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Pressure from top and bottom: Lower food web responses to changes in nutrient cycling and invasive species in western Lake Michigan

Paul M. Engevold [a], Erica B. Young [a,b], Craig D. Sandgren [a,1], John A. Berges [a,b,*]

[a] Department of Biological Sciences, University of Wisconsin-Milwaukee, 3209 N. Maryland Avenue, Milwaukee, WI 53211, USA
[b] School of Freshwater Sciences, University of Wisconsin-Milwaukee, 600 E. Greenfield Avenue, Milwaukee, WI 53204, USA

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ABSTRACT

Over recent decades, Lake Michigan phytoplankton and zooplankton communities have experienced dramatic changes driven both from the bottom (e.g. P loading reduction) and top (e.g. predatory cladoceran invasions) of the food web. We used two data sets from nearly identical sampling at an offshore station (100 m depth) in western Lake Michigan (1988–92 and 2007–09), to test for bottom-up effects (i.e. declines in chlorophyll *a* (chl *a*) or increases in particulate C:P, leading to declines in P-rich cladocerans versus copepods), and top-down effects of invasive predatory cladocerans (i.e. declines in native zooplankton from predation or competition). Between the two periods, total P and particulate C declined, while nitrate and silicate increased. While chl *a* in the largest cells (>53 μm and 10–53 μm fractions) decreased, particulate C:P ratios were unchanged. Total zooplankton abundance and biomass declined significantly between sampling periods, notably cyclopoid copepods, but not *Bosmina* or *Daphnia* species, nor the invasive cladoceran, *Bythotrephes longimanus*. Bottom-up effects, usually associated with 'benthification' attributed to *Dreissena* grazing, are more consistent with the changes observed than are effects of invasive predatory cladocerans. Differences in observations from those in eastern Lake Michigan or other lake-wide surveys are difficult to reconcile but seem more likely due to temporal differences in sampling rather than spatial ones. Discerning the trajectory of Lake Michigan will require better accounting for zooplankton life histories, more sophisticated understanding of nutritional quality and diet for zooplankton, and clearer coupling of pelagic–benthic cycles of elements, including Si and N.

Introduction

Like all the Laurentian Great Lakes, Lake Michigan has experienced substantial changes over the past several decades due to changes in climate, nutrient inputs, fisheries pressure, as well as a succession of non-indigenous invasive species (Bunnell et al., 2014; Cuhel and Aguilar, 2013). Due to the size and spatial complexity of the lake, it has proven difficult to generalize about the effects of changes on the food web; studies have typically focused on intense spatial or temporal coverage, but have seldom done both (see Mida et al., 2010). Eastern Lake Michigan is generally much better represented in published research than the western side of the lake.

Considering Lake Michigan's plankton, dramatic changes have occurred at both the bottom and the top of the food web and include reductions in phosphorus (e.g. Barbiero et al., 2002), increases in water clarity and silicate concentrations, coincident with declines in diatom blooms (Barbiero et al., 2012; Kerfoot et al., 2008, 2010; Vanderploeg et al., 2010), and shifts in zooplankton species (Evans, 1986; Barbiero et al., 2005). Invasive species such as dressenid mussels have undoubtedly played major roles in such changes (Hecky et al., 2004; Nalepa et al., 2010), while the effects of others such as the predatory cladocerans *Bythotrephes longimanus* (which was detected in the lake in 1986) and *Cercopagis pengoi* (which was established in the lake by 1999) (Branstrator and Lehman, 1991; Cavaletto et al., 2010; Lehman, 1991) have been less clear. For example, in the case of *B. longimanus*, large initial declines in herbivore biomass were readily attributed to the invader (e.g. Lehman, 1991), but subsequently populations stabilized (e.g. Barbiero and Tuchman, 2004) and the picture has been complicated by more recent changes in a number of biotic and abiotic factors in the lake (Vanderploeg et al., 2012).

Two powerful concepts that have helped in the interpretation of such complex situations have been bottom-up and top-down control (McQueen et al., 1986) and ecological stoichiometry (e.g. Sterner and Hessen, 1994). McQueen et al. (1986) reviewed a broad ecological literature and concluded that bottom-up (resource-mediated) effects controlled biomass and were dominant at the nutrient-to-phytoplankton step of freshwater pelagic food webs, but weakened by approximately a factor of two at each subsequent step. Conversely, top-down (predator-mediated) effects dominated at the top of the pelagic food web,

* Corresponding author at: Department of Biological Sciences, University of Wisconsin-Milwaukee, 3209 N. Maryland Avenue, Milwaukee, WI 53211, USA. Tel.: +1 414 229 3258.
E-mail address: berges@uwm.edu (J.A. Berges).
[1] Deceased on December 24, 2011.

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and weakened towards the bottom. However, McQueen et al. (1986) predicted that in oligotrophic freshwater systems such as Lake Michigan, zooplankton effects on phytoplankton would be significant. Sterner and Hessen (1994) pointed out that a critical aspect of bottom-up control was related to the food quality of prey; phytoplankton that were limited by phosphorus (and thus had high C:P elemental ratios) could in turn be nutritionally limiting to their predators. Significantly, they also noted that, of the dominant herbivorous zooplankton found in Lake Michigan, cladocerans show much higher P requirements than do copepods. Therefore, a phytoplankton community with high C:P (i.e. relatively impoverished in P) may more strongly limit cladocerans than copepods (Sterner and Hessen, 1994).

The availability of nearly identical data sets from two series of cruises to an offshore (100 m depth) station near Milwaukee in western Lake Michigan, conducted in 1988–1992 and 2007–2009, gave us the opportunity to explore food web changes in the context of food web control and ecological stoichiometry. In particular, we expected that if bottom-up effects of nutrient (P) changes driven by reductions in P loading and 'benthification' due to dressenid mussel colonization (Hecky et al., 2004) are prevalent, then we should see declines in water column P, decreases in phytoplankton biomass, increases in the C:P ratio of particulate matter in the lake, and declines in zooplankton such as *Daphnia* spp. that require larger amounts of P, with shifts towards calanoid copepods with smaller P requirements (Schulz and Sterner, 1999; Sterner and Hessen, 1994). Secondly, we considered that if top-down effects of invasive predatory cladocerans continued to increase between 1988–1992 and 2007–2009, then we should see declines of putative prey species (such as *Bosmina* spp.) and also decreases in native species which occupy similar dietary niches as the invaders (such as *Leptodora kindtii*, see Cavaletto et al., 2010 and references therein).

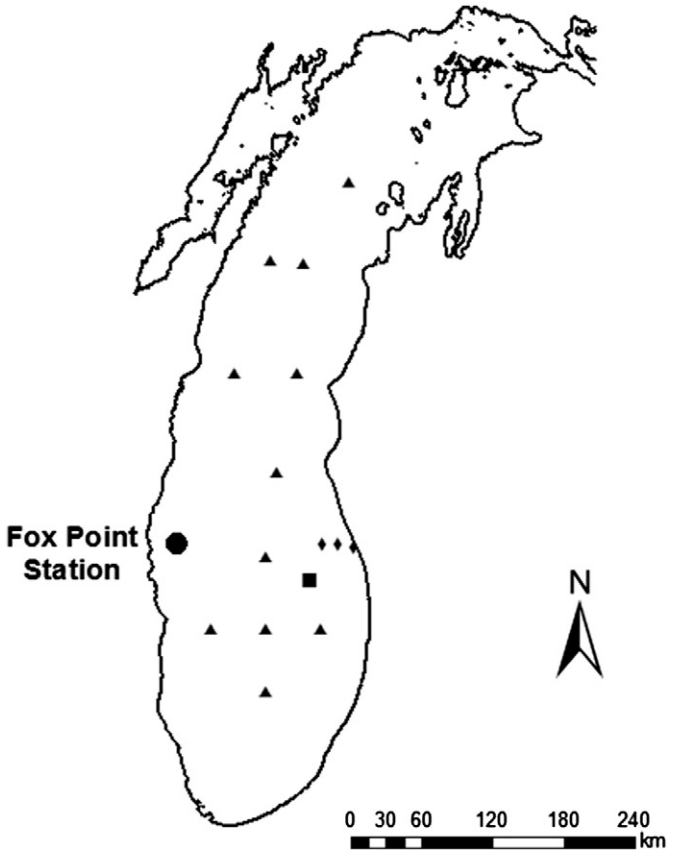

Fig. 1. Map of sampling location in Lake Michigan showing the Fox Point sampling station in relation to other long-term monitoring stations: Grand Haven station (e.g. Lehman and Cacéres, 1993); ▲ US EPA GLNPO monitoring stations; ♦ NOAA GLERL monitoring stations.

Methods

Sampling

Sampling was conducted aboard the *R/V Neeskay* at one station, "Fox Point", in western Lake Michigan (43° 11.77′ N, 87° 40.29′ W), 27 km NE of Milwaukee, Wisconsin, 104 m water depth (Fig. 1, locations of other commonly-used sampling stations are included for reference). This station has served as a reference location for many studies conducted at UWM (see waterbase.glwi.uwm.edu; Brooks and Edgington, 1994). Identical sampling and analysis protocols (except as noted below) were used for June–August during two periods, 1988–1992 and 2007–2009. During the earlier sampling period, two cruises were undertaken in 1988, 5 each in 1989 and 1990, 7 in 1991, and 3 in 1992, and in the later period, 2 cruises in 2007, 6 in 2008, and 1 in 2009.

Vertical water column profiles for light and temperature were determined during the 1988–1992 cruises using a spherical irradiance sensor (LI-193 Li-Cor, Lincoln NE, USA) and bathythermograph as described by Brooks and Edgington (1994). During 2007–9, temperature profiles were collected using a calibrated Seabird CTD (model 25 Sealogger, Sea-bird Electronic Bellevue, WA, USA) with an attached quantum irradiance sensor (QSP 200L Biospherical Instruments, San Diego, CA, USA).

Downcast data were used to determine the depths to which 60%, 30%, 10%, 1%, 0.3%, and 0.01% of surface irradiance (I_o) penetrated, and these were used as sampling depths. Such a method allows correct comparisons of data related to primary productivity across seasons and interannually (see Talling, 1957). This is analogous to the widely used concept of optical depth in oceanography (e.g. Behrenfeld and Falkowski, 1997), but without the complication of a logarithmic scale; we use the term "light penetration depth" for routine reference (cf. Talling, 1957). Discrete water samples were collected at each light penetration depth in 30 L light-opaque Niskin sampling bottles and used for determination of dissolved and particulate nutrients and chl *a*.

Whole water from each light penetration depth was immediately placed into acid-washed 1 L brown polypropylene bottles and kept on ice before ship-board processing (typically within 20 min). Whole water (500–2000 mL) was vacuum-filtered (<10 mm Hg) onboard ship through pre-combusted (2 h at 450 °C) GF/F filters (Whatman-GE Life Sciences, Pittsburgh, PA, USA). The filtrate was stored on ice for determination of dissolved nutrients and the filters stored a desiccant bottle and frozen (−20 °C) for later analysis of POC and PON. All chemical analyses were performed within 24 h of water collection.

Nutrient determinations

Total phosphorus (TP) and total dissolved phosphorus (TDP) were determined by digesting 40 mL replicate unfiltered (TP) and filtered (TDP) water samples with potassium persulfate solution (5% final concentration) in an autoclave for 30 min (Menzel and Corwin, 1965) before measuring soluble molybdate-reactive phosphorus (SRP) (Murphy and Riley, 1962) spectrophotometrically at 885 nm using a 10 cm cell (Ultrospec II, LKB Biochrom, Cambridge, UK). Particulate phosphorus (PP) was determined by subtraction of TDP from TP. Dissolved silicate was determined using replicate 10 mL filtered water samples by the molybdate-stannous chloride procedure (Golterman, 1969) spectrophotometrically at 815 nm using 10 or 1 cm cells. Dissolved nitrate was determined using replicate 20 mL samples by the spectrophotometric Brucine method (Kahn and Brezenski, 1967) at 410 nm using a 4 cm cell.

For particulate C and N elemental analysis, GF/F filters were air-dried over night at room temperature then fumed with concentrated hydrochloric acid for 20 s to remove inorganic carbonates (Hegdes and Stern, 1984). Particulate C and N were analyzed on a Perkin-Elmer Model 2400 CHN elemental analyzer (1991–1992) (PerkinElmer

Waltham, MA, USA) or a Thermo Scientific CE Flash EA1112 Elemental Analyzer (2007–2008) (CE Elantech, Lakewood, NJ, USA) using acetanilide (71.09% C and 10.36% N) as the reference standard. Sample water volume analyzed ranged from 0.12 to 0.24 L.

Chlorophyll

Chl *a* concentrations were determined fluorometrically (EPA 1997) in whole water, <53 μm, and <10 μm fractions by pre-screening replicate 200 mL whole water samples through 53 or 10 μm Nitex screens and then vacuumed-filtering onto 47 mm 0.2 μm pore size polycarbonate filters (Supor 200, Gelman Pall, Port Washington, NY) . Filters were immediately placed into 4 °C 90% acetone buffered with $MgCO_3$ and then extracted for a minimum of seven days at −20 °C. Samples were then shaken, centrifuged, and analyzed under subdued light using a fluorometer (A-10 fluorometer model for 1988–1992, and TD-700 model for 2007–2009, both Turner Designs, Sunnydale, CA, USA) calibrated using pure *Anacystis* chl *a* (Sigma-Aldrich, St Louis, MS). Samples were subsequently acidified with 10% HCl and reanalyzed to correct for phaeopigment (Lorenzen, 1966).

Zooplankton

Zooplankton were collected during daylight hours in triplicate, using whole water column vertical tows (0–90 m) with a 1 m diameter Puget Sound-type closing net (1:4 aspect ratio, 130 μm mesh), towed at ~0.5 m/s. All samples were immediately preserved with a final concentration of either 5% sucrose formalin (1989–1992, 2008–2009) (Haney and Hall, 1973) or 70% ethanol (Black and Dodson, 2003) (2007 cruises only) until analyzed. Zooplankton density was calculated by multiplying the number of individuals of each taxon by the volume of water filtered by the net (corrected for net efficiency). Triplicate tows were first split in the laboratory with a Folsom plankton splitter and physically combined for composite counts (Lehman and Cacéres, 1993), then split until aliquots contained 200–400 individuals (EPA, 2003). Two aliquots (A and B splits) were enumerated and all animals were counted and identified. Copepod adults were examined with an Olympus SZH dissecting microscope (75–640× mag.), and an Olympus CX31 compound microscope (40–100× mag.) and identified to the species using Balcer et al. (1984) and Hudson and Lesko (2003). The entire sample was processed to estimate the abundance of large or rare (*Epischura lacustris*, *Limnocalanus macrurus*, *Senecella calanoides*) and predatory (*B. longimanus*, *C. pengoi*, *L. kindtii*, *Polyphemus pediculus*) taxa. Body length measurements were made on the first 20 individuals encountered for each species. Species-specific estimates of zooplankton biomass were calculated by multiplying the estimated abundance for each sampling date by the mean individual dry weight using published length–dry weight relationships (EPA, 2003). The same equations were used for ethanol-preserved samples; Black and Dodson (2003) reported no significant difference in *Daphnia* length after 18 months when preserved in ethanol vs sugar-formalin.

Data analysis

To examine light attenuation in the water column, extinction coefficients (k) were calculated by regressing log of irradiance against depth for each profile from a sampling date, compared over the two sampling periods using Sigmaplot v. 12.5 (Systat Software Inc., Chicago, USA). Statistical differences among nutrients, chl *a* fractions and particulate C and P measured in the water column samples were examined using two-way ANOVAs (with sampling period and light penetration depth as factors) in Sigmaplot v. 12.5 after log transformation to equalize variance and normalize data. Where differences were detected, they were explored using Tukey's tests. Zooplankton abundance and biomass comparisons between 1989–1992 and 2007–2009 periods were compared using either one-way ANOVAs (where logarithmic and square-root transformations normalized data), or a non-parametric test (Kruskal–Wallis one-way ANOVAs on ranks), using Sigmaplot v. 12.5. In each set of zooplankton comparisons, a Bonferroni correction was applied to adjust for multiple comparisons.

Results

Temperature and light

Plots of the temperature–depth profile from the earlier and later sampling period clearly showed thermal stratification during all samplings, but there was no evidence for a systematic shift in stratification depth or temperature from earlier to later sampling periods (Electronic supplementary material (ESM) Fig. S1). Attenuation of light through the water column decreased from the early to later sampling period (Fig. 2). Based on means (±standard deviations) of water column profile, light extinction coefficients were calculated as 0.191 (±0.030) for 1988–1992 (n = 14 profiles) and 0.104 (±0.012) for 2007–2009 (n = 9 profiles), a statistically significant decline (t-test, $p < 0.01$). Plotting physical depth against the calculated light penetration depth (so that slopes are analogous to light extinction coefficients) for different cruises shows the importance of comparing samples on this basis. Particularly for deeper samples, there is relatively large variability in the irradiance experienced at a particular physical depth (Fig. 2).

Nutrients and chlorophyll a

Vertical profiles of nutrient and biomass data for the Fox Point station are shown in Fig. 3. Data are plotted against light penetration depth (as a percentage of surface irradiance), but a second scale with the approximate corresponding physical depth (calculated from relationships in Fig. 2) is also shown. There were distinct differences in vertical profiles between the 1988–1992 and the 2007–2009 sampling periods for all parameters, except for C:P ratio, which did not change either with light penetration depth or sampling period. There were no statistical interactions between light depth and sampling period for any parameter. Water column TP and PP declined significantly between 1988–1992 and 2007–2009 while dissolved silicate and nitrate both increased significantly ($p < 0.001$, ANOVA in all cases). Both silicate and nitrate increased with light penetration depth (Si at 0.01% depth greater than at 10, 30 and 60% depths ($p < 0.005$, Tukey's tests), nitrate higher at

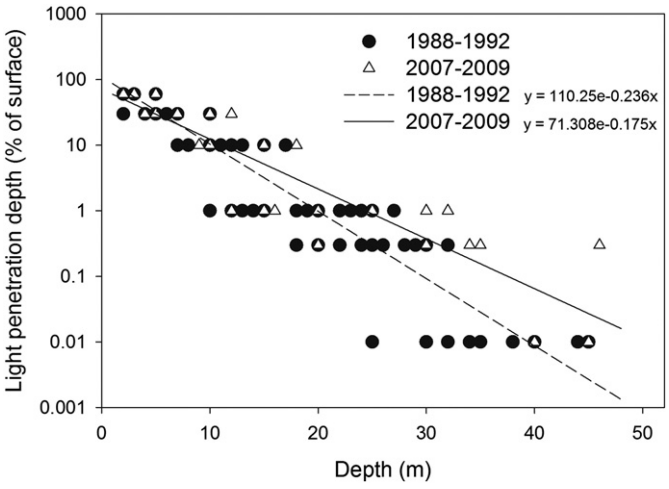

Fig. 2. Relationships between light penetration depth and actual depth in the water column for individual sampling dates in the periods 1988–1992 and 2007–2009, at Fox Point station in Lake Michigan. Lines represent least square regression fits. Mean extinction coefficients (standard deviations) for each period were 0.191 (0.030) for 1988–1992 and 0.104 (0.012) for 2007–2009.

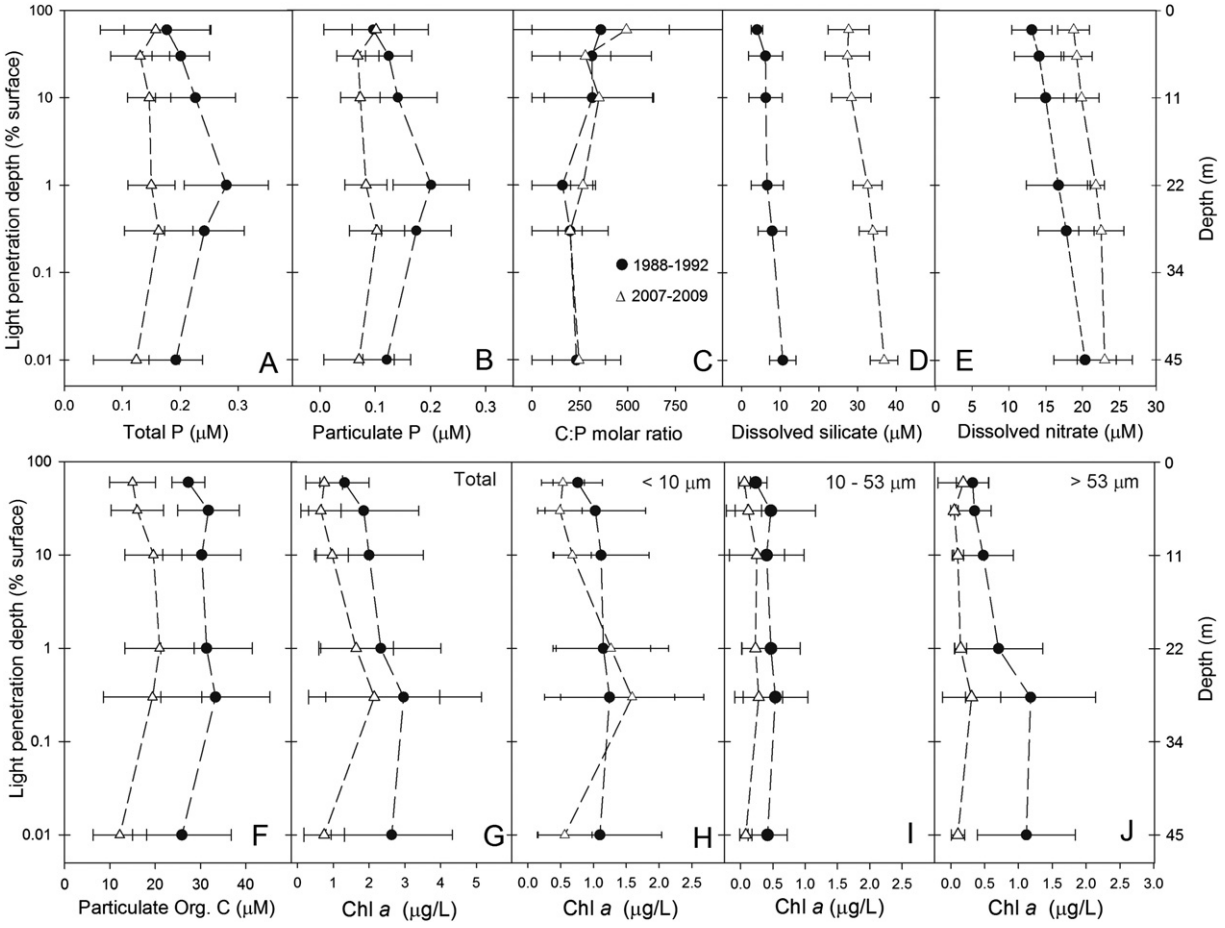

Fig. 3. Nutrient and biomass data for the pooled 1988–1992 (filled circles) and 2007–2009 (open triangles) time periods measured from samples collected at the Fox Point station. Data are plotted against the light penetration depth as a percentage of surface irradiance on that sampling day, shown on left log scale axes, and approximate depths are shown on right axes. A) Total P, B) particulate P, C) C:P molar ratio, D) dissolved silicate, E) dissolved nitrate, F) particulate organic C, G) Total chl *a*, H) <10 µm size fraction chl *a*, I) 10–53 µm fraction chl *a* and J) >53 µm fraction chl *a*. H–J plotted on same scale. Data points represent means of determinations on multiple replicate samples collected on different dates (n = 8–25 for P measurements, n = 8–10 for C determinations, n = 8–19 for SiO_2 and NO_3^-, and n = 8–33 for chl determinations). Error bars are standard deviation.

the 0.01 and 0.3% depths than at the 30 and 60% depths ($p < 0.001$–0.027, Tukey's tests). Particulate organic carbon (POC) also decreased between the earlier and later sampling periods ($p < 0.001$), but C:P molar ratio was unchanged. Total chl *a* and chl *a* within the largest cells (>53 µm and 10–53 µm fractions) decreased significantly between the earlier and more recent sampling periods (both $p < 0.001$; ANOVA). Although POC, total chl *a* and >53 µm chl *a* fraction all appeared to show similar patterns with higher values in the mid water column and lower ones at surface and depth, in only a few cases were these statistically supported, e.g. significantly lower POC at the 0.01% depth than shallower in the water column ($p < 0.05$, Tukey's test) and higher total chl *a* at 0.3% than at 30% or 60% depths ($p < 0.05$, Tukey's test). Chl *a* in the smallest size fraction (<10 µm) was not significantly different between sampling periods, and was notably elevated at 0.3 and 1% depths during the 2007–2009 period which was not observed during 1988–1992 sampling years.

Zooplankton

Total zooplankton abundance declined significantly from 933,427 ± 136,942 organisms/m^2 depth integrated (10,371 organisms/m^3) during 1989–1992, to 349,900 ± 263,138 organisms/m^2 (3887/m^3) in 2007–2009 ($p < 0.001$, ANOVA). Total zooplankton biomass decreased significantly from 3489 ± 756 mg/m^2 (38.8 mg/m^3) during 1989–1992 to 2319 ± 796 mg/m^2 (25.77 ± 8.9 mg/m^3) during 2007–2009 ($p < 0.017$, ANOVA). Conversion of values from areal (per m^2) to volumetric (per m^3) basis can be done by dividing by a factor of 90. Major groups of zooplankton taxa are plotted in Fig. 4 and all of the taxa identified are shown in Table 1. The most diverse group of zooplankton was the calanoid copepods of which the dominant species, *L. macrurus*, and a major subgroup, the diaptomids (consisting of *Leptodiaptomus ashlandi*, *L. minutus*, *L. sicilis*, and *Skistodiaptomus oregonensis*) were also plotted separately (Fig. 4). Abundance of calanoid copepods declined significantly ($p < 0.0001$) though biomass of pooled calanoid copepods did not change significantly over the same period (Fig. 4A, B) as some of the significant decreases in abundance were driven by small-sized components e.g. nauplii and copepodites (Table 1). There were no significant differences in either abundance ($p > 0.6$) or biomass ($p > 0.7$) of diaptomids as a groups between the two periods (Fig. 4). Calanoid copepodites, which significantly declined in abundance and biomass between the two periods were (in terms of abundance) >99% diaptomids in 1989–92 and >87% diaptomids in 2007–9. The abundance and biomass of cyclopoid copepods also decreased ($p \le 0.001$) with decreases in abundance and biomass of cyclopoid copepodites ($p \le 0.002$) and *Diacyclops thomasi* ($p \le 0.001$) and decreases in cyclopoid nauplii biomass ($p < 0.002$). Between the two sampling periods, *C. pengoi* appeared but were still at very low density during the 2007–2009 sampling period, and dressenid mussel veligers increased ($p \le 0.001$) (Fig. 4, Table 1). There were no significant changes in *Bosmina* spp., or pooled *Daphnia* species because some daphnids declined while *Daphnia longiremis* increased significantly in abundance and biomass ($p \le 0.001$).

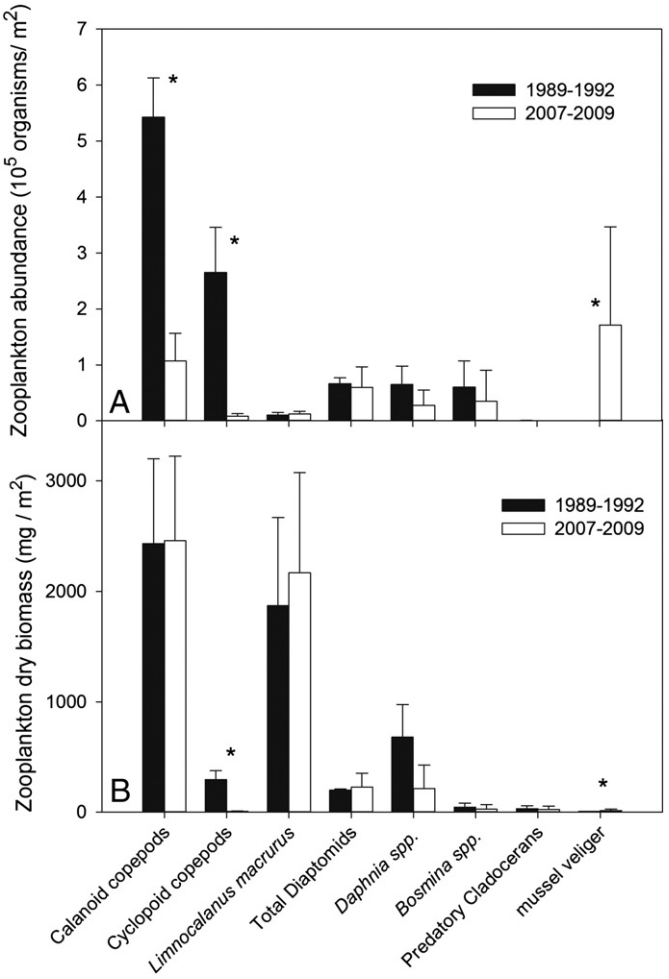

Fig. 4. Zooplankton in samples from Fox Point station pooled for 1989–1992 (filled bars) and 2007–2009 (open bars) time periods. Zooplankton are grouped into taxa or single species integrated over the whole water column, shown as individual counts of abundance (A), and dry biomass (B) calculated from measured body lengths. Note that the 'Calanoid copepods' category includes *Limnocalanus macrurus*, which is also plotted separately. 'Total Diaptomids' includes *Leptodiaptomus ashlandi*, *L. minutus*, *L. sicilis*, and *Skistodiaptomus oregonensis* (see Table 1). Bars are means (+ standard deviations as whiskers on the bars) of 20 (1989–92) or 9 (2007–2009) replicate measurements. Asterisks indicated significant differences between the two time periods.

Discussion

Resource availability

Changes in the water column observed at this deep water western Lake Michigan station were similar to other reports of increased light penetration and reduced particulate matter in the water column associated with dreissenid mussel grazing (Mida et al., 2010). The first sampling period at this site (1988–1992) was over the period when mussels, especially *Dreissena polymorpha*, were establishing in Lake Michigan, but before quagga mussels (*Dreissena rostriformis bugensis*) were identified in western Lake Michigan in the early 2000s (Cuhel and Aguilar, 2013). The second sampling period (2007–2009) was after the quagga mussels expanded into deeper water affecting the offshore water column more dramatically (Mida et al., 2010). Depletion of water column phytoplankton biomass at the Fox Point station was evident from decline in the particulate organic carbon and chl *a* as well as particulate P; these declines were consistent throughout the water column from 0.01 to 60% light penetration depth. The declines in TP and chl *a* were in a similar range to that reported for the southern basin of Lake Michigan (Barbiero et al., 2012) and on the eastern side of Lake Michigan (Pothoven and Fahnenstiel, 2013; Vanderploeg et al., 2012).

Reduction in total P in the water column could reflect slight declines in annual P loading into the southern Lake Michigan basin, especially on the western side of the lake, though this was not shown to have significantly influenced spring chl *a* concentrations (Bunnell et al., 2014; Mida et al., 2010). A more probable explanation is the 'benthification' process associated with *Dreissena* grazing and removing particulate biomass from the water column and releasing nutrients in the benthos, initially in the nearshore (Hecky et al., 2004), but increasingly in deeper waters due to quagga mussels (e.g., Vanderploeg et al., 2010) which have a higher tolerance to colder temperatures and range of substrata (Cuhel and Aguilar, 2013). This process of trapping P in the nearshore resulting in reduced offshore phytoplankton biomass, termed 'oligotrophication', has been of concern for a number of years (Bunnell et al., 2014; Hecky et al., 2004), and this study expands the spatial analysis to western Lake Michigan with a dataset of broad temporal coverage.

Declines in TP and PP seem to have been associated with increases in non-limiting macronutrients. Nitrate is the dominant inorganic N form in Lake Michigan, and increasing nitrate concentrations through the water column suggests reduced phytoplankton demand. However increases in nitrate have been reported for other Laurentian Great Lakes, especially Lake Superior (Sterner et al., 2007; Chapra et al., 2012). Rowe et al. (2014) suggested an increase in nitrate in Lake Michigan of 0.21 μM/year in spring, which between 1990 and 2008 would have been 3.8 μM. Averaged over the water column, we observed a similar increase from 16.2 to 20.9 μM (4.7 μM). Similarly, in Lake Michigan, Mida et al. (2010) reported nitrate concentration changes from ~12.5 to 17.5 μM (5 μM) over a comparable time period to the present study. These data suggest that the 0.21 μM/year estimates (Rowe et al., 2014) may underestimate increasing nitrate in southern Lake Michigan. Reasons for a larger increase in nitrate relative to other nutrients might include: i) higher atmospheric N deposition in southern regions of the lake, ii) lower denitrification rates (Rowe et al., 2014), and/or iii) lower nitrate demand due either to reduced phytoplankton biomass (e.g. from quagga mussel grazing) or limitation of phytoplankton production due to decreasing pelagic P supply. If biological N demand were the major factor, one would expect an N increase to be ~16 times the decrease in P supply (based on Redfield stoichiometry). TP declined by 0.074 μM while nitrate increased by 4.7 μM which is a 63-fold difference, suggesting that declining nitrate demand due to P-limitation is not the only driving force. With respect to changing N-cycles, the increasingly oligotrophic Lake Michigan may represent a good contrast to Lake Superior. Lake Superior also shows increasing N, but for Lake Michigan there is also a greater potential for changes in anthropogenic N loadings (Sterner et al., 2007; Rowe et al., 2014).

Dramatic increases in dissolved Si availability in the water column (Fig. 3D) suggest strong links between the oligotrophication occurring in Lake Michigan and changing Si demand. Silicate is well-appreciated as a significant 'macronutrient' in aquatic ecosystems, chiefly for its role in diatom and other silicate-demanding species. Changes in silica have long been examined as indices of environmental change in Lake Michigan, though their interpretation has been controversial (e.g. Schelske and Stoermer, 1971; Shapiro and Swain, 1983). Moreover, the lack of significant Si depletion in summer suggests that this element is no longer a major structuring element in phytoplankton succession (cf. Scavia and Fahnenstiel, 1987). Increases in dissolved Si in southern Lake Michigan have been reported previously; Barbiero et al. (2002) observed a 16 μM average increase in spring dissolved silicate while this study showed a 24 μM increase in summer concentrations over ~18 years. Increases in Si have been attributed to declining diatoms blooms (Mida et al., 2010), which are in turn related to reduced P loading, and dreissenid mussel grazing (Barbiero et al., 2002). However, the depth-averaged 24 μM dissolved Si increase was more than 300 times the decline in TP concentration over the same time period. This suggests that declining P availability is not the chief factor driving increasing Si

Table 1
Summary of zooplankton taxa abundance and dry biomass (calculated from measured lengths) for key grouped taxa and species. Total calanoid and cyclopoid copepods includes all subcategories including copepodites and nauplii. Values represent means (standard deviation) of 20 (1989–92) or 9 (2007–2009) replicate measurements for the sampling periods 1989–1992 and 2007–2009. Those taxa or groups which changed significantly between the two sampling periods are in bold font ($p < 0.005$ for group comparisons or $p < 0.002$ for species comparisons).

	Mean abundance (individuals/m^2)					Mean biomass (mg/m^2)				
Taxon	1989–1992		2007–2009		p-Value	1989–1992		2007–2009		p-Value
Bosmina spp.	60,044	(46,961)	35,239	(55,268)	0.5[a]	46.2	(36)	27.1	(43)	0.4[a]
Total *Daphnia* spp.	65,293	(32,726)	27,923	(27,108)	0.3	679.6	(296)	215.1	(213)	0.7
Daphnia galeata mendotae	60,131	(25,015)	15,283	(16,392)	0.5	654.6	(272)	166.4	(178)	0.5
Daphnia retrocurva	3926	(7149)	0	0	0.1	16.4	(30)	0.0	0	0.1
Daphnia pulicaria	477	(955)	2137	(1914)	0.015	7.4	(15)	33.0	(30)	0.02
Daphnia longiremis	**759**	(1203)	**10,503**	(9458)	**<0.001**	**1.1**	(2)	**15.7**	(14)	**0.001**
Total calanoid copepods	**542,555**	(70,002)	**107,089**	(49,259)	**<0.001**[a]	2435.0	(764)	2460.2	(761)	0.4[a]
Calanoid copepodites	**340,475**	(57,440)	**20,100**	(14,980)	**<0.001**	**303.1**	(51)	**17.9**	(13)	**0.001**
Calanoid nauplii	**123,476**	(16,815)	**9778**	(8013)	**<0.001**[a]	**49.4**	(7)	**3.9**	(3)	**0.001**[a]
Leptodiaptomus ashlandi	44,013	(10,015)	30,567	(19,512)	0.3[a]	104.3	(24)	72.4	(46)	0.3[a]
Leptodiaptomus minutus	11,277	(6632)	6881	(7919)	0.4[a]	19.1	(11)	11.6	(13)	0.3[a]
Leptodiaptomus sicilis	10,852	(5808)	19,195	(10,679)	0.1[a]	74.7	(40)	132.2	(74)	0.1[a]
Skistodiaptomus oregonensis	620	(745)	3187	(3797)	0.9	1.9	(2)	9.9	(12)	0.9
Limnocalanus macrurus	10,382	(4434)	12,047	(5002)	0.8	1871.3	(799)	2171.4	(902)	0.8
Epischura lacustris	1129	(1001)	4600	(3924)	0.009	7.6	(7)	30.9	(26)	0.01
Senecella calanoides	239	(287)	10	(9)	0.2	2.3	(3)	0.1	(0)	0.2
Eurytemora adults	93	(109)	724	(1255)	0.6[a]	1.3	(1)	9.9	(17)	0.6[a]
Total cyclopoid copepods	**265,197**	(80,458)	**8113**	(4876)	**<0.001**[a]	**296.0**	(79)	**8.0**	(3)	**0.001**[a]
Cyclopoid copepodites	**126,153**	(38,273)	**1738**	(1361)	**<0.002**	**98.9**	(26)	**1.4**	(1)	**0.002**
Cyclopod nauplii	86,655	(42,461)	4563	(3288)	0.003[a]	**34.5**	(17)	**1.8**	(1)	**0.001**[a]
Diacyclops thomasi	**49,316**	(12,964)	**1123**	(314)	**<0.001**[a]	**158.0**	(42)	**3.6**	(1)	**0.001**[a]
Tropocyclops prasinus mexicanus	3052	(2758)	145	(251)	0.04	4.6	(4)	0.2	(0)	0.04
Mesocyclops edax	21	(26)	290	(502)	0.6[a]	0.0	(0)	0.1	(0)	0.6[a]
Leptodora kindti	164	(315)	17	(25)	0.09	1.0	(2)	0.1	(0)	0.09
Polyphemus pediculus	80	(159)	0	0	0.6	1.1	(2)	0.0	0	0.6
Bythotrephes longimanus	94	(75)	101	(125)	0.3	15.2	(13)	12.4	(15)	0.3
Cercopagis pengoi	0	0	42	(72)	0.05	0.0	0	1.5×10^{-5}	(10^{-5})	0.05
Mussel veliger	**0**	0	**171,377**	(175,359)	**<0.001**	**0.0**	0	**14.3**	(15)	**0.001**

[a] Significance tested using one-way ANOVAs (with logarithmic or square-root transformations); all other comparisons made with a non-parametric test Kruskal–Wallis one-way ANOVAs on ranks.

but that specific effects on Si-demanding taxa must be involved, as reported for Lake Michigan (Fahnenstiel and Scavia, 1987; Barbiero et al., 2005). Evans et al. (2011) summarized dramatic declines in Si demand in Lakes Michigan and Huron, which they attributed to expansion of dressenid mussels, while, using a seasonal analysis of Si use in Lake Michigan, Mida et al. (2010) suggested that the proportion of production by diatoms has decreased, as quagga mussels have expanded offshore. Concern about Si cycling has almost entirely focused on growth and sedimentation of planktonic diatoms. More recently, there is increasing appreciation of the impact of benthic processes including benthic and epiphytic diatom production (Carrick and Lowe, 2007; Malkin et al., 2009), and while the connection between the benthic and pelagic environments is not always obvious, the case of dressenids illustrates how significant it can be (Hecky et al., 2004; Cuhel and Aguilar, 2013). However, in contrast to planktonic species, we know little about Si demand in benthic organisms. There is evidence of unusual dissolved Si uptake capabilities among benthic diatoms (Leynaert et al., 2009; e.g. multiphasic kinetics and no clear saturation of uptake at any Si concentration) and silica may be required by many non-diatoms, including higher plants (Epstein, 1999). Moreover, Carrick and Lowe (2007) established that benthic algae in Lake Michigan experience significant seasonal Si limitation similar to phytoplankton. Our preliminary work (Berges and Young, 2008) demonstrates that substantial Si demand by blooms of benthic green filamentous algae and their epiphytic diatoms can affect Si cycling in nearshore waters of Lake Michigan.

Phytoplankton biomass

Chl *a* and particulate organic carbon declines observed at this western Lake Michigan station indicate reduced phytoplankton biomass in Lake Michigan, which has been reported previously, though mostly in terms of total chl *a* (e.g. Fahnenstiel et al., 2010; Mida et al., 2010; Pothoven and Fahnenstiel, 2013). The changes in total chl *a* through the water column were the result of the larger phytoplankton cells (10–53 μm and >53 μm fractions) but not the < 10 μm fraction which did not change between the two sampling periods. The <10 μm fraction includes picocyanobacteria, small green algae, and flagellates but excludes the generally larger diatoms. Significant declines in the larger size fractions, including the larger and often colonial diatoms are consistent with several reports of reduced diatom abundance in Lake Michigan (Barbiero et al., 2005; Fahnenstiel and Scavia, 1987). At a similar depth station on the east side of Lake Michigan, Fahnenstiel et al. (2010) reported declines in diatoms and chrysophytes but a lack of change in cyanobacteria, chlorophytes or cryptophytes in pre- and post-quagga mussel comparisons. The <10 μm fraction of chl *a* in deeper water (light penetration depth of 0.3 and 1% of surface) was actually higher during 2007–9 than in 1988–92, and the 2007–9 peak chl *a* for the size fraction was 1.6 μg/L (Fig. 3G), compared with 0.25–0.75 μg/L reported for the <10 μm fraction for the summer 1985–88 period by Sandgren and Lehman (1990). Together, these data support the idea of the development of a nano- and picophytoplankton-dominated DCM in western Lake Michigan since quagga mussel colonization (cf. Fig. 4, Cuhel and Aguilar, 2013). The significant decline in POC along with total chl *a*, despite no change in the small cell fraction is likely due to the more minor contribution of carbon in pico- and nanoplankton to total POC. However, phytoplankton count data from 2008 (Simmons et al., Accepted for publication) suggest that, based on biovolume, diatoms continue to make up 15–75% of summer phytoplankton biomass in the epilimnion and more in the metalimnion at this Fox Point station, with chrysophytes and dinoflagellates accounting for most of the rest.

Despite declines in TP and PP between the 1988–92 and 2007–9 sampling periods (suggesting increasing P-limitation), the molar C:P ratio of particulate matter in the water column did not change between the two time periods (Fig. 3C). The very high range of C:P for seston

(150–500) over the entire period represents consistently poor (P-limited) food quality for zooplankton (Sterner and Hessen, 1994). Thus, although the pelagic system appears to have been more P-limited in 2007–9 versus 1988–92, this did not result in poorer quality particulate matter, at least not in terms of C:P ratio.

Changes in zooplankton

We observed significant decreases in abundance and biomass of total zooplankton between 1988–92 and 2007–9. In terms of biomass, the decline is approximately 30% and on the same order as that described by Vanderploeg et al. (2012) for 1994–2003 versus 2007–8. Such changes, while dramatic, are nothing like the declines in nearshore regions observed in the early to mid-1980s (90% decline in abundance of most species; Evans, 1986). Like Vanderploeg et al. (2012), we observed declines in the cyclopid copepod *D. thomasi* as well as in calanoid nauplii; but unlike their study, we did not see significant declines in *Daphnia galeata mendotae*, increases in *B. longimanus*, or increases in omnivorous and predatory calanoid copepods. Indeed, significant declines in calanoid copepods as a group were only seen in abundance (not in biomass), driven by declines in nauplii, while declines in cyclopoid species showed up in both abundance and biomass (Table 1).

Revisiting our hypotheses, given decreases in P availability and phytoplankton biomass, to what extent might these explain decreased zooplankton biomass? One simplistic approach would be to compare the magnitude of declines in chl *a* and zooplankton groups. For example, proportional declines in total cyclopoid biomass (>95%) exceed the decreases in both total chl *a* and the larger chl *a* size fractions (50–75%). Calanoid copepodites and nauplii also declined proportionally more than did larger chl *a* fractions, though these organisms comprise relatively small components of the total zooplankton biomass. Such comparisons in terms of biomass are problematic because phytoplankton biomass turns over much more rapidly than does zooplankton biomass, and so these samplings integrate different time periods. Also some zooplankton species have multiple generations within a season (see Torke, 1975), in which case averaging across a season could result in combining organisms that have experienced quite different nutritional environments. More importantly, it must be recognized that there is considerable flexibility in copepod diets, depending on relative prey availability. While nauplii and copepodites of most copepods species and adults of diaptomids are likely herbivore/omnivores, adults of many of the cyclopoids accounting for declines observed (e.g. *D. thomasi*) are omnivore/carnivores (e.g. see Table 1; Vanderploeg et al., 2012). Thus, these groups would be prone to effects of competition from *B. longimanus* as well as bottom-up limitation. However, in comparing Lake Huron zooplankton communities in 2007 to those in 1983–4, Bunnell et al. (2012) found declines in three cyclopoid species, but increases in *D. galatea mendotae* and one calanoid copepod and used this contrast to argue that *B. longimanus* predation was probably not the major driver of these changes. Lack of changes in *D. galatea mendotae* and calanoids in the present study might support a similar argument.

From 1988–92 to 2007–9 we observed no significant changes in the abundance or biomass of *B. longimanus*, *Daphnia* and *Bosmina* that are its putative prey, nor of its major native predatory cladoceran competitors, *L. kindtii* or *P. pediculus* (Table 1). Lehman (1991) and Lehman and Cacéres (1993) saw large effects of the *B. longimanus* invasions on *Daphnia* species (all except *D. galatea mendotae* declined), but it seems likely that such changes had already happened by the beginning of the present study (cf. time series presented in Barbiero and Tuchman, 2004). Vanderploeg et al. (2012) reported declines in *D. galatea mendotae* in eastern Lake Michigan, but we found no significant differences, and indeed our numbers fall in the range reported by Lehman (1988) for 1985–87 for an eastern Lake Michigan station. In the case of *C. pengoi*, no clear conclusion can be drawn because this species was not detected in the lake until 1999, and only occurred in significant numbers on one sampling date at the offshore station; a nearshore distribution with highly variable distribution offshore has been noted before in eastern Lake Michigan (Cavaletto et al., 2010; Witt et al., 2005). *P. pediculus* was also quite rare among cruises making it difficult to draw firm conclusions. Certainly, current *B. longimanus* numbers and biomass are similar to that seen in the eastern lake offshore (Cavaletto et al., 2010), but orders of magnitude lower biomass to that observed by Lehman and Cacéres (1993) off Grand Haven Michigan (*B. longimanus* ~150 mg/m^2; *L. kindtii* 200 mg/m^2). Cavaletto et al. (2010) argued that *L. kindtii*, *B. longimanus* and *C. pengoi* have achieved a degree of coexistence in Lake Michigan due to different spatial and temporal exploitation of the environment, i.e. *C. pengoi* inshore versus *B. longimanus* offshore; *L. kindtii* early in the season versus *B. longimanus* later. Lehman (1991) certainly demonstrated that increases in *B. longimanus* lead to declines in *L. kindtii*, but his observations coincided with the very early period of the present study. It seems reasonable to conclude that whatever changes happened, they may have stabilized over the study period. In the offshore, *C. pengoi* does not appear to be a major competitor with native predators. In any case, our data do provide evidence of sustained negative effects of invasive predatory cladocerans on native predatory cladocerans.

We did find evidence of dramatic increases in dressenid veliger larvae, which were not seen in the sampling period 1989–92 at the Fox Point station. Densities in 2007–9 averaged the equivalent of 2000 / m^2, about 6-fold lower than abundances observed in eastern Lake Michigan by Nalepa et al. (2010) at a station off Muskegon in similar water depth. It is important to note that our sampling, using 130 μm mesh net was not intended to collect veliger larvae; side-by-side comparisons in 2008 of hauls with a 64 μm net suggest mean capture efficiencies for veligers are on the order of 55% with the larger net. While these larvae are not preferred food sources for most species, they can certainly be consumed by calanoid copepods (Liebig and Vanderploeg, 1995).

Had C:P of particulate matter increased significantly over the study period suggesting a deterioration in food quality in terms of P content, we might have hypothesized that higher C:P ratio would favor copepods (which have themselves higher C:P) over cladoceran herbivores. Moreover, because cladocerans and *Bosmina* species appear to tolerate lower P content better than *Daphnia* species (Sterner and Hessen, 1994), we might have anticipated advantages for *Bosmina* spp. relative to *Daphnia* spp. However, the C:P ratio of particulate matter did not change, and we observed no changes in either abundances of biomasses of daphnids, bosminids or their relative abundances between the two periods considered. Interestingly, Lehman and Branstrator (1995) used stoichiometry and a simple food web model to demonstrate that, since *B. longimanus* shows a C:P ratio in the range 36–52, it requires a food source with C:P ratio similar to daphnids. Thus, copepods, which have higher C:P (>100) cannot effectively support its growth, and where copepods begin to dominate over daphnids, *B. longimanus* populations will be in an unfavorable nutritional situation to increase. This may provide an explanation of the inability of *B. longimanus* to expand its invasion of Lake Michigan over the study period.

Contrasting results among studies

Results from the present study contrast in some important respects with previously published work. What are the reasons for these differences? In the first instance, there are spatial differences. We have examined a single station in western Lake Michigan, while most other work is based on the eastern lake (Fig. 1 NOAA stations, e.g. Vanderploeg et al., 2012), or broader survey of the whole lake (Fig. 1; EPA stations, e.g. Barbiero et al., 2012); Mida et al. (2010) previously compared results collected at NOAA and EPA stations and concluded that the spatial differences were relatively minor. Our Fox Point station was chosen to represent the open waters of Lake Michigan, based on evaluation of satellite images and previous sampling experience over many years (see Brooks and Edgington, 1994); so it is difficult to see why there would be

systematic biases in observations. A second possibility is methodological differences. However, the methodologies used are all well established and nearly identical. Except in the case of zooplankton data, which is based on the whole water column, we have opted to compare data scaled by light penetration depth, as opposed to examining discrete water column regions (e.g. upper mixed layer) or crucial features like the deep chlorophyll maximum (Brooks and Torke, 1977). Our results, however, show that there is little evidence of interactions between the periods examined and light penetration depths because similar changes (or lack of change) have occurred throughout the water column. Mida et al. (2010) also concluded that methodological differences were unlikely to cause more than minor variation among studies.

The major issues are quite likely to lie in differences in the time of sampling or temporal resolution. The majority of the sampling in the present study was carried out between late spring and late summer (early June to late August). Thus, not represented in our sampling are the spring bloom, which occurs in May or earlier (Barbiero et al., 2012), and the peak abundances of *B. longimanus* populations, which quite likely occur in October or later (Yurista et al., 2010). This probably provides for a more robust internal comparison of data, but it makes some comparisons with other data sets more challenging. Mida et al. (2010) noted that key differences between NOAA and EPA data sets resulted because limited temporal resolution in the EPA sampling resulted in missing key peaks in chl *a* that would have indicated spring blooms. Another good example might be the calanoid copepod *L. macrurus*. Barbiero et al. (2009, 2012) noted large, recent increases in *L. macrurus* in Lake Michigan: in 2004 and 2006, average biomass (~12 mg/m^3) was about three times greater than the 1988–92 average (~4 mg/m^3), but Kerfoot et al. (2010) reported declines in abundance from 2006 to 2008 from about 364/m^3 to 30/m^3, which based on our dry mass values for *L. macrurus* would equate to about 40 mg/m^3 to 4 mg/m^3. In contrast, our data show no changes, with averages of about 22 mg/m^3 across all years (Table 1). In this case, some of the apparent contradictions are explained by differences in sampling times: Kerfoot et al. (2010) sampled in spring at times when few *L. macrurus* adults would be present in the water column (Torke, 1975) (cf. data for 2006–8 published in Vanderploeg et al., 2012). Abundances reported by Lehman (1988) for *L. macrurus* in 1985–7 ranged from 9550 to 15,520 /m^2, which are quite close to average abundances in the present study, and fit well with more recent values published in Doubek and Lehman (2011). Timing of sampling and life histories of different zooplankton species could actually interact. For example, cyclopoids such as *D. thomasi* are quite likely to have at least two generations in summer, while *L. macrurus* reproduces only once in fall/winter (see Torke, 1975). This means that different species integrate food availability and predation over different periods of time and so that it becomes more difficult to know with what their abundance or biomass can or should be correlated.

Gaps in understanding

Torke (1975) commented that "If we are to understand the fundamental relationships in natural ecosystems … it is clear we must gather basic information on the organisms which comprise these systems". Yet, life histories of zooplankton species have very seldom been examined in situ, i.e. detailed weekly times series in which nauplii and copepodites are identified to species, as Torke (1975) did. Such work is tedious and the necessary taxonomic expertise is increasingly lacking. Worryingly, because crustacean development is so strongly controlled by temperature and food supply, with changing temperature regimes and nutritional environments in the Lake, we can not necessarily rely on details of these life histories from the past (even the 1970s) remaining accurate today. To complicate matters even further, basic tools such as length–weight regression can be biased if zooplankton characteristics such as life history and diet change. Doubek and Lehman (2011) have described potential biases in length–weight regressions for larger *L. macrurus* that result from differences in lipid content, which varies seasonally with reproductive cycles (e.g. Vanderploeg et al., 1998) or with shifts from herbivory to omnivory (e.g. Warren, 1983).

Another aspect of understanding these organisms concerns nutrition. As we discuss above, there is evidence that the impacts of invasion by predatory zooplankton may be constrained by the availability and quality of food, but we have as yet only crude means to judge food 'quality' (e.g. bulk C:P analyses). At another level entirely, we lack means to effectively identify what invasive cladoceran predators are eating because as fluid feeders, little remains to be identified in gut contents. Application of methods to identify and quantify prey (e.g. immunochemical or nucleic-acid-based methods, see Sheppard and Harwood, 2005; Symondson, 2002) is desperately needed. Some progress has been made in developing molecular probes (Gorokhova and Lehtiniemi, 2007) and semi-quantitative antisera against putative prey species (Berges et al., 2013).

Finally, it is easy to neglect the benthic environment when examining pelagic systems. The dressenid invasion serves as a lesson because many of the changes we describe in the present study are correlated with and have been attributed to the establishment and subsequent expansion of two benthic *Dreissena* species (see review by Cuhel and Aguilar, 2013). However, now that effects of quagga mussels are well established in the nearshore and deeper water benthos, what is the likely trajectory of changes to food webs and related nutrient cycling in Lake Michigan? For example, do the plateauing changes in TP and dissolved nitrate since 2005 (Mida et al., 2010), suggest an approaching stability and acclimation in nutrient cycling? Recent data and ongoing monitoring of P may provide insights, but to complement such work, it may be important to include monitoring of dissolved Si and N as indicators of changing nutrient demand and inputs, and more detailed in situ analysis of pelagic–benthic fluxes to incorporation into modeling and understanding of pelagic food webs and nutrient cycling (Vadeboncouer et al., 2002).

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jglr.2015.04.015.

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