



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-Ptácnikova 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- μ m 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-Ptácnikova 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 μ m 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

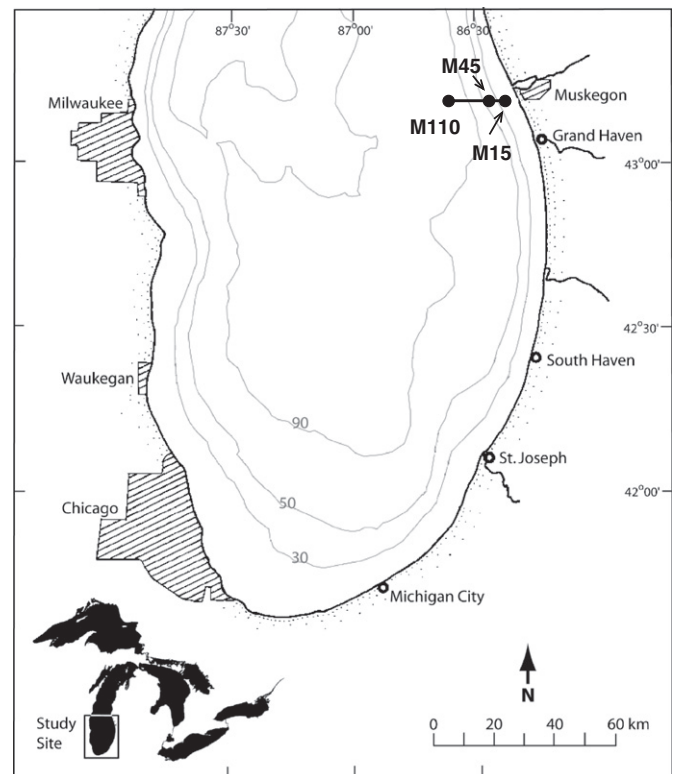


Fig. 1. Location of sampling stations M15, M45 and M110 on Lake Michigan near Muskegon, Michigan.

a station as a fixed effect and the year as a random effect. In the second analysis, we applied the same analytical tool for modeling relationships between each of the three *Cercopagis* population parameters (total biomass of *Cercopagis*, proportion of fecund females and mean clutch size), and the three parameters of environment that we hypothesized may influence *Cercopagis* (total biomass of *Bythotrephes*, density of potential prey and temperature). Here, the environmental parameters were handled as fixed effects, whereas the depth of a station and the year were entered as random effects to generalize over potential idiosyncrasies in the data. Prior to the lme analysis, *Cercopagis* and *Bythotrephes* biomass data as well as zooplankton density data were square-root transformed, as suggested by a preliminary Box–Cox transformation analysis. P-values were obtained by using lmerTest package (Kuznetsova et al., 2013).

Vertical distribution

Vertical distribution of *Bythotrephes* and *Cercopagis* was examined at M45, where we often found the two species co-occurring. We used a choke-off, messenger activated vertical plankton net (0.5-m diameter, 2.5-m long, 153- μ m mesh size) to sample the epilimnion, metalimnion, and hypolimnion, as defined by vertical temperature profile that was determined with a CTD just before taking the net tows. We did one sampling during the day in 2001, one day and one night sampling in 2002, and two sets of day–night samplings in 2003.

Predation experiments

For consumption experiments, we tested several combinations of *Bythotrephes*, *Cercopagis* and *D. mendotae* concentrations in large (2-L) bottles. All *Bythotrephes* and *Cercopagis* were 3rd instars, and the mean body length of *Daphnia* (1.49 mm from top of the head to base of tail spine) was nearly identical to that of *Cercopagis* (1.53 mm). We compared feeding of a single *Bythotrephes* offered ten *Cercopagis* alone, ten *Daphnia* alone, or five *Cercopagis* and five *Daphnia* together. We also included control treatments of five *Cercopagis* and five *Daphnia* without *Bythotrephes* and ten *Cercopagis* only to evaluate possible predator–prey interactions between *Cercopagis* and *Daphnia* and to examine the potential for *Cercopagis* cannibalism or other non-*Bythotrephes* associated mortality. All treatments had six replicates.

Cercopagis and *Bythotrephes* for experiments were carefully collected and handled as described by Pichlova-Ptácnikova and Vanderploeg (2009, 2011). *Daphnia* were isolated from a 153- μ m net tow collected on the same day of the experiment. The water used for holding the animals and for experiments later in the day was taken at the same station where the animals were collected and it was screened through a 37- μ m net to remove zooplankton.

The bottles were placed into a large outdoor deck-top incubator, with a cage rotating at a speed of 0.25 rpm (Vanderploeg et al., 1993), and a blue filter to reduce the light level of incoming solar radiation to simulate light conditions in the lake, with an light intensity of $<10 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. The experiments were conducted in early August 2001 in Muskegon, MI, and ran for 24 h, to cover one complete diurnal cycle (with a day length of about 14 h 15 min). Water temperature in the incubator was kept constant at 21 °C.

After the end of the experiment, the bottle contents were preserved with sugar formalin for later examination. A clear indication that *Cercopagis* was killed and eaten by *Bythotrephes* was presence of only the long caudal spine of *Cercopagis* remaining in the experimental vessel, because *Bythotrephes* consumes only soft body parts. As decomposition of a dead *Cercopagis* body takes more than 24 h under the conditions we used (our observation), the spine would remain with the body when *Cercopagis* died from other causes. Thus, we concluded that all tails without bodies indicated that *Cercopagis* was consumed. We also determined the number of dead, but not consumed, animals separately from consumed animals as an indicator of mortality that could result from handling stress from injury or from stress induced by other cercopagids. A t-test was utilized to compare numbers of prey consumed in different treatments.

Results

Spatial population characteristics of *Cercopagis* and environmental parameters

Cercopagis population characteristics and environmental data (summarized in Electronic supplementary material (ESM) Table S1) show strong seasonal variation in temperature and population characteristics as well as some variations related to station location. Total biomass of *Cercopagis* showed a nearshore–offshore gradient with highest numbers nearshore (M15) significantly different from values from offshore (M110) station ($t = 2.934$, $\text{Pr}(>|t|) = 0.004$). The mid-depth station (M45) did not differ significantly from either M110 or M15. However, the trend for fecundity parameters was not so clear. For both proportion of fecund parthenogenetic females and mean clutch size, the values overlapped across stations with no significant differences found.

Sexually reproducing females and males were detected throughout the season at all stations (though not in all samples), with an average of 4.4% and a range of 0.0–47.4% for gamogenetic females, and an average of 6.4% and a range of 0.0–42.1% for males respectively, with highest numbers being reached towards the end of season.

All three environmental variables had a significant effect on one or more tested *Cercopagis* population features (Table 1, Fig. 2). Only *Bythotrephes* biomass had a negative and significant effect on all population features. Density of potential zooplankton prey was significantly connected with higher mean clutch size (as the best explaining factor); and its effect on ratio of fecund females was practically neutral. However, there was a negative relationship between zooplankton prey density and total *Cercopagis* biomass. Temperature had a significantly positive effect on total biomass (as the best explaining factor), a significantly negative effect on mean clutch size, but no effect on the proportion of fecund females. Among the random effects, variation attributed to sampling year was considerably larger than that attributed to sampling depth for both *Cercopagis* biomass and proportion of fecund females; variance attributable to random effects was negligible for mean clutch size.

Vertical distribution

Bythotrephes and *Cercopagis* populations overlapped in their vertical distribution at the mid-depth station (M45) in all of our collections

Table 1

Results of linear mixed model analysis for effects of environmental parameters on population parameters of *Cercopagis*. For fixed effects, t-statistics and p-values are shown; for random effects, attributable variance is shown. Significant results for fixed effects are labeled in bold.

<i>Cercopagis</i> population parameters	<i>Bythotrephes</i> biomass		Zooplankton density		Mean temperature in upper 15 m		Depth of station	Year
	t	$\text{Pr}(> t)$	t	$\text{Pr}(> t)$	t	$\text{Pr}(> t)$	Variance	
Biomass	−3.511	0.0008	−2.683	0.0360	5.331	1.42e−06	7.486	146.758
Proportion of fecund females	−3.686	0.0016	0.066	0.9477	0.397	0.6955	2.406e−08	1.342e+02
Mean clutch size	−4.170	0.0005	4.615	0.0002	−2.097	0.0489	0.000	0.000

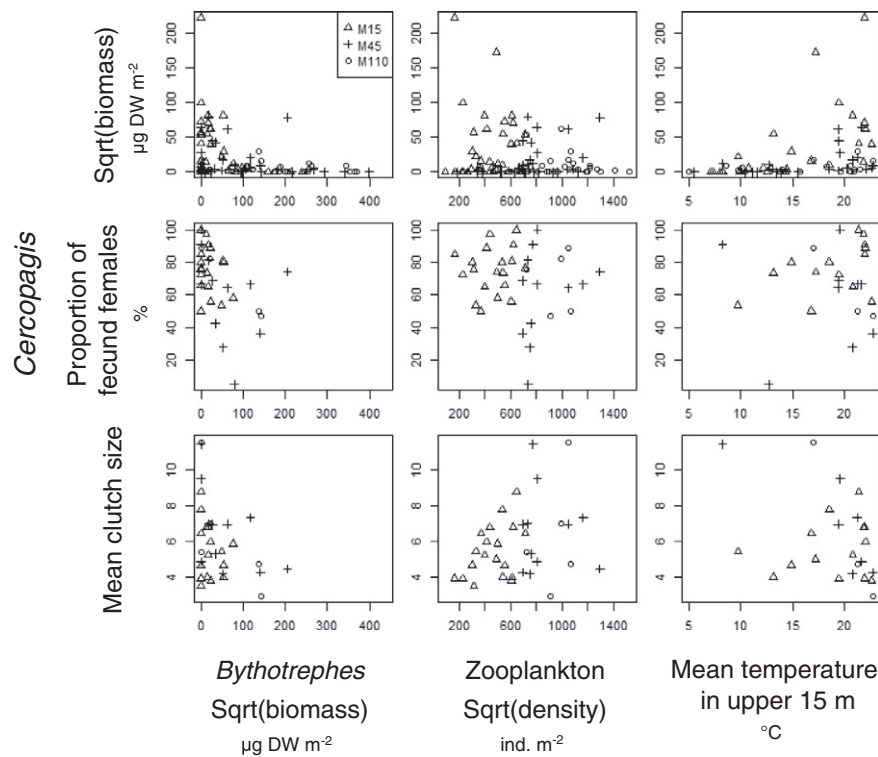


Fig. 2. Scatterplots of relationships explored in the linear mixed effect analysis. Datapoints are coded by the sampling station.

(Fig. 3). *Cercopagis* occurred only in epilimnion, or mostly in epilimnion and partly in metalimnion. A major part of the *Bythotrephes* population was also abundant in the epilimnion; however, they were also relatively abundant in the metalimnion and occasionally we found few individuals in hypolimnion. In neither of the species was there any consistent difference between day and night vertical distributions over all of the sample collections.

Predation experiments

Bythotrephes consumed *Cercopagis* and *D. mendotae* at equal rates— 1.3 ± 0.4 and 1.3 ± 0.2 ind·d⁻¹, respectively—when presented together at identical concentrations (Fig. 4), ($t = 0$, $df = 7.35$, $p = 1$). Thus, there was no preference for *Cercopagis* or *Daphnia* by *Bythotrephes*, and no vulnerability difference between them. When *Cercopagis* and *Daphnia* were offered separately, *Bythotrephes* consumed *Cercopagis* (2.0 ± 0.6 ind·d⁻¹) at a slightly lower rate than *Daphnia* (2.5 ± 0.2 ind·d⁻¹); however, this difference was not significant ($t = 0.74$, $df = 6.23$, $p = 0.48$). In the control treatment with *Daphnia* and *Cercopagis*, *Cercopagis* did not prey on *Daphnia* at all, and in the *Cercopagis*-only control treatment cannibalism was low (0.3 ± 0.3 ind·d⁻¹). Thus, estimates of *Bythotrephes* consumption were not affected by *Cercopagis* predation or cannibalism. Non-predatory mortality of *Cercopagis* was 20 % on average; whereas, for *Daphnia* and *Bythotrephes* it was zero.

Discussion

There has been considerable speculation as to what regulates abundance and spatial distribution of *Cercopagis* and its potential for invading new systems. In the Great Lakes, there has been evidence that another invader, *Bythotrephes*, regulates *Cercopagis* spatial distribution and abundance through direct predation. Moreover, some evidence is consistent with large planktivorous fishes regulating *Bythotrephes* spatial distribution which in turn drives *Cercopagis* distribution. However, there has not been much information available on predation by

Bythotrephes on *Cercopagis* and on vertical spatial overlap to see if these species overlap enabling predation to occur. Lastly, there has not been much consideration given to the role of prey availability and other factors in regulating population response and spatial distribution of *Cercopagis*. In our study, we examined all of these factors through combined field and laboratory investigation.

Spatial population characteristics of *Cercopagis* and environmental parameters

Our analysis on the horizontal distribution confirms the strong negative direct effect of *Bythotrephes* on *Cercopagis* (Table 1 and Fig. 2). Both the share of fecund *Cercopagis* females and the mean clutch size tended to be lower with the increasing *Bythotrephes* biomass as well. We thus hypothesize that *Bythotrephes* may hinder *Cercopagis* not only by a direct predation (Yurista et al., 2010), but also indirectly by a selective predation on fecund females and females with high clutch size which are both optically conspicuous and are not as agile swimmers as barren specimens (our observation). *Bythotrephes* is a visual predator (Muirhead and Sprules, 2003), and it has been already shown earlier that a vulnerability of a prey to *Bythotrephes* predation correlates with visual conspicuousness of a prey (Jokela et al., 2013; Pangle and Peacor, 2009) and/or prey's swimming patterns and escape abilities (Pichlova-Ptácniková and Vanderploeg, 2011). A significant effect of *Bythotrephes* on fecundity of another prey (*Daphnia*) by selecting for large females carrying large clutches has been demonstrated earlier by Manca et al. (2008); however, the hypothesis that there is a similar effect of *Bythotrephes* on *Cercopagis* populations remains to be tested.

In addition to examining spatial overlap and feeding of *Bythotrephes* on *Cercopagis*, we examined how density of potentially edible prey may influence *Cercopagis* population parameters. The effect of zooplankton prey abundance was on the one hand significantly negative (though with rather weak slope) with *Cercopagis* total biomass, but on the other hand significantly positive with the mean clutch size. A positive effect of a sufficient food quantity on clutch sizes of cladocerans has been documented many times (e.g., Gliwicz and Boavida, 1996) and

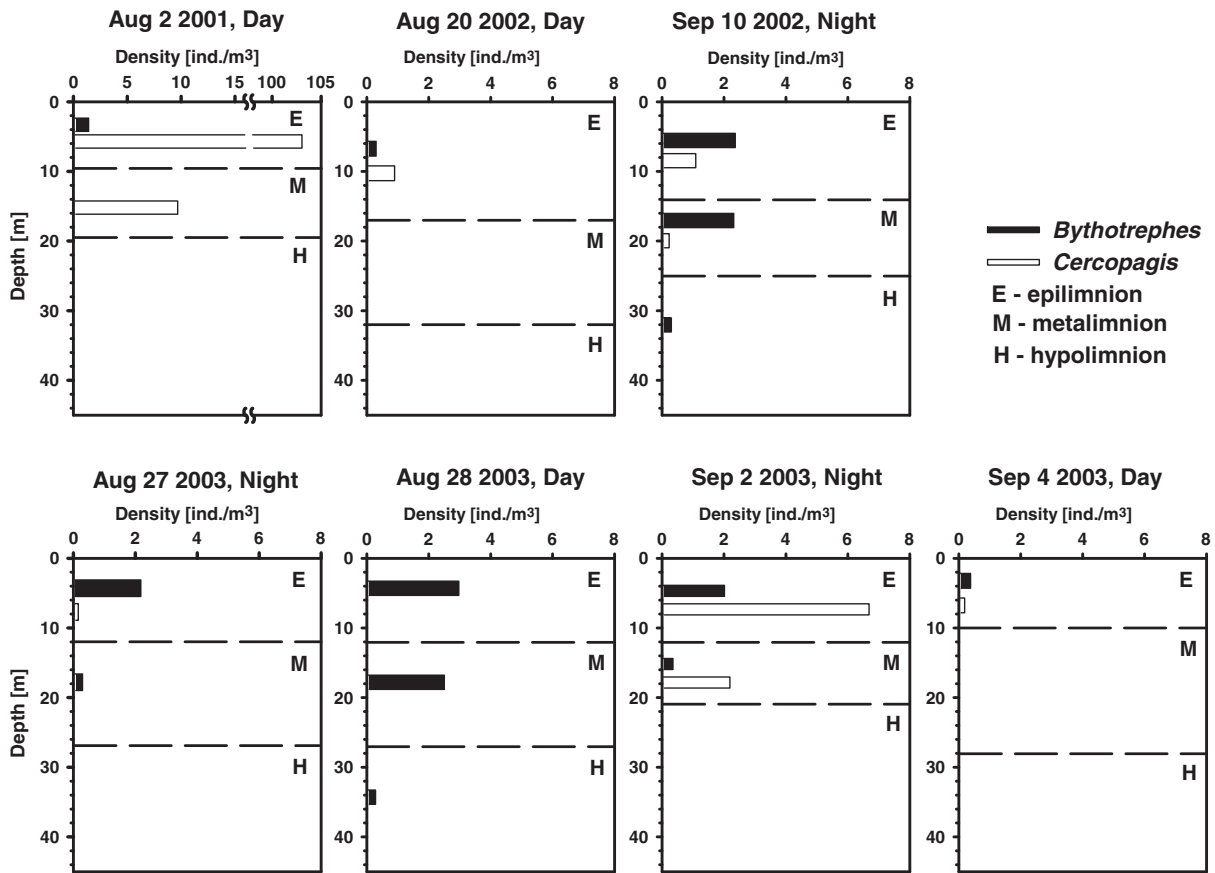


Fig. 3. Vertical distribution of *Bythotrephes* and *Cercopagis* at station M45.

for the closely related *Bythotrephes* recently by Kim and Yan (2013). The higher clutch size may not be necessarily correlated with higher total biomass, as the investment to an individual offspring can differ largely (Straile and Halbach, 2000). The effect of zooplankton prey abundance on proportion of fecund females was not significant—the fecundity level is, however, not only the result of quantity of food but also of its quality, as recently shown by Kim et al. (2014). Further study is needed

to analyze both food quantity and quality requirements for *Cercopagis* and their impacts on its life-history traits.

A high proportion of fecund females in populations of cladocerans typically results from optimal species-specific environmental conditions, such as food and temperature. Unlike other cladocerans, *Cercopagis* are fertile beginning in their first instar after hatching (Grigorovich et al., 2000) which may increase per capita reproduction rate. In our data, the ratio of fecund females varied between 5.3% and 81.5% throughout the season, with an average of 69.2%, whereas the ratio of barren parthenogenetic females ranged between 0.0% and 61.1%, averaging 19.9%. This might indicate that the population experienced favorable environmental conditions at the beginning and the middle of summer. We observed gamogenetic females and males, which is typically a signal of worsening or sub-optimal conditions, throughout the entire growing season, though in relatively small numbers. This seems to be, however, a frequent pattern of *Cercopagis* populations, as it has been documented elsewhere (e.g., Simm and Ojaveer, 2006).

The strongest predictor variable that explained total *Cercopagis* biomass was epilimnetic temperature. This result is in agreement with previous observations that *Cercopagis* reaches highest abundances at higher water temperatures than many other zooplankton species in the temperate zone (Benoît et al., 2002; Cavaletto et al., 2010) although its temperature tolerance is relatively broad (8–30 °C, (Gorokhova et al., 2000)). Mean epilimnion temperatures were, in general, comparable across our sampling transect with the nearshore occasionally influenced by upwelling which implies that the temperature is likely not a driving factor for the nearshore–offshore gradient in *Cercopagis* population.

Contrary to the expectation that clutch size would increase with temperature, we observed a negative effect. The negative relation between temperature and mean clutch size is a phenomenon reported

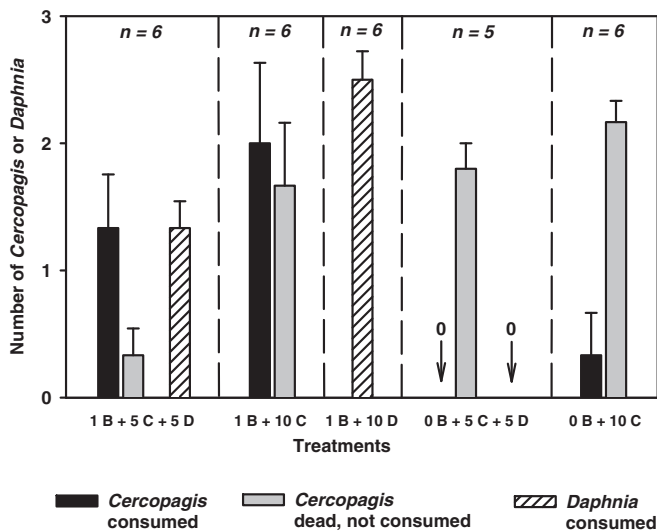


Fig. 4. Consumption of *Cercopagis* and *Daphnia* in *Bythotrephes* predation experiments. Mean and standard error of mean of replicates within a treatment are shown. B = *Bythotrephes*, C = *Cercopagis*, D = *Daphnia*.

elsewhere related to the beginning of population buildup. *Cercopagis* has been shown to have the highest mean clutch size right in the beginning of season (Makarewicz et al., 2001; Simm and Ojaveer, 2006; Witt et al., 2005), when temperature is not yet at a peak, and declines later, when the temperature is high. A reason for this pattern is not understood. One should keep in mind as well that the clutch size, which is relatively easy to quantify, is only a surrogate for the birth rate of a population, that actually matters. In cladocerans, elevated water temperatures reduce development time non-linearly (e.g., Bottrell et al., 1976), but to our knowledge, no such relationship for *Cercopagis* has been quantified yet.

Vertical distribution

Both *Bythotrephes* and *Cercopagis* have been described as predominantly epilimnetic species exhibiting limited or modest vertical migration into the meta- or hypolimnion. Our study is of particular interest in that we observed vertical distribution of both species together. Absent or very weak diel vertical migration together with predominant occurrence in the epilimnion and metalimnion were reported both for *Bythotrephes* (Enz et al., 2001; Lehman and Cáceres, 1993) and for *Cercopagis* (Benoît et al., 2002; Laxson et al., 2003; Ojaveer et al., 2001; Telesh et al., 2000). Unlike Witt et al. (2005) we did not find any *Cercopagis* in hypolimnion. Because *Cercopagis* is capable of the diel vertical migration in its indigenous area (Rivier and Dumont, 1998) and, as shown in this study, can be preyed upon by *Bythotrephes* in which vision plays an important role in prey detection, encounter (Muirhead and Sprules, 2003) and capture (Jokela et al., 2013; Pangle and Peacor, 2009), we expected *Cercopagis* to avoid overlap with *Bythotrephes* during the day at station M45. Such an escape response was exhibited by *D. mendotae* (Lehman and Cáceres, 1993; Pangle and Peacor, 2006; Vanderploeg et al., 2015) and copepods (Bourdeau et al., 2011). If *Cercopagis* had migrated into the metalimnion, it may have escaped some predation pressure by *Bythotrephes* on three of four of our daytime samples and two out of three nighttime samples (Fig. 3). However, we did not observe any signs of vertical avoidance in *Cercopagis* of *Bythotrephes* either in the day or in the night within the scale we worked in (epilimnion, metalimnion, hypolimnion). Therefore, it appears that *Cercopagis* did not use vertical migration as an escape mechanism from *Bythotrephes* in Lake Michigan.

Predation in the laboratory and field

Similar consumption rates for *Cercopagis* and *D. mendotae* of comparable size by *Bythotrephes* imply that there might be similar predation pressure on them in the field too. However, *D. mendotae* did not show any decrease, but rather increased after *Bythotrephes* invasion to the Great Lakes (Barbiero and Tuchman, 2004). It is worth noting that survival of *D. mendotae* and demise of two other congeneric species (*D. retrocurva* and *D. pulicaria*) in offshore waters was attributed to vertical migration of *D. mendotae* that limited overlap with *Bythotrephes*, whereas the other species did not migrate to avoid overlap (Lehman and Cáceres, 1993). The lack of vertical migration of *Cercopagis* may make it, too, especially vulnerable to *Bythotrephes* predation.

The control experiments with *Daphnia* and *Cercopagis* together and with *Cercopagis* alone imply that *Cercopagis* does not engage in significant cannibalism or eat other species of the same size. This is in contrast to high cannibalism reported in *Bythotrephes* (Schulz and Yurista, 1999). On the other hand, *Cercopagis* is obviously very delicate animal and suffered from non-predatory mortalities in the laboratory even if handled very carefully. The number of dead, but not consumed, animals was similar across all our experiments, so we are assuming that the impact of non-predatory mortality was likely similar in all experiments and did not bias our results on prey consumption or selectivity by *Bythotrephes*. The slower swimming speed of *Cercopagis* makes escape

from *Bythotrephes* improbable (unpublished observations; Pichlova-Ptácnikova and Vanderploeg, 2011).

In general, our rates of predation by *Bythotrephes* were lower than in some recent studies (Kim and Yan, 2013; Pangle and Peacor, 2009), though the chosen prey concentrations were higher than in the field. This is likely due to the strong effects of light intensity on predation success (Jokela et al., 2013; Pangle and Peacor, 2009). We performed our experiments in rather low light and our outcomes correspond well with results of Schulz and Yurista (1999), who did their experiments in conditions more similar to ours.

Conclusions

In Lake Michigan it is likely that the horizontal distribution of *Bythotrephes* is regulated by fish predation, and in turn *Bythotrephes* predation regulates *Cercopagis* distribution. Cavaletto et al. (2010) documented a limited horizontal (offshore–onshore) spatial and temporal overlap of *Cercopagis* and *Bythotrephes* in Lake Michigan. Strong evidence for control of *Bythotrephes* by fish in the nearshore zone of Lake Michigan in late summer was presented by Pothoven et al. (2007). *Bythotrephes* unlike *Cercopagis* was highly selected by large alewives, and consumption of *Bythotrephes* exceeded its production. Vanderploeg et al. (2015) demonstrate that at a 60-m-deep site at the same time of the Pothoven et al. (2007) study, alewife consumption was not enough to control *Bythotrephes* populations and that *Bythotrephes* consumed a large fraction of zooplankton production. Further, they observed that because of low abundance, *Bythotrephes* in the nearshore zone (10-m depth) had a minimal impact on *Cercopagis*. Finally, Keeler et al. (in this issue) also reported that consumption by fishes in Lake Michigan exceeded *Bythotrephes* production only in the nearshore zone; while at 46 and 110 m bottom depths, consumption by fish was insufficient to control *Bythotrephes* though this study suggests that besides fish, temperature may significantly influence nearshore *Bythotrephes* biomass.

Densities of small zooplankton were generally an order of magnitude higher offshore than nearshore. Therefore, it is possible that if *Bythotrephes* were not present in Lake Michigan, *Cercopagis* might reach higher densities offshore than nearshore as it does in other basins (Gorokhova et al., 2000; Makarewicz et al., 2001; Rivier and Mordukhai-Boltovskoi, 1966) with no or low *Bythotrephes* populations.

Both high consumption of *Cercopagis* by *Bythotrephes* and vertical spatial overlap are important parts of the predation story. In Lake Michigan, *Bythotrephes* negatively impacts *Cercopagis* populations, by direct predation, which may be of a same rate as of *D. mendotae* and possibly by reducing birth rate of *Cercopagis* by selecting for the most fertile females. Unlike *D. mendotae*, *Cercopagis* did not exhibit a vertical migration strategy to avoid *Bythotrephes* in the areas of horizontal spatial overlap. Further, it is possible that some nutritional limitation of *Cercopagis* may play a role. Food limitation—both quantity and quality—are areas deserving further study.

Our results for Lake Michigan may offer some insight into the invasibility of lakes by *Cercopagis*. It seems unlikely that *Cercopagis* would be able to develop significant populations where *Bythotrephes* already exists in high abundance. There has been rapid spread of *Bythotrephes* throughout lakes in North America. A similar spread has not been observed for *Cercopagis*.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jglr.2015.10.006>.

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