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Changes in the cladoceran community of Lake Superior and the role of *Bythotrephes longimanus*

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ABSTRACT

Introductions of *Bythotrephes longimanus* have resulted in reduced cladoceran species richness and biomass in the Laurentian Great Lakes and many inland lakes. *Bythotrephes* was first observed in Lake Superior in 1987 but its effect on the cladoceran community has been unknown. We compared the composition of the offshore cladoceran community of Western Lake Superior during 2014 and 2015 to zooplankton surveys from 1971–2001 to determine whether changes in the cladoceran community have occurred. Monthly comparisons show that the contribution of *Bosmina longirostris* to offshore cladoceran numbers was generally twice as much in the 1970s than during 2014–2015 while the relative contribution of *Daphnia mendotae* increased after the 1970s. These community changes are consistent with changes due to *Bythotrephes* observed in other lakes. To evaluate evidence for the role of *Bythotrephes* in these community changes, we used data from 2014–2015 to analyze patterns in spatial and vertical overlap between *Bythotrephes* and its cladoceran prey species (*Bosmina*, *Daphnia*, and *Holopedium*) and compared estimates of consumption by *Bythotrephes* to production of these potential prey. *Bosmina* was the species whose vertical position and rate of production made it most vulnerable to suppression by *Bythotrephes*. Of the potential cladoceran prey species, *Bosmina* densities were also the most negatively correlated with *Bythotrephes* densities. These findings support a hypothesis of top-down effects on *Bosmina* by *Bythotrephes* in Lake Superior. This work informs future zooplankton research in Lake Superior and furthers our understanding of the effects of *Bythotrephes* on the Lake Superior food web.

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Introduction

Species introductions in aquatic ecosystems can alter the abundance and community composition of zooplankton (Brooks and Dodson, 1965; Carpenter et al., 1987). In North America, introductions of *Bythotrephes longimanus*, a predatory cladoceran native to northern Europe and Asia (Lehman, 1987; Burkhardt and Lehman, 1994), have resulted in reduced zooplankton species richness (particularly in cladocerans) and abundance in small inland lakes and in the Great Lakes (Barbiero and Tuchman, 2004; Strecker et al., 2006; Azan et al., 2015). *Bythotrephes* selects slow-moving cladocerans such as *Bosmina longirostris* and *Daphnia* spp. (Vanderploeg et al., 1993; Grigorovich et al., 1998; Schulz and Yurista, 1999). *Bosmina* and *Daphnia* consistently become less abundant in lakes following *Bythotrephes* invasion and multiple studies suggest that this is a direct result of consumption by *Bythotrephes* (Yan and Pawson, 1997; Yan et al., 2002; Strecker et al., 2006; Kerfoot et al., 2016).

Rapid cladoceran community changes in the Great Lakes following *Bythotrephes* invasion occurred in Lake Michigan in the late 1980s, when two of three common *Daphnia* species nearly disappeared within a year of the first detection of *Bythotrephes* (Lehman, 1988; Lehman, 1991; Lehman and Cáceres, 1993). *Daphnia mendotae* has remained common in Lake Michigan since *Bythotrephes* establishment, but appears to have done so partly by reducing the extent of its vertical overlap with *Bythotrephes* (Pangle and Peacor, 2006; Pangle et al., 2007). Other small cladocerans such as *Bosmina* have also become less common in Lake Michigan since the establishment of *Bythotrephes* (Makarewicz et al., 1995; Schulz and Yurista, 1999). Similar changes have been described in the cladoceran communities of Lakes Huron and Erie (Barbiero and Tuchman, 2004; Bunnell et al., 2012). In Lake Ontario, *Bosmina longirostris* and *Eubosmina* spp. abundance has declined by more than half since 2003 (Barbiero et al., 2014; Rudstam et al., 2015). These changes coincided with an order of magnitude increase in *Bythotrephes* abundance after 2003 which suggests that *Bythotrephes* has exerted top-down control on bosminids in Lake Ontario.

Bythotrephes was first detected in Lake Superior, the largest lake on Earth by surface area, in 1987 (Cullis and Johnson, 1988), but its effect on the zooplankton community is largely unknown. The Lake Superior zooplankton community is calanoid-dominated in terms of density

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and biomass (Patalas, 1972; Barbiero et al., 2001). Historically, the cladoceran community in Lake Superior was dominated by three species including *Bosmina longirostris*, *Daphnia mendotae*, and *Holopedium gibberum* (hereafter referred to by genus, unless otherwise noted). Brown and Branstrator (2004) reported a lower abundance of *Bosmina* in August of 2001 compared to observations from the early 1970s. Though reductions in *Bosmina* abundance are consistent with planktivory by *Bythotrephes*, the authors could not clearly demonstrate such a relationship given the temporal limitations of their dataset. Zooplankton surveys spanning multiple sampling seasons are needed to determine whether these or other community changes have occurred in the decades since *Bythotrephes* establishment.

Previous studies in Lakes Michigan and Huron have suggested that consumption by *Bythotrephes* can exceed production of cladocerans (Lehman and Cáceres, 1993; Bunnell et al., 2011; Bunnell et al., 2012). Consumption by *Bythotrephes* has not yet been estimated in Lake Superior. *Bythotrephes* densities in Lake Superior are generally lower than in Lakes Michigan and Huron (Barbiero et al., 2001; Brown and Branstrator, 2004; Brown et al., 2012; Pothoven et al., 2012; Bunnell et al., 2014). However, Lake Superior is also colder and less productive than the other Great Lakes (Patalas, 1972) and the consumptive demands of *Bythotrephes* in Lake Superior may still approach the rate of production of their preferred prey species. Cladoceran production is subject to a variety of losses other than by invertebrate predation. Thus, increased mortality due to *Bythotrephes* predation might be enough to reduce cladoceran abundance even if consumption by *Bythotrephes* does not exceed cladoceran production.

The addition of *Bythotrephes* to the Lake Superior food web is not the only important change that has occurred in this ecosystem in recent decades. Since the 1970s, population densities of planktivorous fish have fluctuated in Lake Superior and average summer surface temperatures have increased (Austin and Colman, 2007; Gorman, 2012; Pratt et al., 2016). One key change in the planktivorous fish community since the 1970s has been an overall increase in lake herring (*Coregonus artedii*) densities. Increasing vertebrate planktivory would be expected to cause a downward shift in the average body size of zooplankton (Brooks and Dodson, 1965). Temperature is a key factor driving zooplankton production and spatial aggregation in Lake Superior and increases in surface temperature might increase zooplankton production and density (Watson and Wilson, 1978; Zhou et al., 2001). In addition, the increase in summer surface temperatures in Lake Superior since the 1970s has the potential to favor warm water taxa such as small cladocerans (Lehman, 2002). Though zooplankton abundance and production can also be influenced by changes in primary production, changes in food quality and quantity for herbivorous zooplankton are unknown over the period of *Bythotrephes* invasion. However, changes in food availability would be expected to have similar effects on the densities of all herbivorous zooplankton rather than effects on specific taxa. Therefore, while changes in temperature, vertebrate planktivory, and primary production all can cause changes in zooplankton community structure, the effects of these ecosystem changes on the cladoceran community should be distinguishable from top-down effects by *Bythotrephes*.

The purpose of this study is to determine whether long-term changes in the cladoceran community of Lake Superior have occurred since the introduction of *Bythotrephes*. Based on changes observed in the cladoceran communities of the other Great Lakes and smaller, inland lakes following *Bythotrephes* invasion, we hypothesized that small cladocerans such as *Bosmina* would be less common in offshore areas of Lake Superior than before *Bythotrephes* invasion. To test this, we compared the offshore cladoceran community observed during the 2014 and 2015 growing seasons to past zooplankton surveys. Further, we used the data from 2014 and 2015 to evaluate three lines of evidence that *Bosmina*, *Daphnia*, and *Holopedium* populations are currently negatively impacted by the presence of *Bythotrephes*. These lines of evidence were: 1) the extent of synchronous spatial overlap among the prey taxa and

Bythotrephes, 2) patterns in vertical position of the prey taxa relative to *Bythotrephes*, and 3) the difference in temperature-driven production of the prey taxa versus temperature-driven consumptive demands of *Bythotrephes*.

Methods

Sampling sites and dates

Zooplankton and water temperature data were collected in the western arm of Lake Superior (Fig. 1) from the *R/V Blue Heron*. In 2014, collections occurred on June 3–6, July 23–25, August 11–14, August 17–19, October 1–2, and October 16–19; in 2015 collections occurred on May 20–22, July 15–17, September 8–10, October 5–7, and October 16–19. The number of stations visited in each month is indicated in Table 2. Stations 5, 12, and 15 were sampled in every month and station 7 was sampled in every month except July and October of 2014 (Fig. 1). The remaining stations were sampled on only one or two occasions. Zooplankton samples were collected primarily during low light conditions (between dusk and dawn) although some samples were collected during daylight hours. Additional archived zooplankton samples collected at station 6 were available from the summer of 1996 (see Table 1 for details). All stations visited were >70 m in depth and the depths and coordinates of all stations are described in Electronic Supplementary Material (ESM) Table S1.

Zooplankton collection

Zooplankton were collected using a conical plankton net with a mouth opening of 1-meter diameter, 153 μ m mesh, and a 4:1 aspect ratio (length to opening). A metered winch was used to collect vertical tows to depths of 60 m and 15 m at each site to study both total zooplankton and the shallow dwelling taxa. Recent studies have shown that >90% of the zooplankton biomass in Lake Superior exists at depths <50 m (Oliver et al., 2014; Pratt et al., 2016). At all stations visited after July of 2014, time allowed for triplicate samples to be taken at both depths to increase accuracy in zooplankton density estimates. Zooplankton samples were preserved in 70% ethanol (final concentration). In 2015, nets were equipped with a RBR TWR-2050 pressure gauge to verify that nets reached target depths. The gauge was secured to the steel bridle at the mouth opening of the net and was sensitive to changes of 0.0001 dbar. Pressures were converted to depth according to Sea-Bird Electronics, Inc. (2002) as:

$$\text{depth (m)} = \text{pressure (dbar)} \times 1.0197 \quad (1)$$

Zooplankton processing

Specimens were sorted, counted, and identified under a Nikon SMZ 1500 dissecting microscope. Identification was done to species level according to Balcer et al. (1984). All *Bythotrephes* and *Leptodora kindtii* were removed with forceps and counted in full. Replicate subsamples were taken until approximately 100 individuals of each taxon were counted. For less abundant taxa, larger subsample volumes were used and counting stopped when adequate replication of individuals per subsample was achieved or 10% of the sample volume was counted. The lengths of the first ten individuals in each taxon were measured using the ocular micrometer. The lengths of all *Bythotrephes* and *Leptodora* were measured using the method in Branstrator (2005). For *Bythotrephes*, the number of barbs on the caudal spine (indicator of developmental instar) of each individual was also recorded for later consumption estimates. The length of each taxon was averaged for each sample (June–July 2014) or set of triplicate samples (Aug 2014–Oct 2015).

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