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Recent changes in the offshore crustacean zooplankton community of Lake Ontario

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ABSTRACT

Crustacean zooplankton communities in the offshore of Lake Ontario have undergone substantial changes between 1997 and 2011. A shift was apparent in 2004 from an initial assemblage dominated by cyclopoid copepods (mostly *Diacyclops thomasi*), *Daphnia retrocurva* and bosminids, and with *Cercopagis pengoi* (which invaded the lake in 1998) the dominant predatory cladoceran, to one characterized by reduced numbers of cyclopoids, a more varied predatory cladoceran community, and increased biomass of calanoid copepods. These changes represented a shift from a community which has been relatively stable in the offshore of the lake for at least 40 years. A further change was seen in 2008, marked by increased biomass of *Leptodiaptomus sicilis*, *Bythotrephes longimanus* and *Daphnia mendotae*. Unlike the somewhat similar changes seen recently in the zooplankton communities of Lakes Huron and Michigan, the shifts in Lake Ontario have not been accompanied by a trend towards increased oligotrophy. A more likely explanation for the observed shifts in Lake Ontario is decreased vertebrate predation, likely due to alewife declines, and changes in the predatory invertebrate community.

Introduction

The Great Lakes Water Quality Agreement (GLWQA), signed in 1972 (Holden, 1972), initiated a period of change in the nutrient status of the Laurentian Great Lakes with the setting of measures to control phosphorus loadings into the lakes. Results of these efforts were quickly seen in Lake Ontario; within 10 years of the signing of the GLWQA, phosphorus loading to that lake was reduced by approximately 40% (De Pinto et al., 1986), with equally dramatic decreases in in-lake total phosphorus (TP) concentrations also seen (De Pinto et al., 1986; Johengen et al., 1994; Stevens and Neilson, 1987). Since then the initial rapid rate of decline in phosphorus loading has slowed, and recently updated loading estimates have indicated no further declines between 1994 and 2008 (based on data from Dolan and Chapra, 2012). Since the mid-1980s, rates of decline of in-lake TP concentrations have also apparently slowed (Millard et al., 2003), although they have not entirely stopped (Dove, 2009).

The responses of the lower food web to phosphorus reductions have been somewhat ambiguous. In an early study, Stevens and Neilson (1987) failed to detect any trends in de-seasonalized measures of algal biomass between 1974 and 1982. Subsequently, Millard et al. (2003) found a sudden decline in summer chlorophyll *a* between 1982 and 1985 in a data series extending from 1974 to 1993, although no trend was seen at a mid-lake station between 1981 and 1995. Johengen et al. (1994) did find evidence of a decrease in chlorophyll *a* at the same mid-lake station using an abbreviated (1981–1992) subset of the same data series, although this was not confirmed statistically. Dove (2009) failed to find a trend in open lake summer chlorophyll using an extended (1974–2008) data set.

A number of studies have examined the Lake Ontario zooplankton community for evidence of changes in response to decreased nutrient levels seen in the 1980s, though most of these studies were based on different subsets of the same Canadian Department of Fisheries and Oceans biomonitoring program data series. Johannsson (1987) compared data collected between 1967 and 1972 compiled from various historical reports with new data from 1981 to 1985. No consistent change in total abundance or community structure was found between the two periods. A subsequent study provided some evidence of declines in stratified-season cyclopoid and cladoceran numbers between 1981 and 1995 in the mid-lake region, with less ambiguous decreases in estimated zooplankton production seen during this time period (Johannsson et al., 1998). A broad review of zooplankton in Lake Ontario (Johannsson, 2003) pointed to species shifts away from *Chydorus* and *Ceriodaphnia* species, which are typically associated with nutrient-rich waters, and declines in biomass between 1981 and the early 1990s. These shifts were thought to be a response to phosphorus declines, rather than changes in predation, given both concomitant declines in phosphorus and edible phytoplankton, and a lack of corresponding increases

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in the primary zooplanktivores in the lakes, alewife and *Mysis*, associated with the zooplankton declines. However, there has been some evidence of predation impacts on zooplankton community structure and timing after the period of rapid trophic change in the 1980s. The relative contribution of *Daphnia retrocurva* to zooplankton production increased from the 1981–1985 period to 1986–1995, with decreases in fish predation a likely contributing factor, while the abundance of the larger species *Leptodora kindtii* (henceforth *Leptodora*) and *Epischura lacustris* increased during 1987–1995 in association with alewife declines (Johannsson, 2003). Recent reports have hinted at larger shifts in zooplankton community size and composition (e.g., Holeck et al., 2012; Stewart et al., 2010), but these studies have by and large been hampered by incomplete time series and, more importantly, sampling restricted to the epilimnion.

Another potential determinant of the size and composition of the zooplankton community during this period has been the appearance of two exotic predatory cladocerans. *Bythotrephes longimanus* (henceforth *Bythotrephes*) was first reported in the Great Lakes in a December 1984 sample from Lake Huron (Bur et al., 1986), although it had been found in Lake Ontario in 1982 (Johannsson et al., 1991). In spite of its first detection in the lake, substantial populations have been observed only rarely in Lake Ontario (Johannsson, 2003), probably due to alewife predation (Johannsson et al., 1991; Mills et al., 1992). A second predatory cladoceran, *Cercopagis pengoi* (henceforth *Cercopagis*), was first observed in Lake Ontario in 1998 (MacIsaac et al., 1999). Unlike *Bythotrephes*, *Cercopagis* quickly established itself in the lake (Ojaveer et al., 2001). Bioenergetics modeling has suggested that *Cercopagis* has the potential to impact zooplankton populations in Lake Ontario (Laxson et al., 2003), a possibility corroborated by a lack of overlap between *Cercopagis* and potential prey populations (*D. retrocurva*, *Bosmina longirostris* and *Diacyclops thomasi*) in late summer data (Laxson et al., 2003). In a study of seasonal data from pre- and post-*Cercopagis* years, Warner et al. (2006) observed declines in abundance of bosminids, *D. thomasi* and copepod nauplii during periods of peak *Cercopagis* abundance; declines were not seen for *D. retrocurva*.

Interest in potential changes in the Lake Ontario lower food web, and in particular in crustacean communities, has intensified in recent years given the changes seen in Lake Huron and Lake Michigan (Barbiero et al., 2009a,b, 2012; Fahnenstiel et al., 2010a,b). A recent assessment of the lower food web of Lake Ontario has suggested declines in offshore zooplankton biomass in Lake Ontario have occurred since 2004 (Holeck et al., 2012), but the data used in that study were largely restricted to the epilimnion. Where deeper tows were taken, sub-epilimnetic zooplankton biomass was generally found to be substantially higher than epilimnetic biomass (Holeck et al., 2012). In this paper we examine recent (1997–2011) summer crustacean zooplankton communities in the offshore of Lake Ontario. We were particularly interested in the extent to which any changes observed in Lake Ontario crustacean communities might be consistent with those seen in Lakes Huron and Michigan, and if so, whether similar causal mechanisms could be invoked.

Methods

Sampling

Most of the data used for this study were drawn from the U.S. EPA's Great Lakes National Program Office (GLNPO) biannual off-shore monitoring program. To assess seasonal changes in primary production, chlorophyll *a* concentrations were estimated from observations made by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and the Moderate Resolution Imaging Spectroradiometer (MODIS) which were obtained from the NASA Ocean Color Program (http://oceancolor.gsfc.nasa.gov). GLNPO samples eight offshore stations in Lake Ontario, and these were assigned to either the eastern region of the lake or the western region, roughly divided by the Scotch Bonnet Ridge (Fig. 1). A strong east–west gradient has been observed in zooplankton community composition (Johannsson, 2003), possibly due to differences in timing of thermal development in the lake (Patalas, 1969), with the result that communities in these two regions can differ notably (Barbiero et al., 2001). Station depths in the eastern and western regions ranged from 50 to 180 m (mean = 115 m) and 98 to 130 m (mean = 121 m), respectively.

Two surveys were conducted each year: one each during the spring isothermal period (April 9–26) and the summer stratified period (August 3 to September 3). At each station, samples for nutrients were collected at discrete depths throughout the entire water column with Niskin bottles mounted on a SeaBird Carousel Water Sampler, and vertical profiles of temperature and chlorophyll were measured with a SeaBird CTD (conductivity, temperature, depth) probe equipped with a fluorometer. For the present study, total phosphorus data from samples collected in the upper 12 m of the water column during the spring survey were used to provide an indication of initial growing season nutrient levels, while profiles of temperature and *in vivo* chlorophyll measured during the summer survey were used to assess vertical distribution of chlorophyll during the stratified season. Crustacean zooplankton were collected by vertical tows taken from depths of 100 or 2 m from the bottom, whichever was shallower, using a 0.5-m diameter, 153-μm mesh conical net (D:L = 1:3) equipped with a flow meter. Because tows prior to 1997 differed slightly in terms of depth and net mesh size, and because we were primarily interested in

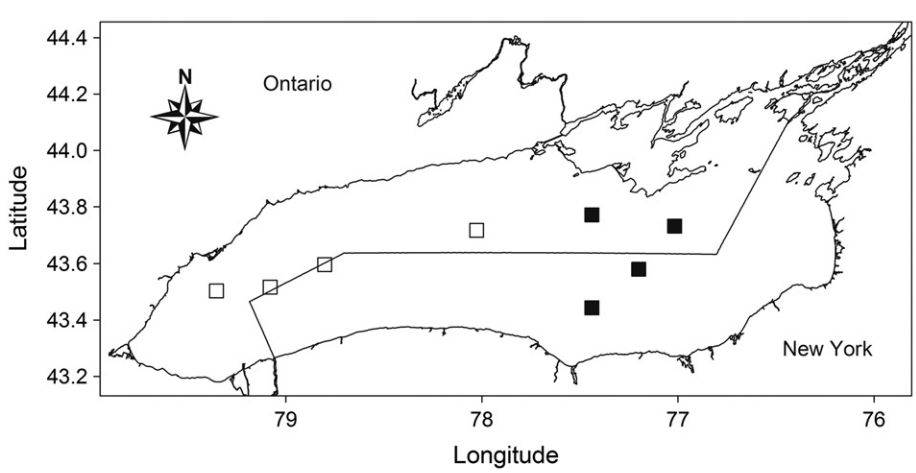

Fig. 1. Map of study site showing locations of EPA sampling stations. Filled symbols indicate those assigned to the eastern region of the lake; open symbols indicate those assigned to the western portion of the lake.