Journal of Great Lakes Research 41 Supplement 3 (2015) 125–142

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

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

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ARTICLE INFO

Article history:
Received 16 October 2014
Accepted 22 September 2015
Available online 25 October 2015

Communicated by Tomas Hook

Index words:
Cercopagis
Bythotrephes
Daphnia
Invasive species
Alewives
Diel vertical migration

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.

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 zooplankter (~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-Ptáčníková 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* (Ptáčníková 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-Ptáčníková 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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http://dx.doi.org/10.1016/j.jglr.2015.10.005
0380-1330/Published by Elsevier B.V. on behalf of International Association for Great Lakes Research.

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-Ptáčníková 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 (2010/20011) 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 GLENDA 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/eegle/), 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 (μmol quanta m^{-2} s^{-1}):

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

Intensive spatial study—experimental design

The broad experimental design included examining spatial and predatory interactions among mesozooplankton and visually preying invasive cercopagids and alewives at a nearshore (M10, 10-m deep site: 43.188° N 86.330°W) and an offshore site (M60, a 60-m-deep site; 43.188° N, 86.453°W) in southeastern Lake Michigan in the same time frame using the short transect approach described by Vanderploeg et al. (2009a,b). We conducted two cruises, each of which consisted of a 1.5-d survey at M10 followed immediately by a 1.5-d survey at M60. The first cruise (August 2–4, 2004) was conducted on days near the full moon, and the second, two weeks later, occurred at the time of the new moon (August 16–19). Thereby, we could contrast vertical migration patterns of zooplankton and alewives, which can have different migratory patterns depending on the phase of the moon (Janssen and Brandt, 1980; Janssen, per. com.). Some of the results for M10 are published in Pothoven et al. (2007), particularly those dealing with fish consumptive impacts. We use these nearshore data and new analyses of *Bythotrephes* and zooplankton for our comparison with M60 results.

Similar technologies, methods, and experimental approaches were used at both sites. We sampled four complete sampling cycles over the diel cycle on the first cruise and six complete sampling cycles on the second cruise at M60 to capture conditions at times near solar noon, midnight, and just before or after day-night transitions. For reference, on August 4, sunrise, solar noon, and sunset were respectively 06:38, 13:50, and 21:04 EDT; on August 18, respective times were: 06:54, 13:49, and 20:44 EDT. M10 was sampled seven times over the diel cycle on August 2–3 and eight times on August 16–17 (Pothoven et al., 2007). Because we did not see any noteworthy patterns of vertical structure of zooplankton in the shallow unstratified water column at M10, we do not report PSS results.

Intensive spatial study—fish, plankton, and physical variables at M60 and M10

To start the cycle sampling sequence, we conducted bottom and midwater trawls to capture alewives for diet analysis. Alewife and other planktivorous fishes were collected using a 7.6-m semi-balloon 4-seam Skate model bottom trawl (13-mm stretched-mesh cod-liner). The bottom trawl was towed along or near the ~60-m or ~10-m depth contour for approximately 15–20 min at a speed of ~1 m s^{-1}, and all fish were immediately frozen (Pothoven et al., 2007). Use of the midwater trawl was abandoned after a few trials because few fish were captured; all data presented are for fish that were captured in the bottom trawl. Sufficient fish for diet analysis were collected only on the first cruise at M60; in contrast, alewives were captured at all sampling times at M10 on both cruises (Pothoven et al., 2007).

Immediately following each deployment of the bottom trawl, the transect was sampled using fishery acoustics with a Biosonics DT6000 129 kHz split beam echosounder (ping rate of 3 pings s^{-1}, a pulse width of 0.4 ms, and a target acquisition threshold of −70 dB) and PSS. Transects were conducted along the ~10-m and ~60-m depth contours in approximately N–S and S–N directions near and N and S of M10 or M60 at a boat speed of 7.5 km h^{-1}. Note that there was not exact overlap between trawl transects and PSS/acoustic transects so that there would not be any effect of trawling on acoustic sampling. The PSS consisted of a mini optical plankton counter (OPC; Model 2 T, Focal Technologies, Dartmouth, NS), an Aquatracka III fluorometer (which has four decade logarithmic amplifiers, Chelsea Technology Group, Surrey, UK), an OS200 CTD (Conductivity, Temperature, Depth sensor; Ocean Sciences, San Diego, CA), and a Biospherical Instruments Model QSP-2300 4π quantum scalar PAR sensor mounted on a V-fin (Ruberg et al., 2001; Vanderploeg et al. 2009a,2009b) that was continuously raised or lowered at 0.25 m s^{-1} between bottom and surface as the boat moved at 2.5 m s^{-1} to create a sinusoidal path along the transect. Data collected from all sensors on the PSS were logged at 2 Hz. The half hour time period allowed us to do four undulations of the PSS for data analyses at M60. The PSS mapped out temperature, chlorophyll fluorescence, and number and biomass of zooplankton-sized particles (>0.25 mm equivalent spherical diameter) using the standard software for conversion of size categories to equivalent volume of spheres (Liebig et al., 2006; Liebig and Vanderploeg, 2008).

At the end of each acoustics/PSS transect, we lowered an instrument package—hereafter referred to as a CTD—consisting of Seabird CTD (conductivity-temperature-depth), scalar PAR (Biospherical Instruments Model QSP-2300 4π quantum scalar) sensor and Sea Tech fluorometer. Temperature profiles were used for choosing depth intervals to sample zooplankton in the epilimnion, metalimnion, and hypolimnion with a messenger actuated, choke-off vertical opening/closing net (1-m diameter, 4-m-long, 153 μm mesh); duplicate tows were made and results are presented as means. This allowed us to obtain species-specific information on zooplankton; but, unlike optical plankton counts, it was limited to relatively coarse vertical spatial resolution (~10 m). Using information from the tows in each depth zone and thickness of the depth zones, we also calculated an integrated full water column concentration at each sampling cycle so we could compare species composition between cruises and between deep-water and shallow sites. We describe completion of all sampling events on a transect at a given time period as a cycle, and we used multiple sampling cycles to capture diel interactions. The same net was used to sample zooplankton at M10. Because of the shallow depth there and lack of stratification, only full water-column tows were made at M10.

Data and sample analysis at M60 and M10

Both PSS and acoustics data were binned in 1-m intervals and presented as 1-D vertical plots. Because the fluorometer on the PSS was functioning intermittently, we determined depth distribution of chlorophyll fluorescence and all physical variables except temperature from vertical casts of the CTD. As with the PSS fluorometer in previous work (Vanderploeg et al., 2007, 2009b), linear regression ($R^2 = 0.97$, $n = 5$, $P < 0.01$) was used to convert fluorometer measurements (volts) on the CTD instrument package to derived chlorophyll *a* from measurements of chlorophyll *a* in grab samples. These samples were collected at night (same time CTD was deployed) using Niskin bottles at different depths at M60 (5, 22, and 35 m on the second cruise) and at M10 (5 m on first and second cruises). Because the CTD was used 0.5–1 h after the PSS/acoustics tow, we back-calculated PAR profiles to time of PSS/acoustics tows using the extinction coefficient determined on the CTD cast and incident PAR measured at the nearby Lake Michigan Field Station at the time of the PSS/acoustics tow. This was pertinent to capturing PAR profiles for PSS/acoustics runs near transitions between day and night.

We used Echoview 3.3 (Sonar Data, www.sonardata.com) software to analyze the acoustic data. Prior to processing, raw acoustic files were inspected for bottom intrusion and noise. All acoustic data were processed using a threshold of −60 dB for the echo-squared integration. Target strength values were converted to estimates of length using the equation developed by Warner et al. (2002) for alewives. All midwater targets were assumed to be alewife since alewives were the only pelagic species collected in day and night bottom trawls. Alewives were binned into small (≤100 mm total length) and large (>100 mm total length) size categories. Since large alewives dominated the biomass at both M60 and M10, and no small alewives were captured for diet analysis at M60, we restricted our analyses to large alewives. Large alewives are of particular interest to our study because of their ability to feed on *Bythotrephes*.

Using known optical plankton counter (OPC) size (equivalent spherical diameter [ESD]) bins for different zooplankton species determined from lab experiments (Liebig and Vanderploeg, 2008), we were able to identify two size regions that corresponded to species of interest: *D. mendotae* (0.75–1.5 mm ESD) and *Bythotrephes longimanus* (1.5–

3.5 mm ESD). Choice of the lower threshold of 0.75 mm for *Daphnia* could exclude the smaller individuals of the population (Liebig and Vanderploeg, 2008). This was necessary to avoid overlap with medium-sized copepods (*Leptodiaptomus sicilis*) that can occur in this size range. Most of the biomass of *Daphnia* population was above this threshold and we do not expect that smaller individuals would have very different DVM patterns from larger individuals. *Limnocalanus macrurus* overlaps in size with large *Daphnia*. This overlap can be a problem if *Limnocalanus* is abundant and mostly affects the hypolimnetic region, where it is usually found (Liebig and Vanderploeg, 2008; Vanderploeg et al., 2012). In some places in the text we refer to size, depth preferences, and feeding habits of different species of zooplankton. Species size can be found in Liebig and Vanderploeg (2008) and most other characteristics found in Table 1 of Vanderploeg et al. (2012). For those characteristics not described in these papers, we cite appropriate literature.

Zooplankton analysis from net tows followed the same protocols detailed by Cavaletto et al. (2010) and Vanderploeg et al. (2012). To determine zooplankton abundance and composition, an aliquot was taken from a known sample volume with a Hensen–Stempel pipette, so that a minimum 550 zooplankters were identified for each sample. To count large predatory cladocerans, which were found in lower densities than other zooplankton, the whole sample was rinsed through a 600 μm mesh sieve, and all specimens were identified and counted.

To determine zooplankton biomass, length measurements were made on a subsample of taxa (10 adult copepods and 25 copepodites or cladocerans from one of the replicate tows) that accounted for over 10% of the total density using Image Pro Plus image analysis software (Media Cybernetics, Silver Spring, MD). Up to 100 individual large predatory cladocerans were measured for each sample. Dry weight biomass of zooplankton taxa collected in plankton nets and fish stomach contents (described below) were determined from length-weight regressions using Culver et al. (1985) for *Leptodiaptomus* spp., *Chydorus*, *Bosmina*, *Leptodora*, *Diacyclops*, copepod nauplii, *D. mendotae*, *Diaphanosoma*, and *Eurycercus* (using relation for similarly shaped *Chydorus*); Grigorovich et al. (2000) for *Cercopagis*; Malley et al. (1989) for *Epischura* and *D. retrocurva*; and Markarewicz and Jones (1990) for *Bythotrephes*. For zooplankton taxa that were less than 10% of the sample, a mean default taxon-specific weight was used from the literature (Hawkins and Evans, 1979).

At M60, alewives for diet analysis were collected in trawls at 07:00 and 19:00 EDT on August 3 (n = 16 in each collection). At M10, large alewives were collected on each sampling cycle for a total of 397 fish (Pothoven et al., 2007). Diet analysis of adult alewives followed methods of Pothoven and Vanderploeg (2004) and Pothoven et al. (2007) summarized below, and selectivity was expressed as Vanderploeg and Scavia's (1979) selectivity coefficient W′ using the full water column abundance of zooplankton as prey concentration. Results from both day and night collections were pooled because results for diet, and W′ for both collections were nearly identical at M60. At M10, diet analyses and W′ were calculated for each cruise (Aug. 2–3; Aug 16–17).

In the laboratory, fish were measured (nearest mm total length) and weighed (nearest gram), stomach contents were removed, and the entire fish (minus stomach contents) was dried at 70 ° C to a constant weight. To determine diet composition, all large prey (*Bythotrephes*, *Cercopagis*, *Leptodora kindtii*) from each stomach were identified and counted. Only bodies with eye-spots of *Bythotrephes* and *Cercopagis* were used to enumerate partial prey, because spines can accumulate in stomachs (Branstrator and Lehman, 1996). Mesozooplankton (e.g. Copepoda, Cladocera) from each stomach were added to a known volume (10–25 mL) of water and sub-sampled with a 1 mL aliquot, so that approximately 100 individuals were counted. If stomachs contained fewer than 100 mesozooplankton, all individuals were counted. Mesozooplankton were classified as Bosminidae, Daphnidae, Cyclopoida, Calanoida, and nauplii. Prey lengths of at least five intact individuals of each prey group, except nauplii, from each stomach (if available) were measured using Image Pro image analysis software (Media Cybernetics, Silver Spring, MD). Prey length was converted to dry weight using weight-length regressions described above. The average dry weight of an individual of each prey type was determined for each size class of alewife and multiplied by the number of each prey type in a stomach. Prey weights of each prey group were summed across all individual fish from a sample date, and diet composition was determined as the percent of the total calculated dry weight.

Table 1
Bythotrephes characteristics used in Yurista et al. (2010) model: Instar compositions (%) and median instar dry weight (μg). Data were pooled from all individuals taken from both M60 and M10.

Instar	Composition (%)	Weight (μg)
1	18	115
2	66	209
3	16	246

Bythotrephes and alewife feeding impact

In comparing consumptive impacts of *Bythotrephes* and alewives at M60 on the first cruise (for which we have diet information for alewives) with results from M10, we had to factor in the roles of vertical migration and prey selection. To explore the potential consequences of vertical migration and prey selection on the pelagic community at M60, we compared consumptive impacts of *Bythotrephes* and fish on dominant zooplankton species in the epilimnion, metalimnion, and hypolimnion day and night using bioenergetics and empirical production and biomass estimates of all predators and prey for the first cruise at M60.

Theoretically, both effects of light intensity and prey selection can be factored into consumptive impact of *Bythotrephes* predation on different prey types (C_i) in a straightforward way:

$$C_i = C(T) \cdot f(L) \cdot r_i, \tag{2}$$

where $C(T)$ is the total consumption from bioenergeticts relationships (see below) for a given temperature (T), $f(L)$ is the light mediated effect function (range: 0–1) on consumption, and r_i is the proportion of prey i in the diet, which we can estimate from known prey selectivity and from abundance at the time of the observation (see below).

As noted above in the description of $f(L)$ (Eq. (1)), light is a major mediator of prey consumption in *Bythotrephes* (Jokela et al., 2013; Muirhead and Sprules, 2003; Pangle and Peacor, 2009). *Bythotrephes* requires much more light (more than an order of magnitude more) than fishes for effective predation (e.g., Vanderploeg et al., 2009a, 2009b). The $f(L)$ vs. L relationship predicts that above ~10 μmol quanta m^{-2} s^{-1}, *Bythotrephes* feed at near maximum rate and that no feeding occurs on *D. mendotae* in the dark. Consumption drops off quickly below ~3 μmol quanta m^{-2} s^{-1}. Jokela et al. (2013) also observed no feeding in the dark on *Daphnia* (*D. pulex* and *D. pulicaria*) in dark-treatment enclosures. In some of the experiments described in Jokela et al. (2013), however, there was feeding on the small cladoceran *Bosmina*; therefore, it is possible there is some predation on small cladocerans under very low light conditions. To approximate consumption, we assumed all consumption would occur during the day, with *Bythotrephes* feeding only on the daytime assemblage with which it overlaps. Because of the high position of *Bythotrephes* in the water column where, $f(L)$ was high throughout much of the daylight hours (see results), $f(L)$ was assigned a value of 1 in Eq. 2.

We estimated total daily (occurring entirely in daytime) *Bythotrephes* consumption, $C(T)$, of zooplankton at M60 and M10 using the bioenergetics model of Yurista et al. (2010), which assumes unlimited prey availability, and the more conservative "*Bythotrephes* efficiency" model (Pothoven and Höök, 2014) of Dumitru et al. (2001) that uses the temperature-production model of Shuter and Ing (1997) for *Cladocera*, divided by

0.27 for prey conversion efficiency. Instar and *Bythotrephes* weights necessary for the bioenergetics model are shown in Table 1. Abundance of *Bythotrephes* in each layer came from averaging abundance in each layer from all the net tows because of high variability of abundance from net tow to net tow and general similarity of depth distribution for day and night samples.

To define the diet proportions (r_i) necessary for partitioning consumption among different prey of *Bythotrephes*, we used published prey selectivity information coupled with measured average daytime prey abundance in the basic definition of selectivity (Eq. (1) of Vanderploeg and Scavia, 1979):

$$r_i = X_i W_i' / \sum X_i W_i', \tag{3}$$

where X_i is abundance (expressed in either number or biomass) of prey *i*, and W_i' is the selectivity coefficient. We assigned values of 1, 0.2, and 0.1 for selectivity coefficients for cladocerans, nauplii, and copepods (e.g., Vanderploeg et al., 1993). Ptáčníková et al. (2015) showed that selectivity for C*ercopagis* was the same as for *D. mendotae*; therefore we assigned a value of 1 also to *Cercopagis*. As noted above, *Leptodora* is known to be consumed by *Bythotrephes*, but selectivity or feeding rates are not known. Consistent with other Cladocera, we assigned them a selectivity coefficient of 1.

Alewives can be either size-selective or not in either the light or dark. Being size-selective can be visual (Janssen 1976) or in the dark using their lateral line (Janssen et al. 1995). Being non-size selective can occur via ram filter feeding in the light (Janssen 1976) or in the dark (Janssen 1980). Pothoven et al. (2007) observed alewife fed during all sampling cycles at M10. Considering all these results, we assumed that alewife consumption at M60, like that at M10, was temperature and not light driven.

We estimated adult alewife consumption on zooplankton and *Bythotrephes* relative to their production on the first alewife cruise at M60 from the information on diet, acoustic abundance, and size of fish collected on this cruise. Total alewife abundance was based on nighttime acoustic abundance. The fraction of fish in each layer during both night and day was multiplied by total abundance to determine abundance in each layer. The day and night abundance was weighted by the fraction of the diel cycle in light (0.59) and dark (0.41).

Maximum consumption (wet weight) was determined as an allometric function of fish mass (Hanson et al., 1997) using the temperature-dependent function from Thornton and Lessem (1978). As done in previous alewife bioenergetics modeling studies (Stewart and Binkowski 1986), we assumed an adult alewife during the summer experienced an average daily water temperature of 7.8 °C at M60 based on the water temperatures and the amount of time spent within each depth strata as determined from acoustics. Parameter inputs for consumption determinations for adult alewife were taken from Stewart and Binkowski (1986). We used a 30.6 g alewife for consumption calculations based on the average weight of adult alewives collected in bottom trawls on August 3–4, 2004. We assumed that the proportion of maximum consumption consumed by an adult alewife during summer was 0.19, based on Stewart and Binkowski (1986); a nearly identical value (0.20) was obtained by Pothoven and Madenjian (2008) from measured growth and bioenergetics estimates of consumption at the time of our experiments. At M10, we estimated alewife consumption with the ration method using the temperature at the site (Pothoven et al., 2007).

Because bioenergetics calculations in fish are based on wet weight, the dry weight of each prey type (copepods, cladocerans, Mysis) was converted to wet weight using wet to dry weight ratios appropriate to each taxon (Hanson et al., 1997), and wet weight diet composition was determined. Consumption as g food g fish^{-1} d^{-1} (wet weight) was multiplied by the average fish weight (30.6 g) to determine g food alewife^{-1} d^{-1}. This amount was multiplied by the proportion of each prey type in the diet to determine the amount of each prey type (wet weight) eaten per day. Because we were interested in knowing consumption in the different regions of the water column to compare directly with the estimated zooplankton production for the different layers, we took total water column consumption and estimated the proportion of consumption occurring in different layers based on alewife abundance in each of the layers.

The amount of each prey eaten was then converted back to a dry weight using taxon-specific wet to dry weight ratios and summed across prey types to determine the total amount of food eaten per day on a dry weight basis. This amount was multiplied by the abundance of adult alewife determined from night acoustics (number m^{-3}) to determine g food eaten m^{-3} d^{-1} and was compared to production estimates of zooplankton (based on dry weight).

Daily production rates for prey groups within the epilimnion, metalimnion, and hypolimnion were determined separately using production/biomass (P/B) relationships. Production for cladocerans (including *Bythotrephes*) and copepods was determined using the temperature-based daily P/B relationships from Shuter and Ing (1997):

$$\log P/B_{daily} = \alpha + \beta T \tag{4}$$

where $\alpha = -1.725$ (Cladocera), -1.766 (Cyclopoida), or -2.458 (Calanoida) and $\beta = 0.044$ (Cladocera), 0.040 (Cyclopoida), or 0.050 (Calanoida). A P/B value of 2.82 was used for *Mysis relicta* (Reynolds and DeGraeve, 1972). Water temperature (T) was measured directly in the field on each date, and epi-, meta-, and hypolimnion temperatures were taken from the mid-depths of each zone. Respective depth zones and midpoint temperatures (in parentheses) were: 0–12 m (20.9 °C), 12–28 m (13.8 °C), and 28–60 m (5.8 °C). All production estimates for prey groups were determined on a volumetric (mg dry weight m^{-3} d^{-1}) basis to allow for comparison with fish consumption data. Production was determined for each time interval and averaged over all sample periods to obtain one estimate of production for each date and depth interval. To express consumptive impacts of both alewives and *Bythotrephes* on the zooplankton community, we report consumption:production (C:P) as a measure of impact; a ratio of ≥1 would imply control of prey populations by predation.

Results

Changing water clarity in Lake Michigan

Lake Michigan water clarity increased in mid-depth and offshore waters in years beginning (2004) and after the expansion of dreissenid mussels into deep water relative to years before (1994–2000) (Fig. 1). Mean k_{PAR} was 0.13 (Range 0.12–0.14) at M60. Respective k_{PAR} values taken from Fig. 1 to represent conditions before, during, and after the expansion to deep water were 0.23, 0.13, and 0.09. As expected light-mediated prey capture efficiency, $f(L)$, was much higher at a given depth during and after the expansion (Fig. 2). At the time of our experiment, PAR was ~10 μmol quanta m^2 s^{-1}, and $f(L)$ was ~0.8 for the upper 40 m of the water column throughout much of a sunny day. At the time of our cruises, light extinction at M10 was highly variable—likely a result of resuspension and riverine input at M10; k_{PAR} varied between 0.24 and 0.44 m^{-1} on the first cruise and 0.14 and 0.29 m^{-1} on the second cruise. Because of the shallow depth at this station, light extinction would not play a factor in *Bythotrephes* predation, since PAR at the 10 m depth would equal or exceed 10 μmol quanta m^{-2} s^{-1}.

Spatial connections: first cruise—full moon cruise

Vertical distribution of zooplankton and fish showed marked changes for the given depth distributions of temperature and chlorophyll as light changed during the four sampling cycles (C1–C4) over the diel sampling period (Figs. 3 and 4). Well-developed stratification is seen with the bottom of the epilimnion occurring at 12 m and the bottom of the metalimnion at 28 m. However, there were subtle changes in the depths of the epilimnetic-metalimnetic and metalimnetic boundaries

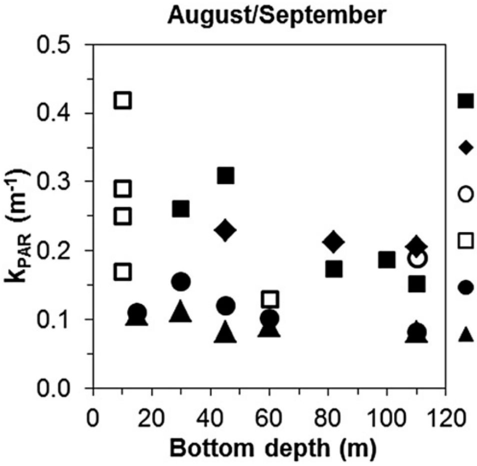

Fig. 1. Extinction coefficient for photosynthetically active radiation (k_{PAR}) at sites on or near the Muskegon transect during late summer. Measurements for 2004 were taken on spatial cruises of present study.

throughout the day (Fig. 3; Table 2). Despite these changes, original boundaries were used throughout the day for sampling with nets. Surface PAR, as expected, was maximal near solar noon under relatively sunny skies and relatively low at 07:45, reflecting early morning incident PAR and overcast conditions. Light rain attenuated surface PAR at 20:00 EDT and moonlight (not reliably measureable) at 00:45 EDT. A deep chlorophyll layer can be seen at the bottom of the metalimnion.

The zooplankton community was dominated by *D. mendotae* and *Leptodiaptomus* copepodites (stages C1–C5) with *Limnocalanus*, *L. sicilis*, and *Epischura* being secondary dominants (Table 3; Fig. 4). On the whole, the zooplankton community was centered in the metalimnion both day and night (Fig. 4a). The cladocerans *Daphnia* and *Bosmina*, the small diaptomid *Leptodiaptomus minutus*, and cyclopoid *Diacyclops* showed a strong shift from epilimnion at night to metalimnion during day. The middle-sized diaptomid, *Leptodiaptomus ashlandi*, stayed in the metalimnion, and the large diaptomid *L. sicilis* was found both in the hypolimnion and metalimnion, with the greatest depth found near solar noon. The highest concentration of the large predatory calanoid *L. macrurus* was found in the hypolimnion. On a biomass basis, the largest diel vertical migration (DVM) of the zooplankton community was for *Daphnia* movement between the metalimnion and epilimnion.

The OPC showed a diffuse distribution of particles in the *D. mendotae* size range (hereafter know as digital *Daphnia*) in the epi- and metalimnion at night, and the concentrated abundance found at depth at other times. Environmental conditions at the depth of the digital *Daphnia* maximum at different times during the diel cycle are shown in Table 2. The lowest position in the water column occurred mid-day near solar noon at a depth of 32 m at the location of the metalimnetic–hypolimnetic boundary (Fig. 3 and Table 2). Here both PAR intensity and *f*(*L*) were high (Figs. 2 and 3, Table 2). There appeared to be some overlap of digital *Daphnia* with the lower portion of the deep chlorophyll layer during the day but little overlap with digital *Bythotrephes*, which were mostly found higher in the water column (Fig. 3 and Table 2). The greatest spatial overlap between fish and digital *Daphnia* occurred in the transition from light to dark and at midnight. At early light (C3),

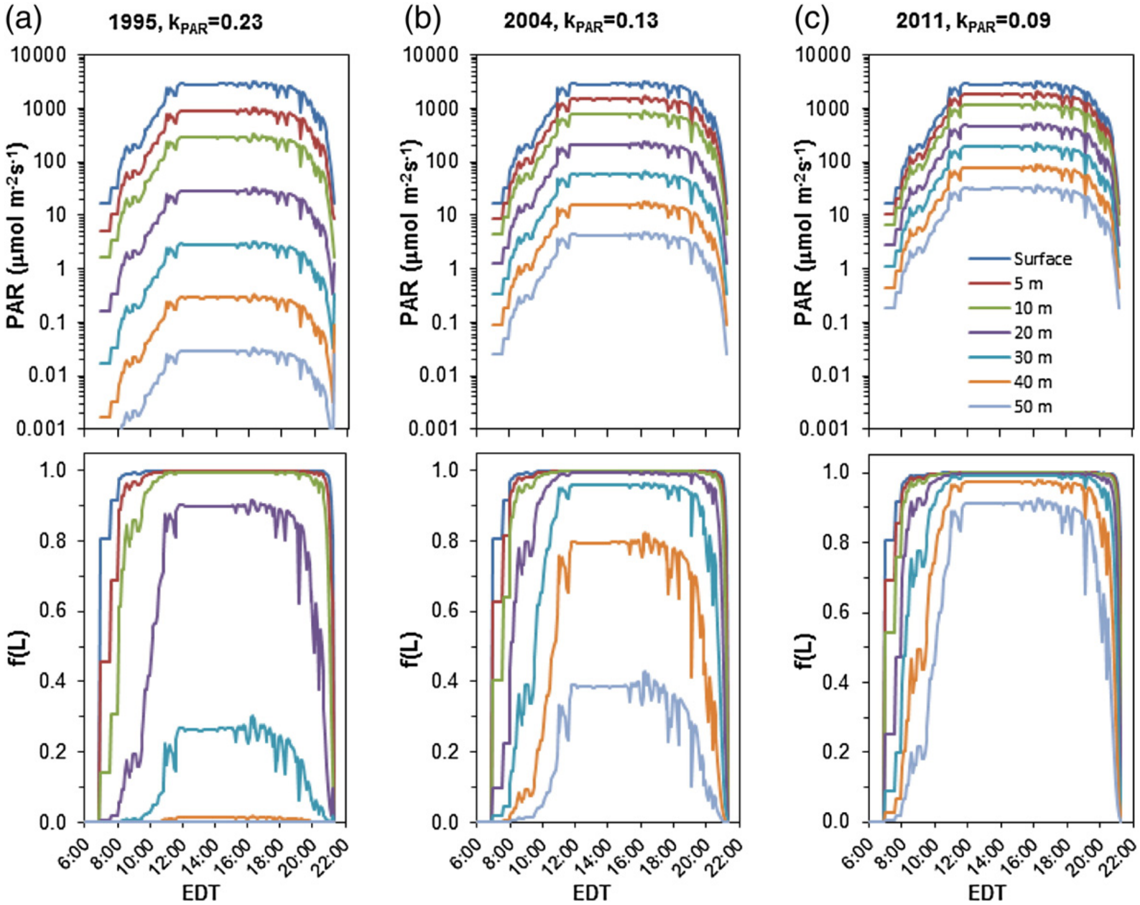

Fig. 2. Photosynthetically active radiation (PAR) and *f*(*L*), the light-mediated prey capture efficiency of *Bythotrephes*, at different depths in the water column at M60 for different extinction coefficients of PAR using surface PAR measured at the Lake Michigan Field Station on August 4, 2004. Results are shown for different k_{PAR} values representing (a) conditions in 1995 before the expansion of dreissenids into deep water, (b) the average measured during the experiments in August 2004 representing the cusp of the dreissenid expansion, and (c) the amount measured at the time of full dreissenid expansion into deep water.

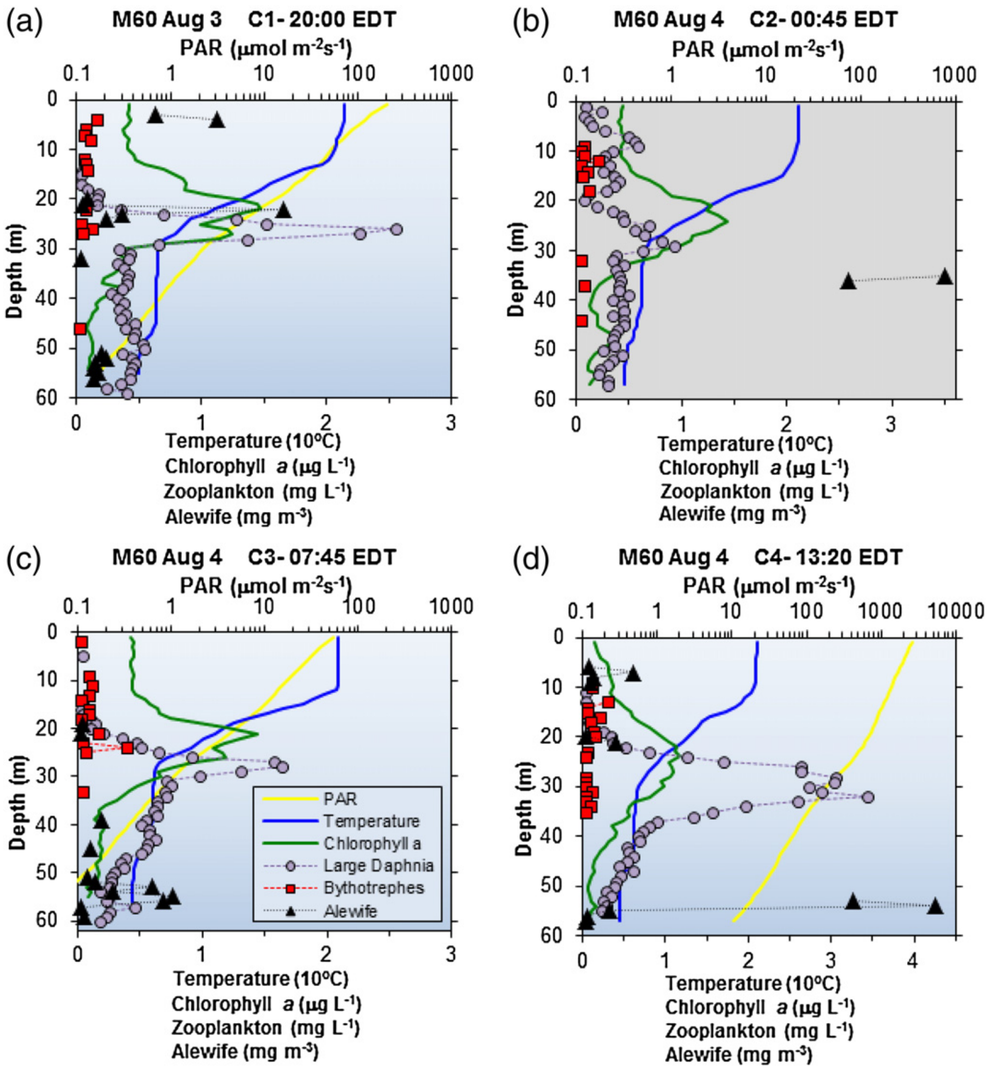

Fig. 3. Vertical distribution of physical variables (temperature and PAR), chlorophyll *a*, zooplankton (*Daphnia mendotae* and *Bythotrephes*), and alewives as seen by the CTD instrument package, plankton survey system, and acoustics on August 3–4. Fish and zooplankton masses are in units of wet weight. The blue background shading is used to indicate day observations and gray shading to indicate night observations. Note temperature scale must be multiplied by 10 for actual values.

digital *Daphnia* were found quite deep at the metalimnion–hypolimnion boundary. At this time, fish are already on or near the bottom. Not much change is observed from early morning to midday in either digital *Daphnia* or fish. Most of the digital *Bythotrephes* biomass was found in the epilimnion or upper metalimnion.

The trends observed with the OPC fit the broad trends observed with net tows for *Daphnia* and *Bythotrephes* in the epilimnion, metalimnion, and hypolimnion (Fig. 4); however, the occurrence of digital *Daphnia* in the deep hypolimnion—not seen in net tows—is likely an artifact caused by abundant *Limnocalanus* that can overlap in size (Liebig and Vanderploeg, 2008).

Spatial connections: second cruise—new moon cruise

On the second cruise, we completed six cycles of sampling (C1–C6) (Fig. 5). The epilimnion and metalimnion were greatly expanded (Fig. 5) relative to the first cruise (Fig. 3), and because of clearer weather, PAR was much higher at a given depth; k_{PAR} was 0.12 m^{-1}, very similar to the first cruise. A combination of mixing and downwelling caused by high winds and winds from the south (measured at Muskegon) between cruises may have led to this structure.

Because of the limitation of sampling relatively broad depth regions with vertical opening/closing nets, the unusual and changing thermal structure over the diel cycle (Fig. 5; Table 2) made sampling of the same discrete well-defined thermal regions difficult. As a result, we sampled somewhat different depth zones over the diel cycle. Sample regions for the epi-, meta-, and hypolimnion were 0–15, 15–48, and 48–59 m for C1 and C2; and 0–20, 20–30, and 30–56 m for C3–C6. For simplicity of presentation of net tow data (Fig. 6), average depths of boundaries for epilimnion–metalimnion and metalimnion–hypolimnion sampled over the diel cycle are shown (dashed lines in Fig. 6), and the data points for abundance for C1 and C2 are shown at different depths than C3–C6 to represent their location in the middle of the zone sampled at those times (Fig. 6).

Zooplankton community structure and biomasses of dominant zooplankton as well as *Bythotrephes* were very similar to the first cruise (Table 3). Zooplankton on the second cruise was again dominated by *D. mendotae* and secondarily by diaptomid copepodites (stages C1–C5). *L. sicilis* and *Limnocalanus* were found in lower abundance, and *Mysis* was absent. Reflecting behavior of *Daphnia*, there was a shift of the total zooplankton at night from the metalimnion to the epilimnion (Fig. 6a, b). Net tow data showed the same broad diel habitat preferences as was seen in the first cruise.

This cruise with its six sampling cycles demonstrated how quickly the zooplankton shift with light changes. Again, digital *Bythotrephes* was found mainly in the epilimnion and the metalimnion. During all daylight collections (C1, C2, C3, C6), digital *Daphnia* were quite deep at the bottom of the metalimnion or on the metalimnion–hypolimnion interface. Although some alewives were seen in the epilimnion near solar noon (C2), most alewives were seen in the water column at night, and most were seen in the hypolimnion and metalimnion (C4 and C5). Digital *Daphnia* found at the 48-m depth at 19:00 were seen in the epilimnion only after dark (23:35 and 04:20) and were diffusely distributed there; therefore, the greatest overlap with digital *Bythotrephes* was seen at these times. These trends observed with the OPC fit broad trends observed with net tows for the hypolimnion, metalimnion, and epilimnion (Fig. 6).

Although there was a deepening of the metalimnion, the deep chlorophyll layer was still found at about the same depth as on the first cruise. Because of its very deep migration, *Daphnia* was far below this layer during the daytime (Fig. 5 and Table 2). Note that the nighttime or dim-light chlorophyll profiles (C3–C6) more accurately capture the chlorophyll concentration in the epilimnion because of nonphotochemical quenching that attenuates fluorometer response under high light conditions (e.g., Vanderploeg et al., 2007).

Prey selection and feeding impact by alewives at M60

Bythotrephes was the preferred prey of adult alewives at M60 (Fig. 7) despite their limited overlap (Figs. 3 and 4; Table 4). As seen in Table 4, the bulk of adult alewives were found in the hypolimnion over the daily cycle, whereas most *Bythotrephes* were found in the epi- and metalimnion. *Bythotrephes* was the largest prey available at M60, except for *Mysis*, a hypolimnetic-metalimnetic macrozooplankton prey, which was not abundant. Relative to *Bythotrephes* ($W' = 1$), W' values of all other prey—including *Daphnia*, *Cercopagis*, and *Mysis*—were < 0.02 (Fig. 7).

Estimated feeding impact of alewives calculated from acoustic abundance information and weight of alewives (Table 4) on all zooplankton species including *Bythotrephes* (Table 5) was small because of low alewife abundance, 19.1 fish ha^{-1} (0.00003 m^{-3}). The analysis of consumption based on time in depth zone and prey abundance suggested that most alewife consumption of *Bythotrephes* and other zooplankton was in the hypolimnion; however, *Bythotrephes* and total zooplankton production was greatest in the epilimnion and metalimnion. C:P for alewife predation on (the few) *Bythotrephes* in the hypolimnion was 5.3, far exceeding the value of 1 needed for control. We also include production information on *Cercopagis* (found in the epilimnion) and the

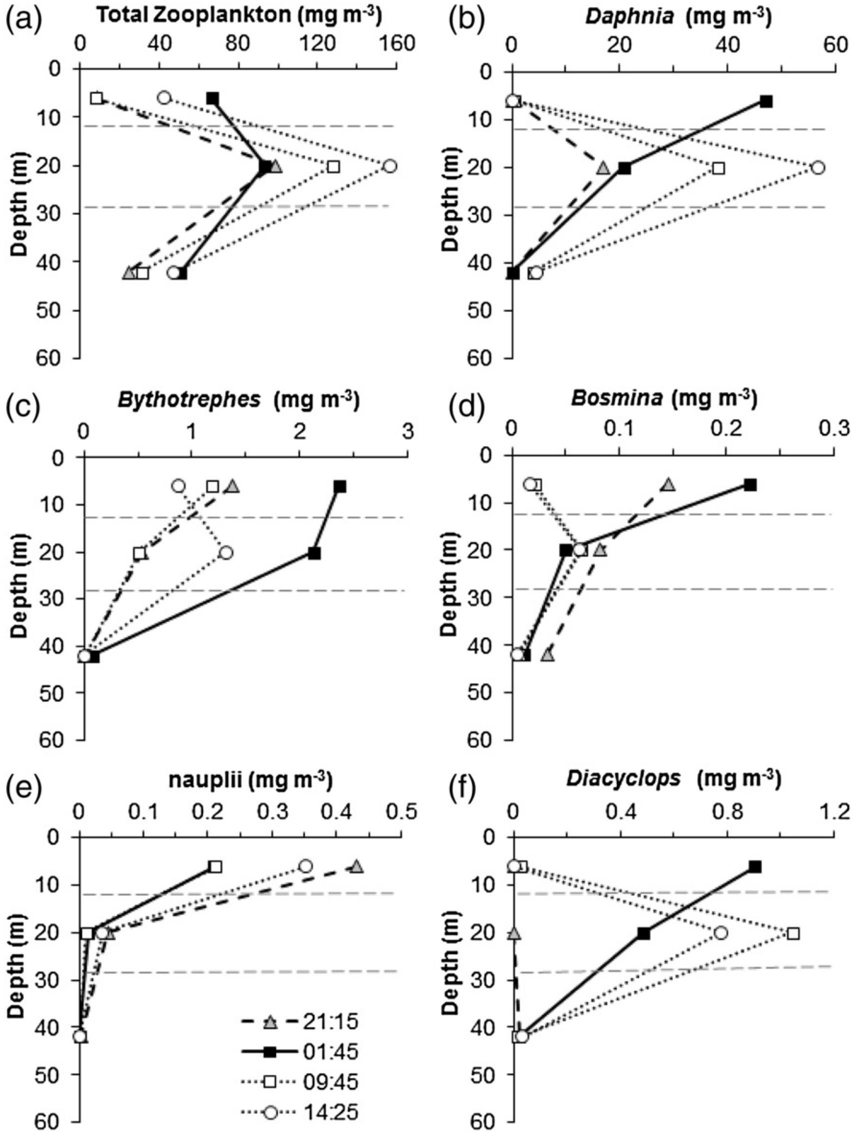

Fig. 4. Vertical distribution of major zooplankton species captured over the diel cycle at M60 on August 3–4. The dashed lines indicate boundaries between epi-, meta-, and hypolimnion.

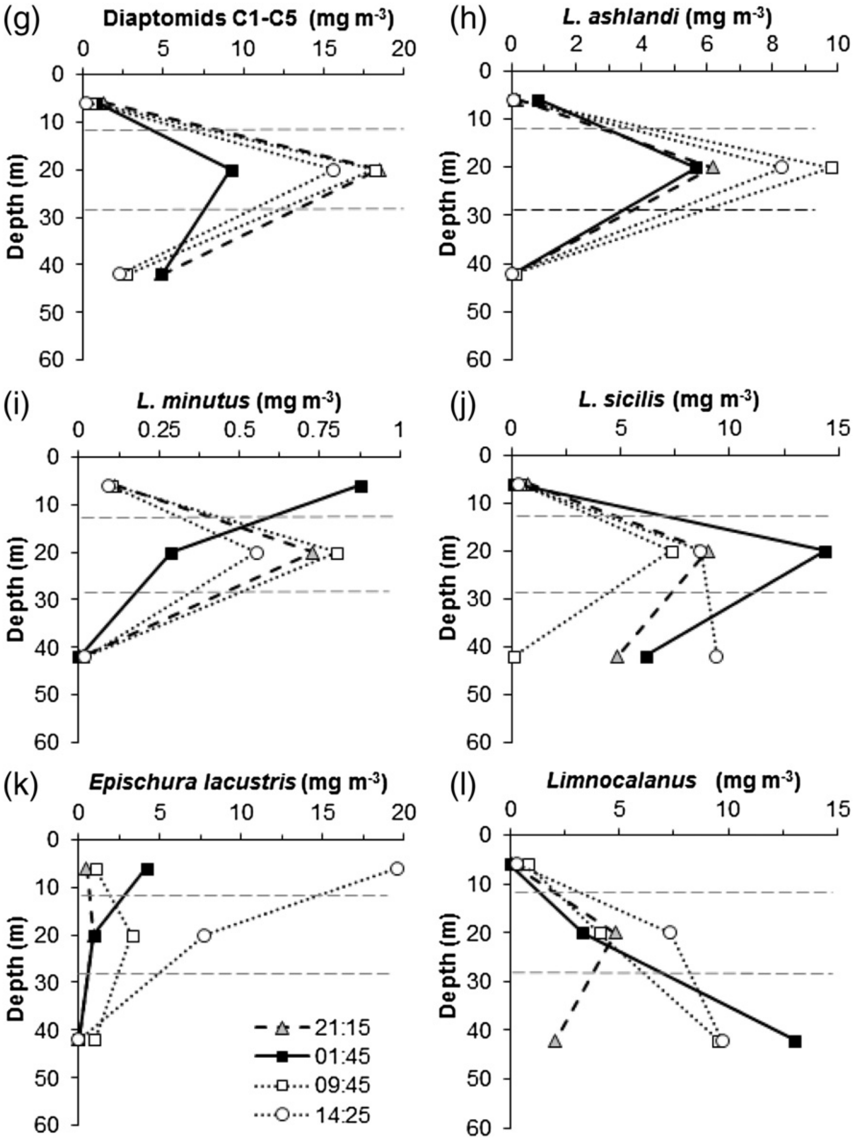

Fig. 4 (*continued*).

native predatory cladoceran *Leptodora* (epi- and metalimnion). They were found in extremely low abundance (Table 3), are not shown on depth distribution plots (Fig. 4), and were not found in any alewife stomachs. The C:P ratio of alewives for the total zooplankton community was <0.01 for the total water column; C:P for the preferred *Bythotrephes* was much higher but still very low (0.05).

Table 2
Depths of epilimnetic–metalimnetic (E-M D, m) and metalimnetic–hypolimnetic (M–H D, m) boundaries and conditions at depth (D, m) of *Daphnia* maxima for different times during diel sampling cycles (C1–C4 on Aug. 3–4; C1–C6 on Aug 18–19): temperature (T, °C), photosynthetically active radiation (PAR, μmol quanta m^{-2} s^{-1}), light mediated capture vulnerability function ($f(L)$, unitless), chlorophyll concentration (Chl, μg L^{-1}), chlorophyll concentration at D relative to maximum chlorophyll concentration (%Chl max, %), and fraction of total *Bythotrephes* concentration found at D (Byth frac). For C2 on Aug. 3, conditions at both primary (1st) and secondary *Daphnia* biomass peaks (2nd) are indicated.

Date	Cycle	Time	E–M D	M–H D	D	T	PAR	$f(L)$	Chl	% Chl max	Byth frac
3-Aug-04	C1	20:00	12	28	26	8.3	4.2	0.38	1.20	82	0.14
3-Aug-04	C2 1st	0:45	15	29	29	6.8	0	0	1.00	70	0
3-Aug-04	C2 2nd	0:45	15	29	9	21.0	0	0	0.43	30	0.10
3-Aug-04	C3	7:45	12	28	28	6.3	1.3	0.11	0.77	54	0
4-Aug-04	C4	13:20	10	31	32	6.5	147	0.99	0.82	70	0.02
18-Aug-04	C1	8:45	14	49	47	6.6	1.3	0.10	0.11	15	0.10
18-Aug-04	C2	14:35	16	47	44	8.2	6.8	0.54	0.14	19	0
18-Aug-04	C3	19:00	20	48	48	4.9	0.8	0.06	0.10	13	0.05
18-Aug-04	C4	23:33	20	48	19	18.0	0	0	0.65	81	0.03
19-Aug-04	C5	4:25	18	45	21	14.5	0	0	0.83	91	0.16
19-Aug-04	C6	7:40	16	46	43	6.6	1.9	0.16	0.21	26	0.02

Table 3
Pelagic zooplankton biomass at M10 and M60 during first (Aug. 2–4) and second (Aug. 16–19) cruise. Respective number of cycles sampled at M10 on first and second cruises were 7 and 8, and at M60 4 and 6.

	Biomass (mg dry weight m^{-3})							
	M10				M60			
	Aug 2–3		Aug 16–17		Aug 3–4		Aug 18–19	
Taxon	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Copepoda nauplii	3.50	0.68	0.46	0.08	0.07	0.01	0.16	0.02
Chydorus spp.	0.32	0.10	0.91	0.37	0.00	0.00	0.00	0.00
Bosmina longirostrus	15.39	3.06	38.52	11.13	0.05	0.01	0.03	0.01
Leptodora kindtii	0.03	0.01	0.03	0.01	0.07	0.04	0.00	0.00
Cercopagis pengoi	0.40	0.17	0.06	0.02	0.00	0.00	0.00	0.00
Diacyclops thomasi	0.43	0.13	0.33	0.07	0.23	0.07	0.56	0.11
Leptodiaptomus (C1–C5)	0.22	0.08	0.14	0.02	6.38	0.62	6.06	0.89
Leptodiaptomus ashlandi	0.01	0.01	0.03	0.01	2.24	0.25	2.58	0.57
Leptodiaptomus minutus	0.02	0.02	0.02	0.01	0.24	0.18	0.19	0.02
Leptodiaptomus sicilis	0.00	0.00	0.00	0.00	5.47	1.18	2.94	0.36
Epischura lacustris (C1–C5)	2.01	0.49	0.39	0.08	2.40	1.36	1.03	0.09
Daphnia mendotae	0.06	0.02	0.10	0.07	13.11	2.93	15.94	3.39
Daphnia retrocurva	0.21	0.08	0.12	0.03	0.00	0.00	0.00	0.00
Diaphanosoma spp.	0.08	0.04	0.03	0.01	0.00	0.00	0.00	0.00
Dreissena veligers	0.14	0.03	0.61	0.38	0.00	0.00	0.00	0.00
Bythotrephes longimanus	0.03	0.03	0.05	0.01	0.64	0.17	0.72	0.18
Limnocalanus macrurus	0.00	0.00	0.00	0.00	1.91	0.38	0.22	0.07
Mysis diluviana	0.00	0.00	0.00	0.00	0.39	0.35	0.00	0.00
Total zooplankton	26.11	3.79	43.48	11.50	37.18	5.32	29.84	4.74

Feeding impact of Bythotrephes at M60

In contrast to alewives, estimated consumption by *Bythotrephes* was high, and they consumed an appreciable portion of total water-column production at M60, with nauplii and cladocerans *Bosmina* and *Leptodora* especially hit hard (Table 5). Total zooplankton production was highest in the metalimnion, matching the high concentration of zooplankton there, whereas *Bythotrephes* consumption was highest in the epilimnion because of a somewhat higher abundance there than in the metalimnion and also because of the higher temperature there (Fig. 3; Table 4). As expected, the model of Dumitru et al. (2001) gave more conservative estimates than the model of Yurista et al. (2010). C:P ratios for the total water-column production for the zooplankton community were 0.29 and 0.11 for the Yurista et al. (2010) and Dumitru et al. (2001) models, respectively. C:P ratios were >1, for nauplii, *Leptodora*, *Bosmina*, and small calanoids using the Yurista et al. (2010) models, whereas C:P was relatively large for these same taxa using the Dumitru et al. (2001) model, but C:P was >1 for only nauplii.

Consumptive impact was highest in the epilimnion, where C:P ratios for the total community were 1.1 and 0.33 by Yurista et al. (2010) and Dumitru et al. (2001) models, respectively. C:P ratios were especially high in the epilimnion for species with high epilimnetic affinities and high W′ values: *Leptodora*, nauplii, and *Bosmina*. Respective C:P values for *Leptodora*, nauplii, and *Bosmina*, were 3.3, 8.5, and 2.0 for the Yurista et al. (2010) model and 1.1, 2.7, and 0.6 for the Dumitru et al. (2001) model.

Nearshore zone zooplankton community and impacts of Bythotrephes and alewives

Temperatures in the nearshore zone in early and mid-August were very similar to epilimnetic temperatures at M60 (Figs. 3 and 5; Table 4). Zooplankton composition in the nearshore zone (Table 3) consisted of essentially all the species associated with the epilimnion in offshore regions (Figs. 4 and 6) and species typically associated with the littoral zone such as *Diaphanosoma* and the epibenthic *Chydorus* (Balcer et al., 1984). In contrast to the offshore zone, there was a high abundance of the small cladoceran *Bosmina* and a low abundance of *Daphnia* spp. *D. retrocurva*, a small species, was the dominant nearshore species of *Daphnia*. *Cercopagis* and *Leptodora* were also abundant nearshore relative to offshore.

Selectivity of large alewives in the nearshore zone showed a strong preference for *Bythotrephes* and a low preference for all other pelagic zooplankton (Fig. 7 bottom panel). *Bythotrephes*, followed by Daphnidae and Bosminidae, were important components of large alewife diet on the first cruise, and Bosminidae and *Bythotrephes* were important on the second cruise (Fig. 7 top panel). As reported by Pothoven et al. (2007), benthos in the form of Chironomidae were important diet items, constituting, respectively, 39 and 45% of the diet biomass on first and second cruises.

Alewife C:P for the total zooplankton community and most zooplankton taxa was low during both cruises at M10; however, C:P was very high for *Bythotrephes* (Tables 6 and 7). On the first cruise, C:P was 15.1 for *Bythotrephes*, far exceeding the C:P assumed necessary for control, *Daphnia* was 0.57 and all other taxa less than or equal to 0.07 (Table 6). On second cruise alewife C:P was 6.0 with cyclopoids having the next highest C:P of 0.09. All other taxa were less than 0.04. Despite the high alewife C:P, *Bythotrephes* was still found at low concentration on the second cruise at M10, at a time when alewife density was even higher than the first cruise (Table 4). In contrast to alewives, *Bythotrephes* C:P on all zooplankton was very low (Table 7) because of its low abundance (Table 4).

Discussion

We used a variety of tools to examine vertical and offshore vs. nearshore spatial and predatory interactions among non-indigenous fish (alewives) and visual-preying *Bythotrephes* and other zooplankton. We used fishery acoustics and PSS to examine fine vertical scale DVM of alewives and zooplankton with special emphasis on understanding the relationship between alewives, *Bythotrephes*, and the dominant offshore herbivorous cladoceran, *D. mendotae*. We were able to examine fine-scale DVM for *D. mendotae* relative to potential predators, food, and physical factors because we were able to assign size categories to large *D. mendotae* and its predator *Bythotrephes* (Liebig and Vanderploeg, 2008). Although we could report DVM of smaller size categories of zooplankton than *D. mendotae* and *Bythotrephes*, these smaller categories would include a broad range of species (e.g., *Bosmina*, nauplii, copepodites, adult *L. minutus*, *L. ashlandi*, and *L. sicilis*); therefore,

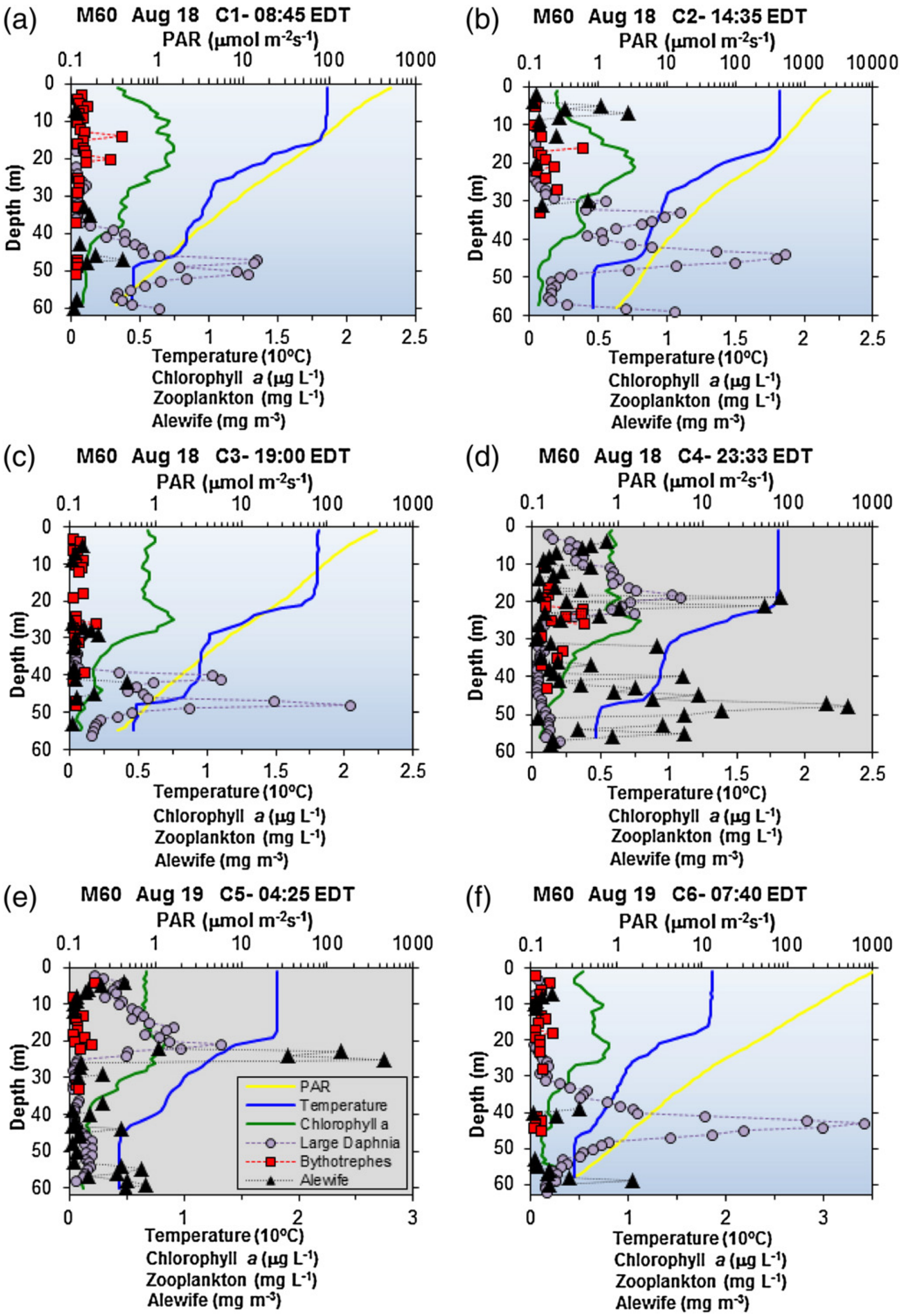

Fig. 5. Vertical distribution of physical variables (temperature and PAR), chlorophyll *a*, zooplankton (*Daphnia mendotae* and *Bythotrephes*), and large alewives as seen by the CTD instrument package, plankton survey system, and acoustics on August 18–19. Fish and zooplankton masses are in units of wet weight. The blue background shading is used to indicate day observations and gray shading to indicate night observations. Note temperature scale must be multiplied by 10 for actual values in degrees C.

it was not possible to assign unique size categories to these smaller species at the time of our experiments (Liebig and Vanderploeg, 2008).

At a coarser vertical scale, we used net tow data and bioenergetics models to examine consequences of spatial overlap by comparing consumption impacts of *Bythotrephes* and alewives on mesozooplankton in the epi-, meta-, and hypolimnion and in the nearshore zone. In addition, we looked at potential impacts of predation by using bioenergetic and P/B models to understand relative inshore-offshore impacts of the visually preying *Bythotrephes* and alewives. These observations were carried out when the ecosystem was in transition due to the expansion of quagga mussels into deep water (Nalepa et al., 2010; Vanderploeg et al., 2010), including increased water clarity (Vanderploeg et al., 2012).

DVM of zooplankton and fish

Net tows revealed that for the zooplankton community as a whole, the metalimnion was a center of distribution, especially on the first cruise. Individual zooplankton species were found in the broad thermal habitat zones (epi-, meta-, and hypolimnion) reviewed by Vanderploeg et al. (2012).

The PSS, like the net tows, revealed that *Daphnia* was found in surface waters at night, which is not surprising in that it would be able to feed in warm surface waters at a time when visual predation from *Bythotrephes* and fish would be at a minimum. Adults of the dominant planktivorous fish, alewives, are known to be found in the hypolimnion during the day with migration into the metalimnion at night (Janssen and Brandt, 1980). On both our cruises, there was some migration of alewives into the meta- and epilimnion. Likewise *Bythotrephes*, the favored prey of alewives, would escape much alewife predation by being in the epilimnion or metalimnion. Although *Bythotrephes* feeding on *Daphnia* is greatly depressed under low light conditions, it can feed to some degree in the dark; and species with lesser escape abilities, such as *Bosmina*, could be vulnerable to predation at night (Jokela et al., 2013).

On both cruises, *D. mendotae* migrated to the metalimnion–hypolimnion boundary (5–8 °C) early in the morning despite the greatly different depths on the first (28 m) and second cruises (48 m) and remained there throughout the day. The 29 m migration from the 48-m depth observed at 19:00 to the 19-m depth by 23:33 on the second cruise demonstrated the extensive and rapid DVM of *Daphnia* as day transitioned to night. The potential effect of *Bythotrephes* abundance on extent of migration of *Daphnia* (Pangle and Peacor, 2006) was not an issue in our experiments because *Bythotrephes* abundances were the same on both cruises. Pangle and Peacor (2006) reported a positive correlation of percentage of *Daphnia* found in the hypolimnion during the day with *Bythotrephes* abundance in Lakes Michigan and Erie. As was seen in the PAR and *f*(*L*) plots, *Daphnia* migrated to a region of low vulnerability to visual predation (0.10–0.11) early in the morning, but shortly thereafter *f*(L) at these depths was quite high. Despite the high *f*(*L*) in deep water during most daylight hours, digital *Bythotrephes* generally did not migrate to these deeper waters, where in theory *f*(*L*) would allow them to forage on *Daphnia*. It may be that the metalimnion–hypolimnion boundary is the lowest point (temperature) to which *Daphnia* will migrate to avoid overlap with *Bythotrephes*. If they migrated deeper, they would not be able to avoid high overlap with fish found in the hypolimnion during the day.

The importance of examining fine-scale spatial distribution of zooplankton can also be appreciated by comparing our results with those reported by Pangle and Peacor (2006) who used a pump system with 40-m-long hose to sample discrete depths on our first spatial cruise immediately after as our net tows. Their observations were reported as

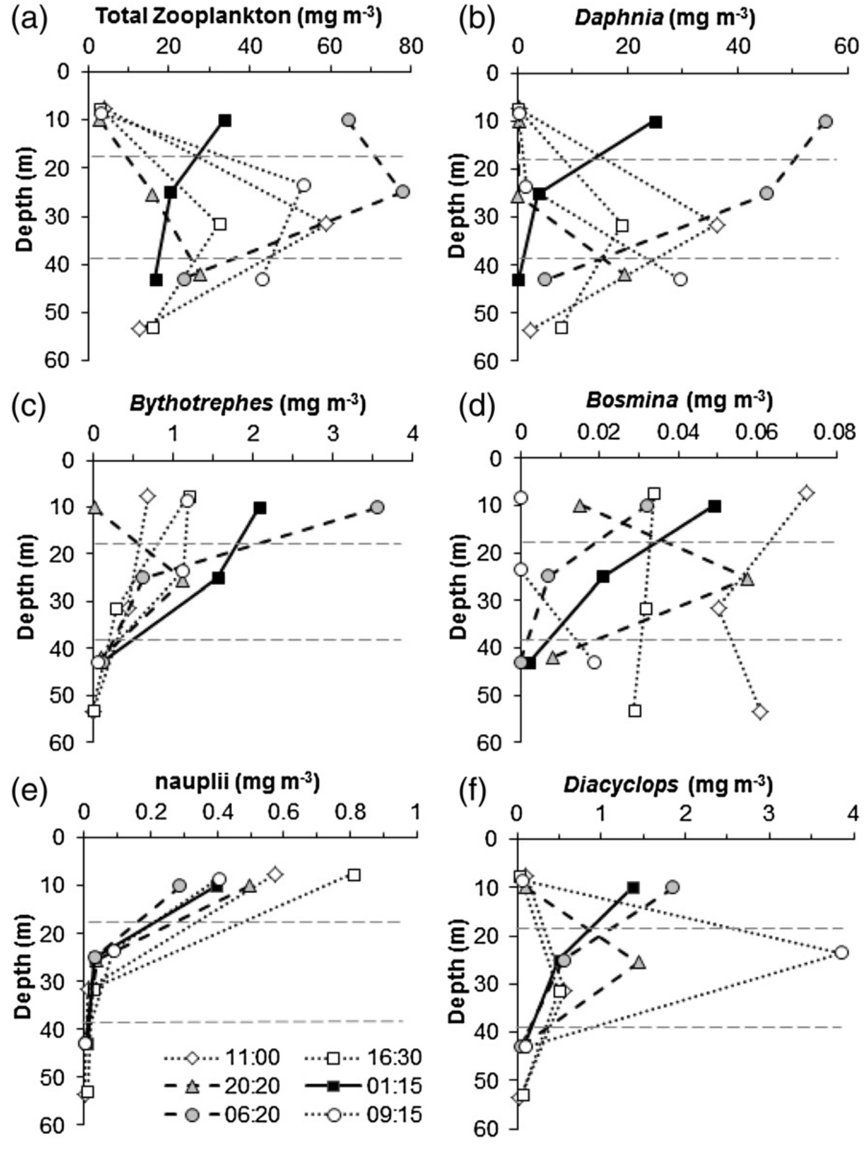

Fig. 6. Vertical distribution of major zooplankton species captured over the diel cycle at M60 on August 18–19. The dashed lines indicate average depths of boundaries between epi-, meta-, and hypolimnion over diel cycle.

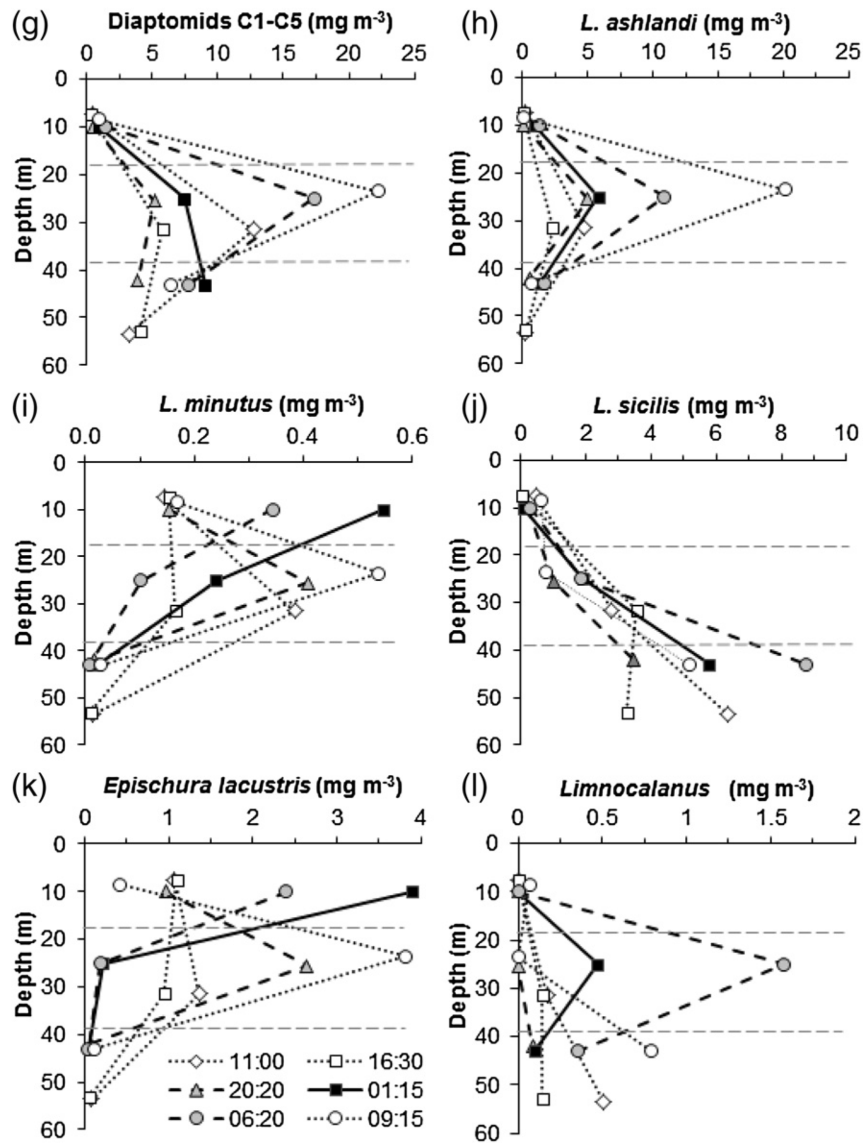

Fig. 6 (*continued*).

part of a larger study that showed a positive correlation of percentage of *Daphnia* found in the hypolimnion during the day with *Bythotrephes* abundance in Lakes Michigan and Erie. Their approach was to sample mid-depths and transitions of thermal regions: 4, 10, 20, 32, and 40 m depths. The upper water column results for both *Bythotrephes* and *Daphnia* were very similar to ours, but the 32-m sample depth missed the peak of *Daphnia* at 28 m (especially at 21:00). Our coarse-scale net tows are also in agreement with PSS observations. Our study and the Pangle and Peacor (2006) study both demonstrate the avoidance of overlap of *Daphnia* with *Bythotrephes* during the day; however, our continuous profiles clearly demonstrate that *Daphnia* is focused in rather narrow bands.

Increased water clarity, a result of mussel expansion into deep water (Vanderploeg et al., 2010), may have improved the feeding abilities of *Bythotrephes*. Using a pre-mussel expansion k_{PAR} of 0.2 would imply that for a typical midday value (10^3 μmol quanta m^{-2} s^{-1}), the depth threshold for visual predation would have been 29 m compared with 45 m in 2004. This implies there is really no place in the epilimnion or metalimnion that *Daphnia* are not vulnerable to visual predation during daylight hours from *Bythotrephes* or fish, assuming they are willing to forage at these depths. We did not factor light into our bioenergetics model other than forcing all consumption to occur in daylight hours where *Bythotrephes* and prey overlapped.

The different extent of migration between the first and second cruise likely had an impact on *Daphnia* feeding success during the day. On the first cruise, DVM brought *Daphnia* into the chlorophyll maximum, but on the second cruise, they remained far below it. This again points to DVM being related to predator avoidance or habitat selection for temperature. It can be argued the lesser migration or co-occurrence of small copepods overlapping with *Bythotrephes* is related to the more rapid escape response of copepods (Vanderploeg et al., 1993; Pichlová-Ptáčníková and Vanderploeg, 2011).

Bourdeau et al. (2015) obtained broadly similar results to ours using regression methods to examine the roles of *Bythotrephe*s density and other environmental factors on daytime zooplankton depth distributions in Lake Michigan for data collected 2004–2011. They used the same pump system and sampling approach of Pangle and Peacor (2006) and sampled at 4-m intervals from surface to 40 m. Mean depth of *D. mendotae* was strongly associated with depth of the metalimnetic-hypolimnetic boundary and secondarily with *Bythotrephes* abundance. Smaller changes in mean depth were seen with other species. In both our experiments and their experiments water clarity would be expected to be high. PSS use in our experiments was particularly useful for defining fine scale distribution missed by gaps in pumping, and we sampled both day and night to define extent of vertical migration. All these data point to

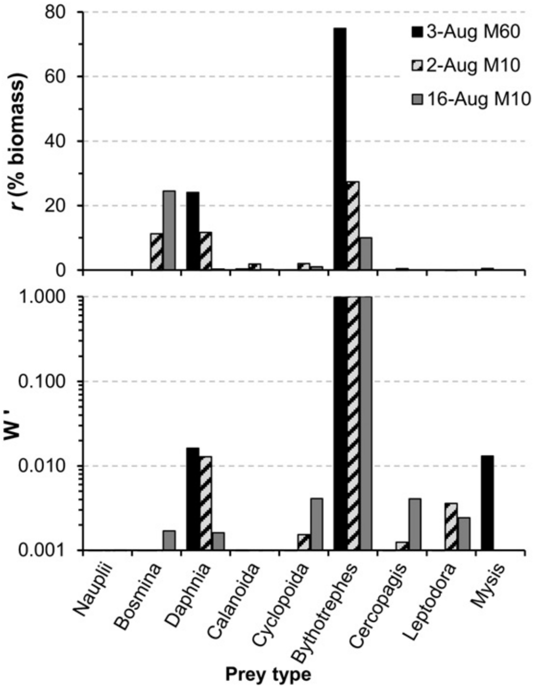

Fig. 7. Percent of large alewife diet (*r*) composed of different pelagic zooplankton taxa and selectivity (*W*′) for these taxa at the mid-depth (M60: 60-m-deep) and nearshore (M10: 10-m-deep) stations.

the hypothesis that *D. mendotae* will be found at the metalimnetic–hypolimnetic boundary throughout much of the summer when *Bythotrephes* are abundant.

Consumption impacts of Bythotrephes and alewives

Similar to previous work by Pothoven and Vanderploeg (2004) and Pothoven et al. (2007) in nearshore and mid-depth zones, *Bythotrephes* was the preferred prey of adult alewives at M60 and constituted more than 70% of their diet by weight. This was the case even though alewives were more abundant in the hypolimnion over the course of the day than in the upper water column. Sampling alewives in bottom trawls could bias our collection of fish to those feeding near the bottom particularly those collected at 19:00, before evening migration. Nevertheless, W′ values for early morning and early evening collections were similar. Using the water-column C:P of 0.05 for alewives feeding on *Bythotrephes* at M60 would imply that an alewife concentration of 550 fish ha^{-1} would exert control over *Bythotrephes*. This is comparable to historically high levels in Lake Michigan (Bunnell et al., 2013); however, this consumption would not be possible because it would largely occur in the hypolimnion where there are few *Bythotrephes*. Control of *Bythotrephes* in the epilimnion and metalimnion given a C:P ratio of 0.01 would require an even higher density of fish.

Because of the high abundance of both adult and young-of-year alewives in the nearshore zone, they had a greater effect on large species of zooplankton than offshore (Tables 5, 6, and 7). In particular, large alewives fed heavily on *Bythotrephes* and secondarily on *Daphnia*, whereas small alewives at M10 as reported by Pothoven et al. (2007) fed heavily on *Daphnia*. However, benthic prey (Chironomidae and Chydoridae) were an important component of the diet at M10 (Pothoven et al. 2007). This is consistent with observations of Sierszen et al. (2014) who showed that benthos in the nearshore zone was important to fishes, whereas in the offshore zone DVM is important for the food web.

Conceptually speaking, Fig. 8 shows links among large alewives, small alewives, and (pelagic) zooplankton occupying the same space in the water column as occurs in the Lake Michigan nearshore zone. Elimination of *Bythotrephes* from the nearshore zone removed its impact and allowed a food web to be dominated by small zooplankton, particularly *Bosmina* and small copepod species such as *Diacyclops*, as large alewives removed *Bythotrephes* and small alewives removed large zooplankton without spines. These small zooplankton species would be expected to be in the nearshore zone as well as the offshore zone because of their close association with the epilimnion.

The question might be asked as to why *Bythotrephes* was found in the nearshore zone at all considering the very high C:P ratios we determined for alewife consumption. Transport of offshore *Bythotrephes* inshore can occur during downwelling events. The same downwelling event that deepened the epilimnion and metalimnion at M60 between cruises would have also transported *Bythotrephes* inshore.

Because Pothoven et al. (2007) reported that the combined feeding impact of small and large alewives at M10 on the second cruise (when large and small alewives were more abundant) was 45 % of *Daphnia* production, the question arises whether they are exerting control on *Daphnia* inshore to explain the large difference between offshore and inshore abundance. Pothoven et al. (2007) point out that their estimates of consumption based on the daily ration method were considerably lower than bioenergetic estimates so that it is possible they were controlling *Daphnia* populations. *Daphnia* in the nearshore zone were likely to be smaller because of dominance of *D. retrocurva*, a species smaller than *D. mendotae* (Balcer et al., 1984); therefore, the fish probably exerted selective pressure on the larger species. The higher abundance of *D. mendotae* in the nearshore zone on the second cruise—like *Bythotrephes*—may represent transport from offshore to nearshore during downwelling.

In contrast, in the offshore region, the lower abundance of large alewives and their spatial separation from *Bythotrephes* released predation pressure on *Bythotrephes*, and allowed it to dominate the predatory impact, with slow moving cladocerans such as *Bosmina*, *Cercopagis*, and *Leptodora* (Ptáčníková et al., 2015) essentially eliminated. We assumed *Leptodora* would have the same vulnerability as other cladocerans to predation from *Bythotrephes*. *Leptodora* could also suffer from competition with *Bythotrephes* because its feeding preferences overlap with *Bythotrephes*, particularly for small cladocerans. These predation patterns described here, in large part, are consistent with horizontal spatial patterns of both predatory and herbivorous cladocerans reported by Cavaletto et al. (2010), Ptáčníková et al. (2015), and Pothoven and Fahnenstiel (2015) during mid-summer (summarized in Fig. 9) The extreme DVM of *D. mendotae* clearly demonstrates that its spatial separation from *Bythotrephes* during the day is an important factor in its survival and dominance in the offshore region.

Our study also complements the extensive work of Bunnell et al. (2011) for offshore Lake Huron who used a similar bioenergetics

Table 4
Comparison of individual alewife wet weight, average temperature experienced by large alewives over diel cycle (T-ALW), and density of large alewife and *Bythotrephes* in different depth zones at M60 and M10 over 24 h period. Midpoint temperatures of epi-, meta-, and hypolimnion on Aug 3–4 were 20.9, 13.8, and 5.8 °C.

Date	Station	T-ALW	Ind. wt.	Alewife density (N ha^{-1})			*Bythotrephes* density (N ha^{-1})		
		(°C)	(g)	Epi	Meta	Hypo	Epi	Meta	Hypo
Aug 2	M10	20.9	21.6	74.1	–	–	20,000	–	–
Aug 16	M10	18.8	15.9	111.9	–	–	32,000	–	–
Aug 3–4	M60	7.8	30.6	2.6	3.1	13.4	966,030	757,962	46,709

Table 5
Estimated zooplankton production (mg dry weight m^{-3} d^{-1}) from temperature and production/biomass relations (Shuter and Ing, 1997) compared to bioenergetic estimates of consumption (cons; mg dry weight m^{-3} d^{-1}) by alewives and by *Bythotrephes* (Bytho) in the epilimnion, metalimnion, hypolimnion at M60 on Aug 3–4. Bioenergetics consumption for *Bythotrephes* was calculated using the bioenergetics models of Yurista et al. (2010) and Dumitru et al. (2001). The ratio of consumption to production (C:P) is also shown to help identify times of control implied by C:P ratios > 1.

Variable	Zone	Zooplankton prey									
		Daphnia	Sm. Calanoid	Cyclopoid	Bytho	Cercopagis	Leptodora	Mysis	Nauplii	Bosmina	Total
Production	Epi	1.877	0.327	0.029	0.231	<0.001	0.033	0	0.012	0.017	2.526
	Meta	2.533	0.709	0.044	0.091	<0.001	0.010	1.263	<0.001	0.005	4.655
	Hypo	0.074	0.120	<0.001	0.001	0	0	1.488	<0.001	<0.001	1.684
	WC	1.163	0.333	0.019	0.076	<0.001	0.010	1.105	0.003	0.006	2.713
Bytho Cons (Yurista)	Epi	0.432	2.074	0.003	–	0	0.110	0	0.099	0.035	2.753
	Meta	0.583	0.056	0.001	–	0	0.002	0	<0.001	0.001	0.644
	Hypo	0.019	0.008	<0.001	–	0	0	0	<0.001	<0.001	0.026
	WC	0.269	0.464	0.001	–	0	0.024	0	0.021	0.008	0.780
Bytho C:P (Yurista)	Epi	0.23	6.34	0.11	–	0	3.33	–	8.48	2.01	1.09
	Meta	0.23	0.08	0.03	–	0	0.16	0	0.13	.17	0.14
	Hypo	0.25	0.06	0.02	–	–	–	0	0.12	0.07	0.02
	WC	0.23	1.39	0.05	–	0	2.40	0	8.06	1.40	0.29
Bytho Cons (Dumitru)	Epi	0.140	0.671	0.001	–	0	0.035	0	0.031	0.011	0.855
	Meta	0.305	0.030	<0.001	–	0	0.001	0	<0.001	<0.001	0.336
	Hypo	0.002	0.001	<0.001	–	0	0	0	<0.001	<0.001	0.003
	WC	0.118	0.153	<0.001	–	0	0.008	0	0.007	0.002	0.288
Bytho C:P (Dumitru)	Epi	0.07	2.05	0.04	–	0	1.08	–	2.74	0.65	0.33
	Meta	0.12	0.04	0.01	–	0	0.08	0	0.07	0.09	0.07
	Hypo	0.03	0.01	0	–	–	–	0	0.01	0.01	<0.01
	WC	0.10	0.46	0.02	–	0	0.79	0	2.61	0.46	0.11
Ale Cons	Epi	<0.001	<0.001	<0.001	0.001	0	0	<0.001	0	0	0.002
	Meta	<0.001	<0.001	<0.001	0.001	0	0	<0.001	0	0	0.002
	Hypo	0.001	<0.001	<0.001	0.004	0	0	<0.001	0	0	0.005
	WC	0.001	<0.001	<0.001	0.003	0	0	<0.001	0	0	0.004
Ale C:P	Epi	<0.01	<0.01	<0.01	0.01	0	0	<0.01	0	0	<0.01
	Meta	<0.01	<0.01	<0.01	0.01	0	0	<0.01	0	0	<0.01
	Hypo	<0.01	<0.01	<0.01	5.28	–	–	<0.01	0	0	<0.01
	WC	<0.01	<0.01	<0.01	0.05	0	0	<0.01	0	0	<0.01

approach to compare consumptive impact of *Bythotrephes* and *Mysis* with those of forage fishes. *Bythotrephes* consumption exceeded zooplankton production July–October. *Bythotrephes* accounted for 78%, Mysis 19%, and forage fishes 3% of the zooplankton consumption. They did not factor in selectivity or DVM into their consumptive impacts to evaluate potential impacts on particular species since only full water column net tows were made. As they point out, the consumptive impact of *Bythotrephes* was much higher than that for fish because of their higher abundance and higher weight-specific consumption. Likewise depth-specific production of zooplankton was not reported, and it was assumed most mesozooplankton production and *Bythotrephes* consumption occurred in the epilimnion. In Lake Huron, they noted that between *Bythotrephes* in the epi- and metalimnion and *Mysis* in the hypolimnion, there is limited spatial refuge for zooplankton prey.

Bunnell et al. (2012) contrasted seasonal zooplankton composition in 1983–1984 (before *Bythotrephes*) with that from 2007 in Lake Huron. They were surprised that *Bosmina* and *D. mendotae* showed contrasting changes: *Bosmina* decreased and *Daphnia* increased after the invasion. Due to the timing of their upper water column net tows, they were not able to specify daytime consumptive impacts. Our detailed spatial study and bioenergetic modeling demonstrated that *D. mendotae* finds a refuge by its migration from surface waters to the boundary between metalimnion and hypolimnion thereby avoiding both *Bythotrephes* and hypolimnetic predators such as adult fish and *Mysis*. *Bosmina* which exhibited a lesser migration suffered a greater consumptive

Table 6
Estimated zooplankton production (mg dry weight m^3 d^{-1}) from temperature and production/biomass relations (Shuter and Ing, 1997) compared to bioenergetic estimates of consumption (mg dry weight m^3 d^{-1}) by *Bythotrephes* at M10 on Aug 2. Bioenergetics consumption was calculated using the bioenergetics models of Yurista et al. (2010) and Dumitru et al. (2001). Alewife (>100 mm) consumption estimates are from Pothoven et al. (2007).

Variable	*Daphnia*	Sm. Calanoid	Cyclopoid	*Bythotrephes*	*Cercopagis*	*Leptodora*	Nauplii	*Bosmina*	Total
Prod	0.056	0.095	0.076	0.005	0.063	0.005	0.135	2.512	2.942
Bytho Cons (Yurista)	0.001	0.001	<0.001	–	0.002	<0.001	0.003	0.064	0.071
Bytho C:P (Yurista)	0.03	0.01	<0.01	–	0.03	0.03	0.02	0.03	0.02
Bytho Cons (Dumitru)	<0.001	<0.001	<0.001	–	<0.001	<0.001	0.001	0.016	0.018
Bytho C:P (Dumitru)	0.01	<0.01	<0.01	–	0.01	0.01	0.01	0.01	0.01
Alewife Cons	0.031	0.005	0.005	0.074	0.001	<0.001	<0.001	0.030	0.148
Alewife C:P	0.56	0.06	0.07	15.10	0.02	0.03	<0.01	0.01	0.05

Table 7
Estimated zooplankton production (mg dry weight m^3 d^{-1}) from temperature and production/biomass relations (Shuter and Ing, 1997) compared to bioenergetic estimates of consumption (mg dry weight m^3 d^{-1}) by *Bythotrephes* at M10 on Aug 17. Bioenergetics consumption was calculated using the bioenergetics models of Yurista et al. (2010) and Dumitru et al. (2001). Alewife (>100 mm) consumption estimates are from Pothoven et al. (2007).

Variable	*Daphnia*	Sm. Calanoid	Cyclopoid	*Bythotrephes*	*Cercopagis*	*Leptodora*	Nauplii	*Bosmina*	Total
Prod	0.032	0.023	0.046	0.007	0.008	0.004	0.014	4.907	5.027
Bytho Cons (Yurista)	<0.001	<0.001	<0.001	–	<0.001	<0.001	<0.001	0.078	0.079
Bytho C:P (Yurista)	0.02	0.01	<0.01	–	0.01	0.01	0.01	0.02	0.02
Bytho Cons (Dumitru)	<0.001	<0.001	<0.001	–	<0.001	<0.001	<0.001	0.024	0.024
Bytho C:P (Dumitru)	<0.01	<0.01	<0.01	–	<0.01	<0.01	<0.01	<0.01	<0.01
Alewife Cons	0.001	0.001	0.004	0.040	<0.001	<0.001	<0.001	0.098	0.145
Alewife C:P	0.04	0.04	0.09	6.03	0.03	0.02	<0.01	0.02	0.03

impact in our study. We suggest similar mechanisms likely explain the pattern observed in Lake Huron.

Fishery management implications

A major impetus to research on *Bythotrephes* has been the concern that it competes for food resources with age-0 fish such as the alewife, the forage base for the salmonid fishery in Lake Michigan. Growth rate of larval alewives, occurring in the epilimnion during summer, increases with zooplankton abundance (e.g., Weber et al., 2015). *Bythotrephes* consumption of zooplankton in the epilimnion would decrease zooplankton abundance and thereby potentially decreasing the growth of the particulate feeding larvae (Janssen, 1976). Bourdeau et al. (2015) presented evidence that high concentrations of *Bythotrephes* induced greater day-time depth distributions of *Daphnia*, *Bosmina*, cyclopoid copepods, and adults of *L. ashlandi* and *L. minutus*. In mid-depth and offshore waters, we have found larval alewives mostly in the epilimnion (E. Rutherford, pers. com.). Alewife larvae are known to prefer prey much smaller than *Daphnia* (e.g., Withers et al., 2015; Rutherford pers. com). *Bythotrephes* by removing smaller zooplankton can be affecting growth potential of larval alewives. The remaining dominant cladoceran, *D. mendotae*, is of little use to the larvae because of its large size and deep migration.

The feeding conditions and abundance of larval alewives inshore versus offshore varies across Lake Michigan. On the western side of the lake, prevailing westerly and southerly winds and accompanying upwelling will transport the larvae, first found in the nearshore zone, offshore (Weber et al., 2015). In contrast on the eastern side of the lake, downwelling associated with these same winds will cause larvae to be retained nearshore. Higher concentrations of larval alewives are found nearshore than offshore on the eastern side of the lake (Rutherford, per. com.). Thus, it is possible that larval alewives could profit from high concentrations of small zooplankton nearshore on the eastern side of the lake in contrast to the western side of the lake, where feeding conditions have been described as better offshore (Weber et al., 2015). Depending on the depth distribution of small juveniles, the loss of small zooplankton and deep distribution of *D. mendotae* could be a problem for them as well. Since the time of our cruises in

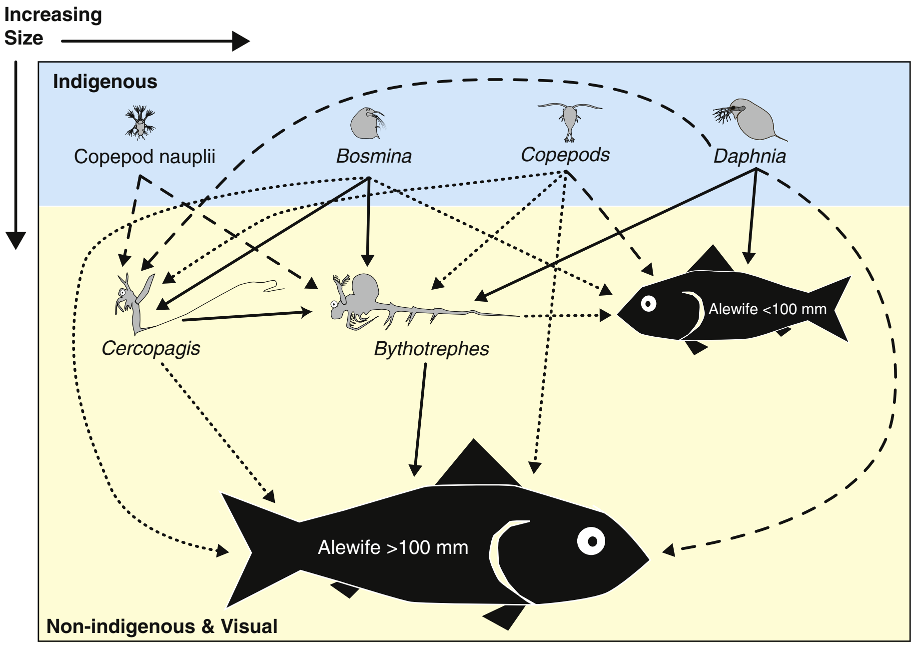

Fig. 8. The non-indigenous food web of Lake Michigan illustrated by feeding preferences of visually feeding non-indigenous invertebrate and vertebrate predators (yellow shading) feeding on each other and indigenous zooplankton (blue shaded) occupying the same volume of water such as the nearshore zone: adult alewives (>100 mm) control *Bythotrephes*, and *Bythotrephes* controls its intraguild prey *Cercopagis* and other zooplankton. The thickness of the lines indicates the values of the selectivity coefficients (W'). Thick lines, thin lines, and dashed lines indicate decreasing selectivity values.

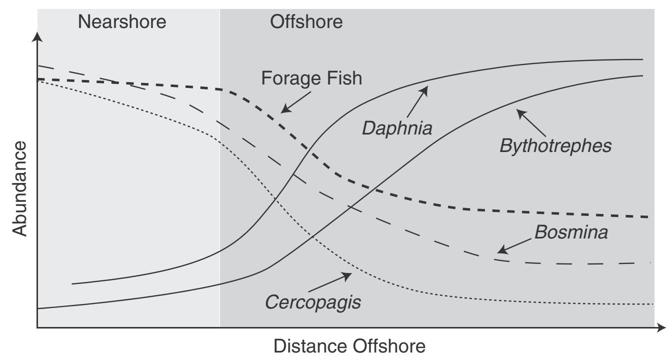

Fig. 9. An idealized perspective of horizontal organization of fish, *Bythotrephes*, *Cercopagis*, *Daphnia*, and *Bosmina*.

2004, there has been a loss of zooplankton associated with the dreissenid invasion. Growth rates have decreased in larval alewives in 2011–2014 compared to 2001 (Rutherford, per. com.).

Future research

Our study has shown that thermal structure and light play important roles in shaping diel spatial interactions among visual predatory zooplankton and fishes and that distribution and feeding interactions can occur at fine spatial scale in the vertical dimension. The study also highlighted the importance of prey selection of the planktivores in determining zooplankton species composition. These insights suggest areas where further research is needed for understanding and forecasting impacts.

Future work should focus on further elucidating fine-scale vertical spatial coupling because we have shown here how important this is for *D. mendotae*, *Bythotrephes*, and alewives. The use of the PSS with its optical plankton counter was one means of examining this spatial coupling. We are now using a laser optical plankton counter, which allows greater sample volume per unit time, measurement of smaller zooplankton, and can give higher resolution separations among size classes because of fewer problems with coincidence counting (e.g., Herman et al., 2004). Opening and closing vertical nets provided species identification, but had poor spatial resolution. Pumps can sample a few discreet layers, but at a relatively low rate. Better targeting of the pump in conjunction with real-time PSS observations may help in some situations. Use of tools like MOCNESS (multiple opening closing net environmental sample system) (Wiebe et al., 2013) would be helpful for sampling large volumes of water in narrow vertical bands to better capture mesozooplankton, *Bythotrephes*, and larval fishes.

Another research area clearly needed is quantifying the functional feeding response of *Bythotrephes* for a broad array of prey, temperature, and light conditions. We have used a bioenergetic approach with assigned selectivity coefficients to approximate feeding in relatively broad regions of the water column: epi-, meta-, and hypolimnion. This is a poor substitute for quantifying predatory impacts of *Bythotrephes* using a functional response approach, considering the important roles of light, temperature, and selectivity as it relates to detection and escape responses of different prey. This would be important in quantifying interactions at smaller spatial scales. We recognize this is a significant problem because of the difficulty of bringing *Bythotrephes* into the lab and the fragility of some of the prey such as *Cercopagis*, *Leptodora*, and other cladocerans (Vanderploeg et al., 1993; Pichlová-Ptáčníková and Vanderploeg, 2009).

DVM itself is at least partially driven by escape from planktivore predation and is an area deserving further research to define its extent and drivers. *D. mendotae* has been shown to migrate in response to both fish (Stirling et al., 1990) and *Bythotrephes* (Pangle and Peacor, 2006) abundance in the epilimnion. The subtleties of the migration and thresholds for response are not well understood for *Daphnia*, and are less well understood for other mesozooplankton particularly copepods, the dominants in all Laurentian Great Lakes except Lake Erie. Bourdeau et al. (2015) show that depth distribution of other zooplankton species such as copepods are also changed with *Bythotrephes* abundance. Likewise DVM of *Bythotrephes* may be responsive to fish. Both alewives and lake ciscoes (*Coregonus artedi*) (Jensen et al. 2006) migrate from the hypolimnion into the metalimnion to feed at night. *Bythotrephes* position in the upper water column may offer some protection from these planktivores. Also, *Bythotrephes* tended to avoid the hypolimnion and have a higher daytime position in the water column in inland lakes in Canada that had lake ciscoes (Young and Yan, 2008).

Many of the same issues that apply to *Bythotrephes* apply to fishes. We were not able to catch fish at all intervals through the day and night to determine their diet at all levels of the water column. Likewise a functional response approach would be useful factoring in their response to different prey, temperature, and light.

These research questions have particular relevance in Lake Michigan now that phytoplankton and zooplankton abundance are greatly reduced and much of the primary production occurs in picophytoplankton, a situation more common of offshore gyres of the oceans than the Great Lakes (Carrick et al., 2015). Understanding spatial predatory interactions in this very changed system at all levels of the food web will be an important goal of future research.

Acknowledgments

Assistance in the field by the crew of the R/V Laurentian is greatly appreciated. Funding was provided by the Great Lakes Fishery Commission and the National Oceanic and Atmospheric Administration. We thank J. Janssen, T. Höök, and an anonymous reviewer whose constructive comments improved the manuscript. D. Beletsky gave us valuable advice on reasons for thermocline deepening. This is Great Lakes Environmental Research Laboratory Contribution No. 1783.

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