



Recent changes in abundance and cell size of pelagic diatoms in the North American Great Lakes

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Abstract

Changes in diatom abundance and cell size in Great Lakes phytoplankton collections were examined from two periods, 1996–1999 and 2007–2008. Trends indicate marked shifts in pelagic diatoms, including diatom total biovolume and cell density declines. Concurrent with these changes have been establishments of invasive species, water quality changes and longer stratification periods resulting from climate warming. No consistent change in cell sizes was observed in diatoms between the two periods in the Great Lakes basin as a whole, but lake- and taxon-specific changes were apparent. Cell size declines include centric and pennate diatoms in the spring in Lake Huron and pennate diatoms in the spring in Lake Superior. Increases in cell size occurred for centric diatoms in Lake Erie and pennate diatoms in the summer in lakes Michigan and Ontario. Some of the more dominant taxa exhibited lake-specific shifts. For instance, lightly-silicified diatoms such as *Nitzschia* increased in length in Lake Huron, possibly as an adaptation to climate warming and/or declining nutrient supplies. Difficulty in explaining the observed changes in cell sizes is acknowledged, but continued study of these trends is critical to understanding impacts on Great Lakes food webs.

Key words: diatom sizes, large lakes, cell density, stressors, grazers, nutrients

Introduction

Phytoplankton size structures are influenced by environmental drivers such as nutrients, thermal structure of the water column and grazing (Parsons & Takahashi 1973). For example, high nutrient concentrations often result in a shift to larger-celled algal assemblages (Watson & Kalff 1981, Peters 1983, Sprules & Munawar 1986). Physiological models generally predict that the proportion of smaller cells in an assemblage will increase with decreasing nutrient availability (Irwin *et al.* 2006). In most related literature this is considered logical because nutrient (and light) acquisition is maximized at high surface area/volume ratios (i.e., small sizes) (Finkel *et al.* 2004). Alternatively, it has also been hypothesized that diatom size decreases in response to increasing nutrients in order to slow the rate of sinking out of the euphotic zone as would be needed if the depth of light penetration decreased with increasing biological content of the epilimnion (Smol *et al.* 1984).

It has been postulated that size-dependent sinking would be constrained by stratification regimes (Rodríguez *et al.* 2001; Winder *et al.* 2009), and so cell sizes and shapes may adjust in response to climate shifts such as warming. Climate influences have been noted to have simultaneous influences on taxonomic composition and cell sizes in diatom communities. Over the period of recent warming, arctic (Smol *et al.* 2005) and temperate lakes in Europe and North America (Rühland *et al.* 2008) have manifested a distinct shift towards smaller planktonic diatom species, especially those in the genus *Cyclotella* (Kützing) de Brébisson (1838: 19). Finkel *et al.* (2009) noted that the median size of diatoms decreased in a comparison of pre-European and modern sedimentary assemblages of diatoms from a suite of alkaline Ontario lakes. The apparent selection of small species was linked to climate-induced increases in the duration and strength of the

stratification period. In agreement, a reduction in diatom size in Lake Tahoe has been linked to climate-induced strengthening of summer stratification (Winder *et al.* 2009).

Size ranges of phytoplankton consumed by grazers are limited by grazer morphology (Burns 1968, Geller & Muller 1981, Bogdan & Gilbert 1984), particularly in the case of filter-feeding cladocerans, and also by size-selective feeding by copepods (Wilson 1973). Therefore, changes in the composition of the herbivore community can impact size distributions of phytoplankton. Sommer *et al.* (2001) have shown differential effects of cladocerans and copepods on the size structure of phytoplankton communities. This is particularly relevant given the dramatic shifts in cladoceran/copepod ratios that have been observed recently in some of the Great Lakes (Barbiero *et al.* 2009a, 2009b). Shifts in algal cell sizes have generally been observed as shifts in the assemblage; i.e., a change in species composition in response to a change in environmental conditions. However, little is known about intra-species changes in algal cell size, with the rare exception of herbivore-algae studies. Some algal species are able to adjust their phenotype (e.g., spines, size) in response to grazing. For instance, grazing pressure has been known to result in changes in the shape and size of certain algae, such as *Scenedesmus* Meyen (1829: 774) (Hessen & Van Donk 1993), but similar evaluations for diatoms have been rare (e.g., Pondaven *et al.* 2007).

The planktonic communities of the Laurentian Great Lakes have been subject to environmental changes in the past several decades that might have an impact on diatom cell size. Successful implementation of phosphorus controls in response to the Great Lakes Water Quality Agreement has resulted in a decrease in nutrient concentrations in many regions of the lakes (Johengen *et al.* 1994, Dolan & McGunagle 2005). This trend towards oligotrophication has accelerated in recent years, perhaps driven by the appearance of dreissenid mussels (Barbiero *et al.* 2009a, 2009b, Dove 2009, Fahnenstiel *et al.* 2010). These more recent reductions in nutrients have been accompanied by sometimes dramatic shifts in zooplankton communities. For example, the cladoceran community of Lake Huron has virtually disappeared since 2003 (Barbiero *et al.* 2009a), while similar, if not quite as dramatic, changes have occurred in Lake Michigan at roughly the same time (Kerfoot *et al.* 2010). There is also recent evidence that climate change has resulted in warming of the Great Lakes and an increase in the period of stratification (e.g., Austin & Coleman 2008, Dobiesz *et al.* 2009, Trumpickas *et al.* 2009).

While some of the effects of these changes on diatom communities have already been documented (e.g., Barbiero *et al.* 2006), much remains unknown about the impacts of recent climate warming, changes in nutrient flux (increases and decreases), herbivore shifts and other stressors on the Great Lakes pelagic system. A cursory analysis of the Great Lakes phytoplankton from the last 15 years reveals declines in cell numbers and biovolume (with the exception of Lake Erie), concurrent with rapid changes in water quality (Osantowski 2010) and other biological communities [zooplankton (Barbiero *et al.* 2009a), the benthic macroinvertebrate *Diporeia* (Nalepa *et al.* 2009)]. In some cases these changes are attributed to establishment of invasive species, such as the quagga mussel which has carpeted the entire Lake Michigan basin (Bunnell *et al.* 2009), likely resulting in dramatic reductions in microorganism biomass. However, changes in the planktonic community, especially those that probably reflect trophic relationships, are not always so easily explained.

A better understanding of the shifts in the Great Lakes phytoplankton is needed to explain past changes in environmental condition, but more importantly to determine future scenarios. The recent, rapid shifts in water quality and biological assemblages are worrisome, and explanations of likely causal factors will be critical to management recommendations. Evaluating changes in diatom assemblages and cell sizes, and comparing these changes with shifts observed in other freshwater lakes, can reveal drivers and trajectories of pelagic condition as they relate to primary producers. Furthermore, future applications of diatom size in sedimentary records could be a useful indicator of ecological change (e.g., warming; Winder *et al.* 2009) in response to changes in a lake's condition.

Since 1983 the USEPA's Great Lakes National Program Office (GLNPO) has undertaken an annual monitoring program for the pelagic Great Lakes. To meet goals of the Great Lakes Water Quality Agreement of 1978 (USEPA 1997), the monitoring program collects environmental information that is important to understanding the Great Lakes food chain. The primary objective of the annual program is to assess the

environmental quality in the open lake basins. Phytoplankton collections are followed by identification and enumeration of diatoms and non-diatomaceous algae. Ultimately these algae data are evaluated for long-term trends in phytoplankton as they relate to stressors and food web dynamics. We quantified the abundance, taxonomic composition and size of diatoms from the Great Lakes phytoplankton collections from two periods; a pre-2000 (1996–1999) and recent (2007–2008) period. Primary aims of this examination of 13-year trends from the pelagic Great Lakes were to substantiate trends in diatom (1) density and biovolume, (2) cell sizes, and (3) assemblage composition. From these trends we affirm the main changes taking place and hypothesize driving influences.

Methods

Twice yearly the U.S. EPA conducts surveillance monitoring of the offshore waters of the Great Lakes to fulfill provisions of the Great Lakes Water Quality Agreement. To track environmental conditions and trends these surveys include phytoplankton collections (Barbiero & Tuchman 2002), and detailed diatom assessments are performed on these samples. The diatom samples in this investigation comprise pelagic collections from spring and summer cruises of the R/V *Peter Wise Lake Guardian* in 1996, 1998, 1999, 2007 and 2008. Integrated phytoplankton samples were created from a composite of water samples taken at discrete depths with a rosette sampler. For an unstratified water column (early spring), the integrated sample was prepared by taking equal volumes of water from depths of 1, 5, 10 and 20 meters unless the depth was less than 20 meters. For epilimnetic sampling of a stratified water column (summer), equal volumes were taken from 1 m, 5 m, 10 m and the lower epilimnion. Aliquots from each depth were combined to form a 1-L composite sample which was preserved with 10 mL each of Lugol's Solution and 37% formalin.

Sample preparation

At least 500 mL of sample water were digested in a 1000 mL beaker using 20 mL of concentrated HNO₃. Beakers were heated at approximately 100 °C (steaming or barely boiling) on a hotplate until the volume was reduced to about 20 mL. In a 300 mL beaker the remaining water was combined with 25 mL of 30% H₂O₂ and a few crystal grains of K₂Cr₂O₇. Samples were re-heated until the volume was reduced to less than 10 mL. Samples were transferred to 15-mL graduated centrifuge tubes and rinsed at least seven times with deionized water as follows: Samples were centrifuged at 1500 rpm for 20 minutes; all but 0.5 mL of supernatant was drawn off; deionized water was added to bring the volume up to at least 10 mL; and the sample was agitated using a vortex mixer. On final centrifugation all but 0.5 mL of supernatant was drawn off and the final slurry volume was brought up to 5 mL with deionized water.

Two microscope slides were made from each sample. Round coverslips were placed on a static-free slide warmer. A homogenized 0.25 mL aliquot of slurry was added to each coverslip and allowed to dry. Heating of the slides was never applied because it resulted in clumping of the diatom remains, so coverslips were allowed to dry at room temperature. Diatom density was observed at 200x magnification under a compound microscope to ensure adequate diatom density for counting. If needed, additional slurry was added and dried. Coverslips were mounted on microscope slides using Hyrax[®] medium.

Sample analysis

Diatoms were identified and enumerated at 1000–1250x using oil immersion. Identification to the lowest taxonomic rank was facilitated using standard references (a full list of the taxonomic literature used is available from the primary author). At least 500 valves were counted per slide. At least 10 specimens of each taxon were measured for cell volume calculations. When fewer than 10 specimens were present, those present were measured as they were encountered. Measurements for each specimen were recorded as one or more of length, width, diameter and depth. For many taxa (such as *Stephanodiscus* Ehrenberg (1845: 72) and *Cyclotella*), depth measurements were problematic because the cells were seldom oriented in girdle view. For

biovolume calculations, when a certain dimension for a specimen could not be measured the average for that taxon was assumed based on measurements from previous years. Cell size as presented in the results refers to the most relevant measured dimension for a given taxon. For instance, because they were typically oriented in valve view the most frequent available measurement for *Cyclotella stelligera* (Cleve & Grunow in Cleve) Van Heurck (1882: pl. 94, fig. 22–26) was valve diameter, whereas for the pennate diatom *Fragilaria crotonensis* Kitton (1869: 110) the valve length was almost always measured. Taxa such as *Aulacoseira* Thwaites (1848: 167) were typically oriented in girdle view, so valve depth was the dominant measurement.

Densities of diatom cells (cells mL⁻¹) were based on quantitative counts of centric and pennate diatoms recorded during detailed assessment of the non-diatomaceous algae (USEPA 2010). Biovolumes of cells (µm³ mL⁻¹) were calculated based on formulas representing the closest approximation of each diatom's geometric shape. A list of the geometric forms and formulae are listed in Chapter 4 of the USEPA's standard operating procedures for the monitoring effort (USEPA 2010). For this article, calculations were used to estimate algal biovolume per unit water volume for all diatoms encountered in a given sample, centric diatoms and pennate diatoms. Pre- and post-2000 analyses were performed by different algal analysts. Although taxonomic workshops were held for consistency we cannot fully discount an analytical artifact on algal abundance estimates.

To evaluate changes over the sampling period, monitoring data (cell dimensions, densities and biovolumes) were averaged for each of the pre- (three years) and post-2000 (two years) periods. Differences in these parameters between the two periods were used to graphically track changes. Significance of changes was determined using the R programming language (version 2.10.0, R Development Core Team 2010) with the R Commander package (version 1.5-6, Fox 2005).

Results

Diatom abundance

The dominant difference in Great Lakes diatoms between the two periods was a decline in assemblage density and biovolume, with spring assemblages exhibiting the most obvious unidirectional differences (Fig. 1). Spring data show consistent declines in both density and biovolume in the upper lakes (Superior, Huron, Michigan) and declines in biovolume in Lake Ontario. Increases in spring diatoms in Lake Erie are attributed to substantial recent blooms of the large-celled centric diatom *Aulacoseira islandica* (O.Müller) Simonsen (1979: 60), especially in the central basin. Trends in summer abundance varied by sample location. In the summer, diatom densities and biovolume in central to northern Lake Huron and southern locations in lake Superior predominantly declined, density and biovolume increased in northern Lake Superior, and biovolume declined in central lake Erie while densities increased. Otherwise there was little evidence of lake-wide summer trends for the other lakes. While not presented here, it is worth noting that other algal forms (chrysophytes, cryptophytes, chlorophytes and cyanophytes) largely exhibited a similar summer change as the diatoms over the study period (unpublished data).

Are cells getting smaller or larger?

By constraining size-based analyses to taxa that occurred in both the pre- and post-2000 assemblages we factored out the influence of assemblage shifts over time and examined whether average cell sizes were collectively changing across the individual taxa (Fig. 2). Overall, the first two columns of scatterplots in Fig. 2 indicate no consistent change in taxon-specific cell sizes. Applying a paired test on taxon-specific differences in each lake for each season revealed no overall change in cell sizes (Wilcoxon paired tests with Bonferroni correction for multiple comparisons, $P = 0.05$). Points that lie farther from the 1:1 line indicate that some taxa may have changed size, but in general these taxa tended to be less common and so may not accurately represent their populations. For instance, the average length of *Amphipleura pellucida* (Kützing) Kützing (1844: 103) (Fig. 2) may have decreased, but this taxon was not commonly observed in phytoplankton samples. More detailed investigation into taxon-specific changes in Lake Erie indicated that

the abundant taxon *Aulacoseira islandica* (an increase from 18 to 21 μm average mantle depth), among others, has increased in average size. Similar shifts were not reflected in most other taxa. A comparison of boxplots indicates no overall change in cell sizes when sizes were averaged within taxa and across both seasons (Fig. 2, third column).

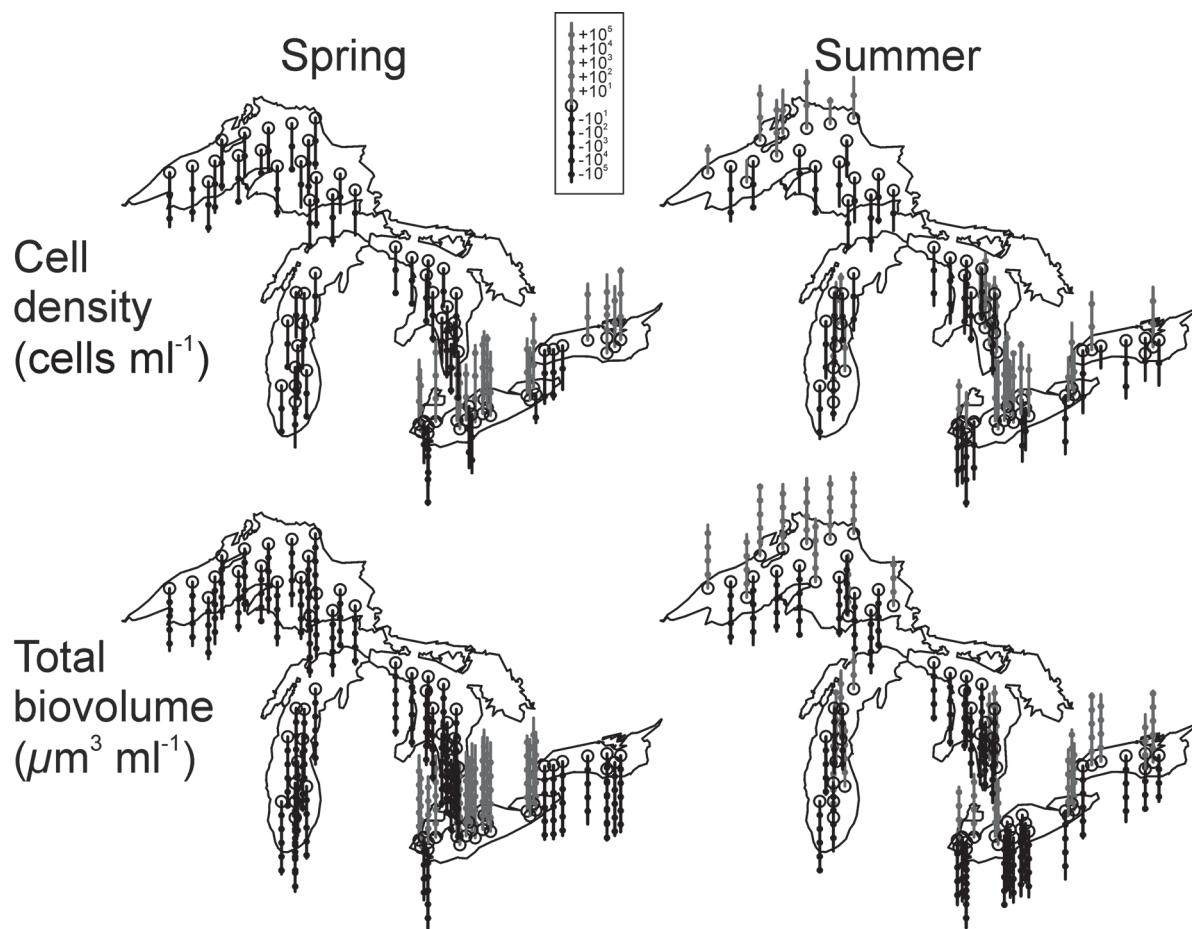


FIGURE 1: Average change in density and biovolume of total diatoms in spring and summer from sample locations throughout the Great Lakes. Lines represent the difference in diatom abundance (density or biovolume) between the average for pre-2000 years (1996, 1998, 1999) and post-2000 years (2007, 2008). Black, down-pointing lines indicate declines in diatom cell densities or biovolumes at each sample location. Gray, up-pointing lines similarly indicate density or biovolume increases over the sampling period.

Examination of the site-specific changes in cell size for total diatoms, centrics and pennates (Fig. 3) reveals no consistent pattern across the Great Lakes. In the spring, cell size decreases are noted in Lake Huron, western Lake Erie and eastern Lake Ontario; these size reductions are largely attributed to the pennate diatoms. In Lake Erie, spring cell sizes increased in the central and eastern basins, mostly due to the dominant *Aulacoseira islandica*. Spring size changes in Lake Superior have no discernable spatial pattern overall, but pennate diatoms may be decreasing in size. Similarly for summer, no Great Lakes basin-wide pattern in size changes were apparent. However, lake-specific changes suggest that summer cells are getting smaller in northern Lake Huron (pennates) and central and eastern Lake Erie (centrics and pennates). Summer size increases are apparent in Lake Michigan (mostly pennate diatoms), and Lake Ontario (mostly pennates). Space limitations prevent inclusion of trend data for all of the common Great Lakes taxa, but trends in cell sizes for some of the species that contribute substantial algal biovolume to the lakes are presented in Fig. 4 (similar plots for all common taxa are available from the primary author). Certain taxa, such as large *Stephanodiscus*, have notably decreased in size in some of the lakes, whereas many of the thin, narrow-lanceolate or rod-shaped taxa (e.g., *Nitzschia* Hassall (1845: 435) and *Asterionella formosa* Hassall (1850: 10)) have become longer. As an example, *Nitzschia acicularis* (Kützing) W. Smith (1853: 43), a common diatom in Lake Superior in spring and summer, has increased in length by an average of 27 μm in that lake.

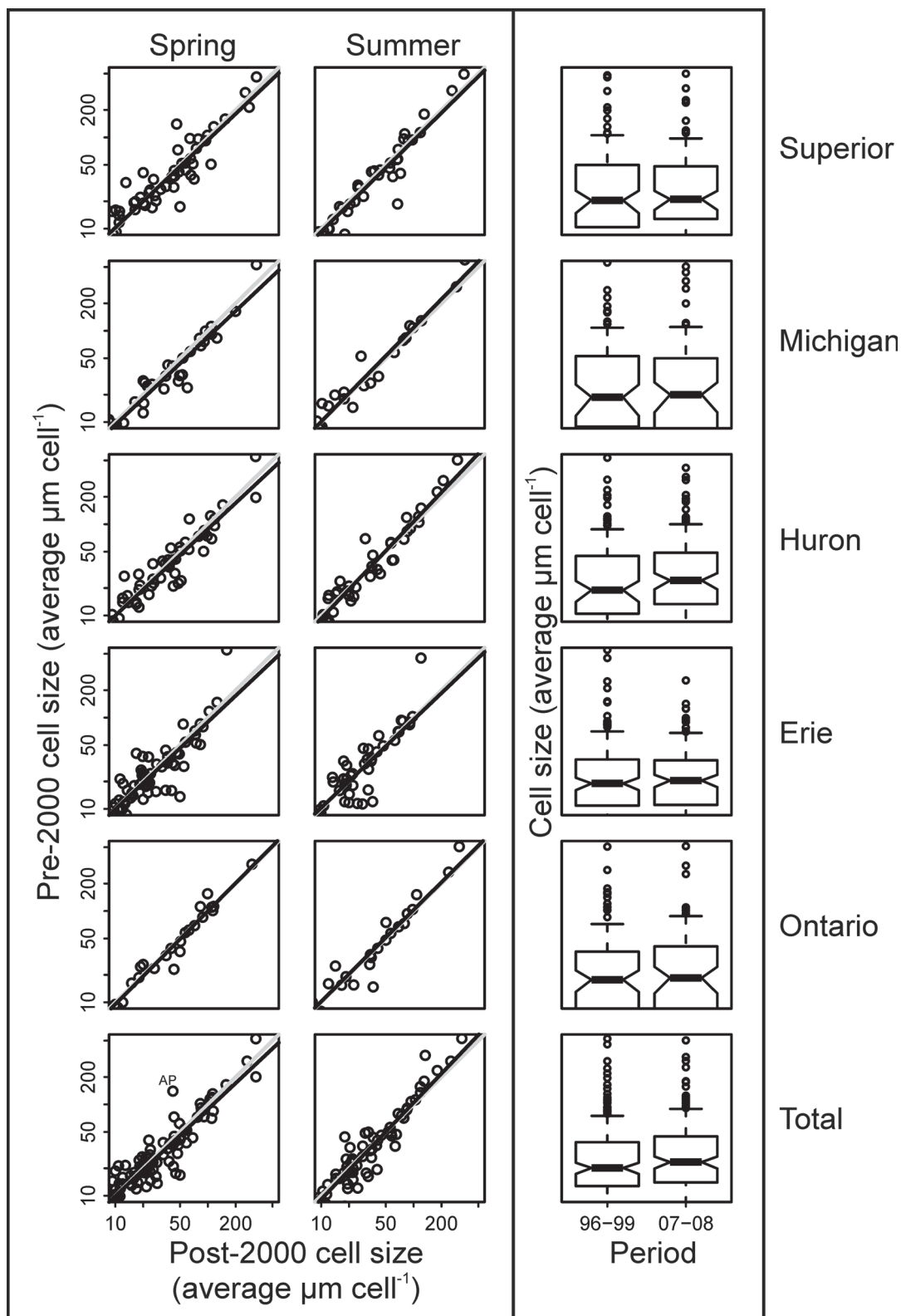


FIGURE 2: Comparison of pre-2000 (1996, 1998, 1999) and post-2000 (2007, 2008) cell sizes. Each circle in the first two columns (spring and summer) represents a comparison of average cell size for a taxon. Taxa that occurred in only one period are not included. Diagonal gray lines are 1:1 and black lines are the fitted regressions. AP indicates *Amphipleura pellucida*, as mentioned in the text. The third column presents boxplot distributions of taxon-specific average cell sizes (spring and summer combined) for the two periods, for all taxa present in each period. Paired t-tests ($P = 0.05$, with Bonferroni correction for multiple comparisons) were used to determine differences between the two periods (no significant differences were noted). The top and bottom of each box are the 25th and 75th percentiles, a line is drawn through the middle of each box at the median, with pinches representing ± 10 percentiles. The upper and lower tails respectively indicate the largest and smallest scores beyond 1.5 interquartile ranges of the box percentiles.

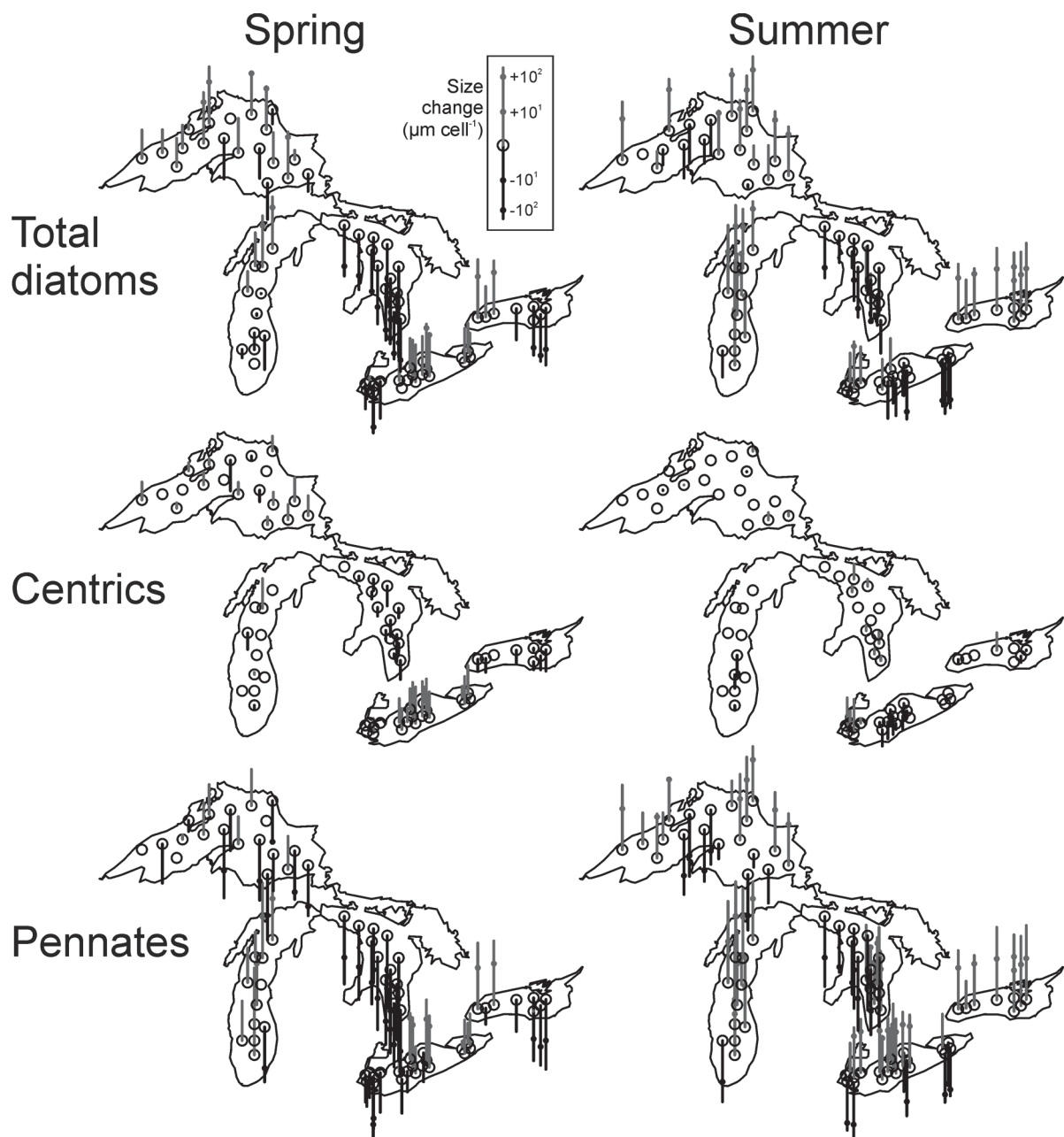


FIGURE 3: Change in cell size (μm) for diatoms from sample locations throughout the Great Lakes. Line lengths represent the difference in size between the average for pre-2000 years (1996, 1998, 1999) and post-2000 years (2007, 2008). Sizes for the two periods were based on an average of all measured cells at each location. Seasonal data are presented for all, centric and pennate diatoms. Black, down-pointing lines indicate declines in average cell size at each sample location. Gray, up-pointing lines similarly indicate cell size increases over the sampling period.

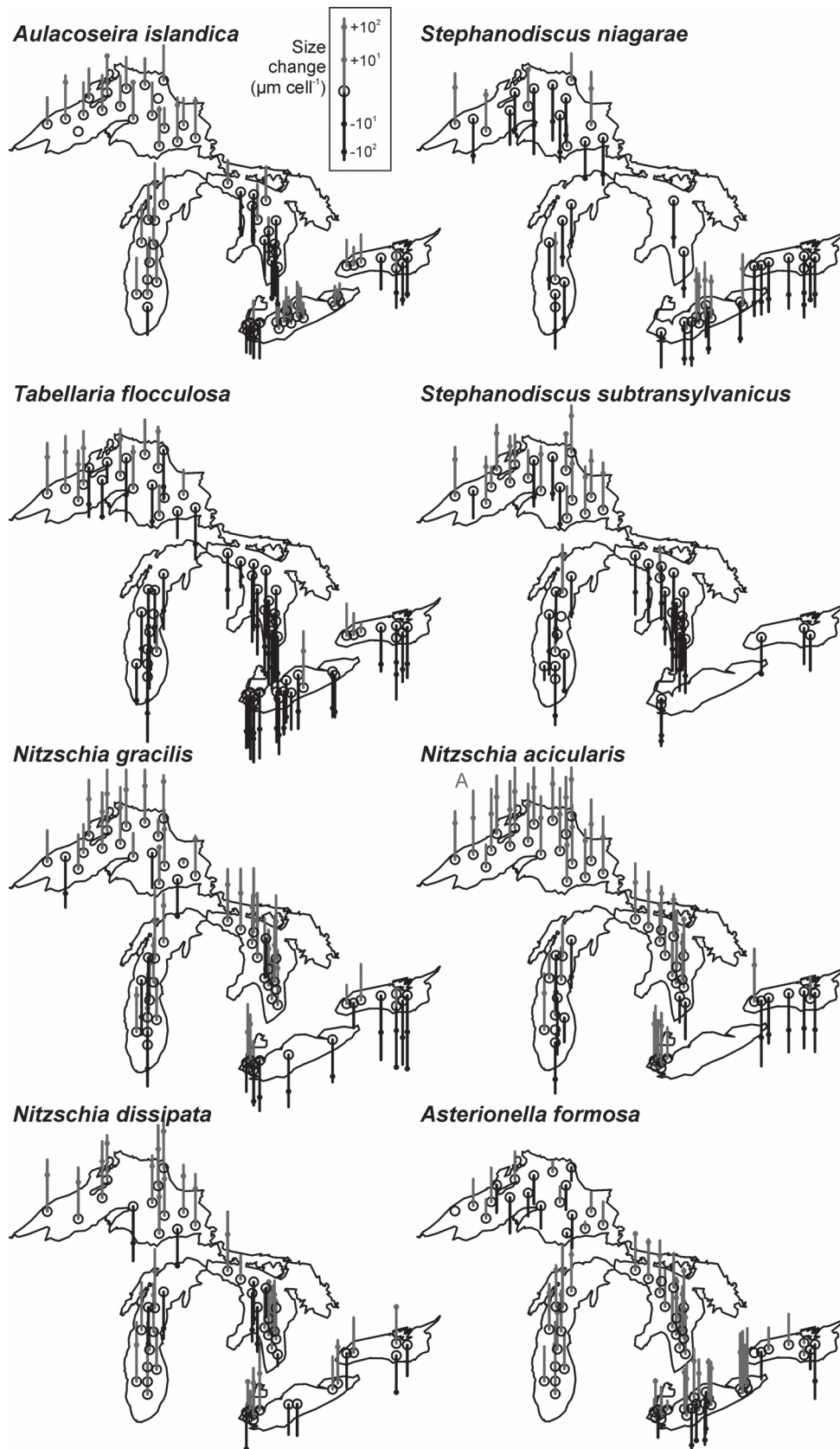


FIGURE 4: Change in cell size (μm) for select diatom species from spring sample locations throughout the Great Lakes. Line lengths represent the difference in size between the average for pre-2000 years (1996, 1998, 1999) and post-2000 years (2007, 2008). Black, down-pointing lines indicate declines in average cell size at each sample location. Gray, up-pointing lines similarly indicate cell size increases over the sampling period. The presence of a circle at a sampling station indicates that the taxon was observed during both periods.

Discussion

With the exception of Lake Erie, recent declines in the density and biovolume of diatoms have occurred in the Great Lakes basin. Lake- and taxon-specific changes in cell sizes were also observed for the study period. These changes in the diatoms are attributed to some known changes in environmental condition, but in many cases it has been difficult to confirm reasons for the observed shifts.

Despite substantial changes in physical, chemical and biological conditions in the Great Lakes over the 13-year study period, no consistent shift in diatom sizes has occurred across all taxa. While shifts to smaller diatoms have been the norm in lakes throughout the Northern Hemisphere (Rühland *et al.* 2008), a similar trend does not appear to apply to the recent history of the Great Lakes, likely owing to the significant physicochemical differences between the Great Lakes and the smaller lakes used in the paleoecological data summary of Rühland *et al.* To understand the observed trends it is clear that the Great Lakes need to be considered individually, and in cases like Lake Erie there are obvious spatial differences among sub-basins.

There has been a distinct shift to smaller taxa in Lake Huron, particularly in spring assemblages. Closer examination of taxonomic shifts reveals that large-celled taxa such as *Stephanodiscus subtransylvanicus* Gasse (1980: 47–48) have been replaced by smaller-celled taxa including *Cyclotella cf. atomus* Hustedt (1937: 143). Lake Huron has undergone the most dramatic ecological changes between the two periods compared in our study. These include the crash of cladoceran populations in the offshore of the lake (Barbiero *et al.* 2009a) and the collapse of alewife (*Alosa pseudoharengus* Wilson), previously the main prey fish in the lake (Riley *et al.* 2008), both in 2003. That same year saw an abrupt decline in the magnitude of the spring algal bloom, according to higher water clarity (Barbiero *et al.* 2011). During the study period Huron has simultaneously experienced declines in nutrients (Barbiero 2009a) and overall algal biomass (Barbiero *et al.* 2011), factors that may be related to the establishment of the quagga mussel (Nalepa *et al.* 2007). Similar chemical and biological trends have been observed in Lake Michigan (Fahnenstiel *et al.* 2010), but Michigan experienced an average increase in the length of pennate diatoms. It may be that, due to the rapid expansion of the filter-feeding quagga mussel throughout the Michigan basin between the two periods investigated in our study (Nalepa *et al.* 2009), the diatoms, albeit lower in number, are becoming larger as smaller cells are selectively grazed. It is unclear, though, whether such shifts would be manifested at the species level, as opposed to the community level.

In general it appears that, as Huron became more oligotrophic, large, heavy diatoms such as *Aulacoseira islandica* and *Stephanodiscus subtransylvanicus* decreased in size while needle-like taxa, such as *Nitzschia acicularis* and *Asterionella formosa*, became longer. Such a change might suggest adaptation of needle-like cells to increase surface area for nutrient absorption in an increasingly limited environment. Increasing in length is also considered an adaptation to reduce sinking rates (Hutchinson 1967), which may be a result of a longer ice-free season and stronger late-summer stratification (higher epilimnetic temperatures and greater density differential in the thermocline; King *et al.* 1997).

Although dreissenids appear to be a driving force behind algal declines in Lake Michigan (Vanderploeg *et al.* 2010), some of the changes in diatom assemblage composition and cell sizes in the other lakes are probably not explainable by grazing pressure. Lake Huron has a smaller dreissenid population (Nalepa *et al.* 2007) and has seen substantial declines in zooplankton, yet algal densities are also declining (Barbiero *et al.* 2011). In Lake Superior there is no known change in herbivores that could account for the observed spring declines in cell density and biovolume. This decrease in Huron and Superior's algal density and biovolume may be associated with warming climate, which has reduced the average period and extent of ice cover, increased average annual surface water temperatures and extended the annual stratification period (e.g., Austin & Coleman 2008). Similar phenomena on other large lakes, such as Lake Tahoe (Winder *et al.* 2009), resulted in a decrease in the median size of diatoms as an adaptation to reduce sinking velocity. A similar overall change in cell sizes did not occur in Lake Superior, but certain taxa have had clear unidirectional shifts in cell size; some taxa have decreased (e.g., *Stephanodiscus niagarae* Ehrenberg) or increased (e.g., *Nitzschia acicularis*) in size. Physical and chemical changes in the lake are probably affecting these changes, but

additional work is needed to better understand mechanisms. Despite an increase in average surface water temperature it may be that there has not been sufficient time to monitor or observe class-wide changes in diatom cell size in Lake Superior as a result of warming (note that reductions in the size of diatoms observed by Rühland *et al.* [2008] were derived from paleoecological records covering a period of more than 100 years.) Concurrent changes in water quality, such as nutrients (Chapra *et al.* 2009), are probably limiting planktonic assemblages, but adaptational explanations for these changes are only speculative at this time.

While diatom biovolume and densities predominantly declined across the Great Lakes basin, recent phytoplankton collections from Lake Erie indicate increased diatom production. Most notable is the predictable spring bloom of *Aulacoseira islandica*. The dominance of this taxon contributes to the increase in average cell size in the assemblage, especially in Erie's central basin. This change further supports the premise that eutrophication may lead to larger cells (Winder *et al.* 2009), particularly in a well-mixed, enriched lake such as Erie. However there are contrasting views in the published literature, such as Stoermer *et al.* (1989), who noted in Lake Ontario that the diatom *Stephanodiscus niagarae* Ehrenberg (1845: 80) decreased in diameter following eutrophication and an apparent prevention of sexual reproduction in the species. Further, Stoermer *et al.* (1985) determined that eutrophication and resulting silica depletion caused specimens of *Melosira (Aulacoseira) islandica* to become more finely-structured in more recent sediments of a Lake Ontario core. The paleoecological data reflect size changes within particular taxa caused by environmental drivers. Such unidirectional, taxon-specific changes were not as obvious in our 13-year analyses. Based on inter-lake differences, a given taxon could increase or decrease in size based on each lake's unique and complex interaction of environmental factors. Even though there have been significant environmental and assemblage changes over our study period, changes in nutrients and silica do not appear to be having consistent impact on cell sizes within taxa.

Reasons for the augmentation of these spring diatom blooms are uncertain at this time. Nutrient trends suggest that individual nutrient concentrations have not changed significantly in the last decade, although the central and eastern basins of Lake Erie are the only pelagic regions in the Great Lakes with a declining N:P ratio (USEPA, unpublished data). The success of *Aulacoseira* in Lake Erie may be a competitive response to this changing ratio, so nutrient ratios may be worth additional exploration.

Study of changes in the size and shape of specific organisms in response to environmental influences has been performed largely on higher trophic levels (e.g., cladoceran morphological responses to predation pressure; Chang & Hanazato 2003). This analysis of Great Lakes diatoms indicates that some algal taxa may also respond to environmental cues by changing size. However, the predominant shift in sizes, where detectable, is attributed to temporal shifts in the taxa comprising each lake's assemblage. Long-term changes in Great Lakes phytoplanktonic algal assemblages have been documented previously using fossil material (e.g., Stoermer 1993), and it is recommended that further paleoecological investigations be used to clarify long-term, size-related changes in the algal communities.

Biotic and abiotic factors are determining the size structure in diatom communities in the Great Lakes, and the relative effects of these factors vary by lake. These lake-specific considerations will be important in future tracking of diatom-based trends, especially in paleoecological and other applications that require long-term information on environmental quality and food web dynamics.

Acknowledgements

Michael Agbeti, Joseph Volerman and Jennifer Gronefeld supported diatom assessments of the GLNPO phytoplankton samples. This research was supported by a grant to E. Reavie from the U.S. Environmental Protection Agency under Cooperative Agreements GL-00E23101. This document has not been subjected to the Agency'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 is contribution number 539 of the Center for Water and the Environment, Natural Resources Research Institute, University of Minnesota Duluth.

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