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Long-term changes in Lake Ontario rotifer abundance and composition: A response to *Cercopagis* predation?



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Rotifers and the predatory Cercopagis, Bythotrephes, Leptodora, and Diacyclops were collected from 1984 to 2013 in Lake Ontario. In contrast to a previous study, total rotifer abundance decreased. Of the six common genera, Polyarthra and Keratella abundances significantly decreased; Conochilus, Kellicottia, Synchaeta, and Asplanchna abundances did not. Relative abundances of Conochilus and Keratella remained the same, but relative abundance of Kellicottia increased from 12.6% to 24.7% of the population after 1999. Bythotrephes predation on rotifers was minimal, as this species was not observed in quantity during the summer months when rotifers were present. Although Leptodora and Diacyclops predation cannot be ruled out, populations of these genera were higher prior to the Cercopagis invasion and did not appear to be causal in the observed decline in rotifers. The changes in rotifer populations observed did coincide with the introduction of the exotic, predaceous cladoceran Cercopagis. Selective feeding on rotifers by Cercopagis was likely, as relative abundance of colonial and loricated large-spine species increased and non-loricated forms such as Polyarthra decreased in abundance and relative abundance. However, with the long-term decrease in chlorophyll and phosphorus, which were reduced to ~10 from ~25 µg P/L in the late 1990s, a definitive causal factor cannot be determined. The decrease in abundance of total rotifers was likely a response to decreased chlorophyll levels in Lake Ontario, while the change in relative abundance and composition of loricated and colonial forms suggests that a top-down selective response may be occurring.

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Introduction

Anthropogenic-driven change to biologic populations characterizes the recent history of Lake Ontario. Lake Ontario has experienced overfishing, cultural eutrophication, and contaminant discharge responsible for degradation of water quality, loss and change of habitats, and the decline in native fish communities (Mills et al., 2003). Implementation of binational agreements and subsequent management plans, such as the reduction of phosphorus loading to the lake and the stocking of hatchery-released trout and salmon, reversed cultural eutrophication and restored the lake trout and salmon populations, albeit with non-native Pacific salmon. For example, reductions in epilimnetic phosphorus from over 25 to $<10 \ \mu g P/L$ via the phosphorus abatement program led to major decreases in chlorophyll and increases in secchi disk depth (Holeck et al., 2008; Mills et al., 2003; Rudstam et al., in press) and a shift to oligotrophy (Mills et al., 2003). Another major factor of change was the successful decision to stock salmonines in Lake Ontario ostensibly not only to reduce the planktivorous feeding alewife stocks but also to develop what is now a substantial sport fishery (O'Gorman and Stewart, 1999; Stewart et al., 2003).

Superimposed on these changes are the invasions of exotic species. In Lake Ontario, perhaps the most consequential have been the addition of the filter-feeding dreissenids and the addition of the large, exotic predaceous cladocerans Bythotrephes longimanus and Cercopagis pengoi. Consequently, substantial top-down and bottom-up pressures existed on the food web of Lake Ontario. Prior to the introduction of the exotic cladocerans, alewife predation on zooplankton was intense and structured the zooplankton community towards small species (Mills et al., 2003). With the addition of the exotic cladoceran species, there were associated changes in the composition of the plankton. High Cercopagis abundance has been associated with declines of several crustaceans, including Diacyclops thomasi, Daphnia retrocurva, and Eubosmina spp. (Laxson et al., 2003; Makarewicz et al., 2002; Warner et al., 2006). From 1980 to 2003, the epilimnetic crustacean zooplankton density declined almost an order of magnitude (Holeck et al., 2008), and there was an additional decline of almost an order of magnitude from 2003 to 2008 (Rudstam et al., in press). This decline was primarily due to declines in cladocerans and cyclopoid copepods, whereas calanoid copepods increased within the entire water column (Rudstam et al., in press).

In lakes, rotifers play a major role in energy transfer and nutrient cycling (Makarewicz and Likens, 1979; Schindler, 1972). Even so, little information exists on rotifers in Lake Ontario during this period of

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substantial change in structure of the food web and in trophic status. In the Great Lakes, most early studies of rotifers are descriptive (e.g., Ahlstrom, 1936; Eddy, 1934; Tressler and Austin, 1940) while later studies (Nauwerck, 1978; Stemberger, 1974; Stemberger and Evans, 1984) have focused on regional spatial and seasonal distributions. Benoit et al. (2002) suspected that rotifers, which fall into the body sizes most vulnerable to predation by Cercopagis, would be strongly affected in Lake Ontario by invasive cladocerans. Similarly, Witt et al. (2005) suggested that in Lake Michigan the decline in rotifer abundance was associated with Cercopagis establishment and thus predation but was concerned that the rotifer declines occurred prior to Cercopagis entering the system. Barbiero and Warren (2011), in a comparison of rotifer abundances among the Great Lakes from 1983 to 2006, suggested that rotifer communities were responding to trophic state as well as to predation by exotic predatory cladocerans. However, they concluded that changes in rotifer species composition in Lake Ontario occurred, but a change in rotifer abundance was not observed.

In the Barbiero and Warren (2011) study of Lake Ontario rotifers, temporal trends were determined based on spatially sensitive data of samples taken on two offshore cruises within 3 days of each other in the month of August. Since rotifer species populations pulse very strongly from late spring to early autumn, sampling in one month of the year may not reflect abundance patterns for an entire summer. Here we consider a different set of rotifer data with the addition of *Cercopagis, Bythotrephes, Leptodora*, and *Diacyclops* data, seasonally sensitive (May–October) for the period of 1984 to 2013, and reconsider the hypothesis that rotifer abundance did not change and that species composition did change in Lake Ontario.

Materials and methods

Lake Ontario zooplankton samples were taken north of Hamlin Beach State Park, NY, in the offshore region (100-m depth) in 1984, 1987, 1999, 2003, 2005, 2007, and 2013 (Fig. 1). Zooplankton tows were from 20 m to the surface and taken every other week (generally May–October, Table 1) with a vertical tow net (63-µm mesh net, 50-cm diameter) equipped with a General Oceanics flow meter. The contents of the nets were washed in a sampling bucket, transferred to bottles, relaxed with tonic water, and preserved with 10% buffered formalin. The 1984 and 1987 tows were replicated (n = 3), while the 1999, 2003, 2005, 2007, and 2013 tows were not. Thus zooplankton abundance represented tow averages (n = 3) in 1984 and 1987. In other years one vertical tow (n = 1) was taken, but various volumes of samples were counted for rotifers and crustaceans with a Sedgewick-Rafter cell in each year [1984 and 1987 (1 to 3 mL), 2005 (1 to 12 mL), 2007 (1 to 12 mL), and 2013 (1 to 6 mL)] to enumerate at least 100 crustaceans. In 2013 and as a result of these criteria, the average number of rotifers counted was 677 per mL (range 48 to 2010). Rotifers (see Electronic Supplementary material Table S1 for a species list) were generally identified to species following Stemberger (1979) and Ruttner-Kolisko (1974). Only rotifers and Diacyclops are reported on here. Common rotifers were defined as genera, accounting for >2%of the total rotifer abundance in at least 5 years of the study.

Starting in 1999, *C. pengoi*, *B. longimanus*, and *Leptodora kindtii* were collected by vertical hauls (20 m to the surface) of a flow-metered double Bongo net (571- μ m mesh net, 50-cm diameter, n = 2) and preserved in 10% buffered formalin. Sample collections for *Cercopagis* and



Fig. 1. Map showing sampling sites on Lake Ontario of EPA (1986–1991) and of this study (offshore of Hamlin Beach).

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