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ORIGINAL ARTICLE

Size matters: diatom establishment and extirpation timing in the Laurentian Great Lakes has been influenced by cell size

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The Laurentian Great Lakes are among the planet's fastest-warming lakes. Recent paleolimnological studies have shown changes in the diatom community of the system, including shifts towards taxa characteristic of strongly stratified systems and ongoing cell-size diminution. Relationships between species' cell size and establishment in—or extirpation from—the system have not been addressed. Examining patterns of establishment and extirpation provides insight into the effects of multiple stressors at the ecosystem scale. We evaluate the timing of the establishment or extirpation of diatom taxa from fossil records post-European settlement within the Great Lakes as a function of cell size. Relationships between establishment or extirpation date and cell size were not random, and were best expressed as cubic curves. Generally, large taxa became established early in the record, while establishments of smaller taxa continued apace until the late 20th century. Extirpations of taxa of all sizes accelerated in the late 20th and early 21st centuries, and large-celled taxa were disproportionately extirpated over the last two decades. We discuss the implications of these relationships on the overall cell-size characteristics of the community, and consider the influences of propagule pressure, nutrient status, species invasions, and climate change upon diatom establishment and extirpation.

KEYWORDS: Great Lakes; paleolimnolgy; diatoms; cell size; community change

INTRODUCTION

Despite their status as a relatively young lake system (ca. 11,000 years since Wisconsin glacial period; Dyke and Prest, 1987; Larson and Schaetzl, 2001), the Laurentian Great Lakes (LGL) have been influenced by a wide variety of environmental factors, both natural and anthropogenic. As the lakes transitioned from a glacial meltwater system to the present-day configuration, draining eastward through the St Lawrence River, they were influenced by changing flow regimes (Larson and Schaetzl, 2001; Breckenridge *et al.*, 2004), isostatic rebound (Larsen, 1994; Lewis *et al.*, 2005), and fluctuating air temperatures (Breckenridge *et al.*, 2004). Subsequent to the initial European colonization of the area during the 17th century, the lakes have seen changing land use (Whitney, 1987; Wolter *et al.*, 2006; Schulte *et al.*, 2007), fishing (1973; Link, 2002), eutrophication (Schelske *et al.*, 1983; Conley *et al.*, 2009), toxic pollution (Marvin *et al.*, 2004), biological invasions (Ricciardi and MacIsaac, 2011), and rapid climate change (Austin and Colman, 2007; O'Reilly *et al.*, 2015). These stressors have resulted in a system that has changed markedly through time, and the biota of the system have responded accordingly. Several notable taxa have been extirpated (e.g. *Stephanodiscus niagarae*—Julius *et al.*, 1998; Unionid mussels—Schloesser *et al.*, 2006) or driven to historically low abundances (alewife, *Diporeia*, etc.; O'Gorman and Stewart, 1999; Pothoven *et al.*, 2010) within some or all of the Great Lakes system during the last century, while the lakes have been inundated by a host of both intentionally and accidentally introduced non-native species (Mills *et al.*, 1993).

The planktonic diatom community of the LGL has also changed in response to the influence of multiple stressors within the Great Lakes Basin, particularly in the last century (e.g. Makarewicz *et al.*, 1999; Barbiero *et al.*, 2006; Fahnenstiel *et al.*, 2010; Reavie *et al.*, 2014, 2017; Sgro and Reavie, 2018a). Due to their ubiquitous, well-preserved silica frustules and high fidelity to environmental conditions, diatoms lend themselves well to inference and reconstruction of historical limnological conditions (Dixit *et al.*, 1992, Smol and Cumming, 2000). The diatom record in each of the five LGL shows that assemblages over the last ~160 years have generally become increasingly dissimilar in composition and structure to their pre-European colonization counterparts (Fig. 1). During this time, the diatoms suggest basin-wide increases in cultural eutrophication beginning early after European colonization (Schelske *et al.*, 1983) and culminating in the mid-20th century preceding a period of oligotrophication or recovery following phosphorus abatement measures in the 1970s (Stoermer *et al.* 1996; Allinger and Reavie, 2013; Sgro and Reavie 2018a). Inferences from diatom stratigraphic sequences in multiple lakes have also demonstrated the influence of ongoing deforestation and industrialization within the Great Lakes Basin (Stoermer *et al.*, 1993), as well as effects of non-indigenous species colonization (Stoermer *et al.*, 1996), and anthropogenic impacts to water quality (Reavie *et al.*, 1998).

Rates of surface temperature increase in the LGL are among the fastest of all aquatic systems in the world (Austin and Colman, 2008; O'Reilly *et al.*, 2015) and despite the confounding influence of multiple stressors, the diatom record of the lakes reflects this warming trend. Reavie *et al.* (2017) demonstrated that diatom species within *Cyclotella sensu lato (s.l.)* have increased in relative abundance (RA) and biovolume accumulation rates within all of the LGL over the course of the last ~50 years. Within the Great Lakes, these taxa have been described as a major component of the summertime epilimnetic assemblage (Reavie *et al.*, 2014; Bramburger and Reavie, 2016). Further, *Cyclotella s.l.* are broadly characteristic of relatively deep, highly stratified lakes including tropical lakes, and have increased in RA in temperate, alpine, and polar lakes worldwide (Rühland *et al.*, 2008, 2015). The *Cyclotella s.l.* taxa that have increased most markedly within the Great Lakes were typically those characterized by their smaller cell size (Reavie *et al.*, 2017; Bramburger *et al.*, 2017). This increase in smaller-celled diatom taxa was not limited to *Cyclotella s.l.*, and combined with demographic shifts towards smaller-celled individuals within taxa, has contributed to a reported basin-wide decrease of 587 μm^3 in assemblage mean diatom cell size between 1900 and 2015 (Bramburger *et al.*, 2017).

While Bramburger *et al.* (2017) focused on the effects of size-dependent RA changes among diatom taxa and reviewed mechanisms that could have contributed to this phenomenon, they did not address patterns or effects of species' establishments into—or extirpations from—the LGL phytoplankton community. In this study, we re-examined paleolimnological data from the same

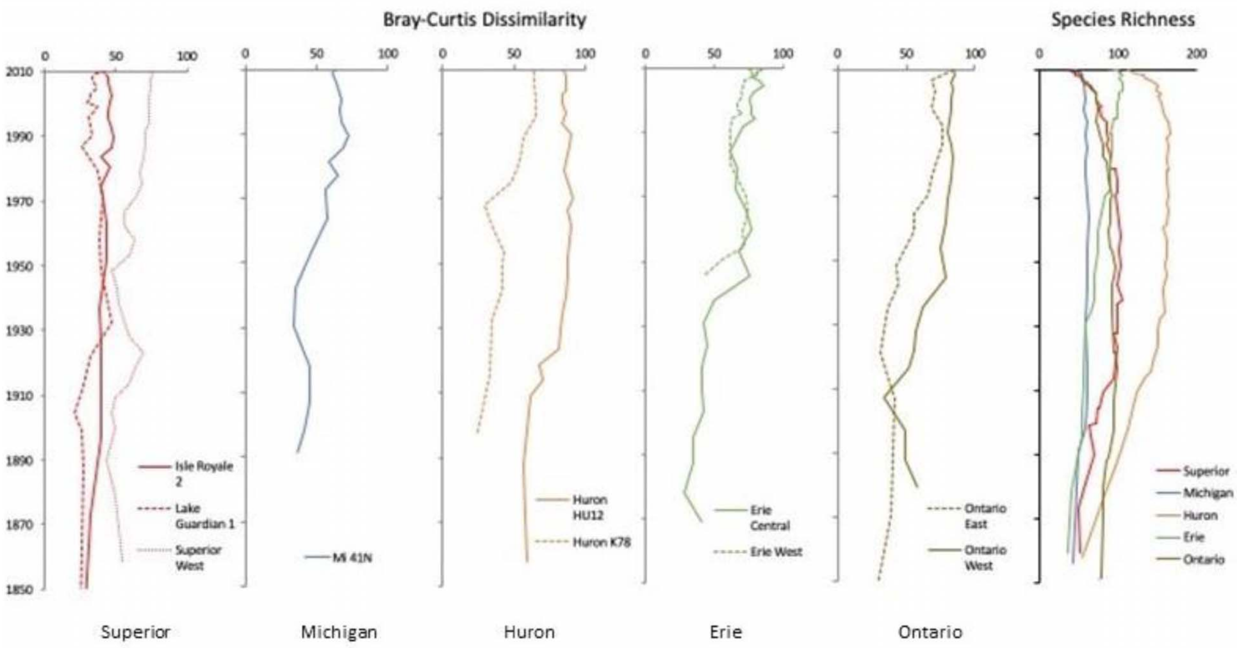

Fig. 1. Community change (left four panels; expressed as Bray–Curtis dissimilarity compared to the oldest sedimentary interval; each line represents a single core and each plot represents a single lake) and accumulated species richness (right-most panel; calculated as core bottom richness + establishments—extirpations for each lake; each line represents a single lake) in the LGL from 1850 to 2010. Sedimentary date represents the mid-date of each sedimentary interval.

10 cores from the LGL and assessed the timing of the first and last detectable appearances of diatom taxa in the sedimentary record as a function of their cell size in order to determine if the timing of *de facto* establishment and extirpation events contributed to the overall size structure of diatom paleo-assemblages within the LGL. We also evaluated patterns of establishments and extirpations within the context of concurrent environmental conditions and stressors, and discuss the implications of these events for overall cell-size trends within the Great Lakes planktonic diatom community over the 20th century. Based on the well-documented warming of the Great Lakes (Austin and Colman, 2008; O'Reilly *et al.*, 2015), the cell-size differences between spring and summer diatom assemblages (Bramburger and Reavie, 2016), and the recently decreasing RA of large-celled taxa within the system (Bramburger *et al.*, 2017), we hypothesized that larger-celled diatom taxa became established within the diatom community primarily in earlier sedimentary intervals (early 1900s) and were extirpated with increasing frequency in more recent sediments (1990s–present). Conversely, we anticipated that smaller-celled taxa that are less constrained by buoyancy and nutrient requirements would exhibit relatively consistent rates of establishment and extirpation from the early 1900s and extending through the anthropocene.

Successful establishment of a novel species within an assemblage is a multi-faceted process. Lodge (1993) suggested that three "filters" (dispersal, physicochemical, and ecological) constrain the establishment of species within new systems. First, an adequate number of viable propagules from a source population must be successfully entrained by a dispersal vector and deposited in the new habitat. Subsequently, newly arrived propagules must be able to tolerate the physical and chemical conditions of the new habitat. If these criteria are met, the colonizing species must be able to maintain a viable population size under the predation and competition regimes that exist in the new habitat. Accordingly, species that are rejected by any of these filters may occur sporadically within a new system, but fail to become established in consistently detectable abundances. Similarly, previously established taxa may be extirpated from a system if they are unable to adapt to changes in the physicochemical or ecological characteristics of the habitat.

Here, establishment and extirpation events for each lake were defined as the first or last appearance of a diatom taxon within a core from that lake. The LGL have been subjected to increased propagule flow across multiple taxonomic groups since the opening of the Welland Canal in the mid-19th century (Colautti *et al.*, 2003). Further, physicochemical (e.g. temperature;

McCormick and Fahnenstiel, 1999, nutrient status; Bourbonniere and Meyers, 1996) and ecological (e.g. dreissenid mussels; Mills *et al.*, 1993) changes have been well-documented within the system spanning back to initial European colonization. If the mechanisms that regulate establishment and extirpation have affected diatoms of all size classes equivalently, we would expect to observe consistent patterns of establishment and extirpation across all size classes, as well as a random distribution of species' cell sizes corresponding to establishment and extirpation events throughout the sedimentary record of the last ∼150 years. Alternatively, if these mechanisms are size dependent, we would expect to observe differential rates of establishment or extirpation among different size classes in different periods of the sedimentary record.

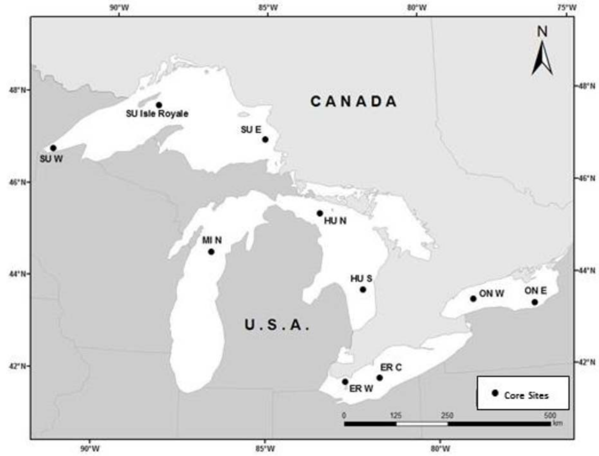

Fig. 2. Map of the LGL showing positions of core sampling aboard the *R/V Lake Guardian* following Bramburger *et al.* (2017). An additional coring site in southern Lake Michigan had poor diatom preservation, and has been omitted.

METHOD

Sediment core sampling and stratigraphy

Sediment cores were collected at 10 locations throughout the Great Lakes, including three cores from Lake Superior, two cores from each of Lakes Huron, Erie, and Ontario, and a single core from Lake Michigan (Fig. 2). Coring was conducted aboard the USEPA research vessel *Lake Guardian* using an Ocean Instruments model 750 box corer (30 × 30 × 90 cm). Supplementary cores were collected aboard the research vessels *Lake Guardian* and *Blue Heron* using an Ocean Instruments model MC-400 multi-corer (9.4 cm diameter tubes). For each location, one core was extruded and sectioned at fine intervals (0.25 cm in upper intervals to 1 cm at the core bottom) depending on estimated accumulation rates and temporal resolution requirements. Extruded samples were used for ^{210}Pb dating and diatom analysis. We employed supplementary ^{137}Cs dating in the western Lake Erie core in order to pinpoint the 1963 peak associated with weapons testing (Appleby, 2001). ^{210}Pb and ^{137}Cs were quantified by low-background gamma spectroscopy as described by Appleby (2001) and ^{210}Pb dating followed methods described by Chraïbi *et al.* (2014). ^{210}Pb profiles indicated typical isotopic decay through time, and dating errors ranged from ±1 to 2 years in the most recent three decades, to ±10–20 years ca. 1850. Although sedimentary records for this study were longer and extended beyond the ^{210}Pb dating range (∼150 years), we focused on sedimentary intervals with ^{210}Pb-inferred median dates no older than ∼1850. Details of the dating models for these cores are provided by Aliff et al. (2020).

Diatom processing

Organic material was removed from diatom samples by digestion in a concentrated, hot (100°C) acid solution. Diatom material was rinsed eight times and permanent slides were prepared using the Battarbee (1986) method. Diatoms were identified to the lowest possible taxonomic level (species or variety) and enumerated at 1000–1200× magnification using light microscopy (Olympus BX51 or Olympus BMAX compound scopes equipped with Nomarski DIC optics). On each slide, at least 500 diatom valves were enumerated, and the valve size (length, width, diameter, and/or depth) was measured for the first 10 valves encountered in each subsample for each taxon in order to calculate species' mean cell size. Biovolume calculations for each individual were conducted based on standardized shape formulas for each taxon (Reavie *et al.*, 2010), and mean biovolumes were calculated for each taxon based on average valve dimensions within each lake (Reavie *et al.*, 2010).

Statistical approaches

In order to minimize the influence of rare taxa on observed trends, taxa that did not account for at least 0.5% of the total valve count in any lake were excluded from further analysis. Simple stratigraphic analyses were used to illustrate trends of species richness and community change in each lake over the past ∼150 years. In order to examine richness trends in each lake, data from multiple cores (where available) were combined into a single stratigraphy, and "accumulated species richness" (*S*) for each sedimentary interval was calculated by the following formula:

$$S_n = S_{n-1} + (S_{est} – S_{ext})$$

wherein S_n is richness of the sedimentary interval of interest, S_{n-1} is the richness of the temporally previous interval, S_{est} is the number of species established in the interval of interest, and S_{ext} is the number of species extirpated since the previous interval (further explanation of establishment and extirpation definitions follows in next paragraph). This metric was used to minimize noise associated with taxa that appeared and/or disappeared periodically through the stratigraphy. Community change is expressed as Bray–Curtis dissimilarity relative to the oldest sedimentary interval for each individual core.

In order to explore the relationship between the size of established/extirpated taxa and the date of their appearance in/disappearance from the sedimentary record, we constructed a null model for comparison to actual data. This allowed us to assess observed trends while accounting for inherent pattern that may have been introduced due to the non-random assignment of individual diatoms to taxa within the assemblage. In the null model, model sedimentary intervals (median dates analogous to actual intervals) were randomly populated with diatom valves based on total abundances from actual count data (500 valves per sedimentary interval). The model was run for 50 iterations per lake, and the earliest and latest occurrences of each taxon were determined in each model iteration. Taxa were considered "present" if they were detectable within at least one sediment interval per lake. Those taxa that were not present in at least five sedimentary intervals within a lake were considered "transient" within that lake, and were excluded from further analysis. Similarly, in order to minimize artifacts associated with differences in temporal resolution between early and recent core intervals, taxa whose first and last appearances were less than a decade apart were also excluded. This allowed us to examine broad trends while minimizing the noise associated with species that never became established within the standing community. Taxa were considered to have become established when their earliest occurrence was more recent than the oldest sediment interval and followed by presence in at least four subsequent sedimentary intervals. Similarly, taxa were considered extirpated if their latest occurrence was prior to the most recent sedimentary interval and was preceded by presence in at least four earlier sedimentary intervals. In order to simultaneously investigate establishment/extirpation and mean cell-size trends, we expressed establishment events as positive cell size and extirpation events as negative cell sizes. We used a variety of regression techniques (linear regression, third degree polynomial regression) to evaluate the relationship between cell sizes and the date of the establishment/extirpation event.

In order to evaluate relationships between the size of established/extirpated taxa and the date of their appearance in/disappearance from the sedimentary record, we used actual count data to determine the mean cell size and earliest and latest occurrence of each taxon in each of the LGL. As with null model data, taxa were considered transient if they did not occur in at least five sedimentary intervals, and were considered to have become established within a lake when their earliest occurrence was more recent than the oldest sediment interval (core bottom) and followed by presence in at least four subsequent sedimentary intervals. Similarly, taxa were considered extirpated from a lake if their latest occurrence was prior to the most recent sedimentary interval (core top) and was preceded by presence in at least four earlier sedimentary intervals. We again expressed establishment events as positive cell sizes and extirpation events as negative cell sizes. We used linear regression analysis and polynomial regression analysis to examine relationships between species cell size and event date in each of the LGL.

RESULTS

In each of the Great Lakes, the planktonic diatom community has changed through time. While there is considerable fluctuation in the level of community dissimilarity from the core bottom through time, dissimilarity to the basal sedimentary interval has generally increased in each lake (Fig. 1). This dissimilarity increase is associated with both the establishments and extirpations of species. Accumulated species richness increased steadily from 1850 through the middle of the 20th century in all of the Great Lakes. With the exception of Lake Erie, all lakes saw a decline in species richness beginning approximately in the 1970s and all lakes have undergone an acceleration of species loss over the past two decades (Superior $\Delta S = -57$ since 1948; Michigan $\Delta S = -9$ since 1963; Huron $\Delta S = -61$ since 1966; Erie $\Delta S = -21$ since 2008; Ontario $\Delta S = -53$ since 1916; Fig. 1).

In examining relationships between cell size of established/extirpated species and the date of the establishment or extirpation event, we observed that in all lakes, larger-celled taxa proportionately became established within lake assemblages early in the sedimentary record, while establishments of smaller taxa continued consistently across all sediment intervals (Fig. 3). Extirpations of smaller-celled taxa have also remained relatively consistent since roughly the turn of the 20th century. In contrast, extirpations of all taxa, and especially larger-celled taxa, have occurred with increasing frequency in more recent sediment intervals, particularly since the 1970s (Fig. 3). Linear regression was used to evaluate general trends in establishment and extirpation, and revealed a significant negative relationship between event date and cell size (i.e. large positive cell sizes earlier, large negative cell sizes later) in all five lakes (Superior $y = -8.62x$, $R^2 = 0.34$, $P < 0.0001$; Michigan $y = -10.54x$, $R^2 = 0.07$, $P < 0.0001$; Huron $y = -4.23x$, $R^2 = 0.28$, $P < 0.0001$; Erie $y = -24.41x$, $R^2 = 0.09$, $P = 0.0094$; Ontario $y = -6.49x$, $R^2 = 0.27$, $P < 0.0001$). While this regression technique suggested a general trend, we found that it did not effectively characterize nuances in the data. Therefore, we applied more complex non-linear regression techniques.

In order to better characterize the cell-size/event-date relationship, we used polynomial regression and were able to fit negatively sloping cubic relationships for all lakes (Fig. 3). These fits were universally more representative of the data than simple linear fits, and demonstrated that unlike the null model, all lakes had a significant, negatively sloping relationship between event date and cell size (i.e. large positive cell sizes earlier, large negative cell sizes later.

DISCUSSION

Recent reports of decreasing diatom cell size within the LGL (Bramburger *et al.*, 2017) suggested that historically changing cell sizes in the system were influenced by both demographic (i.e. smaller individual cells within species) and community (i.e. shifts towards higher abundances of smaller-celled taxa) effects. Often, shifts in community structure are subtle, and comprise changes in the RA of species, while additions and deletions of species to/from an assemblage are less common and can be reflective of more pronounced changes in environmental conditions. In diatom paleolimnology, establishment and extirpation events may be seen as a species' first and last appearances in the sedimentary record (e.g. Julius *et al.*, 1998; Edlund *et al.*, 2000, respectively). Establishments are constrained by species' dispersal dynamics, physiological tolerance of novel conditions, and ability to successfully compete for resources and avoid predation in the new habitat (Lodge, 1993). Similarly, species may be extirpated from a habitat due to changes in the physicochemical or ecological characteristics of the habitat.

Classically, diatoms have been thought to be dispersed readily, and often broadly, by a variety of vectors (Finlay, 2002). The opening of the St Lawrence Seaway and the widening and deepening of the Welland Canal in the late 19th century allowed unimpeded access for trans-oceanic ship traffic into the Great Lakes for the first time (Colautti *et al.*, 2003), and represented a potent dispersal vector exposing the LGL to diatom propagules from a variety of regions. Per Lodge (1993), taxa that became successfully established within a system are reflective not only of adequate dispersal, but also physicochemical and ecological characteristics of the host system that are suitable to the novel taxa (i.e. taxa that were previously undocumented within the system). However, establishment events are not necessarily limited to colonization of the system by taxa from other locales. Several taxa thought to have been recently established within the LGL were demonstrated to have occupied the basin in low abundances prior to European colonization and subsequently increased to detectable abundances within the system (e.g. *Stephanodiscus binderanus*; Hawryshyn *et al.*, 2012). Regardless of the mechanism of a species' first appearance within the fossil record, we can infer that given taxa encountered hospitable conditions at the time of their appearance in the sedimentary record, and we can gain insight into historical conditions by evaluating ecological tolerances and optima of taxa that successfully established themselves within the system. Conditions across the Great Lakes basin were largely meso-oligotrophic and relatively non-impacted until the early part of the 20th century (Reavie and Allinger, 2011; Allinger and Reavie, 2013). As shipping increased among—and from beyond—the lakes, cities grew along the shores of the system, and anthropogenic development proliferated rapidly within the basin in subsequent years. In the earliest parts of the diatom records we investigated (~1850) until the turn of the 20th century, many diatom taxa representing all size classes became established in the Great Lakes. Thereafter, the rate of novel establishments subsided, particularly the establishment of large-celled diatom taxa. These results are also reflected in patterns of accumulated diatom species richness in each of the lakes. Species establishments continued at fairly consistent rates from the early 20th century until the last few decades, when they declined markedly in all lakes except Erie. However, establishment events during the late 20th century were dominated by smaller-celled taxa. When cultural eutrophication was most pronounced during the mid-20th century, conditions were more amenable to larger-celled taxa due to increased nutrient loadings and this was reflected in an increase in the size of taxa that became established around that time. After the implementation of the Great Lakes Water Quality Agreement in 1972, overall nutrient levels declined (Dolan and Chapra, 2012) and with the exception of Lake Erie, the size of species that became established, as well as the rate of establishments, declined across the basin.

In all lakes, species extirpations occurred sporadically throughout the sedimentary record from 1850 through the mid-20th century. However, from ~1970 through the most recent sedimentary intervals, we observed a marked increase in the frequency of extirpation events, and an increase in the cell size of the extirpated taxa. In fact, extirpations have outpaced establishments among

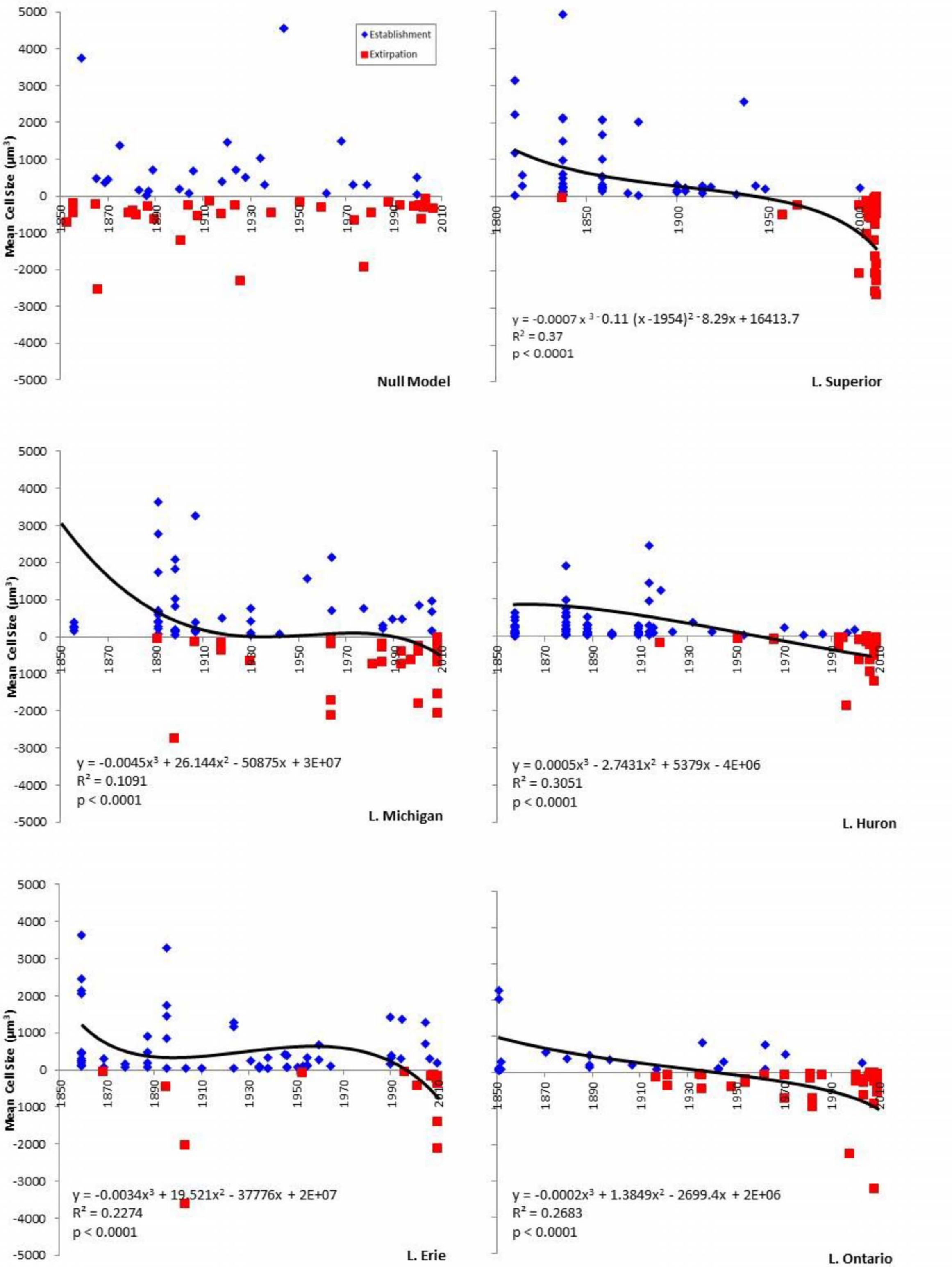

Fig. 3. Relationships between species' mean cell size and establishment/extirpation event date for null model (plot for the null model is an example of a single iteration of the model; no significant relationship between mean cell size and event date was observed in any null model iteration) and Lakes Superior, Michigan, Huron, Erie, and Ontario. Species' mean cell sizes are expressed as positive for establishment events (blue) and negative for extirpation events (red).

both large- and small-celled taxa over the last two decades, and have led to an overall reduction in species richness across the basin. Taxa with cell sizes in the highest quartile (≥700 μm³) have been extirpated at an especially high rate since the 1990s in all lakes. This high rate of extirpation among large-celled taxa has likely been driven by high loss rates due to sinking (as per Reynolds 2006) compared to smaller taxa (Bramburger and Reavie, 2016; Bramburger *et al.*, 2017) associated with warmer, more intensely stratified water columns, as well as declining nutrient availability across the basin (Evans *et al.*, 2011; Dove and Chapra, 2015), and the effects of filter feeding by dreissenid mussels, particularly in Lakes Huron and Michigan (Nalepa *et al.*, 2009; Cuhel and Aguilar, 2013; Sgro and Reavie, 2018b). At a basin-wide scale, the recent extirpation of numerous diatom taxa in general, and large-celled taxa in particular, have contributed to the reduction of assemblage mean cell size (541 μm over the last ~115 years) reported by Bramburger *et al.* (2017) and recent decreases in diatom biovolume (Reavie and Barbiero, 2013) within the LGL.

As with overall cell-size trends (Bramburger *et al.*, 2017), relationships between species' cell size and establishment/extirpation event date show broad consistency across the basin, with subtle lake-to-lake differences. Notably, relatively high rates of small-celled species establishment have been maintained in recent sedimentary intervals in both Lake Erie and Lake Michigan compared to the other three LGLs. In Lake Erie, it is likely that readily available agricultural nutrients associated with recent re-eutrophication (Baker *et al.*, 2014; Kane *et al.*, 2014) have facilitated recent establishments and lower extirpation rates than in other lakes. In Lake Michigan, we speculate that warmer water temperatures and surplus silica resulting from low diatom standing biomass have created novel conditions that supported the handful of establishments we have observed since the turn of the 21st century. It should be noted that in both of these lakes, as in the others, extirpations have still outpaced establishments during this period, and the few taxa that have become established are all characterized by small cell size. These results further support the assertion of Bramburger *et al.* (2017) that warmer, increasingly stratified water columns and longer growing seasons within the LGL are not hospitable to large-celled diatom taxa (Winder *et al.*, 2009). The shift of the Great Lakes planktonic diatom community towards smaller taxa, including the outright disappearance of many larger-celled forms, is just one example of the many changes recently reported in the Great Lakes phytoplankton. In various lakes, large spring diatom blooms and low summer diatom biovolumes (Reavie *et al.*, 2016; Bramburger and Reavie, 2016), as well as record or near-record harmful cyanobacteria blooms (Michalak *et al.*, 2013) and broader changes in the overall algal community composition of the system (e.g. Bridgeman *et al.*, 2012) have become more pronounced during the last decade, and bear many unaddressed implications for higher trophic levels within the Great Lakes food webs.

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