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Zooplankton-phytoplankton interactions in Green Bay, Lake Michigan: Lower food web responses to biological invasions

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ABSTRACT

As the largest freshwater estuary in the Laurentian Great Lakes, Green Bay, Lake Michigan (USA) is an important ecosystem presenting both challenges and opportunities for investigating changes in the face of multiple anthropogenic stressors. We collected new data from 2000 to 2007 to assess changes in lower food web interactions after establishment of invasive species (*Bythotrephes longimanus* and *Morone americana* in 1988 and *Dreissena polymorpha* in 1993) and nutrient reductions (1990s). Phytoplankton and zooplankton biomass and composition, as well as primary productivity and zooplankton community grazing rates, were determined along the previously well-studied trophic gradient from the shallow Lower bay to the stratified, open-water Middle bay. A clear trophic gradient still occurred during 2000–2007, with higher nutrients, phytoplankton and zooplankton in Lower bay compared to Middle bay. Phytoplankton abundance and cyanobacteria dominance increased significantly compared to earlier studies. However, integrated primary productivity did not change significantly at either Lower or Middle bay. Zooplankton standing stock decreased in Lower bay, driven primarily by reductions of bosminids, chydorids, and cyclopoid copepods, but did not change in Middle bay. Zooplankton community grazing rates did not change significantly, but shifts in magnitude and seasonality of net phytoplankton growth rates are consistent with increased phytoplankton standing stocks. Changes in zooplankton composition indicate increased predation by invertebrates and decreased fish predation. Shifts in both bottom-up and top-down factors have occurred, with Lower and Middle bay regions more eutrophic and similar to each other as a result of changes in this highly productive Great Lakes embayment.

Introduction

The Laurentian Great Lakes have been increasingly exposed to multiple stressors in recent decades, including changes in nutrient loading, climate change, and biological invasions (Stow, 2014; Vanderploeg et al., 2015; Cotner et al., 2017). Depending on the nature of the stressor, each can create bottom-up or top-down effects that can change food web interactions and function. For example, increased nutrient loading during the middle of the 20th century led to strong bottom-up effects, leading to eutrophication of the Great Lakes (Schindler and Vallentyne, 2008; Egan, 2017). In the 1980s, invasion of North America by the predatory cladoceran *Bythotrephes longimanus* resulted in strong top-down effects causing changes in crustacean zooplankton communities and lower food web interactions (Lehman and Caceres, 1993; Barbiero and Tuchman, 2004). Invasion of the Great Lakes by white perch (*Morone americana*) led to major shifts in planktivory and top-down effects due to declines of yellow perch in Lake Erie (Bur and Klarer, 1991) and effects on minnows, walleye and white bass in the Bay of Quinte, Lake Ontario (Schaeffer and Margraf, 1987). Understanding how ecosystems respond to such stressors has become a major goal of Great Lakes research.

Green Bay of Lake Michigan is the largest embayment, and one of the most productive ecosystems of the Laurentian Great Lakes (Bertrand et al., 1976; Klump et al., 2009). Extensive studies during the 1970s and 1980s demonstrated that it was heavily influenced by excessive nutrient loading, resulting in strong bottom-up effects driving a trophic gradient for phytoplankton (Sager and Richman, 1991), zooplankton (Richman et al., 1984), and fish (Smith and Magnuson, 1990). As occurred in many of the Great Lakes, this system was also stressed by biological invasions in the 1980s and 1990s. The spiny water flea *Bythotrephes longimanus* and white perch *Morone americana* invaded by 1988 (Jin and Sprules, 1990; Cochran and Hesse, 1994), followed by the zebra mussel *Dreissena polymorpha* in 1992–93 (Kraft, 1993). During this same period, nutrient reduction efforts became more

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effective as well, reducing phosphorus loading from the main source, the Fox River, by approximately 1.5% per year (Qualls et al., 2013). Given the combination of nutrient reductions and invasion by *D. polymorpha* it was expected that phytoplankton abundance and overall productivity of the system would decrease, as had occurred in other Great Lakes (Padilla et al., 1996). However, basic water quality conditions have not noticeably improved following these changes (De Stasio et al., 2008, 2014; Qualls et al., 2013), raising the question of why this system has responded differently than other Great Lakes locations to invasions and remediation efforts.

Probably the most well-known and documented response of Great Lakes ecosystems to biological invasions has been the example of *D. polymorpha*, where decreases in phytoplankton and increases in water transparency occurred due to high filtering capacity and rapid population growth of mussels (Lavrentyev et al., 1995; Barbiero et al., 2006; Fishman et al., 2009; Fahnenstiel et al., 2016). However, recent work shows that dreissenid impacts are context dependent (Sarnelle et al., 2005; Qualls et al., 2007; Vanderploeg et al., 2014), and some systems exhibit increased cyanobacteria following invasion (Vanderploeg et al., 2001; Strayer, 2009). These situations, where responses differ from expected changes, have led to multiple hypotheses about mechanisms leading to increased cyanobacteria blooms. These include increased light penetration following water clearing by mussels (leading to favorable conditions for light-tolerant cyanobacteria like *Microcystis*), and/or selective predation on competitive algae that leads to increased cyanobacteria dominance (Fishman et al., 2010). There is also evidence that responses depend on starting trophic condition of water bodies, with largest negative effects on the cyanobacteria *Microcystis* observed in more oligotrophic systems and positive effects in more eutrophic conditions (Sarnelle et al., 2005). Another possibility is that recycling of nutrients by mussels may improve conditions for cyanobacteria growth (Arnott and Vanni, 1996; Vanderploeg et al., 2002, 2014). Although zebra mussels are known to decrease the ratio of nitrogen to phosphorus due to their higher retention of nitrogen, the overall release of nitrogen to the water in eutrophic systems with high phosphorus concentrations may be more important than the ratios. This could help explain the recent increased dominance of non nitrogen fixing groups like *Microcystis* during late summer in eutrophic systems like lower Green Bay.

Understanding responses in the Green Bay ecosystem is complex because of the invasions by *D. polymorpha*, *B. longimanus*, and *M. americana* along with nutrient reduction efforts, and requires examining changes in multiple trophic levels to assess the relative roles of bottom-up and top-down factors. Only recently have the effects of *B. longimanus* in productive systems like Green Bay been examined, demonstrating that this invertebrate predator may have had stronger impacts than previously suspected in nearshore regions and embayments (Pothoven and Höök, 2014; Merkle and De Stasio, 2018).

Here we report results of studies on lower food web dynamics in Green Bay during the years 2000–2007 along the previously well studied trophic gradient. These data are then compared to earlier published and unpublished data to assess changes in phytoplankton and zooplankton biomass and productivity, as well as grazing interactions from before and after the invasions and nutrient reductions in Green Bay, Lake Michigan. Our analyses of recent changes in lower food web interactions provide new insights into the relative importance of various forces that are affecting this and other ecosystems of the Laurentian Great Lakes.

Methods

Green Bay was sampled during the summers of 2000, 2004, 2005, 2006, and 2007 at five locations established during previous studies along a trophic gradient (Fig. 1; Richman et al., 1984; De Stasio and Richman, 1998; Sager and Richman, 1991). Sites sampled range from shallow Lower bay sites with hypereutrophic conditions to a deeper mesotrophic Middle bay region (maximum depths: GB1A = 1.5 m, GB2 = 3 m, GB3 = 7 m, GB4 = 11 m, GB6 = 15 m). The region south of Long Tail Point and Point Sable are often referred to as the "inner bay" and included stations GB1A and GB2. This area is highly influenced by river water from the lower Fox River, and has water residence times on the order of a few months, depending on river inflows (Klump et al., 2009). Station GB2 corresponds to the "Lower bay" site used in earlier work (Richman and Sager, 1990; Richman et al., 1990; Sager and Richman, 1990, 1991) and GB6 represents "Middle bay" for comparisons of our data with the studies from 1986 to 1988 and 1990–1992. Our samples were collected approximately biweekly each year from June through August, as was done earlier. As reported elsewhere (De Stasio et al., 2008, 2014), standard measures of physical and chemical limnological features were obtained on each date (Secchi depth, vertical profiles of photon flux density, temperature, dissolved oxygen, pH, conductivity, oxidative-reductive potential). Water clarity was measured on each date using a black and white Secchi disk (0.20 m diameter). Vertical profiles of photon flux density were determined at each location with 2π underwater and incident PAR quantum sensors (LI-192S and LI-190) and datalogger (Model LI-1000, LI-COR Co., Lincoln, NE), while other parameters were measured with a multiparameter data sonde (Model DS5, Hydrolab, Loveland, USA). For chlorophyll *a* (chl-*a*), phytoplankton composition and primary productivity analyses, duplicate integrated samples were collected from the top 4 m of the water column using a submersible pump (or to just above the bottom at sites shallower than 4 m). Water for chl-*a* analysis and productivity determinations was transported in opaque bottles kept on ice in the dark until returned to the laboratory later the same day, while phytoplankton samples were preserved in 1% Lugol's solution.

In the laboratory chl-*a* concentration was determined using the standard acetone extraction procedure (Wetzel and Likens, 1991). As in earlier work, replicate subsamples (15–50 mL) for phytoplankton identification and enumeration were examined using settling chambers viewed on an inverted microscope or on permanent slides made by filtering subsamples onto membrane filters (0.45 μm pore size) under low vacuum. Filters were cleared with immersion oil, sealed with Permount and enumerated at 100–500× magnification. Cell linear dimensions were determined with an ocular micrometer and used to estimate cell biovolume based on published relationships between linear dimensions and volume (Wetzel and Likens, 1991). Biovolume was converted to dry weight of biomass assuming 10^6 μm^3 is equivalent to 0.22 μg dry weight (Lind, 1985; Rocha and Duncan, 1985).

In 2006 and 2007 phytoplankton community photosynthetic rates were also determined at all five stations using standard ^{14}C-uptake methodology employing photosynthesis versus light intensity curves (*P* vs. *I*) according to the procedure of Fee (1998). Duplicate light bottles and one "DCMU" bottle were incubated for ca. 3 h at each of four light intensities and at ambient epilimnetic temperatures. All bottles (50 mL Pyrex) received 0.5 mL (148 kBq) of [^{14}C]$NaHCO_3$ while DCMU bottles also received 0.5 mL of 0.005 M DCMU (Diuron, 3-(3,4-dichlorophenyl)-1,1-dimethyl urea) as a photosynthetic inhibitor (Legendre et al., 1983). Uptake of ^{14}C was determined with standard methodology using liquid scintillation counting as performed in Sager and Richman (1991). Total alkalinity and pH were determined for each sample to compute total dissolved inorganic carbon. Estimates of photosynthetic parameters were obtained from *P* vs. *I* curves using the curve-fitting programs provided by Fee (1998). Field data on incident solar irradiance, light penetration, chlorophyll, and mixing depths were used with the programs to calculate daily areal photosynthetic rates ($\sum P$ = mg C/m^2/d), volumetric rates at optimal light intensity (P_{opt} = mg C/m^3/h), and maximum biomass-specific rates of photosynthesis ($P^B{}_m$ = mg C/mg chl-*a*/h). Comparison data are available for Lower and Middle bay locations for earlier years. Photosynthetic rates from 1986 to 1988 and 1990–1992 were corrected as explained in Millard and Sager (1994) for differences in calculation methodology between the Fee program approach we employed and earlier methods

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