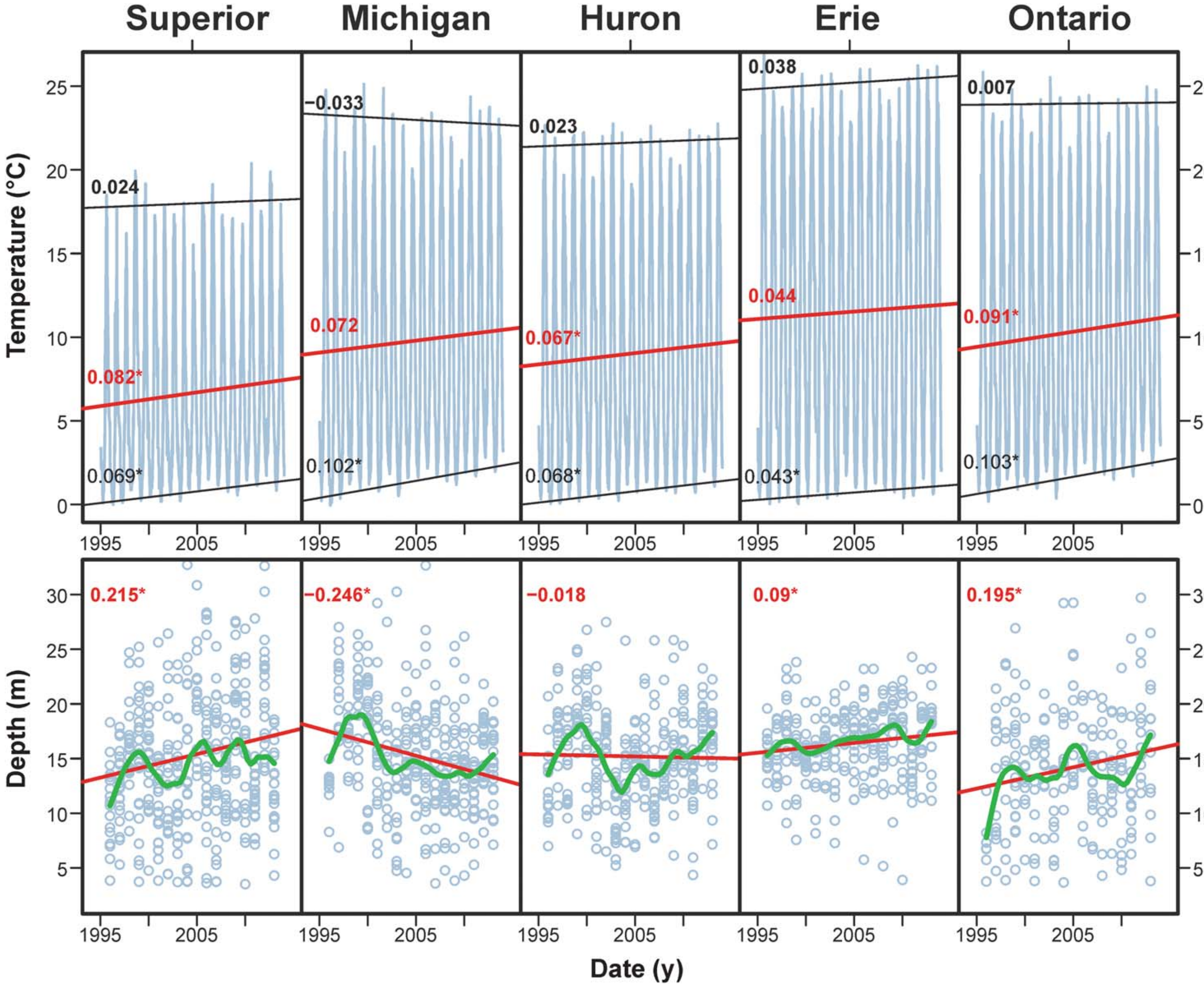

Fig. 2. Measured and linear model fits for Great Lakes surface water temperatures (upper plots) and summer thermocline depths (lower plots). For surface temperatures, linear regressions are provided for annual mean data (red lines) as well as winter minima and summer maxima (black lines), including slopes indicating change in °C yr^{-1}. Asterisks indicate a significant *t*-test of the slope ($p < 0.05$). For thermocline depths the slope (m yr^{-1}) is provided for the linear regression (red), and a locally weighted scatterplot smooth line with a span of 2 yr (green) is included to better indicate year-to-year changes.

the most substantial changes occurred around 1970–1980 across all lakes, although a much earlier shift ∼ 1938 was observed in the Isle Royale core from Lake Superior. In Lake Huron and central Lake Erie the shift to *Cyclotella* was abrupt, but in the cases of Lake Michigan (changepoint at 1998), Lake Ontario (west and east core changepoints at 2001 and 2003) and Lake Superior (west and east core changepoints at 1975 and 1971) it is clear that the shift started several years prior to the changepoints. The polymictic western basin of Lake Erie had a much more subtle recent increase since ∼ 2000. Increases in cell and biovolume accumulation rates occurred in western Superior, central Erie and Huron. Increases in accumulation rates also occurred in other cores (Michigan, Ontario, Superior east), but primarily within the most recent 10 yr. Increases in relative biovolume were especially prominent in Lakes Superior and Huron, lakes that have diatom assemblages composed of the highest contemporary relative abundances of *Cyclotella* (Reavie et al. 2014*a*).

Species in the *Cyclotella comensis* complex, which tend to occur more commonly in August phytoplankton samples, consistently increased in recent decades in the lakes (Table 1). The small spring taxon *Cyclotella atomus* "fine form" (*C. atomus* var. 1; Reavie and Kireta 2015) also increased. Other taxa had

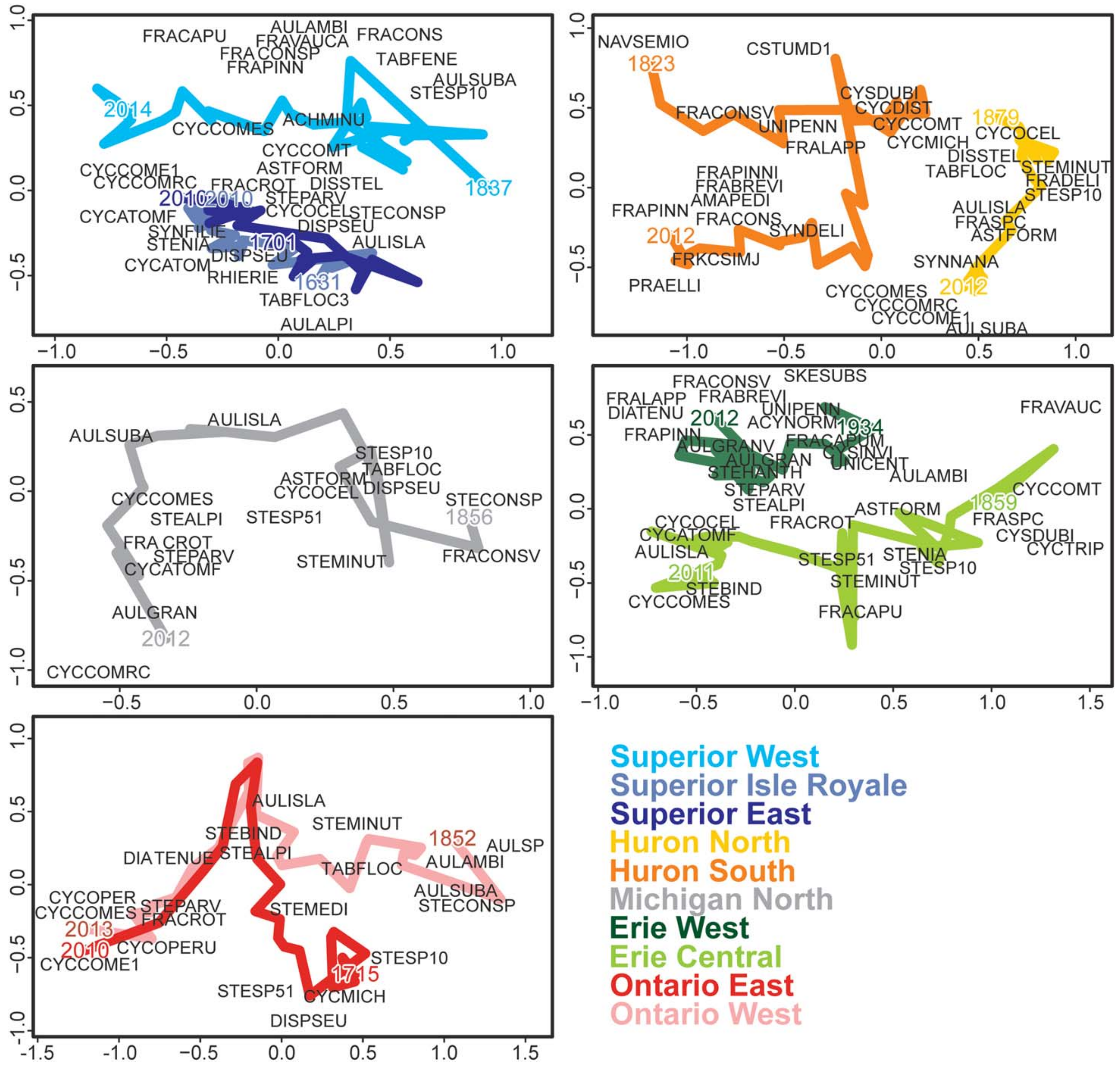

Fig. 3. Two-dimensional non-metric multidimensional scaling (NMDS) analysis of diatom relative abundance data in each lake. Codes for species that occurred at 5% or more in at least one sample are plotted. Historical trajectories are illustrated using a line for each core, with the oldest and most recent ^{210}Pb dates also plotted. Species codes for *Cyclotella sensu lato* match those in Table 1, and all codes are defined by Reavie et al. (2014*a*).

variable responses across lakes, while some showed no change. Because of its summer dominance it is not surprising that the *C. comensis* complex had a significant, positive response along the water temperature gradient. Six of the 12 *Cyclotella* taxa had significant, negative responses to phosphorus while only two taxa responded negatively along the nitrogen gradient. Taxa from the *C. comensis* and *C. atomus* groups were significantly, positively correlated with thermocline depth, whereas *Cyclotella ocellata* responded negatively. Although we do not present all of the historical data for these taxa, all of them appeared to occur in at least trace numbers in pre-20th century sediments; i.e., they do not appear to be new to the lakes.

Long-term environmental data (mostly post-1970 for nutrients and post-1900 for ice, temperature and water level

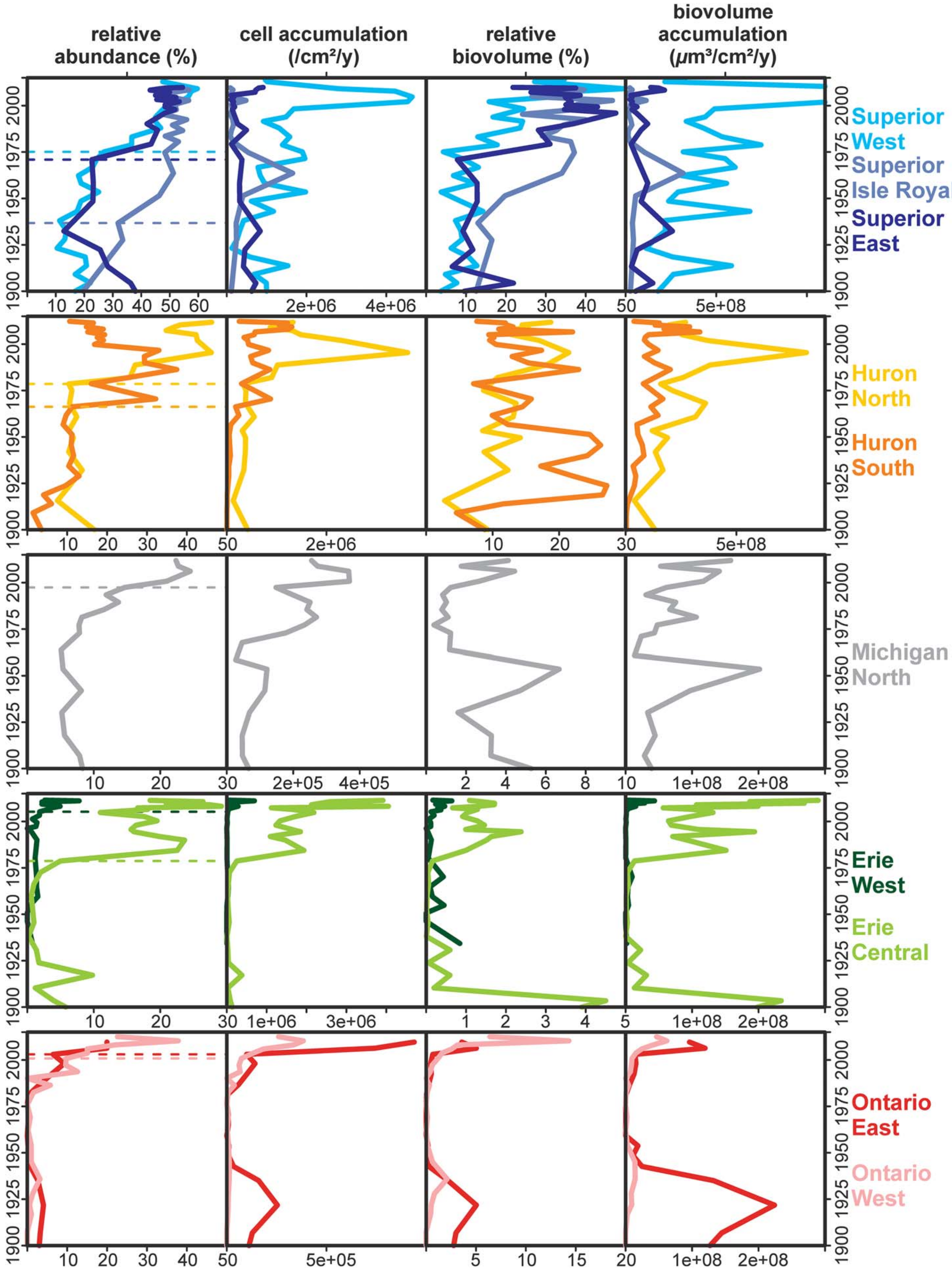

Fig. 4. Sedimentary profiles of *Cyclotella sensu lato* in Great Lakes sediment cores. Data are represented as relative density, cell accumulation rates, relative biovolume and biovolume accumulation rates. For relative abundance data (left-hand plots) dashed lines indicate the changepoint date marking the greatest difference in means between upper (recent) and lower (older) *Cyclotella* data. Diatom taxa included in these summary plots are listed in Table 1.

Table 1. Common *Cyclotella sensu lato* taxa in the Great Lakes sediment cores. Arrows indicate increasing or decreasing trends in relative abundance in the upper 100 yr of cores from each lake. "O" indicates presence but no discernable trend over time. Symbols are shown for taxa that occurred at a minimum of 1% in at least one sample, and bold symbols indicate taxa that occurred at a minimum of 10% in any sample (i.e., dominant taxa). The season indicates when (spring, summer or both evenly) that the species occurs most abundantly in modern diatom-phytoplankton collections from 2007 to 2011 (Reavie et al. 2014*b*). Significant linear relationships (Spearman correlation, $p < 0.05$) with measured epilimnetic (summer) or isothermal water column (spring) temperature (Temp), nitrates + nitrites (N), phosphorus (P = total or dissolved phosphorus) and thermocline depth (Therm) are indicated by positive or negative symbols. Environmental data for correlations were acquired from the USEPA's Great Lakes National Program Office.

		Lake-specific trends						Correlations with water column parameters			
	Code	Season	Superior	Michigan	Huron	Erie	Ontario	Therm	Temp	N	P
Cyclotella atomus "fine form"	CYCATOMF	Spring	o	↑	↑	↑	↑	+	-		
Cyclotella atomus Hust.	CYCATOM	Both	o					+	-		
Cyclotella cf. *delicatula* Hust. (*comensis* "rough center with process")	CYCCOMRC	Both	**↑**	↑	**↑**	↑		+		-	-
Cyclotella comensis Grun.	CYCCOMES	Summer	**↑**	**↑**	**↑**	**↑**	↑	+	+		-
Cyclotella comensis var. 1	CYCCOME1	Summer	↑	↑	↑	↑	**↑**	+	+		-
Handmannia bodanica (Eulen.) Koc. and Khurs. (complex)	CYCCOMT	Summer	o	o	o		o				
Cyclotella distinguenda	CYCDIST	Summer			**O**						
Cyclotella michiganiana Skv.	CYCMICH	Summer	o	o	o		o		+	-	-
Cyclotella ocellata Pant.	CYCOCEL	Summer	**↓**	o	**↓**	**↑**	↓	-			
Cyclotella tripartita Pant.	CYCTRIP	Summer	o	o	o		↓		+		
Cyclotella operculata (Ag.) Kütz. + *operculata* var. *unipunctata* Hust.	CYCOPER, CYCOPERU	Summer	↑	o		↑	↑		-		-
Discostella stelligera (Cl. and Grun.) V.H. + *Discostella pseudostelligera* Hust.	DISSTEL, DISPSEU	Summer	**O**	↓	**↓**	o	↓		+		-

data) reveal some consistencies across the Great Lakes basin (Fig. 5). Water nitrate + nitrite concentrations are increasing while TP is decreasing (Fig. 5b), with the exception of Lake Erie which has had a more erratic condition since ~ 1970. Nitrate, total inorganic N and chloride deposition are declining while ammonium has subtly increased (Fig. 5c). Air temperatures are increasing, particularly since ~ 1980 and especially annual minimum temperature (Fig. 5d). Water levels have been variable but generally show a decline since ~ 1980 (Fig. 5e). The proportion of lake ice coverage has shown a clear decline in all lakes since the last measured peak in 1980 (Fig. 5e).

Simultaneous examination of Fig. 5 and Table 2 permits an assessment of *Cyclotella sensu lato* relative abundance with long-term environmental data. The most consistent variable explaining *Cyclotella* relative abundance was minimum annual temperature, which was positively related across all lakes. Annual mean temperature was correlated in some lakes but not at all in Lake Michigan and Lake Erie. Maximum atmospheric temperature was positively related to *Cyclotella* relative abundance in all lakes except western Lake Ontario. Atmospheric loading of chemicals (N and Cl) tended to be negatively correlated with *Cyclotella* relative abundance, but mainly in the southeastern region of the Great Lakes basin. $NO_2 + NO_3$ water concentrations were strongly, positively correlated with *Cyclotella* in Lake Superior, Lake Ontario and one core from Lake Huron, which is not surprising given the distinct rise in $NO_2 + NO_3$ along with *Cyclotella* in those lakes (Fig. 5). However, this correlation did not exist in the remaining cores. While a recent rise in both water N and *Cyclotella* is apparent across the basin, the relationship was sometimes decoupled, particularly in Lake Ontario where the water $NO_2 + NO_3$ rise began about 20 yr before the initiation of the *Cyclotella* rise (Fig. 5). Strong negative relationships between TP and *Cyclotella* occurred in the Superior cores, Lake Michigan, northern Lake Huron and Lake Ontario.

Synchrony analysis (Table 3) indicated strong similarities in *Cyclotella* relative abundance trends across most core pairs, and a significant average synchrony ($r = 0.63$, $p < 0.001$). Exceptions were the non-significant relationships between the Lake Huron south core and Lake Ontario and western Lake Erie cores.

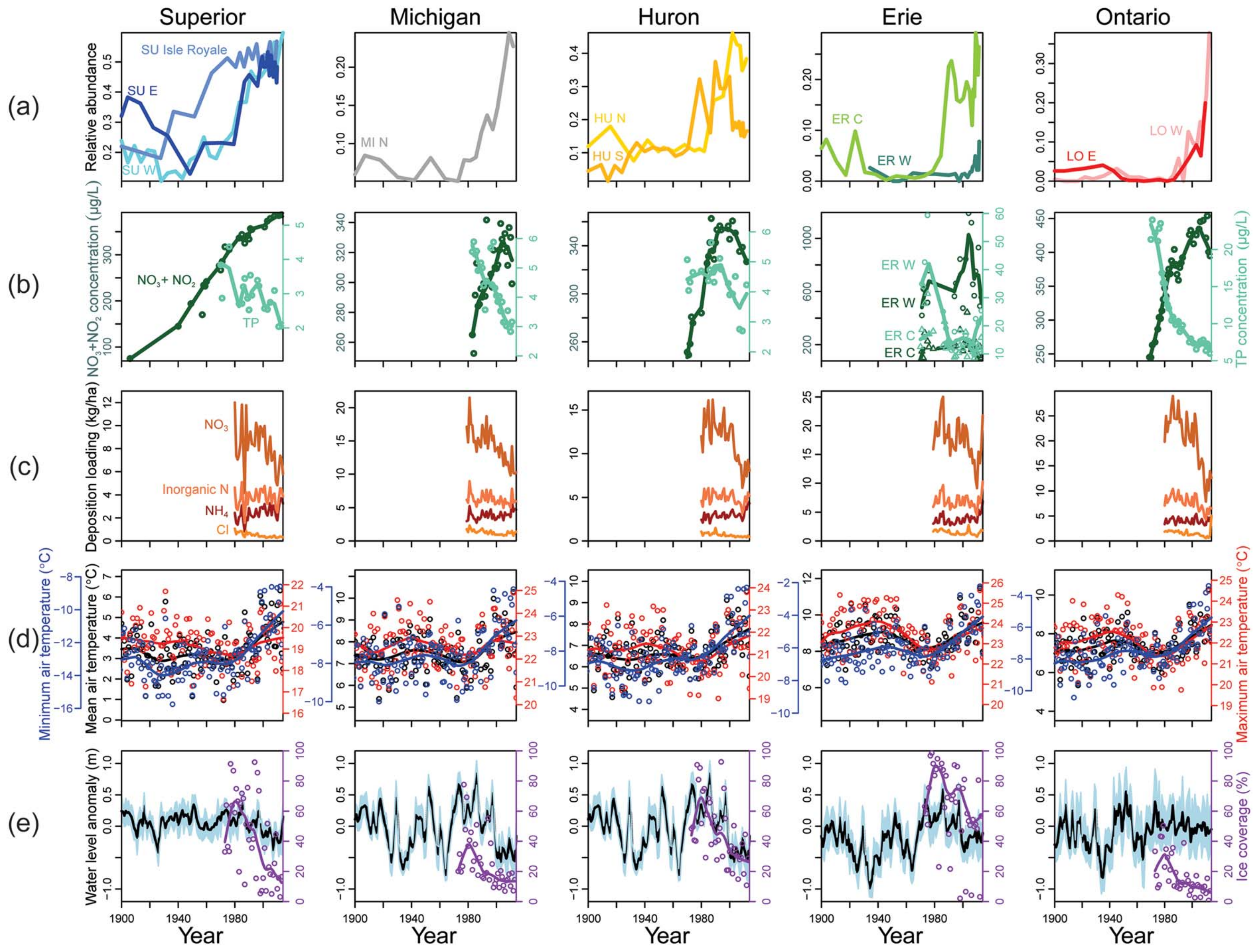

Fig. 5. Stacked plots of *Cyclotella sensu lato* relative abundance from sediment cores (**a**) and measured historical data from each lake. Nitrates + nitrites and total phosphorus (**b**), nitrogen and chloride deposition (**c**), air temperatures (**d**) and ice cover data (**e**, purple line and circles) were fitted with lowess curves with 5-yr spans to smooth trends. Air temperature data are presented as annual minimum (blue), maximum (red), and mean (black), noting the unique *y*-axis scales for each air temperature variable to better illustrate long-term changes. For water levels (**e**, black line), the blue, shaded band shows the range of monthly average water levels and the black line is the annual average. Water level anomalies are based on the 1981–2010 average as a baseline.

Table 2. Spearman correlation coefficients for fossil *Cyclotella sensu lato* relative abundance vs. historical records of physical and chemical variables. Only significant correlations are shown (*t*-test; $p < 0.05$; with Bonferroni correction for multiple comparisons). Numbers in parentheses indicate the number of points in the correlation analysis. Core acronyms match those in Fig. 1.

Group	Variables	SU W	SU IR	SU E	MI N	HU N	HU S	ER W	ER C	ON E	ON W
Atmospheric loading	Chloride	−0.68 (11)	(13)	(14)	(09)	(09)	(14)	−0.58 (18)	(16)	−0.89 (07)	−0.87 (11)
	Inorganic N	(11)	(13)	(14)	(09)	(09)	0.57 (14)	−0.62 (18)	(16)	(07)	−0.75 (11)
	NH_4	0.83 (11)	(13)	(14)	(09)	(09)	(14)	(18)	(16)	(07)	(11)
	NO_3	(11)	(13)	(14)	−0.85 (09)	(09)	0.70 (14)	−0.86 (18)	(16)	−0.86 (07)	−0.80 (11)
Ice cover	Annual maximum %	(12)	(14)	−0.75 (15)	−0.88 (10)	−0.87 (11)	(15)	(18)	(17)	−0.71 (08)	−0.77 (12)
Local atmospheric temperature	Annual mean	0.42 (29)	(19)	0.69 (23)	(18)	(20)	0.39 (29)	(25)	(31)	(18)	0.82 (24)
	Annual maximum	(29)	(19)	(23)	(18)	(20)	(29)	(25)	(31)	(18)	0.63 (24)
	Annual minimum	0.69 (29)	0.59 (19)	0.75 (23)	0.67 (18)	0.60 (20)	0.63 (29)	0.50 (25)	0.53 (31)	0.63 (18)	0.81 (24)
Water level (anomaly from historic mean)	Annual mean	−0.43 (31)	(20)	−0.61 (24)	(19)	(20)	(29)	(25)	(32)	(19)	(24)
	Annual minimum	−0.43 (31)	(20)	−0.61 (24)	(19)	(20)	(29)	(25)	(32)	(19)	(24)
	Annual maximum	−0.46 (31)	−0.53 (20)	−0.64 (24)	(19)	(20)	(29)	(25)	(32)	(19)	(24)
Water quality	Chl *a*, ug/L	(11)	(14)	(15)	(07)	−0.71 (11)	(14)	(18)	(17)	(08)	(12)
	NH_3, ug/L	(13)	(14)	(16)	(02)	(11)	(15)	−0.67 (19)	(18)	0.74 (08)	(12)
	$NO_2 + NO_3$, ug/L	0.86 (26)	0.67 (18)	0.72 (21)	(07)	0.74 (11)	(15)	(19)	(18)	0.78 (09)	0.74 (13)
	SD, m	0.64 (11)	(14)	(15)	(08)	0.69 (12)	(15)	(19)	(18)	0.93 (09)	0.55 (13)
	SiO_2, mg/L	(13)	(14)	(16)	0.99 (04)	(11)	(15)	(18)	(18)	0.88 (09)	0.88 (13)
	SRP, ug/L	(13)	(14)	(16)	(02)	(11)	(15)	(19)	(18)	−0.92 (09)	−0.72 (13)
	TP, ug/L	−0.70 (13)	−0.55 (14)	−0.58 (16)	−0.93 (07)	−0.67 (11)	(15)	(19)	(18)	−0.92 (09)	−0.88 (12)

Table 3. Synchrony analysis using Pearson correlation coefficients for fossil *Cyclotella sensu lato* relative abundance across all possible core pairs. Significance (*t*-test) is indicated by asterisks (**, $p < 0.001$; *, $p < 0.05$; Bonferroni correction for multiple comparisons applied). Core acronyms match those in Fig. 1.

	SU W	SU IR	SU E	HU N	HU S	MI N	ER W	ER C	LO E
SU IR	0.67**								
SU E	0.88**	0.53**							
HU N	0.88**	0.51*	0.85**						
HU S	0.56**	0.70**	0.46**	0.51**					
MI N	0.90**	0.54**	0.79**	0.87**	0.35*				
ER W	0.57**	0.47*	0.37*	0.41*	−0.06	0.63**			
ER C	0.88**	0.62**	0.80**	0.82**	0.57**	0.80**	0.55**		
LO E	0.73**	0.28**	0.64**	0.74**	0.15	0.87**	0.77**	0.71**	
LO W	0.78**	0.51**	0.66**	0.75**	0.23	0.84**	0.68**	0.72**	0.89**

Discussion

The major community changes in Great Lakes diatom phytoplankton presented here are correlated with changes in water column properties that are indirectly related to warmer air temperatures, including a longer open-water season and associated effects on light, thermal structure and mixing depth, as noted by others in smaller lakes (e.g., Rühland et al. 2008). Climate-driven changes in diatom communities can be difficult to decipher owing to simultaneous anthropogenic disturbances, which may be contributing to some of the recent species changes. In the Great Lakes, these anthropogenic impacts include eutrophication and the recent effects of invasive mussels which are contributing to oligotrophication. All of these impacts are unevenly distributed across the Great Lakes. However, the concordance between air and water temperatures, ice cover, and ice-free period reinforces the contribution of recent climate warming to primary producer changes.

Increases in planktonic diatoms in these deep lakes are consistent with findings from top-bottom analyses of 147 lake sediment cores from the central Canadian subarctic, Ontario and Nova Scotia (Rühland et al. 2008), as well as from 40 lakes in northwestern Ontario (Enache et al. 2011), where deeper ($> \sim 6$–10 m) lakes generally recorded the largest increases in small *Cyclotella* taxa in the modern sediments. It is likely that a longer open-water period favors a longer period of radiative heating, changes in light habitat, and associated physical changes that favored the onset of diatom plankton development. Planktonic taxa like *Cyclotella* are known to thrive in longer ice-free periods and in stratified waters and so can outcompete heavier taxa such as *Aulacoseira*, which require more frequent mixing to maintain a position in the photic zone (Fahnenstiel and Glime 1983; Pannard et al. 2008). Further, Winder et al. (2009) observed that these small-celled taxa thrive in deep Lake Tahoe due to their high surface area to volume ratios, enabling them to more efficiently harvest light and nutrients.

Strong correlations exist between increasing abundance of *Cyclotella* in sediment cores and increasing atmospheric temperatures and ice-free periods (e.g., this work and Hawryshyn et al. 2012; North et al. 2013). Other variables show strong correlations, such as the relationship between *Cyclotella* and nitrogen compounds, the latter having a well-documented rise over many decades in Lake Superior (Sterner et al. 2007), but those variables show less coherence across our 10 paleolimnological profiles. It is probable that changes in physical properties such as stratification, resource availability, and water clarity are key factors leading to these shifts. Despite significant efforts to determine reasons for variations among long-term *Cyclotella* increases (in terms of species composition, timing, and magnitude of the rise), the mechanisms remain uncertain and are obviously variable among taxa and lakes. Saros and Anderson (2015) theorized that interactions among multiple variables, i.e., higher nitrates, deeper mixing depths and greater water clarity, may result in a greater relative abundance of *Cyclotella*. It has been noted that changes in wind energy are variably affecting lakes by changing thermal stability and thermocline depths, which in turn can affect light and nutrient availability in the epilimnion (Fee et al. 1996). This is a complex set of integrated variables, as the *Cyclotella* rise has been observed in large lakes with only subtle change in mechanical energy from wind (e.g., Lake of the Woods; Herb et al. 2005).

Among the temperature variables we evaluated, minimum annual temperature showed the most consistent, positive relationship with *Cyclotella* relative abundance. Globally in the last century, minimum annual and seasonal atmospheric temperatures have increased faster than maximum temperatures (Easterling et al. 1997), and minimum temperature may be the most biologically important in lakes. Minimum atmospheric temperature (i.e., the coldest winter extreme) may be a particularly strong determinant of annual ice formation and the length of the ice-free season, thereby having the greatest influence on phytoplankton communities.

Although deeper summer mixing depths (Fig. 2) are apparent in lakes Superior, Erie, and Ontario, the same is not true of Lakes Michigan and Huron, which exhibit a similar increase in sedimentary *Cyclotella* abundance (Fig. 4). Deepening thermoclines are expected with increasing wind speeds as observed on Lake Superior (Austin and Colman 2008) but the same wind dynamics may not be present over the other lakes. The lack of a deepening thermocline in Lakes Michigan and Huron may be related to pelagic food web disturbances in the last ~ 15 yr possibly resulting from the filter-feeding effect of invasive mussels (dreissenids). It may be that, prior to the widespread establishment of dreissenids in the early 2000s (Warner and Lesht 2015), Michigan and Huron had a similarly deepening thermocline (note the uptick in the late 1990s, Fig. 2). Stabilization or reversal of the *Cyclotella* rise in these lakes (Fig. 4; especially Huron) corresponds with the spread of mussels, particularly in southern Lake Huron where the algal decline was most prominent (Reavie et al. 2014*a*), although further work is needed to determine the mechanisms for this change. This very recent *Cyclotella* decline in Huron caused the poor synchrony with Lake Ontario and western Lake Erie core data, where there occurred a recent *Cyclotella* increase. A shallowing thermocline as observed in Lake Michigan would typically arise from increasing water column turbidity or productivity, contradicting the increased water clarity that has been observed (i.e., in Lake Michigan and Lake Huron; Binding et al. 2015; Dove and Chapra 2015); reasons for this physical change therefore require study. Further to this complexity, increasing the mixing depth does not necessarily mean thickening of the photic zone, so diatoms being mixed convectively could spend time in darkness. Simultaneously increasing the thermocline and photic zone depth may favor smaller cyclotelloid diatoms, whereas increasing the mixing depth without increasing the photic zone depth could be detrimental for small *Cyclotella*.

In recent decades there have been clear responses to reduced nutrient flux to the Great Lakes resulting from management of phosphorus (e.g., Makarewicz and Bertram 1991), and standing nutrient and algal loads have also dropped as a result of the shunting effect of invasive dreissenids (Warner and Lesht 2015). Pelagic total phosphorus has declined in all of the Great Lakes since the 1970s (Dove and Chapra 2015). In Lake Superior, for example, there has been a complete return to pre-impact nutrient standing loads (Shaw Chraïbi et al. 2014), but interactions with climate change may be preventing re-establishment of the biotic composition that existed prior to fertilization. Contrasting phosphorus, nitrate levels have increased over the last ~ 40 yr, with a slowing rate of increase and even declines shown for some Great Lakes over the most recent decade (Dove and Chapra 2015). In our analysis of species responses across environmental gradients (Table 1), *Cyclotella* abundance was proportionally higher at lower nutrient concentrations, or had no response along nutrient gradients. There is correlation between declining nutrient loads and increasing *Cyclotella* abundance, but it is remarkable that more recent sedimentary assemblages have not returned to pre-impact conditions, indicating a new ecological state irrespective of nutrient remediation. While climate-driven effects on pelagic nutrients may contribute to shifts in phytoplankton, our observations suggest that nutrients alone are not the major determinants of higher *Cyclotella* abundance in the Great Lakes. Novel climate-related stressors are probably contributing to limnological (and resulting biological) conditions that have no historical analogs.

The biological effects of recent warming on the Great Lakes are confounded by multiple environmental stressors that may obscure a response to climatic change. Indeed, recent decades have seen substantial, well-evidenced changes to the pelagic ecosystems due to the dreissenid invasion (since the early 1990s; Hecky et al. 2004) and re-eutrophication (especially in western and central Lake Erie in the last decade; Michalak et al. 2013), which are undoubtedly simultaneous determinants of some of the diatom taxa we observed in recent sediments. However, the shift to a greater sedimentary dominance by cyclotelloid diatoms began prior to these changes in some lakes, especially Superior, Huron, and Michigan. Changes in Ontario and Erie (the more southerly lakes) began in the 1980s, making it difficult to separate from the remedial effects of lower nutrient flux following implementation of the Clean Water Act. However, there was no reversion to a pre-impact diatom assemblage that was present when nutrient levels were naturally lower in the lake. Further, combined with substantial corresponding evidence of cyclotelloid increases in nearby temperate and otherwise unimpacted boreal and arctic lakes, there is support for a climate response in Great Lakes diatoms.

As for the Laurentian Great Lakes, *Cyclotella* has increased in relative abundance elsewhere, and individual taxa have shown distinct responses. For instance, *Discostella* (formerly *Cyclotella*) *stelligera* increased in Lake of the Woods while it decreased in Siskiwit Lake (on Isle Royale, Lake Superior; Saros et al. 2012). Similarly, unlike the dominant *C. comensis* complex, the *Discostella* complex decreased upcore in the Great Lakes. Recent investigations of vertical distributions of phytoplankton during summer stratification reveal partitioning of *Cyclotella* by depth according to cell size (Bramburger and Reavie 2016). Smaller-celled taxa, including *C. comensis* var. 1 (Reavie and Kireta 2015) are more abundant in the epilimnion of the Great Lakes, while larger-celled taxa (e.g., *Handmannia*) are typically more abundant in the deep chlorophyll layer. Taxa with broader cell size ranges are distributed more evenly between the two layers, and often exhibit within-species size partitioning (Bramburger unpubl.), indicating that intensifying stratification regimes associated with warming may be an important sorting mechanism. However, environmental context is critical to understanding assemblage shifts (Rühland et al. 2015), and clearly the many species of *Cyclotella sensu lato* will vary in their response to climate-induced changes based on multiple autecological optima. A diatom species would not respond to a single environmental variable in isolation (Rühland et al. 2015), hence several studies have attempted to figure out the effects of multiple simultaneous variables on *Cyclotella* growth (e.g., Saros et al. 2012). It is probable each Great Lake has a unique context for each rise, as evidenced by the fact that the selection of dominant *Cyclotella* species varies by lake. For instance, the *Cyclotella* rise includes *C. ocellata* in Lake Erie but not in the other lakes.

Most Great Lakes *Cyclotella* species tend to occur more commonly in summer (Table 1; Reavie et al. 2014) so their increase in abundance may be a result of a longer late-summer-fall growing season, as suggested by Rühland et al. (2013) for Arctic lakes. Smaller *Cyclotella* species are capable of prolific reproduction (Fahnenstiel and Glime 1983; Winder and Hunter 2008) so it is further plausible that a longer growing season would contribute more frustules of *Cyclotella* to sedimentary records. Such an explanation for our observed paleolimnological trends assumes late-year diatoms are repeatedly lost to the sedimentary record while their organic components are recycled to form new diatoms. This is conceivable given the abundant dissolved late-summer silica recorded in the upper lakes that could support an extended period of diatom growth. Negative correlations between *Cyclotella* relative abundance and percent ice cover in some lakes (Table 2) suggest this may be happening, but more detailed year-round phytoplankton collections are needed to test such a hypothesis. Also, with physical changes to the water column the importance of light effects and loss terms need to be better understood. Species-specific resistance to ultraviolet light may favor certain, light-tolerant phytoplankton species under increasing light penetration in the water column. Thermal stratification and vertical mixing determine the sinking velocities of diatoms, and decreased turbulence, as would occur under increased thermal stabilization, should favor small-celled species (Daufresne et al. 2009; Reavie and Barbiero 2013).

Saros and Anderson (2015) summarized the difficulty of using *Cyclotella* species in paleolimnological reconstructions due to their extremely variable responses to contemporary changes in environmental parameters. We, too, acknowledge the difficulty confirming mechanisms for the observed changes. While there is considerable evidence that changes in lake phytoplankton in northern latitudes are due to changing climate and related variables, and even some mechanistic understanding is being developed, little effort has focused on whether these changes are meaningful to lake management. Undoubtedly this reorganization of primary producers is having some bottom-up impact on food webs, and assuming the current trajectory of warming, phytoplankton populations will continue to change. Despite predictions (e.g., for fish; Magnuson et al. 1990*b*), to date in the Great Lakes there are no recorded changes in higher trophic levels that are known to be driven by climate-induced changes in primary producers. Shifts in phytoplankton have had measureable bottom-up effects on species composition and abundance of zooplankton and fish in marine systems (Ware and Thomson 2005) and Everglades wetlands (Rader and Richardson 1994), but the importance of phytoplankton species composition in such relationships is not known. Further experimentation is needed to predict whether changes are likely given the assumption that the shift in primary producers will continue. This would include studies on food preferences of the dominant grazing zooplankton (e.g., *Limnocalanus*) to determine whether they can adequately shift to a diet of *Cyclotella* and other taxa that are favored under the new climate regime. Contemporary research techniques probably have the precision to detect these bottom-up effects, but studies need to be better focused, allocated and funded to determine mechanisms.

Conclusions

There is strong evidence that recent atmospheric warming is having an effect on the structure of Great Lakes phytoplankton assemblages. Diatom taxa in the group *Cyclotella sensu lato* are increasing in relative and (in some lakes) absolute abundance in concord with recent, rapid warming. Such a widespread change in the pelagic Great Lakes due to climate change has not been previously observed. The eventual environmental consequences of this basin-wide change are unknown, but it may serve as a warning of future impacts. We recommend that the following research questions should be initiated (or continue to be intensively studied) to understand and support future management of the Great Lakes pelagic system under the likelihood of continued climate-driven changes.

What is the cause of the *Cyclotella sensu lato* rise in the Great Lakes? Species-specific investigations and ongoing assessments of contemporary assemblages are needed to fully understand the interactions of driving variables on pelagic primary producers. The many changes in water column properties that are associated with warming include changes in the duration and extent of open water and ice cover, changes in light and nutrients and changes in stratification and mixing strength. Assessments would include bench-scale experiments of select taxa from the lakes, and more detailed, year-round sampling of algae and water quality parameters.

Assuming this shift in primary producers will continue, what are the potential future impacts on pelagic food webs? Again, detailed year-round sampling of phytoplankton and grazers is needed to better characterize interactions among trophic levels. Food preferences of the dominant Great Lakes zooplankton need to be known, and whether they are able to tolerate shifting diets. When a better understanding is gathered it may be possible to predict future effects on cold-water fisheries.

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. Springer.

Assel, R., K. Cronk, and D. Norton. 2003. Recent trends in Laurentian Great Lakes ice cover. Clim. Change **57**: 185–204. doi:10.1023/A:1022140604052

Austin, J., and S. Colman. 2008. A century of temperature variability in Lake Superior. Limnol. Oceanogr. **53**: 2724–2730. doi:10.4319/lo.2008.53.6.2724

Battarbee, R. W., V. J. Jones, R. J. Flower, N. G. Cameron, H. Bennion, L. Carvalho, and S. Juggins. 2001. Diatoms, p. 155–202. *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 Academic.

Beall, B. F. N., and others. 2016. Ice cover extent drives phytoplankton- and bacterial community structure in a large north-temperate lake: Implications for a warming climate. Environ. Microbiol. **18**: 1704–1719. doi:10.1111/1462-2920.12819

Binding, C. E., T. A. Greenberg, S. B. Watson, S. Rastin, and J. Gould. 2015. Long term water clarity changes in North America's Great Lakes from multi-sensor satellite observations. Limnol. Oceanogr. **60**: 1976–1995. doi:10.1002/lno.10146

Bramburger, A. J., and E. D. Reavie. 2016. A comparison of phytoplankton communities of the deep chlorophyll layers and epilimnia of the Laurentian Great Lakes. J. Great Lakes Res. **42**: 1016–1025. doi:10.1016/j.jglr.2016.07.004

CASTNET. 2015. Clean air status and trends network [accessed 2015 November]. Available from http://www.epa.gov/castnet

Daufresne, M., K. Lengfellner, and U. Sommer. 2009. Global warming benefits the small in aquatic ecosystems. Proc. Natl. Acad. Sci. USA **106**: 12788–12793. doi:10.1073/pnas.0902080106 [19620720]

Dobiesz, N. E., and others. 2010. Metrics of ecosystem status for large aquatic systems: A global comparison. J. Great Lakes Res. **36**: 123–138. doi:10.1016/j.jglr.2009.11.003

Dove, A., and S. C. Chapra. 2015. Long-term trends of nutrients and trophic response variables for the Great Lakes. Limnol. Oceanogr. **60**: 696–721. doi:10.1002/lno.10055

Easterling, D. R., and others. 1997. Maximum and minimum temperature trends for the globe. Science **277**: 364–367. doi:10.1126/science.277.5324.364

Enache, M. D., A. M. Paterson, and B. F. Cumming. 2011. Changes in diatom assemblages since pre-industrial times in 40 reference lakes from the Experimental Lakes Area (northwestern Ontario, Canada). J. Paleolimnol. **46**: 1–15. doi:10.1007/s10933-011-9504-2

Environment and Climate Change Canada. 2016. National climate services [accessed 2016 February]. Available from http://climate.weather.gc.ca

Fahnenstiel, G. L., and J. Glime. 1983. Subsurface chlorophyll maximum and associated Cyclotella pulse in Lake Superior. Int. Rev. Gesamten Hydrobiol. Hydrogr. **68**: 605–616. doi:10.1002/iroh.3510680502

Fee, E. J., R. E. Hecky, S. E. M. Kasian, and D. R. Cruikshank. 1996. Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. Limnol. Oceanogr. **41**: 912–920. doi:10.4319/lo.1996.41.5.0912

GLAHF. 2016. Great Lakes aquatic habitat framework data; an aquatic, geospatial database for the Great Lakes [accessed February 2016]. Available from http://glahf.org/data/

Hawryshyn, J., K. M. Rühland, R. Quinlan, and J. P. Smol. 2012. Long-term water quality changes in a multiple-stressor system: A diatom-based paleolimnological study of Lake Simcoe (Ontario, Canada). Can. J. Fish. Aquat. Sci. **69**: 24–40. doi:10.1139/f2011-134

Hecky, R. E., R. E. Smith, D. R. Barton, S. J. Guildford, W. D. Taylor, M. N. Charlton, and T. Howell. 2004. The nearshore phosphorus shunt: A consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. **61**: 1285–1293. doi:10.1139/f04-065

Herb, W., O. Mohseni, and S. Heinz. 2005. Lake of the Woods Shoreline Erosion: Analysis of historical shorelines, climate and lake level. University of Minnesota Project Report No. 466.

Hunter, T. S., A. H. Clites, K. B. Campbell, and A. D. Gronewold. 2015. Development and application of a North American Great Lakes hydrometeorological database – Part i: Precipitation, evaporation, runoff, and air temperature. J. Great Lakes Res. **41**: 65–77. doi:10.1016/j.jglr.2014.12.006

Killick, R., and I. Eckley. 2014. changepoint: An R package for changepoint analysis. J. Stat. Softw. **58**: 1–19. doi:10.18637/jss.v058.i03

Magnuson, J. J., B. J. Benson, and T. K. Kratz. 1990*a*. Temporal coherence in the limnology of a suite of lakes in Wisconsin, U.S.A. Freshw. Biol. **23**: 145–159. doi:10.1111/j.1365-2427.1990.tb00259.x

Magnuson, J. J., J. D. Meisner, and D. K. Hill. 1990*b*. Potential changes in the thermal habitat of Great Lakes fish after global climate warming. Trans. Am. Fish. Soc. **119**: 254–264. doi:10.1577/1548-8659(1990)119<0254:PCITTH>2.3.CO;2

Makarewicz, J. C., and P. Bertram. 1991. Evidence for the restoration of the Lake Erie ecosystem: Water quality, oxygen levels, and pelagic function appear to be improving. Bioscience **41**: 216–223. doi:10.2307/1311411

Mason, L. A., C. M. Riseng, A. D. Gronewold, E. S. Rutherford, J. Wang, A. Clites, S. D. Smith, and P. B.

McIntyre. 2016. Fine-scale spatial variation in ice cover and surface temperature trends across the surface of the Laurentian Great Lakes. Clim. Change 1–13. doi:10.1007/s10584-016-1721-2

Michalak, A. M., and others. 2013. Record-setting algal bloom in Lake Erie caused by agricultural and meteorological trends consistent with expected future conditions. Proc. Natl. Acad. Sci. USA **110**: 6448–6452. doi:10.1073/pnas.1216006110

NADP. 2015. National Atmospheric Deposition Program [accessed 2015 November]. Available from http://nadp.sws.uiuc.edu/

National Oceanic and Atmospheric Association (NOAA). 2015. Data from: Great lakes coastal forecasting system [accessed 2015 May]. Available from http://www.glerl.noaa.gov/res/glcfs

NCDC. 2016. NOAA National Centers for Environmental Information [accessed 2016 February]. Available from https://www.ncdc.noaa.gov/cdo-web/search

North, R. L., and others. 2013. The state of Lake Simcoe (Ontario, Canada): The effects of multiple stressors on phosphorus and oxygen dynamics. Inland Waters **3**: 51–74. doi:10.5268/IW-3.1.529

Oksanen, J., and others. 2016. vegan: Community ecology package, R package version 2.3-3 [accessed 2016 June]. Available from http://cran.r-project.org/package=vegan

Pannard, A., M. Bormans, and Y. Lagadeuc. 2008. Phytoplankton species turnover controlled by physical forcing at different time scales. Can. J. Fish. Aquat. Sci. **65**: 47–60. doi:10.1139/f07-149

R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Available from http://www.R-project.org

Rader, R. B., and C. J. Richardson. 1994. Response of macroinvertebrates and small fish to nutrient enrichment in the northern Everglades. Wetlands **14**: 134–146. doi:10.1007/BF03160629

Reavie, E. D., T. M. Jicha, T. R. Angradi, D. W. Bolgrien, and B. H. Hill. 2010. Algal assemblages for large river monitoring: Comparison among biovolume, absolute and relative abundance metrics. Ecol. Indic. **10**: 167–177. doi:10.1016/j.ecolind.2009.04.009

Reavie, E. D., and R. P. Barbiero. 2013. Recent changes in abundance and cell size of pelagic diatoms in the North American Great Lakes. Phytotaxa **127**: 150–162. doi:10.11646/phytotaxa.127.1.15

Reavie, E. D., R. P. Barbiero, L. E. Allinger, and G. J. Warren. 2014*a*. Phytoplankton trends in the Great Lakes, 2001-2011. J. Great Lakes Res. **40**: 618–639. doi:10.1111/1462-2920.12819

Reavie, E. D., A. J. Heathcote, and V. L. Shaw Chraïbi. 2014*b*. Data from: Laurentian Great Lakes phytoplankton and their water quality characteristics, including a diatom-based model for paleoreconstruction of phosphorus. PLoS One **9**: e104705. doi:10.1371/journal.pone. 0104705

Reavie, E. D., and A. R. Kireta. 2015. Centric, araphid and eunotioid diatoms of the coastal Laurentian Great Lakes, v. 62. J Cramer.

Rühland, K. M., A. M. Paterson, and J. P. Smol. 2008. Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. Glob. Change Biol. **14**: 2740–2754. doi:10.1111/j.1365-2486.2008.01670.x

Rühland, K. M., A. M. Paterson, W. Keller, N. Michelutti, and J. P. Smol. 2013. Global warming triggers the loss of a key Arctic refugium. Proc. R. Soc. B **280**: 20131887. doi:10.1098/rspb.2013.1887 [24107529]

Rühland, K. M., K. E. Hargan, A. Jeziorski, A. M. Paterson, W. B. Keller, and J. P. Smol. 2014. A multi-trophic exploratory survey of recent environmental changes using lake sediments in the Hudson Bay Lowlands, Ontario, Canada. Arct. Antarct. Alp. Res. **46**: 139–158. doi:10.1657/1938-4246-46.1.139

Rühland, K. M., A. M. Paterson, and J. P. Smol. 2015. Lake diatom responses to warming: Reviewing the evidence. J. Paleolimnol. **54**: 1–35. doi:10.1007/s10933-015-9837-3

Saros, J. E., and others. 2012. Climate-induced changes in lake ecosystem structure inferred from coupled neo- and paleoecological approaches. Ecology **93**: 2155–2164. doi:10.1890/11-2218.1

Saros, J. E., and N. J. Anderson. 2015. The ecology of the planktonic diatom *Cyclotella* and its implications for global environmental change studies. Biol. Rev. Camb. Philos. Soc. **90**: 522–541. doi:10.1111/brv.12120 [24917134]

Shaw Chraïbi, V. L., A. R. Kireta, E. D. Reavie, T. N. Brown, and M. Cai. 2014. A paleolimnological assessment of human impacts on Lake Superior. J. Great Lakes Res. **40**: 886–897. doi:10.1016/j.jglr.2014.09.016

Smol, J. P. 2012. Climate change: A planet in flux. Nature **483**: S12–S15. doi:10.1038/483S12a [22378120]

Sorvari, S., A. Korhola, and R. Thompson. 2002. Lake diatom response to recent Arctic warming in Finnish Lapland. Glob. Change Biol. **8**: 171–181. doi:10.1046/j.1365-2486.2002.00463.x

Sterner, R. W., E. Anagnostou, S. Brovold, G. S. Bullerjahn, J. C. Finlay, S. Kumar, R. M. L. McKay, and R. M. Sherrell. 2007. Increasing stoichiometric imbalance in North America's largest lake: Nitrification in Lake Superior. Geophys. Res. Lett. **34**: L10406. doi:10.1029/2006GL028861

U. S. Environmental Protection Agency. 2010. Sampling and analytical procedures for GLNPO's open lake water quality survey of the Great Lakes. EPA 905-R-05-001.

U. S. Environmental Protection Agency. 2015. Climate change indicators in the United States – ecosystems [accessed 2015 November]. Available from https://www3.epa.gov/climatechange/science/indicators/ecosystems/great-lakes.html

Ware, D. M., and R. E. Thomson. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. Science **308**: 1280–1284. doi:10.1126/science.1109049 [15845876]

Warner, D. M., and B. M. Lesht. 2015. Relative importance of phosphorus, invasive mussels and climate for patterns in chlorophyll *a* and primary production in Lakes Michigan and Huron. Freshw. Biol. **60**: 1029–1043. doi:10.1111/fwb.12569

Winder, M., and D. A. Hunter. 2008. Temporal organization of phytoplankton communities linked to physical forcing. Oecologia **156**: 179–192. doi:10.1007/s00442-008-0964-7 [18274782]

Winder, M., J. E. Reuter, and S. G. Schladow. 2009. Lake warming favours small-sized planktonic diatom species. Proc. R. Soc. B **276**: 427–435. doi:10.1098/rspb.2008.1200 [18812287]

Acknowledgments

We thank K. Kennedy, A.R. Kireta, R. Sterner and the Research Vessel Lake Guardian and Blue Heron field crews for their help collecting core samples. Compilation of physical and chemical data was supported by R.P. Barbiero and scripts to calculate thermocline depths were developed by B.M. Lesht. Sediment dating was supported by D.R. Engstrom and personnel at the St. Croix Watershed Research Station. This research was supported by a grant to E. Reavie from the U.S. Environmental Protection Agency under Cooperative Agreement GL-00E23101-2. This document has not been subjected to the EPA's required peer and policy review and therefore does not necessarily reflect the view of the Agency, and no official endorsement should be inferred. This article was conceived and designed by ER, CS supported field work, ER, VC and MC analyzed the dataset, GS, LE, AB, VC and RP analyzed samples and compiled data, and ER, GS, LE, AB, VC, RP, CS, MC and AD wrote the paper. This is GLERL contribution number [1836]. This is NRRI contribution number [616].

Conflict of Interest

None declared.

Submitted 15 June 2016
Revised 13 August 2016; 23 September 2016
Accepted 30 September 2016

Associate editor: Marguerite Xenopoulos