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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

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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.

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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 dreissenid 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,

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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 dreissenid 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).

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.glwii.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_0) 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*.

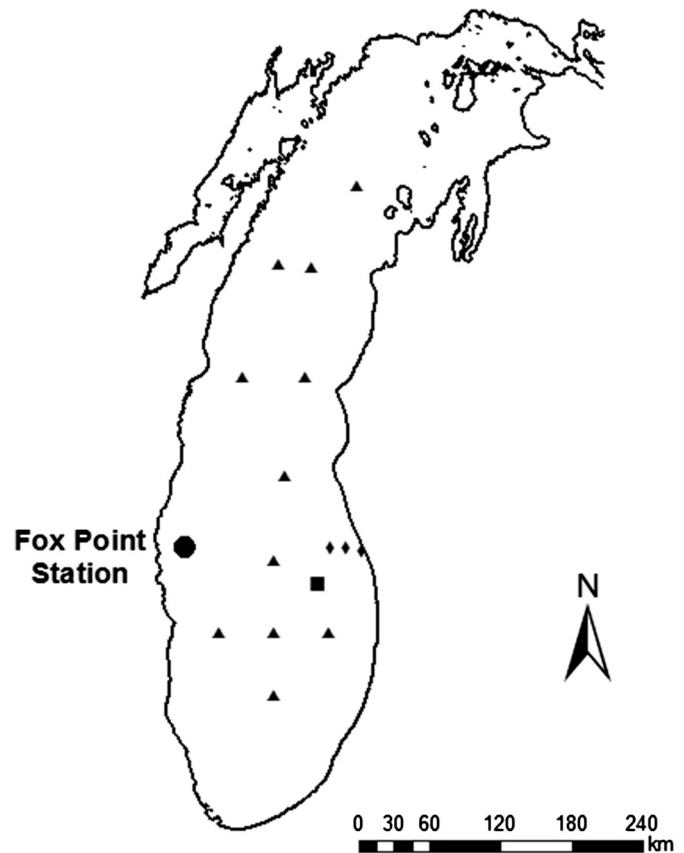


Fig. 1. Map of sampling location in Lake Michigan showing the Fox Point sampling station in relation to other long-term monitoring stations: Grand Haven station (e.g. Lehman and Cacères, 1993); ▲ US EPA GLNPO monitoring stations; ◆ NOAA GLERL monitoring stations.

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 overnight 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

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