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Big versus small: Does *Bythotrephes longimanus* predation regulate spatial distribution of another invasive predatory cladoceran, *Cercopagis pengoi*?

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ABSTRACT

Offshore–onshore spatial distribution and abundance of *Cercopagis pengoi*, a small non-indigenous predatory cercopagid, in Lake Michigan have been hypothesized to be regulated by the larger non-indigenous predatory cercopagid, *Bythotrephes longimanus*, through predation and/or competition. However, temperature and prey abundance are other factors that could be affecting *Cercopagis*. First, we examined all these factors on *Cercopagis* population abundance, life history traits and spatio-temporal distribution. In addition, we examined vertical spatial overlap between these species and determined predation rate of *Bythotrephes* on *Cercopagis*. Linear mixed effects analysis of spatial–temporal data showed that biomass of *B. longimanus* had the strongest effect, which was significantly negative on biomass, proportion of fecund females and mean clutch size of *Cercopagis*. Fecundity increased significantly with density of potential prey zooplankton, whereas *Cercopagis* total biomass increased significantly with the mean epilimnion temperature. *Cercopagis* and *Bythotrephes* overlapped vertically in the epi- and metalimnion, and neither of them showed any appreciable diel vertical migration. In predation experiments, *Bythotrephes* consumed *Cercopagis* at the same rate as *Daphnia mendotae*, a known preferred prey, when offered at equal concentrations. Overall, this observation, together with vertical overlap of *Cercopagis* with *Bythotrephes* implies that *Bythotrephes* predation has a strong influence on *Cercopagis* distribution; however, prey availability, temperature, and competition may be important secondary factors. These results imply that invasion success of *Cercopagis* may be limited by prior invasion by *Bythotrephes*.

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Introduction

In a new environment, non-indigenous species establish ecological interactions not only with native species, but also with other non-indigenous species that invaded prior to them. For example, Ricciardi (2001) has described a number of pairwise interactions among invaders of the Laurentian Great Lakes including both positive and negative interactions among various species. Two closely related exotic cercopagid cladocerans, *Bythotrephes longimanus* and *Cercopagis pengoi* that co-occur in Lake Michigan are of particular interest in terms of their potential negative interactions because of their ecological similarities (Case, 1990). Both are predators of zooplankton, both possess a long tail spine protecting them from predation by small fishes, and both may exhibit rapid population growth (Vanderploeg et al., 2002). *Bythotrephes* successfully invaded all of the Great Lakes during the 1980s and in Lake Michigan remains an important part of pelagic food web structure (Pothoven et al., 2003, 2007, in this issue; Vanderploeg et al., 2012). *Bythotrephes* is reported to have caused changes in the zooplankton community (Barbiero and Tuchman, 2004; Lehman and Cáceres, 1993) and is also hypothesized to have suppressed a native invertebrate predator *Leptodora* in Lake Michigan (Branstrator, 1995). Both *Leptodora* and *Bythotrephes* still coexist, but abundance and biomass of *Leptodora* are much lower than those of *Bythotrephes* (Cavaletto et al., 2010).

Cercopagis was first observed in 1998 in Lake Ontario (MacIsaac et al., 1999), where it quickly reached high densities (Makarewicz et al., 2001), and has likely caused a decline in small zooplankton, such as *Bosmina longirostris*, nauplii and *Daphnia retrocurva* (Benoît et al., 2002; Laxson et al., 2003). In Lake Michigan, *Cercopagis* was first discovered in 1999 (Charlebois et al., 2001) and has since dispersed throughout the whole lake, though they can likely attain high densities at only limited temporal and spatial scales (Cavaletto et al., 2010; Charlebois et al., 2001; Witt et al., 2005).

The similarities in ecological traits of *Cercopagis* and *Bythotrephes* imply competitive and/or predatory interactions between these two species. Because *Cercopagis* is smaller than *Bythotrephes* and *Cercopagis* has smaller thoracopods used for capturing and holding prey, it is likely to have preference for smaller prey than *Bythotrephes*. Nevertheless, both species obviously overlap in prey species and prey size that they

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are capable to feed on (Kim and Yan, 2013; Pichlova-Ptacnikova and Vanderploeg, 2009; Schulz and Yurista, 1995). Also, it was hypothesized that by nature of its size *Cercopagis* could be preyed upon by *Bythotrephes* (Vanderploeg et al., 2002) which has been experimentally confirmed (Witt and Cáceres, 2004). If *Bythotrephes* predation was strong enough, it could keep *Cercopagis* from dominating Lake Michigan, particularly in offshore waters where *Bythotrephes* is usually more abundant than nearshore (Pothoven et al., 2003). Cavaletto et al. (2010) have shown that in *Cercopagis*, densities are highest when *Bythotrephes* densities are low or zero and that in Lake Michigan a temporal and spatial separation occurs between these two related invasive species. Cavaletto et al. (2010) further hypothesized that spatial distribution and abundance of planktivorous fish controlled abundance and spatial distribution of *Bythotrephes*, which in turn affected spatial distribution and abundance of *Cercopagis*. The foundation for potential predatory control of *Bythotrephes* was observations of Pothoven et al. (2007) who demonstrated that adult alewives had high feeding selectivity for *Bythotrephes* and low feeding selectivity for *Cercopagis* and that consumption of *Bythotrephes* exceeded its production in the nearshore zone of Lake Michigan in late summer.

Predators may control their prey not only by direct consumption, but also indirectly, such as lowering its reproduction rate by inducing vertical migration into less favorable habitats. Pangle et al. (2007) and Bourdeau et al. (2011) described a significant indirect negative effect of *Bythotrephes* on populations of *Daphnia* and copepods, respectively, by causing the prey to stay in deeper and colder layers of the water column. Possible indirect effects of *Bythotrephes* on *Cercopagis* have not yet been studied, e.g., neither vertical avoidance nor other potential means. Furthermore, there is little known about the extent of direct predation of *Bythotrephes* on *Cercopagis*. For example, how much would *Cercopagis* be consumed by *Bythotrephes* in comparison with other available prey?

Although alewife control of *Bythotrephes* abundance and *Bythotrephes* direct predatory impact on *Cercopagis* is a plausible explanation of offshore–onshore spatial distribution of *Cercopagis*, other mechanisms can come into play. Different preferences for physical environmental conditions and differences in seasonality between *Cercopagis* and *Bythotrephes* would not seem likely. In other basins, including its native area, *Cercopagis* actually prefers offshore to nearshore waters (Gorokhova et al., 2000; Makarewicz et al., 2001; Rivier and Mordukhai-Boltovskoi, 1966) and remains in the plankton later than in Lake Michigan (Gorokhova et al., 2000; Makarewicz et al., 2001; Telesh et al., 2000).

To test the hypothesis that *Bythotrephes* is (directly or indirectly) responsible for *Cercopagis* spatial and temporal regulation in Lake Michigan, we studied three, so far neglected, features of the *Cercopagis*–*Bythotrephes* relationship:

1) Life history traits and demographic data of the *Cercopagis* population (as revealed by total biomass, proportion of fecund females and mean clutch size) and their relation to simultaneously analyzed effects of a) biomass of *Bythotrephes*, b) prey concentration, c) temperature in epilimnion, across a nearshore to offshore transect;
2) Vertical overlap of *Cercopagis* and *Bythotrephes* in stations with simultaneous occurrence of both species;
3) *Bythotrephes* predation rate on *Cercopagis* in comparison with *Daphnia mendotae*, a known preferred prey species of *Bythotrephes*.

Materials and methods

Field observations

Methods for collecting, preserving, and examining of zooplankton samples used in this study have been described earlier in detail by Cavaletto et al. (2010) and Vanderploeg et al. (2012). Briefly, in 2000–2003, we collected zooplankton samples biweekly to monthly from spring to fall at sites on a nearshore–offshore transect in Lake Michigan off Muskegon, MI (Fig. 1). Duplicate bottom to surface vertical tows were taken with a 153-μm mesh size conical net (0.5-m diameter) at three stations representing the shallow nearshore zone (M15, depth 15 m), the transitional middle zone (M45, depth 45 m), and the deep open-lake zone (M110, depth 110 m).

We converted density data reported by Cavaletto et al. (2010) to total biomass of *Cercopagis* and *Bythotrephes* by multiplying the density by the mean individual weight of *Cercopagis* and *Bythotrephes*. These were determined by measuring 30–100 specimens under dissecting microscope in each of the samples and application of length–weight equations (Grigorovich et al., 2000; Makarewicz and Jones, 1990). Fecundity parameters (ratio of fecund females and mean clutch size) were determined for *Cercopagis* under dissecting microscope by analyzing all specimens in a sample or up to 100 specimens in samples with high *Cercopagis* density.

To analyze a potential effect of prey concentration on *Cercopagis*, a sub-set of total zooplankton density data was selected based on documented *Cercopagis* prey preference (Holliland et al., 2012; Laxson et al., 2003; Lehtiniemi and Gorokhova, 2008; Pichlova-Ptacnikova and Vanderploeg, 2009). The zooplankton prey included *B. longirostris*, *Eubosmina coregoni*, *Ceriodaphnia* sp., *Chydorus sphaericus*, *D. retrocurva*, copepod nauplii, copepodites of cyclopoids, diaptomids and *Eurytemora affinis*, a rotifer *Asplanchna* sp. and zebra mussel veligers. One has to keep in mind though that for small zooplankton such as *Asplanchna* and veligers, the use of a 153 μm mesh size net retains only large specimens of the population. Both zooplankton densities and biomass of *Cercopagis* and *Bythotrephes* are reported on a per m^2 basis to make sites with different depths comparable. As a large proportion of *Bythotrephes*, *Cercopagis*, and prey populations occurs in the epilimnion (see results; Vanderploeg et al., (2015), we calculated mean temperature in upper 15 m from Seabird CTD (conductivity–temperature–depth) instrument casts.

We used linear mixed effects analysis (lme4 package (Bates et al., 2013) of R (R Core Team, 2014)) for testing differences for *Cercopagis* population parameters among sampling stations, with the depth of

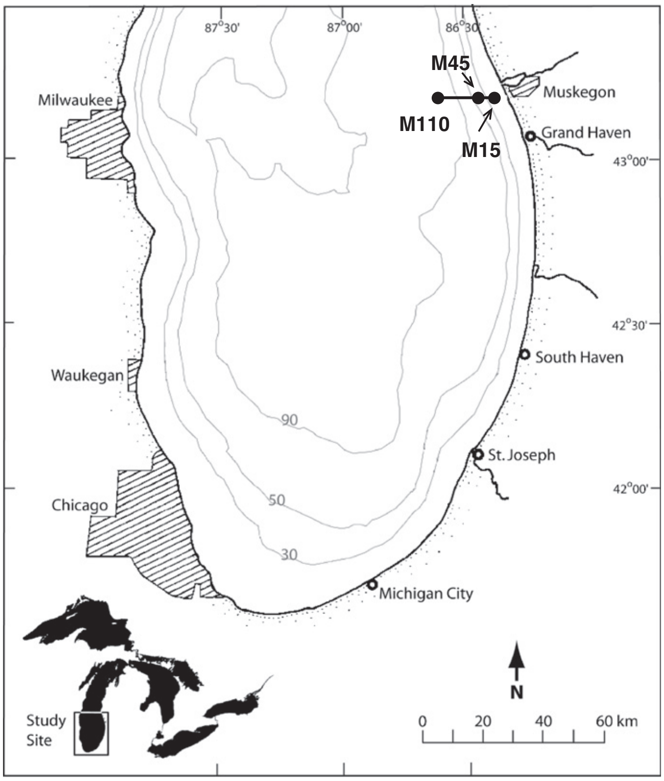

Fig. 1. Location of sampling stations M15, M45 and M110 on Lake Michigan near Muskegon, Michigan.

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