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Decreases in diatom cell size during the 20th century in the Laurentian Great Lakes: a response to warming waters?

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Several authors have postulated that lake warming favors diatom taxa characterized by smaller cell sizes and suggested that this phenomenon may affect freshwater phytoplankton communities worldwide. Here, we examined historical (~1900–2015) trends in diatom cell size in the Laurentian Great Lakes. Cell size decreased in Lakes Superior, Erie and Ontario, while no significant trends were observed for Michigan and Huron. In Lakes Superior and Ontario, cell size within species decreased over the course of the 20th century, suggesting demographic shifts toward smaller, later-generation individuals. Contrastingly, species-specific mean cell size increased in Michigan and Erie, likely as a result of accelerated loss rates during summer stratification. Size-specific rates of relative abundance change (larger taxa decreased while smaller taxa increased), were observed in all lakes except Michigan. These shifts toward communities dominated by smaller celled taxa either reinforced (Superior, Huron, Ontario) or dampened (Michigan, Erie) the influence of demographic shifts. Notwithstanding the influences of multiple stressors on diatom cell size at the within-lake scale, we demonstrated a gradual ($5.11 \mu\text{m}^3/\text{y}$) decline in mean diatom cell size across the basin. Historical, basin-wide decreases in cell size demonstrate the likelihood of climate change driving changes in the primary producer community of large, freshwater systems.

KEYWORDS: Great Lakes; diatoms; cell size change; climate change; paleolimnology

INTRODUCTION

Due to their relatively short generation times, well-understood autecology and ubiquitous silica frustules, the diatoms (Bacillariophyta) lend themselves well to environmental analysis and monitoring studies. They

are also well preserved in sedimentary records, and have been used extensively in paleolimnology in order to infer historical lake conditions (Dixit *et al.*, 1992; Smol and Cumming, 2000). A number of parameters including density, biovolume accumulation rate and community

composition have been used to reconstruct temperature, primary productivity and trophic status (e.g. Manny *et al.*, 1977; Bradbury, 1988; Reavie *et al.*, 1995; Hall and Smol, 1999; Anderson, 2000), and evaluate the effects of anthropogenic stressors and restoration efforts (Brenner *et al.*, 1993; Smol *et al.*, 1998; Hamilton *et al.*, 2015). In the Laurentian Great Lakes, the diatom record reflects a history of increasing cultural eutrophication stretching back to the time of the first colonization by European settlers (Stoermer *et al.*, 1993). This is followed by a period of oligotrophication coincident with the onset of phosphorus abatement programs, improved municipal wastewater treatment and colonization by invasive, filter-feeding mussels within the basin beginning in the latter half of the 20th century (Stoermer *et al.*, 1996).

Recently, several authors reported increases in the frequency and extent of harmful and nuisance algae blooms within the Great Lakes basin (Paerl *et al.*, 2011; O’Neil *et al.*, 2012), and evidence of re-eutrophication in historically problematic areas across the system (Kane *et al.*, 2014; Scavia *et al.*, 2014). Despite multiple stressors driving phytoplankton composition, diatom records from dated sediment cores in all five lakes suggest that climate change has been an important stressor affecting diatom community composition over the past century (Reavie *et al.*, 2016b). Reavie *et al.* (2016b) demonstrated increases in the relative abundance (RA) of *Cyclotella sensu lato* species, exemplified by *Cyclotella comensis* var. #1 (Reavie and Kireta, 2015) and *Cyclotella* cf. *delicatula*, within the Great Lakes during the 20th century. Similar shifts toward increasing abundance of *Cyclotella* within the planktonic diatom community have been reported from freshwater systems worldwide, spanning latitudes from tropical to subpolar (Telford and Lamb, 1999; Rühland *et al.*, 2008, 2015). While the mechanisms that favor dominance by small centric taxa are not well understood, it has been suggested that the earlier onset of stratification, coupled with steeper water column stratification gradients are consistent with the rise of *Cyclotella* taxa worldwide (Rühland *et al.*, 2008, 2015).

In an examination of modern assemblages, Reavie *et al.* (Reavie *et al.*, 2014) demonstrated that *Cyclotella sensu lato* species are an important component of the summer phytoplankton community in the Great Lakes, where they are more abundant in the epilimnion than in the deep chlorophyll layer (DCL) (Bramburger and Reavie, 2016). This pattern is in contrast to larger centric diatoms within the genera *Aulacoseira* and *Stephanodiscus* that are observed more frequently in spring assemblages and later occur in the DCL during stratification. In addition, both pennate and centric diatoms typically exhibited larger cell sizes

within species in spring integrated water column samples and summer epilimnetic samples than in summer DCL samples, suggesting preferential sinking of larger individuals during periods of stratification. These findings imply that assemblages of warmer epilimnetic waters are characterized by smaller diatoms.

The relative importance of environmental variables in determining diatom community size structure varies across aquatic environments (Finkel *et al.*, 2009). Several authors have reported that phytoplankton communities in marine systems show pronounced increases in mean size with increased water column concentrations of chlorophyll *a* (Chisholm, 1992), macronutrients (especially nitrate—Tremblay *et al.*, 1997; Duarte *et al.*, 2000; Vidal and Duarte, 2000) and micronutrients (Howarth and Cole, 1985; Tsuda *et al.*, 2003). Similarly, freshwater algal cell volume is positively related with nutrient concentrations (Sprules and Munawar, 1986; Cattaneo *et al.*, 1998; Lavoie *et al.*, 2006). While diatom growth rate and individual cell size can be influenced by trophic status and nutrient conditions, diatom loss rates are regulated primarily by zooplankton grazing and sinking (Jewson *et al.*, 1981). Diatom loss rates due to sinking are intrinsically linked to both cell size and morphology (Litchman *et al.*, 2009). While the wide variety of cell morphologies exhibited by diatoms contributes differentially to sinking resistance and sinking rate (Smol *et al.*, 1984; Round *et al.*, 1990), larger, more heavily silicified cells generally sink faster than smaller individuals (Reynolds, 2006).

In the Great Lakes, surface water temperature has been increasing gradually over the course of the last century (Reavie *et al.*, 2016b), in accordance with global trends (Austin and Coleman, 2008; O’Reilly *et al.*, 2015). Several authors have discussed the effects of multiple stressors associated with warmer water temperatures on diatom cell size. Density gradients between the epilimnion and lower layers become increasingly steep at warmer water temperatures (Verburg *et al.*, 2003; Behrenfeld *et al.*, 2006). This intense stratification results not only in increased sinking rates for larger celled taxa (i.e. larger taxa require turbulent mixing to remain suspended) but also in decreased rates of nutrient flux into the euphotic zone from lower waters (Winder *et al.*, 2009). Diatom surface area-to-volume ratios are maximized at small cell volumes, resulting in substantial competitive advantages for smaller phytoplankton cells in terms of sinking resistance (Reynolds *et al.*, 2002; Litchman *et al.*, 2006) and nutrient assimilation (Litchman *et al.*, 2006). As such, warmer water temperatures associated with climate change are widely hypothesized to favor smaller algae as their high surface area to

volume ratios enable them to more efficiently harvest light, take up nutrients and maintain vertical position in the water column (Winder *et al.*, 2009). Bramburger and Reavie (2016) noted that the Great Lakes epilimnetic phytoplankton community is becoming increasingly dominated by small, soft bodied algae and small centric diatoms, especially during the stratified period. It follows that increasing surface water temperatures, extended summer stratification periods, and intensified stratification gradients during the last century in the Laurentian Great Lakes would be reflected not only by changes in the taxonomic makeup of the diatom community, but also by a detectable reduction in diatom size through time. To our knowledge, this paper represents the first documentation of historical diatom size diminution in a large, multi-lake, freshwater system.

Several mechanisms influence the mean diatom size in an assemblage. These include community-level effects such as shifts in the RA of small and large taxa within the assemblage (Snoejis *et al.*, 2002), as well as population-level effects including demographics (Round, 1972; Crawford, 1981) and adaptive responses to size selection. Classically accepted paradigms of microbial ecology (e.g. Baas Becking, 1934; Hutchinson, 1961) imply that changes in the RA of taxa are most likely to account for short-term (intra-annual) changes in mean size within an assemblage. In contrast, demographic shifts to populations with higher proportions of smaller, late-generation individuals (i.e. progressively smaller diatom valves) or the evolution of smaller initial valves within a diatom species would account for changes in size over longer periods of time (inter-annual or longer; Yoshiyama *et al.*, 2009). Diatom growth form can also affect the size of “entities” or “natural units.” An increase in the RA of taxa that exhibit solitary, rather than colonial, growth forms would decrease the mean entity size of a community.

In this study, we evaluated changes in diatom cell size within sediments from the Laurentian Great Lakes deposited over the course of the 20th century. In addition to investigating assemblage mean size, we also examined trends in mean entity size, and relationships between species’ cell size and changes in RA, and changes in taxon-specific mean size through time. Based on broadly assumed changes to the stratification regime associated with warmer water temperatures, as well as the observed differences in cell size between spring and summer diatom assemblages (Bramburger and Reavie, 2016) we hypothesized that mean diatom cell size has decreased within the Great Lakes during the past ~100 years. Further, we anticipate that RAs of typically smaller taxa have increased, and that taxon-specific cell size has decreased.

METHOD

Sediment core sampling and stratigraphy

We collected sediment cores at 10 locations throughout the Great Lakes (Fig. 1), including three cores from Lake Superior, two cores from Lakes Huron, Erie and Ontario, and one core from Lake Michigan. Coring activities were conducted primarily aboard the USEPA 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. Additional cores were collected from the research vessels *Lake Guardian* or *Blue Heron* with an Ocean Instruments model MC-400 multicorer (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. Extruded cores were used for ^{210}Pb dating and diatom analysis. ^{210}Pb and ^{137}Cs were measured by low-background gamma spectroscopy as described by Appleby (2001). ^{210}Pb dating followed methods described by Chraïbi *et al.* (2014) and all cores had exponential ^{210}Pb profiles indicating typical isotopic decay with time, and errors associated with dates ranged from ± 1 to 2 years in the most recent three decades to ± 10 –20 years ca. The western Lake Erie core dating included supplementary ^{137}Cs analysis to pinpoint the 1963 peak resulting from weapons testing (Appleby, 2001). Although sedimentary records extended to earlier than time scales supported ^{210}Pb dating (detailed ^{210}Pb profiles available in Chraïbi *et al.* 2014, supplementary Fig. 4), we focused on sediment intervals with ^{210}Pb -inferred median dates later than 1900.

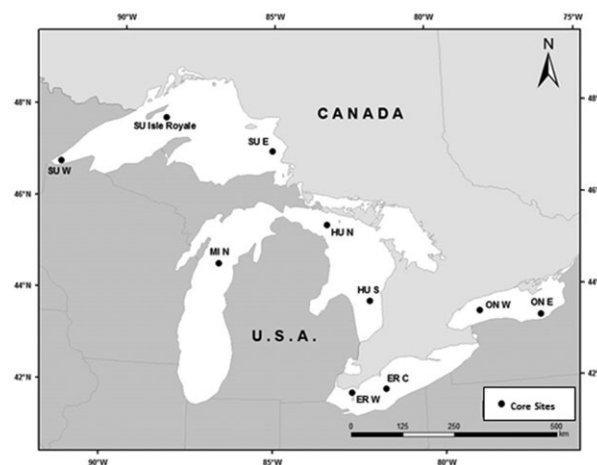


Fig. 1. Map of the Laurentian Great Lakes showing positions of core locations.

Diatom processing

Organic material was cleaned from diatom material by digestion in a concentrated acid solution. Diatom samples were rinsed eight times and slides were prepared using the Battarbee (1986) method. Diatoms were identified and enumerated at $\times 1000$ – 1250 magnification under light microscope. At least 500 diatom valves were counted per slide. For each slide analyzed, the valve sizes (length, width, diameter and/or depth) of the first 10 valves encountered of each taxon were measured using Lumenera Infinity cameras and Infinity Analyze imaging and image analysis software to determine average valve dimensions in each sediment interval (Reavie *et al.*, 2010) for subsequent biovolume calculations. Biovolume for each individual was calculated based on standardized shape formulas for each taxon (Reavie *et al.*, 2010). In addition, we calculated average entity dimensions for diatom species that exhibit colonial growth forms. Entity dimensions were calculated based on the number of individuals within a colony and colony shape (i.e. radial, back-to-back chain, end-to-end chain). Because colonies tend to disarticulate during sample preparation we assigned the number of frustules per colony based on the following assumptions:

- (1.) 1. Radial colony – 6 frustules (e.g. *Asterionella formosa*).
- (2.) 2. Short chain – 6 frustules (e.g. *Staurosira construens*).
- (3.) 3. Moderate chain – 12 frustules (e.g. *Fragilaria crotonensis*).
- (4.) 4. Long chain – 20 frustules (*Aulacoseira spp.*).

These numbers represent a consensus of anecdotal colony size estimates from analysts within our group based on measurements and observations of modern Great Lakes flora. Diatom taxonomy and enumeration techniques were based on USEPA photographic records and plates, and several diatom iconographs (see Chraïbi *et al.*, 2014 for details).

Statistical approaches

For each taxon, diatom counts and measured valve dimensions were used to determine RA, sample biovolume and individual cell biovolume (cell size) for each taxon within each sediment interval. We employed linear regression analysis using assemblage mean cell size (RA-weighted mean individual biovolume for each sediment interval) and taxon-specific mean cell size (normalized to species means for each taxon in each sediment interval) to evaluate temporal trends in diatom size. For

taxon-specific analyses, we included taxa that were present in at least five sedimentary intervals with a minimum of 50 years between first and last appearance in individual lakes. This analysis was also conducted using maximum individual dimension (the longest linear measurement of a diatom valve—length, width or depth—within a species, as well as entity biovolume—individual biovolume \times number of individuals—and entity maximum dimension—maximum colony length, width or depth in filamentous colonies; maximum diameter in radial colonies). In order to evaluate the effect of changing taxonomic composition on mean diatom size, we calculated the standardized rate of RA change over time (standard deviations per century) for each taxon that was present in at least five sedimentary intervals spanning ≥ 50 years between first and last occurrence within a single core, and regressed this against the corresponding taxon-specific mean individual biovolume. In this analysis, a positively sloped relationship indicates increased abundance of larger celled taxa in more recent sedimentary intervals, while a negatively sloped relationship indicates increased representation of smaller celled taxa in more recent sediments. We also used linear regression to examine changes in taxon-specific mean cell size through time in order to quantify population-level effects.

RESULTS

When we examined diatom cell size trends within individual lakes, it became apparent that each lake contributed differently to the overall basin-wide pattern. Assemblage mean cell sizes decreased in Lakes Superior, Erie and Ontario, but not in Michigan or Huron. In Lake Superior, both assemblage mean cell size and taxon-specific mean cell size decreased through time ($y = -3.00x$, $P = 0.0028$; $y = -0.004x$, $P < 0.0001$, Fig. 2), while maximum cell dimension has increased slightly ($y = 0.008x$, $P = 0.023$). In Lake Michigan, there was no trend in assemblage mean cell size through time ($P = 0.421$, Fig. 2, top panel), but we observed increases in both taxon-specific mean cell size ($y = 0.007x$, $P < 0.0001$, Fig. 2, middle panel) and maximum cell dimension ($y = 0.069x$, $P = 0.0485$). In Lake Huron, no trend was observed in either of these metrics ($P = 0.643$; $P = 0.648$, Fig. 2). In Lake Erie, assemblage mean cell size and maximum dimension both decreased through time ($y = -7.5x$, $P = 0.0026$, Fig. 2, top panel; $y = -0.121x$, $P < 0.0001$) while taxon-specific mean cell size increased slightly ($y = 0.004x$, $P = 0.002$, Fig. 4, middle panel). Finally, in Lake Ontario, both assemblage mean cell size and taxon-specific mean cell size decreased over the 20th

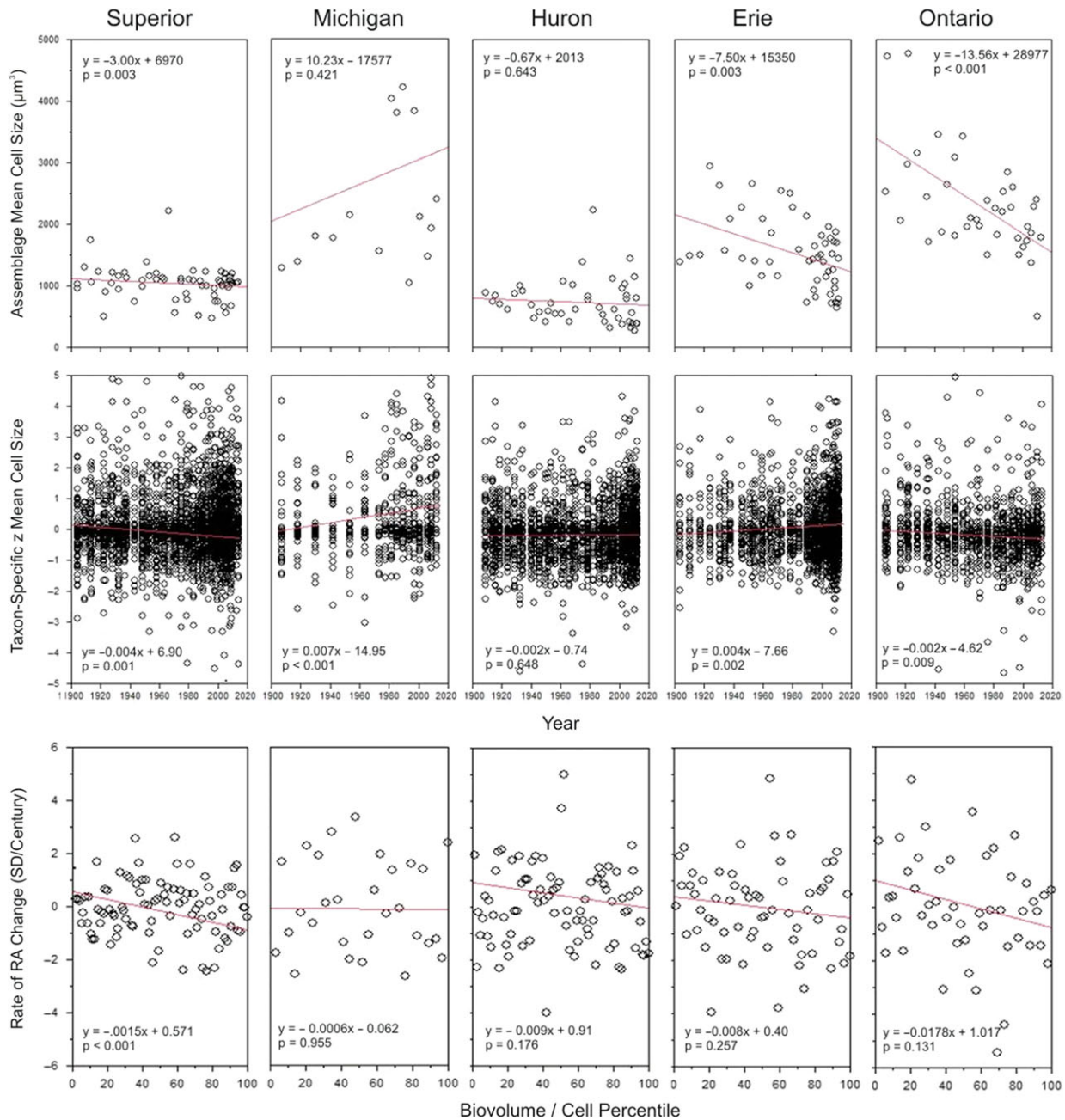


Fig. 2. Lake-to-lake trends. Top panel: Assemblage mean cell size for each lake, 1900–2015. Each point represents a single core mean for each sedimentary interval. Trendline slope is representative of cell size trend across community. Middle panel: Taxon-specific z -normalized mean cell size for each lake, 1900–2015. Each point represents a single species' mean per sedimentary interval, normalized to corresponding mean and standard deviation. Trendline slope is representative of trend in taxon-specific cell size through time. Bottom panel: Relationship between species mean cell biovolume (by percentile, smallest [0] to largest [100]) and rate of RA change (expressed as standard deviations per century) for diatoms from each of the Great Lakes. Each point represents a single species that occurred in >5 sedimentary intervals spanning at least 50 years. Negative slope of trendlines indicates increased representation of smaller celled taxa within the system, while positive trendlines indicate increased representation by larger celled taxa.

century ($y = -13.56x$, $P < 0.001$; $y = -0.002x$, $P = 0.009$, Fig. 2).

When we examined relationships between cell size percentile and rate of RA change in each of the lakes,

we found that generally, taxa characterized by larger cell sizes became less abundant through time, while smaller celled taxa became more abundant. For the most abundant taxa observed in our cores (basin-wide),

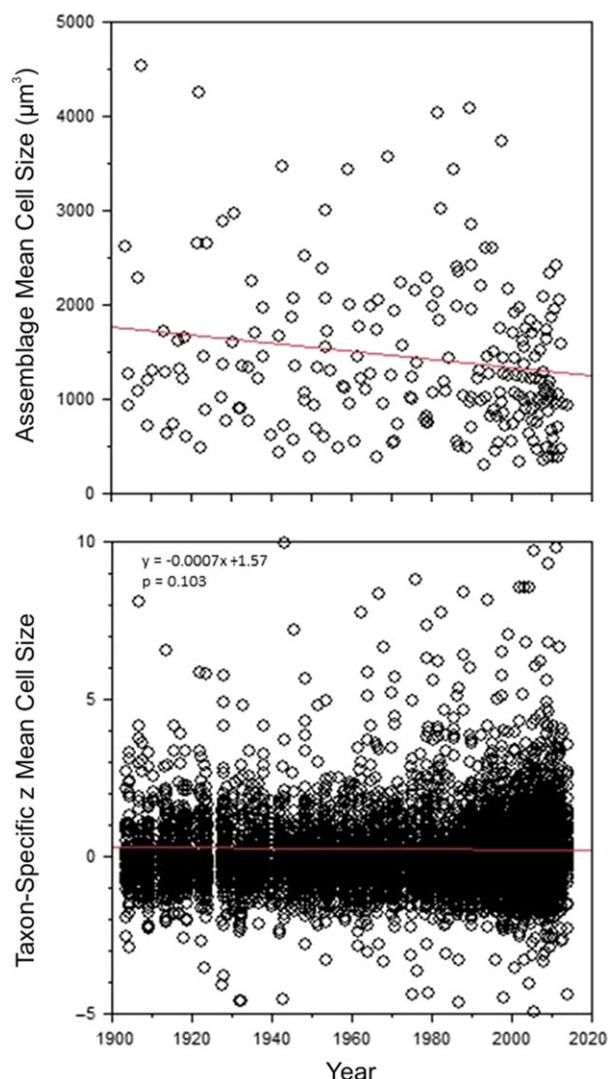


Fig. 3. Basin-wide trends. Top panel: Assemblage mean biovolume/cell (cell size) trends in the Great Lakes, 1900–2015. All lakes are represented in the analysis. Each point represents a single sedimentary interval. Trendline slope is representative of cell size trend across community. Bottom panel: Taxon-specific z -normalized mean biovolume/cell (cell size) trends in the Great Lakes, 1900–2015. Trendline slope is representative of trend in taxon-specific cell size through time. All lakes are represented in the analysis. Each point represents a single species' mean per sedimentary interval, normalized to corresponding species overall mean and standard deviation.

the smallest celled taxa, particularly those within the genus *Cyclotella sensu lato*, exhibited relatively large increases in RA through time, while larger celled taxa typically decreased in RA over the same period (Table I). In Lake Superior, we observed a negative relationship between mean cell size percentile and rate of RA change ($y = -0.0154x$, $P < 0.001$, Fig. 2, bottom panel). While negative trends were exhibited in all other lakes, none of these relationships were significant (Michigan: $y = -0.0006x$, $P = 0.955$;

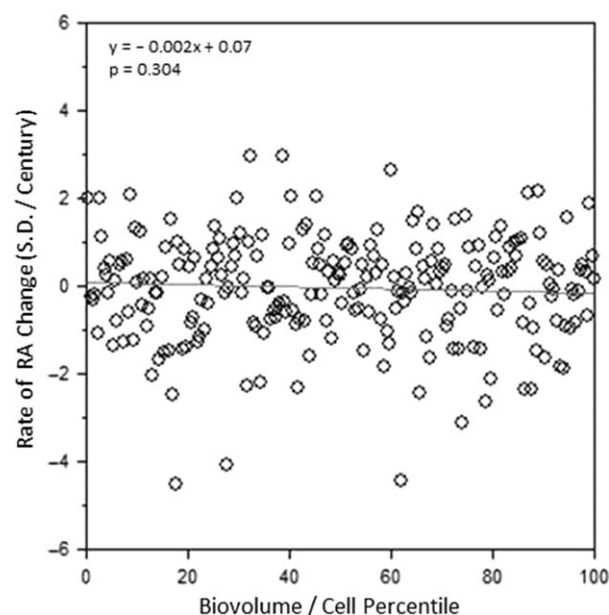


Fig. 4. Relationship between species mean cell biovolume (by percentile, smallest [0] to largest [100]) and rate of RA change (expressed as standard deviations per century) for Great Lakes diatoms. All lakes are represented in the analysis. Each point represents a single species that occurred in >5 sedimentary intervals spanning at least 50 years. Negative slope of trendline indicates increased representation of smaller celled taxa within the system.

Huron: $y = -0.009x$, $P = 0.176$; Erie: $y = -0.008$, $P = 0.257$; Ontario: $y = -0.018$, $P = 0.131$, Fig. 2, bottom panel). Negatively sloped relationships in these analyses indicated that smaller celled taxa increased in RA in more recent sedimentary intervals.

At the whole-basin scale, linear regression analysis demonstrated that mean diatom cell sizes have decreased by $587 \mu\text{m}^3$ within the Great Lakes over the last ~ 115 years ($-5.11 \mu\text{m}^3/\text{year}$, $P = 0.018$, $R^2 = 0.012$, Fig. 3, top panel). However, taxon-specific mean cell size has remained unchanged ($P = 0.103$, $R^2 < 0.001$, Fig. 3, bottom panel). RA-weighted mean maximum cell dimension was also unchanged through time (linear regression, $P > 0.50$, $R^2 < 0.001$). Further, while RA tended to decrease in larger taxa and increase in smaller taxa (Table I), the relationship between mean cell size percentile and RA change was not significant ($y = -0.002x$, $P = 0.304$, $R^2 = 0.009$, Fig. 4).

When we examined historical changes in entity size across all lakes (data not shown graphically), we found decreases in both entity biovolume ($y = -28.213x$, $P < 0.0001$) and entity maximum dimension ($y = -1.351x$, $P < 0.0001$). Among single lakes, we observed decreases in entity biovolume in Lake Superior ($y = -46.264x$, $P < 0.0001$) and Lake Ontario ($y = -30.210x$, $P = 0.0016$), as well as

Table I: Rate of abundance change of the 15 most common (mean abundance) taxa in the Great Lakes

Taxon	Mean RA	Mean cell biovolume (μm^3)	Rank cell biovolume (of 234 taxa)	Rate of RA change (SD/ Century)
<i>Aulacoseira islandica</i>	0.15	2386.15	17	-0.01
<i>Discostella pseudostelligera</i>	0.11	39.06	221	0.18
<i>Cyclotella cf. delicatula</i>	0.09	366.55	81	1.19
<i>Cyclotella ocellata</i>	0.08	172.25	142	-0.86
<i>Fragilaria crotonensis</i>	0.08	414.03	74	0.55
<i>Aulacoseira islandica alpha</i>	0.07	1308.36	32	0.95
<i>Stephanodiscus parvus</i>	0.06	117.98	163	0.67
<i>Cyclotella comensis</i>	0.06	73.42	195	0.99
<i>Fragilaria capucina</i>	0.06	158.78	145	-0.55
<i>Aulacoseira ambigua</i>	0.05	1024.31	42	-1.00
<i>Tabellaria fenestrata</i>	0.05	1488.81	30	-2.30
<i>Aulacoseira subarctica</i>	0.05	732.76	49	0.35
<i>Fragilaria pinnata</i> var. <i>intercedens</i>	0.05	153.00	146	-0.74
<i>Stephanodiscus</i> sp. #10	0.05	267.41	104	-1.34
<i>Cyclotella bodanica</i>	0.04	2161.97	18	-0.43
<i>Frankophila cf. similoides</i> JCU	0.04	45.56	214	1.28
<i>Stephanodiscus conspicueporus</i>	0.04	859.94	44	-2.08
<i>Aulacoseira granulata</i> var. <i>valida</i>	0.04	1291.25	33	0.98
<i>Stephanodiscus medius</i>	0.03	668.97	53	-1.36
<i>Fragilaria brevistriata</i> var. <i>inflata</i>	0.03	77.32	192	0.48

Mean RA represents mean RA in all core intervals in all lakes. Individual cell biovolume is ranked from largest (1) to smallest. Taxa included in analysis were present within at least five sedimentary intervals within a core with the first and last occurrences spanning at least 50 years. A total of 234 taxa met these criteria.

decreases in entity maximum dimension in all lakes except Lake Huron (Superior $y = -1.518x$, $P < 0.0001$; Michigan $y = -1.425x$, $P = 0.043$; Erie $y = -0.696x$, $P = 0.0001$; Ontario $y = 2.180x$, $P < 0.0001$). Decreases in entity size were associated with decreases in the mean number of frustules per colony both at the basin-wide scale ($y = -0.005x$, $P = 0.0007$) and within Lake Superior ($y = -0.022x$, $P < 0.0001$). Given that colony sizes were assigned to each taxon and were kept constant, this finding is reflective of a decrease in the RA of colonial taxa.

DISCUSSION

The responses of diatom assemblages to climate are complex and influenced by a suite of factors including temperature, ice cover, wind, precipitation and solar radiation. While many of these mechanisms function on regional scales, diatom responses to climate are further confounded by non-climate stressors operating within single lakes (i.e. nutrients, non-native species, physical habitat alterations; Rühland *et al.*, 2015). In individual lakes, physical limnological responses to climate forcing are largely constrained by lake morphology. Specifically, larger, cooler lakes are characterized by lower levels of interaction between surface inputs and lakebeds, and are predicted to exhibit simple responses to warmer air temperature, primarily manifested as deeper, more intense and prolonged stratification, as well as extended ice-free periods. Warmer, shallower lakes are more susceptible to evaporative cooling of surface waters and deep, wind-driven mixing and

therefore are more likely exhibit more complex thermal responses to changing climate (Wagner and Adrian, 2009; Foley *et al.*, 2011).

With the deepest average depths (149m, 86m mean depth, respectively) and steepest littoral zone profiles among the Great Lakes, Lakes Superior and Ontario would be expected to best exemplify these simple response patterns. Recent monitoring data have shown that mean thermocline depths have been increasing in both Lakes Superior and Ontario (and to a lesser extent in Lake Erie) over the last ~20 years, while Lake Michigan's epilimnion became thinner during the same period, and no trend was observed in Lake Huron (Reavie *et al.*, 2016a, b). Further, Lakes Superior and Ontario experienced the fastest surface warming since 1995 (0.082°C/year, 0.091°C/year, respectively; Reavie *et al.*, 2016a, b), as well as greatest losses in annual lake ice coverage (79% and 88%, respectively) during the period between 1973 and 2010 (Wang *et al.*, 2012). In the diatom community, extended open water and stratified seasons would be manifested as a demographic shift toward smaller frustules within species (i.e. decreased taxon-specific mean cell size) representative of an increase in the number of rounds of cell division within a single population (per Smetacek, 1985) during each growing season. Our results reflect this pattern for these two lakes. The overall shift to smaller cell sizes in both Lake Superior and Lake Ontario is further exacerbated by taxonomic shifts toward communities increasingly comprised of smaller taxa. Differential changes in RA by large- and small-celled taxa in these lakes are exemplified by *Cyclotella atomus* "fine

form” (also tentatively characterized as *C. atomus* var. 1; Reavie and Kireta, 2015), the smallest species in these two lakes (cell biovolume $\sim 13\text{--}30\ \mu\text{m}^3$), whose RA increased at a rate of 1.40 standard deviations per century in Lake Superior and 2.48 standard deviations per century in Lake Ontario. In contrast, the RA of *Stephanodiscus niagarae*, the largest species in Lake Superior and the second largest in Lake Ontario (cell biovolume $\sim 20\,000\ \mu\text{m}^3$), decreased by 0.41 standard deviations per century and 2.14 standard deviations per century, respectively in these lakes during the period described by these sedimentary series.

While Lakes Michigan and Huron are deep, cool lakes in their own right, recent monitoring data shows that these lakes are not responding to climatic drivers as quickly as Lakes Ontario and Superior (Wang *et al.*, 2012; Reavie *et al.*, 2016a, b), and we did not observe the same changes in assemblage mean cell size through time. The lack of distinct changes in assemblage mean cell size and taxon-specific mean cell size was likely the result of interactions among various stressors during several phases of the lake histories (e.g. silica limitation in the 1960s, Schelske and Stoermer, 1971; dreissenid mussel invasion in the late 20th century, Fahnenstiel *et al.*, 2010) that differed in nature and timing from analogous stressors in Lake Ontario (Estepp and Reavie, 2015). These include taxon-specific cell size increases associated with increased nutrient availability during times of eutrophication and selection against small cells through dreissenid filter-feeding (as per Holland, 1993; Baker *et al.*, 1998), as well as decreases in assemblage mean size associated with demographic and community effects linked to intensified stratification and decreased nutrient availability due to recent oligotrophication. During the mid-20th century, cultural eutrophication provided elevated nutrient concentrations (especially P) that could have sustained larger cell sizes (e.g. *S. niagarae*) in the phytoplankton community (as per Suttle *et al.*, 1987; Chisholm, 1992). While subsequent nutrient abatement efforts reduced the available resources to support algal growth (Conley *et al.*, 2009), cell size remained consistent during this period in the sedimentary record. It is likely that filter-feeding by invasive mussels, especially the quagga mussel (*Dreissena bugensis*) late in the 20th century (Nalepa *et al.*, 2009), has influenced sestonic community composition and deposition of diatoms to the sediments of these lakes. Baker *et al.* (1998) demonstrated that dreissenid mussels reject diatoms as pseudofaeces in favor of smaller food items, and diatoms representing the largest celled taxa included in selective feeding experiments were rejected in favor of all other items, including smaller diatoms. Only in Lake Michigan did we fail to observe the taxonomic shifting

to smaller taxa that were observed (to varying degrees) within other lakes. Thus, increases in species-specific cell size were not dampened by the effects of changing community composition, resulting in overall cell size trends that mirror the species-specific cell size patterns.

Diatom size patterns in Lake Erie differ subtly from those of the other Great Lakes. Decreasing assemblage mean cell size, coupled with increasing taxon-specific mean cell size, suggests that Lake Erie's planktonic diatom community has undergone a shift toward smaller taxa, but with larger cells within each taxon, suggesting that individuals representing earlier cell divisions make up a large portion of the community. Bramburger and Reavie (2016) reported distinct spring and summer phytoplankton assemblages in the lake, and seasonal trends in taxon-specific mean cell size. During summer, surface temperatures often exceed 25°C (Schwab *et al.*, 1999; Burns *et al.*, 2005; Millie *et al.*, 2009). During the stratified season, diatom densities decline markedly in the epilimnion (Bramburger and Reavie, 2016), and large frustules within each taxon, representative of the spring assemblage, have become more heavily represented within the sedimentary record. This simple demographic effect is reinforced by increased availability of legacy nutrients re-mobilized from sediments, coupled with silica subsidies advectively transported from an increasingly oligotrophic Lake Huron (Barbiero *et al.*, 2012). These nutrient pulses help to support the growth of relatively large diatom frustules, particularly those of *Aulacoseira islandica*, under the ice in winter and during the early part of the ice-free season (Twiss *et al.*, 2012; Allinger and Reavie, 2013; Reavie *et al.*, 2016a).

With the exception of Lake Michigan, all lakes displayed a negative relationship between species' mean biovolume per cell and the rate of RA change. This suggests that ongoing community re-organization has occurred in such a fashion as to favor smaller celled diatom taxa, and select against large-celled taxa. Stressors that could be responsible for this type of trend include selection against large, “heavy” individuals in a warmer water column with steeper density differential between the epilimnion and hypolimnion (Smetacek, 1985; Waite *et al.*, 1992), intensified photosynthetically active radiation in less-turbid waters (as per Skubinna *et al.*, 1995; Binding *et al.*, 2007), silica limitation (Schelske *et al.*, 1986) and simple numerical favoring of species with short generation times (Malone *et al.*, 1996). If we consider the intersection of the RA Change: Biovolume/Cell relationship line with the x -axis (Fig. 2), we gain insight into the relative proportion of the assemblage that has increased or decreased in RA through time. In other words, if the position of the x -intercept is $<50\%$, community evenness has decreased,

and the assemblage has become dominated by fewer, smaller celled taxa. In Lakes Erie and Ontario, ~50% of the community has increased in RA, while the other ~50% has decreased, suggesting that, on average, larger taxa have been replaced by smaller taxa as the dominant members of the community. In Lake Superior, only the smallest ~38% of the taxa have increased in RA, indicating that the community has become increasingly dominated by a few small-celled taxa. This trend exemplifies the basin-wide rise of several small *Cyclotella sensu lato* species including *Cyclotella* cf. *delicatula*, +2.59 SD/century), *C. comensis* (+1.69 SD/century) and *C. atomus* fine form (+1.40 SD/century). Contrastingly, in Lake Huron, the position of the x -axis intercept suggests that all but the largest 1% of taxa (x -intercept at ~99%) have increased in RA over the last 115 years. This finding alludes to a decline in the RA of a few previously dominant, large-celled taxa. In fact, several large, centric forms have decreased rapidly in RA across the Great Lakes during the period described here (*Stephanodiscus alpinus* type II/III, -1.77 SD/century; *Cyclotella bodanica* aff. *lemanica* JCU, -1.85 SD/century; *Stephanodiscus oregonicus*, -2.66 SD/century).

While the relative influences of multiple stressors differ from lake to lake within the Great Lakes ecosystem, a few consistent patterns are apparent at a basin-wide scale. We have demonstrated that assemblage mean diatom cell size across the basin has been declining slowly but significantly over the course of the 20th century (Fig. 3). This trend is consistent with recent reports of diatom cell size reductions associated with the warming of surface waters globally (Atkinson *et al.*, 2003; Winder *et al.*, 2009), as well as indirect effects of warmer air temperatures on other water column characteristics including mixing depth, stratification duration and intensity, length of the open water season and nutrient dynamics (Rühland *et al.*, 2008, 2015). Some of these mechanisms exert direct selective pressure on diatom cell size [e.g. differential sinking loss rates (per Litchman *et al.*, 2009), extended stratification supporting multiple generations (Smetacek, 1985)], while others indirectly affect cell size by influencing the RA of taxa occurring within the assemblage [e.g. via re-mobilization of phosphorus from sediments (Jiang *et al.*, 2008), nutrient flux from runoff (Jeppesen *et al.*, 2009)]. In the context of the basin-wide decrease in assemblage mean cell size observed here, these mechanisms would be represented by a decrease in the size of individuals within species and/or a community-level shift toward dominance by smaller celled taxa. At the basin-wide scale, we did not observe a significant relationship between mean cell size and RA change (Fig. 3), nor did we see a decrease in taxon-specific mean cell size through time (Fig. 4), and consideration of the

contribution of individual lakes (as described above) to basin-wide patterns is necessary to understand the mechanisms regulating basin-wide diatom size diminution in the Great Lakes.

Despite lake-to-lake patterns of size change that reflect within-lake stressors and processes, demographic and taxonomic shifts toward smaller cell sizes have caused a decrease in overall diatom cell size in the Great Lakes over the 20th century. These patterns are consistent with the assertion of other researchers that warmer water temperatures, especially in rapidly warming lake ecosystems, favor smaller celled diatoms. These findings demonstrate the ability of climate-related stressors to drive changes in the primary producer community of large freshwater systems. Contributions of these changes to overall primary producer biovolume in the Great Lakes are currently not well studied. However, the implications of a changing primary producer community upon food availability and quality for higher trophic levels should be a consideration of importance to resource managers and regulatory bodies for all large freshwater systems.

CONCLUSION

Both population (i.e. demographic shift toward smaller, later-generational individuals within taxa) and community-level (i.e. compositional shift toward smaller celled taxa) can bring about an overall decrease in assemblage mean cell size within diatom communities. In the Laurentian Great Lakes, interactions between these two mechanisms have led to significant decreases in assemblage mean cell size in individual lakes (Superior, Erie, Ontario), as well as at the basin-wide scale (mean of all lakes; $587 \mu\text{m}^3$ over the last ~115 years). Differences in patterns of demographic, within-species cell size change, as well as size-specific RA change among lakes were influenced by a suite of stressors including lake morphology, trophic status and the presence of invasive mussels. Broader patterns of decreasing cell size within the Great Lakes are reflective of ongoing increases in lake surface temperature, vertical stratification intensity, and open water period associated with climate change. Ongoing changes to the taxonomic composition and size structure of primary producers may affect food quality and availability for higher trophic levels within the system.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Plankton Research* online.

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