



Spatial and predatory interactions of visually preying nonindigenous zooplankton and fish in Lake Michigan during midsummer



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ABSTRACT

A plankton survey system, fisheries acoustics, and opening/closing nets were used to define fine-scale diel vertical spatial interactions among non-indigenous alewives and visually preying cercopagids (*Bythotrephes longimanus* and *Cercopagis pengoi*) and indigenous zooplankton in nearshore and offshore Lake Michigan during August 2004. Because of increased water clarity associated with dreissenid mussel expansion and radically different thermal structure between cruises, we were able to observe the effects of thermal structure on diel vertical migration under high light conditions favorable especially to visual predation by cercopagids. Vertical position and overlap between alewives, *Bythotrephes*, and *Daphnia mendotae* at a 60-m site were strongly driven by thermal structure. *Daphnia* showed the strongest diel vertical migration of zooplankton that included migration between the epilimnion at night and the metalimnion–hypolimnion boundary during the day, whereas its major predator, *Bythotrephes*, was confined at all times to the epilimnion–metalimnion. Some alewives migrated from the hypolimnion to the metalimnion and epilimnion at night. As a result, most spatial overlap of *Daphnia*, *Bythotrephes*, and alewives occurred at night. Simple bioenergetics models were used to contrast predatory interactions between alewives and cercopagids at nearshore and offshore sites. *Bythotrephes* was the preferred prey of alewives, and at the 10-m site, alewives were the major controller of zooplankton because of its elimination of *Bythotrephes*. In contrast, *Bythotrephes* offshore likely escaped predation because of low spatial overlap with a low concentration of alewives and was the major predator and shaper of zooplankton community structure.

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Introduction

Lake Michigan zooplankton community structure and function has been strongly impacted by top-down control from planktivorous non-indigenous alewife (*Alosa pseudoharengus*) as well as predation from visual predatory cladoceran (cercopagid) invaders (*Bythotrephes longimanus* and *Cercopagis pengoi*), potential competitors with age-0 alewives and other fishes (e.g. reviews of Madenjian et al. 2002; Vanderploeg et al. 2002). By studying predatory interactions among these predators, we gain insight into factors that will affect survival of age-0 fishes, including the alewife, previously a nuisance species and now an important forage species for salmonids (Madenjian et al., 2002). *Bythotrephes*, a very large zooplankton (~150 µg dry weight), and the much smaller *Cercopagis* (~5 µg dry weight) both possess a long tail spine and can prey upon zooplankton, particularly cladocerans, nearly as large as they are (Pichlová-Ptáčnicková and Vanderploeg, 2009;

Schulz and Yurista, 1999; Vanderploeg et al. 1993). Their long tail spines largely prevent ingestion by age-0 fishes (Barnhisel, 1991), yet *Bythotrephes* are the preferred prey of large (>100 mm) alewives and other fishes that overlap spatially with it (Pothoven and Vanderploeg, 2004). Because of the size difference between *Bythotrephes* and *Cercopagis*, *Cercopagis* is a potential intraguild prey of *Bythotrephes* (Ptáčnicková et al., 2015; Vanderploeg et al. 2002; Witt and Caceres, 2004).

After the *Bythotrephes* invasion of Lake Michigan in the mid 1980s, two of three dominant species of *Daphnia* (*D. pulicaria* and *D. retrocurva*) immediately declined precipitously in offshore waters (Lehman and Caceres, 1993). *Daphnia mendotae* was thought to persist because of its faster escape reaction (Pichlová-Ptáčnicková and Vanderploeg, 2011) and migration to greater depths during the day to avoid spatial overlap with *Bythotrephes* (Lehman and Caceres 1993; Pangle and Peacor, 2006). Now, *D. pulicaria* and *D. retrocurva* can be found only in very low concentrations offshore (Pothoven and Fahnenstiel, 2015). Coincident with the *Bythotrephes* invasion, the population of *Leptodora kindtii*, a native predatory cladoceran that preys on small zooplankton, greatly declined in offshore waters likely due to competition and predation, because *Bythotrephes* can consume

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Leptodora (Branstrator 1995). Overall, *Bythotrephes* continues to be the dominant species in terms of biomass in mid-depth (45-m) and offshore waters (100-m-deep), and often even in nearshore waters (15-m-depth) (Pothoven and Fahnenstiel, 2015), but all three predatory cladoceran species are still present, due, in part, to earlier phenology of the *Cercopagis* and *Leptodora* populations (Cavaletto et al., 2010).

During midsummer, a considerable fraction of the alewife population can be found in nearshore waters (<20 m depth zone) in association with shoreward spawning migration in spring, while some of the population can be found in transitional (40–60 m) depths (Pothoven et al. 2007). Pothoven et al. (2007) examined alewife prey selection and consumption of different zooplankton including *Cercopagis* and *Bythotrephes* at M10, a 10-m site near Muskegon, Michigan, in August 2004. In this shallow, unstratified water column, large alewife (>100 mm length) prey selection was strongly size dependent, which included high selectivity for *Bythotrephes* and low selectivity for *Cercopagis*. In contrast, small (<100 mm) alewives had very low selectivity for both *Cercopagis* and *Bythotrephes*, while at the same time preferring larger prey without spines. Estimated *Bythotrephes* consumption by large alewives exceeded its production, whereas estimated consumption was less than production for *Cercopagis* and other species of small zooplankton. The predatory impact of *Bythotrephes* was not examined. Although cercopagids consume a broad size range of prey relative to their body size, there is preference for slower moving prey such as cladocerans (Jokela et al., 2013; Pichlová-Ptáčnicková and Vanderploeg, 2009; Vanderploeg et al., 1993).

In offshore and transitional (40–60 m water depth) waters, alewives and zooplankton may vertically migrate and, thereby occupy different depth zones over the diel cycle. In addition there are different zooplankton species not found in the nearshore zone associated with deeper metalimnetic and hypolimnetic portions of the water column (e.g., Pothoven and Fahnenstiel, 2015; Vanderploeg et al., 2012). As a step toward understanding their potential impacts on one another in transitional or offshore waters, we were interested in defining vertical spatial overlap among *Bythotrephes*, *Daphnia*, other zooplankton, and alewives over the diel cycle and examining the potential implications of this overlap to predatory impacts of alewives and *Bythotrephes*. Two cruises at M60, a 60-m deep site due west of Muskegon, Michigan, were performed: one in early August during the full moon phase and another two weeks later in the new-moon phase. Because there was a great deepening of the epilimnion and metalimnion between cruises, this provided us with a natural experiment to explore impacts of different thermal structure on spatial overlap. These cruises were paired with cruises at M10 (Pothoven et al., 2007) to give a comprehensive picture of not only vertical spatial interactions but also inshore-offshore differences.

To define spatial interactions, we used a variety of technologies to define simultaneous diel vertical structure. High resolution fine-scale (1-m resolution) vertical structure of *Daphnia*, *Bythotrephes*, and alewives were captured throughout day and night using a plankton survey system (PSS: with optical plankton counter [OPC], PAR sensor, CTD, and fluorometer) (Vanderploeg et al., 2009a, 2009b) and fishery acoustics. Broader scale (~10-m resolution) vertical structure of different zooplankton species was captured by tows with an opening/closing net.

To evaluate the potential consequences of vertical spatial overlap, we determined prey selectivity and consumption of alewives on zooplankton prey at M60 using a bioenergetics model and compared it to zooplankton production in different depth zones day and night. This was contrasted with bioenergetic estimates of consumption by *Bythotrephes*.

Bioenergetic estimates of *Bythotrephes* consumption have not considered the role of light climate or vertical migration as it relates to individual prey species vulnerability and consumption (e.g., Bunnell et al., 2011). Nor has prey selection of *Bythotrephes* been factored into estimates of consumptive impacts (e.g., Bunnell et al., 2011; Pothoven and Höök, 2014; Yurista et al., 2010). Consumptive impacts on zooplankton community structure are impossible to specify without this information. Water clarity

has increased with expansion of dreissenid mussels into deep water (Vanderploeg et al., 2012) and may have affected visual predatory interactions.

Our experiments occurred on the cusp of expansion of mussels into deep water; therefore we document changes in light climate in years before, during, and after our experiments to put observations in the context of Lake Michigan's changing light climate. Further we explore what these changes may mean to foraging efficiency of *Bythotrephes* and zooplankton diel vertical migration (DVM).

Using a simple bioenergetic modeling approach, we explored potential effects of light climate, vertical migration, and prey selection on zooplankton community structure. Because our study objective was to understand spatial interactions in both vertical and horizontal space, we calculated consumptive impacts of *Bythotrephes* at M10 and compared them with impacts of alewives reported by Pothoven et al. (2007). By examining results from both sites, we attempt to develop a comprehensive picture of spatial and predatory interactions in both offshore and nearshore regions during mid-summer.

Our observations are particularly relevant to the theme of understanding complex interactions in Lake Michigan's rapidly changing ecosystem because we examine factors driving both inshore and offshore zooplankton and fish interactions on the cusp of major ecosystem change. This is the only study that we are aware of that considers simultaneous distributions of mesozooplankton, invasive invertebrate visual predators and zooplanktivorous fishes at high vertical resolution in Lake Michigan or any large, very deep lake.

Methods

Light climate history and implications to DVM

The extinction coefficient of light (k_{PAR}), measured as PAR (photosynthetically active radiation: 400–700 nm), was used in conjunction with incident PAR to examine light climate in the years before, during and after our experiments and its potential effects on DVM and prey vulnerability to predation by *Bythotrephes*. We generated depth profiles of PAR at times of interest during our experiments from incident solar radiation measured at the nearby Lake Michigan Field Station in Muskegon (<http://www.glerl.noaa.gov/metdata/mkg/>) and extinction coefficients determined from shipboard measurements of PAR-depth profiles (described below).

In addition, on August 4, 2004, a clear, sunny day, we generated profiles throughout the 24-h cycle to represent conditions typical of clear weather at Muskegon during early and mid-August. PAR profiles were generated for years before (1994/1995 and 2000) and after (2010/2011) expansion of mussels into deep water by using incident PAR from August 4, and k_{PAR} values measured during these different years. We took k_{PAR} data from the U.S. EPA GLENDATA data base (http://www.epa.gov/greatlakes/monitoring/data_proj/glenda/) for 1994/1995, the EEGLE data base for 2000 (<http://www.glerl.noaa.gov/eeagle/>), and unpublished observations from 2010/2011 for stations located at or near our study sites.

Using these data, we generated depth profiles of $f(L)$, the light mediated prey vulnerability function of *Daphnia* to *Bythotrephes*, to help understand *Bythotrephes*, *Daphnia*, and other zooplankton DVM and consumptive impacts of *Bythotrephes*. That is, would *Daphnia* and other zooplankton seek out light levels where $f(L)$ were below the threshold for efficient predation by *Bythotrephes*? We calculated $f(L)$, which ranges between 0 and 1, from a relationship presented by Pangle and Peacor (2009) predicting relative consumption *Bythotrephes* feeding on *D. mendotae* as a function of PAR intensity L ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$):

$$f(L) = 1 / \left[1 + (L/5.97)^{-1.40} \right]. \quad (1)$$

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