



Evidence for bottom–up control of recent shifts in the pelagic food web of Lake Huron

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ABSTRACT

The magnitude of the spring bloom in the open waters of Lake Huron has declined dramatically in recent years, beginning in 2003. May chlorophyll values, as estimated by SeaWiFS imagery, for 2003–2006 have been 50–60% of 1998–2002 values. April phytoplankton biovolumes have also declined; average biovolume in 2003–2004 was approximately 25% of 2001–2002. Most of this decline was due to reduction in biovolume of colonial diatoms. Reductions in the spring bloom have been closely associated with abrupt declines in cladoceran populations, as well as with declines in cyclopoid copepod populations. In addition, *Daphnia* population egg ratios in August exhibited a pronounced decrease between 2002 and 2003 and have remained depressed through 2005. Taken together, these data suggest a role for reduced food supply in the dramatic shifts seen in the Lake Huron crustacean zooplankton community since 2003. Additionally, summer chlorophyll values have shown signs of decline in 2005 and 2006 in spite of the historically low populations of cladocerans, suggesting that control of summer phytoplankton populations in Lake Huron is determined by nutrient supply rather than grazing pressure.

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Introduction

The relative importance of resource-driven (bottom–up) as opposed to predation-driven (top–down) factors in structuring aquatic ecosystems has been a dominant concern for the past 30 years (Carpenter et al., 1985; McQueen et al., 1986). Some of the earliest support for top–down structuring of zooplankton communities came from the Great Lakes, notably Wells' (1970) classic study of alewife–zooplankton interactions in Lake Michigan. Subsequently, a number of studies have averred cascading impacts of top predator populations on preyfish, zooplankton, and phytoplankton community structure in the Great Lakes (Dorazio et al., 1987; Scavia et al., 1986; Scavia et al., 1988), although the importance of predation in structuring lower trophic levels has not been unquestioned (Evans, 1992). In a system where top predator populations are largely controlled through stocking (Dobiesz et al., 2005; Madenjian et al., 2002) and where extensive effort and expense have gone into controlling nutrient inputs, discerning pathways of top–down and bottom–up control is not only of theoretical interest but has substantial economic and management implications as well.

The food web in Lake Huron has recently undergone a number of unprecedented changes. Cladoceran populations in the offshore of the

lake declined abruptly in 2003 and have remained at historically low levels through at least 2006 (Barbiero et al., 2009). Populations of adult alewife (*Alosa pseudoharengus*), one of the main prey fish in the lake, also collapsed in 2003 and have since been reduced to record low levels in the main basin (Riley et al., 2008), while harvests of the main piscivore in the lake, Chinook salmon (*Oncorhynchus tshawytscha*), have declined precipitously since 2003 (Lake Huron Binational Partnership Action Plan, 2008–2010 2008). These concurrent declines in populations at multiple trophic levels in Lake Huron are consistent with decreased overall production in the open waters of the lake and raise the possibility of a causal role of bottom–up forcings in structuring the open water ecosystem.

A previous attempt to assess the possible role of resource limitation in the cladoceran collapse in Lake Huron failed to reach an unambiguous conclusion; increases in soluble nutrients and Secchi depth suggested reduced primary production, but corroboratory trends in chlorophyll *a* concentrations were not seen (Barbiero et al., 2009). Concerns about possible inconsistencies in our chlorophyll dataset due to a change in both instrumentation and analysts in the middle of the period of interest, however, compounded by lack of agreement between variables noted above, led us to seek alternate sources of data. Satellite remote sensing has been shown to have promise in discerning both spatial and temporal patterns in optical properties of the Great Lakes. In particular, sea-viewing wide field-of-view sensor (SeaWiFS) imagery has enabled detection of both large-scale spatial patterns (Kerfoot et al., 2008) and short-term

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temporal patterns (Lesht et al., 2002) in Lake Michigan chlorophyll. While not immune to problems of analysis and interpretation, compositing of the highly dense data generated by SeaWiFS can permit extraction of meaningful trends, in spite of the inherent variability of the data and uncertainty about their absolute accuracy (Lohrenz et al., 2008).

In this paper, we revisit the recent crashes seen in the crustacean community of Lake Huron in light of chlorophyll estimates derived from SeaWiFS imagery. We were specifically interested in answering the following question: have the changes in zooplankton populations in Lake Huron been associated with a declining base of production?

Methods

Sampling

Most data used for this study were drawn from the US EPA Great Lakes National Program Office (GLNPO) offshore monitoring cruises conducted between 1998 and 2006. A total of 15 stations were visited for plankton and nutrient sampling during this time (Fig. 1). Past analyses have shown that differences exist both in the biology and the chemistry of different regions of the lake, which largely correspond to differences in lake basin morphometry. Therefore, for most analyses, stations were allocated to either the deeper northern or the shallower southern portion of the lake (Fig. 1).

Sampling surveys were conducted during the spring isothermal period and summer stratified period. Spring (April) surveys were conducted as early as possible after ice out to provide estimates of initial growing season concentrations of nutrients and summer (August) surveys were conducted during the period of stable thermal stratification. At each station, samples for nutrients were taken at discrete depths throughout the entire water column with Niskin bottles mounted on a SeaBird Carousel Water Sampler. For the present study, only water quality samples from the isothermal upper (≤ 12 m) water column were used for nutrient analyses. Composite samples for spring phytoplankton analyses were composed of equal aliquots collected from 1, 5, 10, and 20 m. Zooplankton were collected by vertical tows taken from depths of 100 m or 2 m from the bottom, whichever was

shallower, using a 0.5-m diameter, 153- μ m mesh, conical net (D:L=1:3) equipped with a flow meter.

Analytical methods

Chlorophyll *a*, uncorrected for pheophytin, was determined on a Turner Designs 10-AU fluorometer following the method of Welschmeyer (1994).

Phytoplankton abundances were estimated, and *Urosolenia* species and all non-diatom phytoplankton were identified, using the Utermöhl technique (Lund et al., 1958) at a magnification of 500 \times , with diatoms other than *Urosolenia* identified as either centrics or pennates at this stage. At least 250 individuals were enumerated along parallel transects across the middle of the chamber. Identification of diatoms (aside from *Urosolenia*) was done from permanent slide mounts at 1250 \times , with approximately 500 frustules identified per sample. Relative proportions of each taxon of centrics and pennates were then multiplied by the appropriate Utermöhl counts. At least 10 individuals of each taxon were measured per sample, and cell volumes were computed using appropriate geometrical formulae. To ensure consistency, only phytoplankton data generated by a single analyst were used. Such data were available for the period 2001–2004, which bracketed the decline in crustacean populations.

After collection, zooplankton samples were narcotized with soda water and preserved with 5% formaldehyde solution. Samples were split in the laboratory using a Folsom plankton splitter, and four stratified aliquots were examined per sample using a stereoscopic microscope such that rare species were enumerated from the less dilute aliquots. Biomass (as dry weight) was calculated using length–weight relationships derived from the literature (Downing and Rigler, 1984). A fuller presentation of the zooplankton data, along with more detail on methods, is available elsewhere (Barbiero et al., 2009).

Because food supply is an important determinant of the number of eggs produced by daphnids (Boersma, 1995; Green, 1966; Taylor, 1985), population egg ratios of *Daphnia* were determined to further assess whether the population declines in *Daphnia* could be the result of resource limitation. August samples for years bracketing the population decline (pre-decline: 2000, 2002; post-decline: 2003, 2004, and 2005) were examined, with analyses restricted to southern Lake Huron, where *Daphnia* persisted in somewhat higher numbers than in the northern basin of the lake. Samples from five sites were examined for 2000, and samples from four sites were examined for the remaining years. Repeated 1 ml subsamples were taken with a Stempel pipette and *Daphnia* and eggs counted and identified at 30 \times magnification under a dissecting microscope until at least 50 *Daphnia* had been counted. In one case, extremely low *Daphnia* densities resulted in slightly less than 50 individuals being enumerated. *Daphnia mendotae* were overwhelmingly predominant in all samples. Both loose and attached eggs and embryos of *Daphnia* were counted for estimation of population egg ratios (Edmondson, 1965; Goldman et al., 1979). While it is possible that some loose eggs could be lost through the 153- μ m mesh net used to collect zooplankton, we assumed that losses were consistent from year to year and thus would not affect assessment of inter-annual trends.

SeaWiFS chlorophyll estimation and NOAA buoy data

Chlorophyll *a* concentrations were estimated from SeaWiFS Level 1 data obtained from the NASA Ocean Color Archive (<http://oceancolor.gsfc.nasa.gov>). We processed Level 1 data to Level 2 by using Version 5.4 of the NASA SeaDAS software (Baith et al., 2001). Analyses were limited to images recorded within 35 min of 18:20 UTC to reduce distorting effects of extreme satellite viewing angles. Chlorophyll values were estimated using the standard OC4v4 algorithm (O'Reilly et al., 2000) as implemented in SeaDAS. This algorithm has been shown to produce chlorophyll *a* values that agree

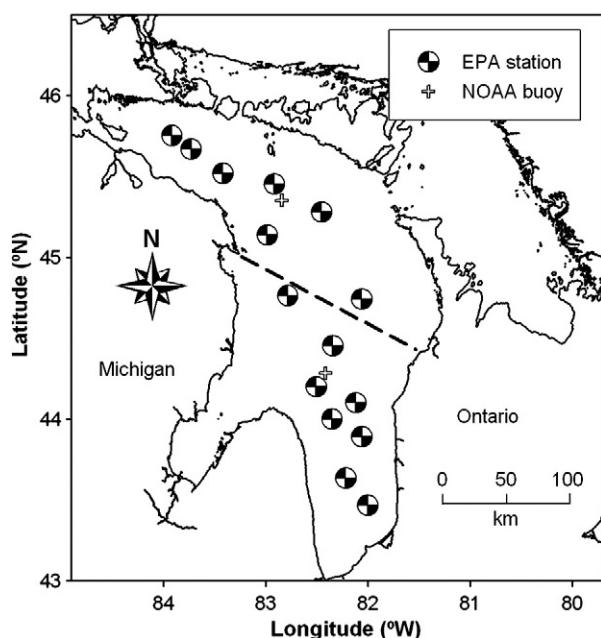


Fig. 1. Map of Lake Huron showing locations of EPA sampling stations and NOAA buoys. Dashed line indicates division between northern and southern stations.

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