



Comparing seasonal dynamics of the Lake Huron zooplankton community between 1983–1984 and 2007 and revisiting the impact of *Bythotrephes* planktivory

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ABSTRACT

Zooplankton community composition can be influenced by lake productivity as well as planktivory by fish or invertebrates. Previous analyses based on long-term Lake Huron zooplankton data from August reported a shift in community composition between the 1980s and 2000s: proportional biomass of calanoid copepods increased while that of cyclopoid copepods and herbivorous cladocerans decreased. Herein, we used seasonally collected data from Lake Huron in 1983–1984 and 2007 and reported similar shifts in proportional biomass. We also used a series of generalized additive models to explore differences in seasonal abundance by species and found that all three cyclopoid copepod species (*Diacyclops thomasi*, *Mesocyclops edax*, *Tropocyclops prasinus mexicanus*) exhibited higher abundance in 1983–1984 than in 2007. Surprisingly, only one (*Epischura lacustris*) of seven calanoid species exhibited higher abundance in 2007. The results for cladocerans were also mixed with *Bosmina* spp. exhibiting higher abundance in 1983–1984, while *Daphnia galeata mendotae* reached a higher level of abundance in 2007. We used a subset of the 2007 data to estimate not only the vertical distribution of *Bythotrephes longimanus* and their prey, but also the consumption by *Bythotrephes* in the top 20 m of water. This epilimnetic layer was dominated by copepod copepodites and nauplii, and consumption either exceeded (Hammond Bay site) or equaled 65% (Detour site) of epilimnetic zooplankton production. The lack of spatial overlap between *Bythotrephes* and herbivorous cladocerans and cyclopoid copepod prey casts doubt on the hypothesis that *Bythotrephes* planktivory was the primary driver underlying the community composition changes in the 2000s.

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Introduction

The Laurentian Great Lakes have generally differed in their community composition of zooplankton, likely owing to differences in productivity and planktivore density. To generalize, Lake Superior (the least productive, deepest, and coldest lake) has been dominated by calanoid copepods, whereas cladocerans and cyclopoids have been relatively more abundant in the lower four lakes (Barbiero et al., 2001; Patalas, 1972). Over the past decade, however, the zooplankton communities in Lakes Michigan and Huron have changed with cladocerans and cyclopoids declining in abundance (Barbiero et al., 2009a; Fernandez et al., 2009; Kerfoot et al., 2010), while calanoid copepods are either

remaining stable or even increasing (Barbiero et al., 2009b; Fernandez et al., 2009). Possible explanations for these changes include: 1) ongoing declines in offshore nutrient concentrations (Barbiero et al., 2009a; Evans et al., 2011; Mida et al., 2010) and the resultant competitive advantages to calanoids (McNaught, 1975; Richman and Dodson, 1983; Santer, 1994); 2) the expansion of quagga mussels and their filtering of phytoplankton (Fahnenstiel et al., 1995; Vanderploeg et al., 2010) and microzooplankton (Kissman et al., 2010; MacIsaac et al., 1991; Pace et al., 1998) that herbivorous and omnivorous cladocerans and cyclopoids feed upon; 3) excessive planktivory from invertebrate predators such as *Bythotrephes longimanus* (Bunnell et al., 2011; Lehman, 1991; Lehman and Cáceres, 1993) that prefer herbivorous cladocerans (Schulz and Yurista, 1999; Vanderploeg et al., 1993).

Zooplankton sampling in Lake Huron has been historically limited, relative to the other Laurentian Great Lakes. For example, more frequent (at least monthly) monitoring in nearby lakes Michigan and Erie has provided a better understanding of zooplankton dynamics for species that exhibit high seasonal variability (e.g., Conroy et al., 2005; Dettmers et al., 2003; Vanderploeg et al., 2012). To facilitate more intensive sampling of zooplankton (and other trophic levels) at regular intervals, the US Environmental Protection Agency (USEPA) and Environment Canada coordinate a year of intensive sampling on

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one Laurentian Great Lake per year. In this paper, we sought to combine the intensive efforts of two federal agencies [US Geological Survey (USGS) and National Oceanic and Atmospheric Association (NOAA)] in Lake Huron in 2007. These data offer the ability to evaluate whether the dramatic shifts in the Lake Huron zooplankton community composition identified by Barbiero et al. (2009a) from August data remain apparent when data from spring, summer, and fall are included. For example, it is likely that some cyclopoid (e.g., *Diacyclops thomasi*) and calanoid (e.g., *Limnocalanus macrurus*) copepod species peak in abundance as early as June and July (Vanderploeg et al., 2012), whereas *Bythotrephes* abundance can peak in October or November (Cavaletto et al., 2010).

Furthermore, the vertical distribution of the zooplankton community is commonly undescribed in studies that explore community-level zooplankton dynamics. Describing the vertical distribution of zooplankton can reveal the extent to which planktivores spatially overlap with their prey. For example, a related paper that used 2007 Lake Huron zooplankton data (based on the entire water column) revealed *Bythotrephes* to be the dominant planktivore, relative to *Mysis*, rainbow smelt, and bloater (Bunnell et al., 2011). One missing element of that work, however, was vertical distribution data for *Bythotrephes* and its potential prey. Beyond the direct effect of *Bythotrephes* consumption on the zooplankton community (see also Dumitru et al., 2001; Strecker and Arnott, 2008), *Bythotrephes* also has been documented to indirectly influence herbivorous cladocerans and copepods by inducing them to migrate into deeper, colder waters where planktivory

might be avoided but productivity is compromised (Bourdeau et al., 2011; Pangle and Peacor, 2006; Pangle et al., 2007).

Herein, we describe the 2007 seasonal dynamics of the Lake Huron zooplankton community and compare them to seasonal data collected in nearby sites in 1983–1984 (Makarewicz, 1987, 1988; see Fig. 1). Although sampling the zooplankton community for only 1 year is not ideal for most studies, the Lake Huron zooplankton community underwent such a dramatic shift in community composition in the mid-2000s (Barbiero et al., 2009a) that we assume that any interannual changes in the mid-2000s would still pale in comparison to the zooplankton community composition in the 1980s. Our analyses also go beyond descriptions of seasonal dynamics in 2007: for a subset of the data, we also used newly estimated vertical distribution data to revisit the *Bythotrephes* consumption modeling results from Bunnell et al. (2011). In particular, we wanted to determine not only the extent of spatial overlap between *Bythotrephes* and its preferred cladoceran and copepod prey, but also the likelihood that planktivory by *Bythotrephes* could have been underlying the changes in community composition that were observed in the mid-2000s.

Materials and methods

Data for this study derived from multiple sources (Table 1), each with slightly different methods (details below). In general, the 2007 northern basin sampling was conducted by USGS and was the only sampling reported herein that sampled both the whole-water column

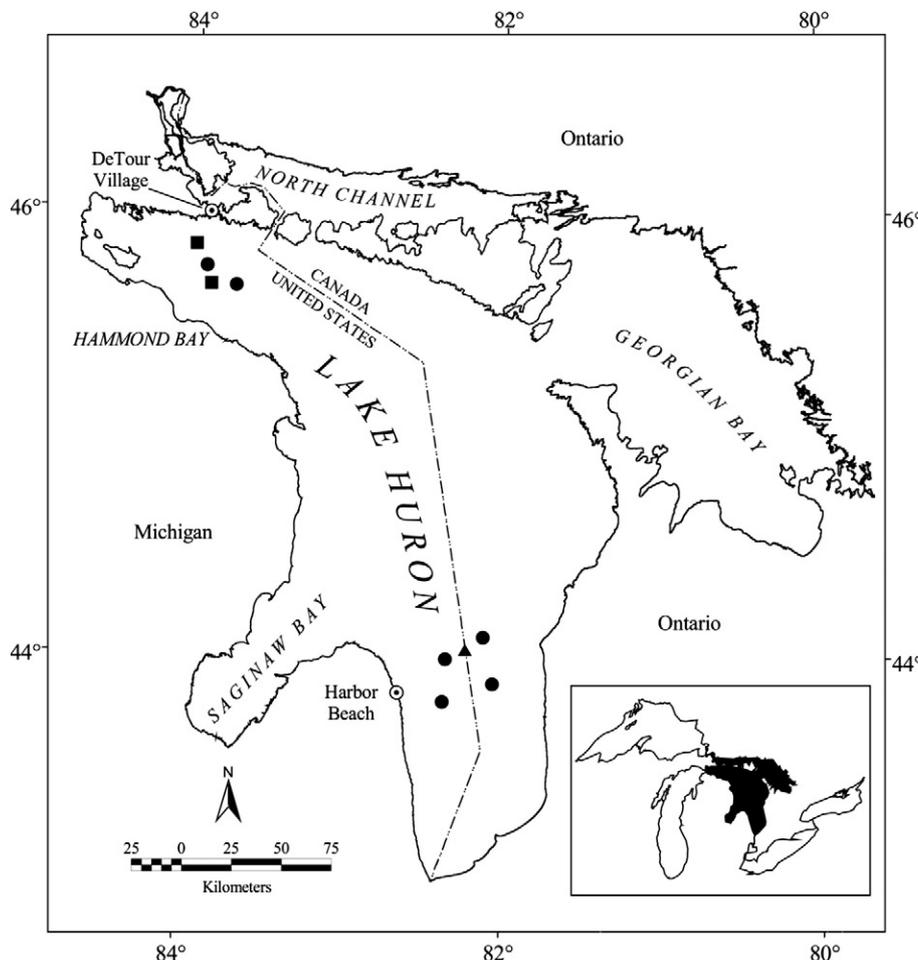


Fig. 1. Map of Lake Huron sampling sites where zooplankton were sampled seasonally in 1983, 1984, and 2007. Sites in the northern basin included those sampled by USGS in 2007 offshore from DeTour and Hammond Bay, Michigan (squares), and those sampled by USEPA in 1983 and 1984 (circles). Sites in the southern basin included those sampled by NOAA in 2007 offshore from Harbor Beach, Michigan (triangle), and those sampled by USEPA in 1983 and 1984 (circles). See Table 1 for more details on sampling times at each site.

Table 1

Summary of the number of sites that were sampled in a given month, year, and basin in Lake Huron. All samples were a whole-water column tow. Samples from 1983 to 1984 (see Makarewicz, 1987, 1988) were collected by USEPA, whereas samples from 2007 were collected by USGS in the northern basin and NOAA in the southern basin. See Fig. 1 for locations of the sampling sites in each basin.

Basin	Year	April	May	June	July	Aug	Sept	Oct	Nov	Dec
North	1983		1			2		2		
North	1984		1			2			1	1
North	2007		2	2	2	2	2	2		
South	1983		2			4		4		
South	1984		2			3			2	2
South	2007	1	1	1	1	1		1		

and the top 20 m of water. As a result, only the 2007 northern basin sampling was used to estimate vertical distribution and consumption by *Bythotrephes*. The 2007 southern basin samples were collected by NOAA, and the 1983–1984 northern and southern basin samples (Makarewicz, 1987, 1988) were collected by USEPA; these data were based on whole-water column sampling (we ignored the results from sampling the top 20 m in 1984 because time of sampling was not recorded). Data from other published time series of seasonal Lake Huron data (e.g., Evans, 1986; Watson and Carpenter, 1974) were less comparable to our 2007 data because they were not collected at similar water-column depths or nearby sites.

2007 Northern basin field sampling and laboratory processing (USGS)

At two sites (offshore of Hammond Bay and Detour, MI) in the northern basin, the entire water column (minus 1 m above the bottom of the lake) was sampled with a set of replicate tows using a 153- μm mesh, 0.5-m diameter net fitted with a calibrated flowmeter. The net was retrieved at a speed of 0.5 m/s, and the samples were bathed in antacid for up to 5 min prior to preservation in 5% sucrose formalin. A Seabird bathythermograph was deployed after each set of samples to estimate the vertical water temperature profile. A second set of replicate tows sampled the top 20 m of the water column with a 63- μm mesh, 0.5-m diameter net fitted with a calibrated flowmeter. Sampling occurred monthly between May and October, and time of day differed among months (Table 1).

Laboratory processing followed USEPA protocol (Anonymous, 2003). To estimate densities of crustacean zooplankton with the 153- μm mesh net, samples were split using a Folsom plankton splitter. Samples were subdivided until the number of zooplankton within the smallest subsample (referred to as the 'A' and 'B' splits) contained between 200 and 400 total individuals. All individuals in these splits were identified, counted, and the first 20 in each taxon were measured with an ocular micrometer. All adults were identified to species (except for *Bosmina* spp.) and copepodites (immature) were identified to species except *Leptodiaptomus* spp. and *Epischura lacustris* (which were classified as calanoid copepodites). Less abundant species (i.e., those whose counts summed to less than 40 in the 'A' and 'B' splits) were counted in the 'C' split (which equaled the sum of the 'A' and 'B' splits). Only large (i.e., *L. macrurus*, *Senecella calanoides*, *E. lacustris*) and rare (i.e., not typically seen at that time of year or depth) taxa were counted in the 'D' split (which equaled the sum of the 'A', 'B', and 'C' splits). Split-specific densities for each taxa were averaged, with a weighting based on the proportion of the split that was examined. Finally, the entire sample was processed to estimate abundance of *Bythotrephes* and any other large predatory cladocerans.

Cladocerans were measured from either the top of their head or the front of their rostrum to the base of the caudal spine or the distal-most part of their carapace, except for *Bythotrephes* which was measured from the proximal end of its spine to the base of the 'S-curve' of the spine (Garton and Berg, 1990). Copepods were measured from the

anterior-most part of the cephalosome to the distal end of the caudal ramus.

Samples from the 63- μm mesh zooplankton net were processed differently. First, they were processed for rotifers, copepod nauplii, and dreissenid veligers by splitting the sample such that between 200 and 400 individuals would be counted in each of two 1-mL subsamples withdrawn from a Hensen-Stempel pipette. Each subsample was placed in a Sedgwick-Rafter cell, covered with a glass cover slip, and all target organisms were identified, counted, and measured with a compound microscope under 100 \times magnification. The abundance for each species equals the average of the two 1-mL subsamples. Later, we returned to these samples to estimate densities of crustacean zooplankton using the same protocol as described for the 153- μm mesh samples. For these top 20 m samples only, *Bythotrephes* were classified to instar (based on the number of barbs on the spine), and for each instar that occurred up to ten measurements were recorded.

2007 Southern basin field sampling and laboratory processing (NOAA)

Procedures from the southern basin in 2007 were largely similar to those in the northern basin in 2007, save for the following differences. The 153- μm mesh, 0.5-m diameter zooplankton net was not fitted with a flowmeter; hence volume of water sampled was based on the length of cable deployed and the area of the mouth of the zooplankton net. In the laboratory, a Hensen-Stempel pipette was used to draw an aliquot subsample such that approximately 600 individuals were available for enumeration and identification. All cladocerans and adult copepods were identified to species, immature copepodites to genus, and cyclopoid and calanoid nauplii were combined into one group. To count large predatory cladocerans, such as *Bythotrephes*, the whole sample was rinsed through a 600- μm mesh sieve, and all individuals were counted. Length measurements were made on a subsample of taxa (10 adult copepods and 25 copepodites or cladocerans) that were over 10% of the total density using Image Pro Plus, image analysis software (Media Cybernetics, Silver Spring, MD). In the case of large predatory cladocerans, all individuals were measured (body length) or up to 100 individuals if more than that were present.

1983–1984 Northern and southern basin field sampling and laboratory processing (USEPA)

Data were obtained from microfiche included in USEPA reports (Makarewicz, 1987, 1988). The report containing data from 1983 (Makarewicz, 1987) reported abundance ($\#/m^3$) by species and life stage, whereas the report with data from 1984 (Makarewicz, 1988) reported both abundance and biomass ($\mu\text{g}/m^3$). A 62- μm mesh, 0.5-m diameter net fitted with a flowmeter was used to sample the entire water column (i.e., from 2 m above the bottom to the surface). After collection, samples were narcotized with club soda and then preserved with 5% formalin. Laboratory processing for crustacean zooplankton cited Gannon (1971), whereby all individuals within a subsampled aliquot were counted and identified in a chambered counting cell. We focused on samples collected adjacent to our 2007 sampling sites (see Fig. 1).

Data analyses

To estimate biomass ($\mu\text{g}/m^3$) for 2007 samples, weight was estimated for each individual length using the appropriate length versus dry weight regression (Doubek and Lehman, 2011; Dumont et al., 1975; Persson and Ekbohm, 1980; Rosen, 1981). The mean dry weight for each species and life stage was then calculated and multiplied by the density to estimate biomass. When lengths were reported in the samples from the southern basin, we applied the same length versus weight regression that was used for the northern basin. When lengths were not recorded from the southern basin, we applied the mean dry

weight from the northern basin to the southern basin densities to estimate biomass.

To compare seasonal biomass between 1984 and 2007 (recalling that biomass was not reported in 1983; Makarewicz, 1987), we focused on three broad taxonomic categories (calanoid copepods, cyclopoid copepods, herbivorous cladoceran), and for each sampling unit (i.e., the mean of the two replicate samples at a given site in 2007 or the biomass reported at a given site in 1984) we estimated the proportion of each broad taxon. We did not want to make biomass comparisons at a finer taxonomic level because we do not know which length vs. dry weight regressions were applied in 1984. For these proportional estimates, we did not include predatory cladocerans (given that *Bythotrephes* were not captured at our sites in 1984) or copepod nauplii (given that 2007 north basin estimates of nauplii were based only on samples of the top 20 m of the water column). To determine whether biomass proportions differed seasonally between 1984 and 2007, we used a generalized additive modeling (GAM) approach (Wood, 2004) in R 2.14.1 (R Development Core Team, 2011) with mgcv package 1.7–12. Relative to a generalized linear model, a GAM can more easily accommodate the non-linear relationship (sometimes unimodal) between biomass of zooplankton taxa and day of the year (DOY). Where appropriate, GAM allows for the estimation of smoothing parameters to describe these non-linear relationships and can also estimate parameters based on linear relationships. These separate functions are then “added” (see Hastie and Tibshirani, 1990). We ran two models for each of the three broad taxonomic categories: a full model with year effects included (model 1) and a reduced model with no year effects (model 2). We used Akaike’s Information Criterion (AIC) to compare the two models; if model 1 had an AIC value at least 2 less than the AIC for model 2 (Burnham and Anderson, 2002), then we concluded that model 1 was the most parsimonious model and that inclusion of year (i.e., 1984 vs. 2007) explained significant variation in proportional biomass. Other explanatory variables included basin (*B*: north or south), as previous research has found differences in zooplankton dynamics between these two basins (i.e., Barbiero et al., 2009a); DOY (which accommodated seasonality of zooplankton dynamics); and interaction terms between DOY and *B* and between DOY and *Y*. The form for model 1 was:

$$\text{proportion}_{\text{biomass}} = \beta_0 + s(\text{DOY}) + Y + B + s(\text{DOY}) \times Y + s(\text{DOY}) \times B + \varepsilon,$$

where β_0 is the estimated overall mean, $s(\text{DOY})$ is the smoothing function for DOY, *Y* was an indicator variable for year, *B* was an indicator variable for basin (see Table 1), two interactions terms ($s(\text{DOY}) \times Y$ and $s(\text{DOY}) \times B$), and ε is the normally distributed error with mean 0 and variance σ^2 . Model 2 did not include the *Y* term or the $s(\text{DOY}) \times Y$ term. Because the normality of the $\text{proportion}_{\text{biomass}}$ response variable was not improved by any transformation, we left it untransformed.

When model 1 was the most parsimonious model, we examined the parameter estimate (and P-value) for the *Y* parameter (main effect) and interaction terms involving *Y*. When the main effect *Y* had a P-value < 0.05 (i.e., $\alpha = 0.05$), we concluded that there was an overall effect of year and that the sign of the parameter estimate revealed which year had the overall greatest abundance. In some cases, however, the main effect *Y* was not significant, but inclusion of *Y* still resulted in model 1 being more parsimonious than model 2 because it allowed for different smoothing functions to be fit between DOY and biomass for different combinations of years and basins.

To compare seasonal abundance ($\#/\text{m}^3$) trends between the 1980s and 2000s, we were able to use data from 1983–1984 as well as 2007. For all years, zooplankton were identified either *i*) to species, for all adult crustaceans (except for *Bosmina* spp.), *ii*) as calanoid copepodites, or *iii*) as cyclopoid copepodites. This resulted in 15 different taxa groupings, and we excluded four species (*Daphnia longiremis*, *Daphnia pulicaria*, *Daphnia retrocurva*, and *Eubosmina* spp.) that were relatively abundant in 1983–1984 but rare by 2007, likely owing to the invasion

of *Bythotrephes* (Barbiero and Tuchman, 2004) in the 1980s. As before, our sampling unit equaled the mean density of a given zooplankton taxa at a given site on a given day. We evaluated whether seasonal zooplankton abundance differed between collections in 1983–1984 and 2007 using the same GAM approach as described above; we pooled data from 1983–1984 into one “year” for the model because we were more interested in broad temporal differences measured between the early 1980s and 2007 rather than finding statistical differences between 1983 and 1984. To improve the normality of the response variable (abundance) in the GAM, we applied a ln-transformation (plus 0.65, the smallest non-zero abundance estimated).

To determine the percentage of each population that occupied the top 20 m in the water column at the northern sites in 2007, we assumed that the different mesh sizes generated no biases in areal density estimates ($\#/\text{m}^2$), which have been confirmed by paired-tow data for all crustacean species except *Mesocyclops* copepodites (Barbiero et al., 2001), including *Bythotrephes* (Pothoven et al., 2012). At each site, we calculated the proportion in the top 20 m as the mean areal density ($\#/\text{m}^2$) estimated in the top 20 m divided by the mean areal density estimated in the whole water column sample. We then calculated the average proportion in the top 20 m across the two sites. Water temperature profiles revealed that the metalimnion (defined as the depth at which water temperature changed by $\sim 1^\circ\text{C}$ per m) occurred at different depths in each month: May – isothermal, June – 10–15 m, July – 8–17 m, August – 24–34 m, September – 23–29 m, October – 34–38 m. As a result, we pooled the months into one of four groupings, based on the depth of the metalimnion (and consequently how much of the epilimnion was sampled in our 20-m tows) and the time of sampling (day vs. dusk/night): 1) May (isothermal sampled at dusk or night); 2) June, July (entire epilimnion and metalimnion sampled at dusk); 3) August, September ($\sim 85\%$ of epilimnion sampled at night); and 4) October ($\sim 60\%$ of the epilimnion sampled during the day). For each grouping, we report the mean proportion in the top 20 m. We focused only on the most abundant species, given that the proportion in the top 20 m for rare species (i.e., *S. calanoides*, *Mesocyclops edax*, *T. prasinus mexicanus*) was highly variable. Predicted vertical distribution and other life history characteristics for each species studied in Lake Huron are summarized in Table 2.

To evaluate the potential effects of *Bythotrephes* planktivory on zooplankton, we focused on samples collected in the top 20 m of water during October 2007 at the two northern basin sites. Previous analyses of the impact of *Bythotrephes* on the Lake Huron zooplankton community were based on whole-water column samples, which was acknowledged to possibly overestimate the prey available to *Bythotrephes* (Bunnell et al., 2011), given that *Bythotrephes* generally occurs in the epilimnion and perhaps as deep as the metalimnion during autumn (Lehman and Cáceres, 1993; Pangle et al., 2007; Young and Yan, 2008) leaving a refuge for hypolimnetic zooplankton prey. To calculate daily consumption (dry mg/m^2) of *Bythotrephes*, we used two approaches. First, we used a bioenergetic (BE) model (Yurista et al., 2010) that assumed *Bythotrephes* were feeding under “ideal” feeding conditions (i.e., unlimited prey). This model required epilimnetic temperature, and mean size and biomass of each instar. Second, we used a more conservative growth efficiency (GE) method that has been used in other studies (e.g., Dumitru et al., 2001; Foster and Sprules, 2009; Strecker and Arnott, 2008), whereby consumption = production/0.27, which assumed that 27% of the food consumed by *Bythotrephes* resulted in production. We calculated daily production (mg/m^2 , dry weight) by *Bythotrephes* with the Shuter and Ing (1997) cladoceran regression model (which requires temperature and standing stock biomass). Although the Shuter and Ing (1997) model was not developed with large predatory cladocerans, its predictions were statistically similar to those of an egg-ratio production model for *Bythotrephes* (Foster and Sprules, 2009). To estimate daily production of potential zooplankton prey in the top 20 m of water, we used

Table 2

Summary of life history characteristics of zooplankton species sampled on at least five sampling occasions in Lake Huron in 2007. For vertical location, epi = epilimnion, meta = metalimnion, and hypo = hypolimnion. Information summarized from Balcer et al. (1984) and D.B. Bunnell, unpublished data.

Species	Coarse taxonomic grouping	Vertical location		Season of peak abundance	Feeding preference	Size range (mm)
		Day	Night			
<i>Leptodiatomus ashlandi</i>	Calanoid	Hypo	Epi-meta	Spring/fall	Herbivorous	0.9–1.1
<i>Leptodiatomus minutus</i>	Calanoid	Hypo	Epi-meta	Spring/summer	Herbivorous	0.9–1.1
<i>Leptodiatomus sicilis</i>	Calanoid	Hypo	Hypo	Spring/fall	Herbivorous	1.1–1.8
<i>Skistodiatomus oregonensis</i>	Calanoid	Epi	Epi	Spring/fall	Herbivorous	1.2–1.4
<i>Epischura lacustris</i>	Calanoid	Meta	Epi	Summer/fall	Omnivorous	1.4–2.0
<i>Limnocalanus macrurus</i>	Calanoid	Hypo	Meta	Summer	Omnivorous	2.2–3.2
<i>Senecella calanoides</i>	Calanoid	Hypo	Meta	Fall	Omnivorous	2.4–3.3
<i>Diacyclops thomasi</i>	Cyclopoid	Meta	Epi	Spring/summer	Carnivorous	0.9–1.2
<i>Tropocyclops prasinus mexicanus</i>	Cyclopoid	Epi	Epi	Fall	Omnivorous	0.5–0.9
<i>Mesocyclops edax</i>	Cyclopoid	Epi	Epi	Summer	Carnivorous	0.7–1.7
<i>Daphnia galeata mendotae</i>	Cladoceran	Meta	Epi	Summer	Herbivorous	1.0–3.0
<i>Bosmina</i>	Cladoceran	Epi	Meta	Summer	Herbivorous	0.2–0.6
<i>Holopedium gibberum</i>	Cladoceran	Epi	Meta	Summer	Omnivorous	1.5–2.2
<i>Bythotrephes longimanus</i>	Cladoceran	Epi-meta	Epi	Fall	Carnivorous	5.1–10.6

the same Shuter and Ing (1997) regressions to calculate daily production (mg/m^2 , dry weight) of cladocerans, and cyclopoid and calanoid copepods; these models required estimates of standing stock biomass and epilimnetic temperature. To estimate production of copepod nauplii, we applied the ratio of calanoid:cyclopoid copepods to nauplii, such that the appropriate calanoid or cyclopoid regression could be used.

Results

Seasonal differences in zooplankton biomass and abundance between 1984 and 2007

Comparing seasonal biomass trends for broad taxonomic categories between 1984 and 2007 revealed that calanoid copepods were generally a greater proportion of the zooplankton community in 2007 than in 1984, whereas cyclopoid copepods and cladocerans were generally a smaller proportion of the community in 2007 than in 1984 (Fig. 2). For each broad taxa, the GAM that included year effects (model 1) was the most parsimonious, based on the AIC values for models 1 and 2, respectively: calanoid (−51.6, −30.1), cyclopoid (−91.7, −75.9), herbivorous cladocerans (−58.3, −41.6). For model 1 of each taxon, the main effect of Y was significant (i.e., proportional biomass differed between years).

Comparing seasonal abundance between 1983–1984 and 2007 at a finer taxonomic resolution revealed that the inclusion of year (model 1) nearly always resulted in the most parsimonious model (*Holopedium gibberum* was the exception, Table 3). Recalling that model 1 could be the most parsimonious for two reasons (the main effect of Y being significant and/or the non-linear relationship between DOY and abundance differing between combinations of Y and B), we focused on whether the main effect of Y was significant (see Table 3), given that it best addressed whether seasonal abundance differed between 1983–1984 and 2007. Among the cladoceran taxa, abundance of *Bosmina* spp. (Fig. 3e) was higher in 1983–1984 than in 2007, whereas abundance of *Daphnia galeata mendotae* (Fig. 3f) was actually higher in 2007 than in 1983–1984. Abundance of *H. gibberum* (Fig. 3g) did not differ between time periods. For the four categories of cyclopoid copepods, however, seasonal abundance was always higher in 1983–1984 than in 2007: *D. thomasi* (Fig. 3a), *M. edax* (Fig. 3b), *T. prasinus mexicanus* (Fig. 3c), cyclopoid copepodites (Fig. 3d).

For seven out of eight calanoid taxa, the main effect of year was not significant despite model 1 being most parsimonious. *E. lacustris* (Fig. 4a) was the only taxon for which seasonal abundance in 2007 was greater than in 1983–1984. For three other taxa, however, (*Leptodiatomus ashlandi*, *Leptodiatomus minutus*, *L. macrurus*; Figs. 4b, c, e, respectively), the P-values for the main effect of year ranged 0.051–

0.069 (Table 3), which were very close to $\alpha = 0.05$. As a result, these calanoids are suggestive of different overall seasonal abundances between 1983–1984 and 2007: higher in 1983–1984 for *L. ashlandi* and higher in 2007 for *L. minutus* and *L. macrurus*. For the remaining taxa (*Leptodiatomus sicilis*, *S. calanoides*, *Skistodiatomus oregonensis*, calanoid copepodites; Figs. 4d, f, g, h), only the shape of the non-linear relationship between DOY and abundance differed between B and Y.

Zooplankton vertical distribution in northern Lake Huron in 2007

The vertical distribution of zooplankton differed across the four groupings. For samples collected in May (pre-stratification, samples collected at dusk or night), only *Bosmina* spp., *L. macrurus*, and *L. minutus* had at least 50% of their individuals sampled in the top 20 m of water (Fig. 5). For those samples in June–July at dusk, which included the entire epilimnion and metalimnion, all of the species except *H. gibberum* had at least 50% of their individuals in the top 20 m of water. By August–September, however, far fewer zooplankton taxa (i.e., only *L. minutus*, *S. oregonensis*, *E. lacustris*, and *Bythotrephes*) had a majority of individuals sampled in the top 20 m at night (which encompassed 85% of epilimnion); of particular note was only 5% of bosminids in the top 20 m, following all individuals in the top 20 m in previous months. October samples during the day encompassed 60% of the epilimnion, and most zooplankton taxa had the majority of individuals sampled below 20 m. Relative to August–September, however, only a few taxa revealed marked declines in October: *E. lacustris* (proportion in top 20 m declined from 0.64 to 0.20), *D. thomasi* (0.46 to 0.11), and *D. galeata mendotae* (from 0.49 to 0.03).

Comparing *Bythotrephes* consumption to zooplankton production

For diurnal northern basin samples collected in October in the top 20 m of water, daily consumption estimates for *Bythotrephes* ranged from 3.3 to 9.3 mg/m^2 off Hammond Bay and 1.5–4.3 mg/m^2 off Detour (Fig. 6), depending on the method used. For Hammond Bay, both estimates exceeded the total daily production of crustacean zooplankton (3.1 mg/m^2) in the top 20 m of water. For Detour, only the BE consumption method exceeded total daily production (2.3 mg/m^2); the GE method of consumption was only 65% of zooplankton production. For both sites, the dominant prey taxon in the top 20 m, in terms of biomass, was calanoid copepodites (57 and 48% of the biomass, respectively, in Hammond Bay and Detour). Other taxa that exceeded 10% of the biomass at a site included copepod nauplii (17%, 18%) and adult *L. sicilis* (15% at Hammond Bay). Preferred prey for *Bythotrephes* (*D. galeata mendotae*, *Bosmina* spp.) comprised less than 1% of the biomass at each site.

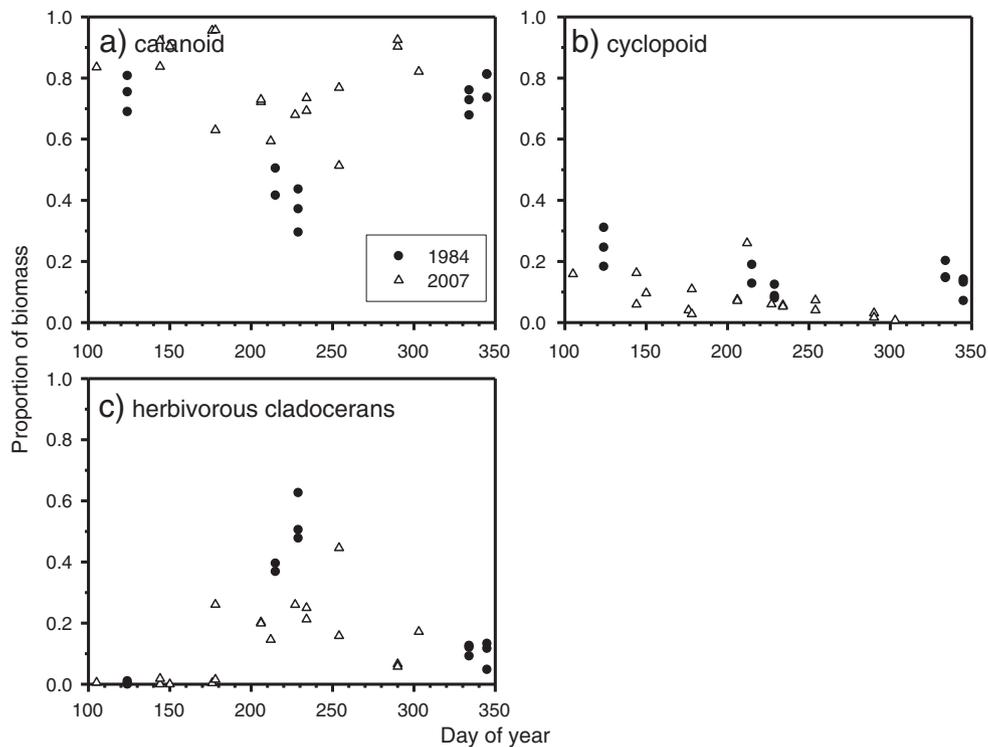


Fig. 2. Proportion of zooplankton biomass ($\mu\text{g}/\text{m}^3$, dry weight) as a function of day of year in 1984 (filled circles) and 2007 (open triangles), sampled with whole-water column, 153- μm mesh zooplankton nets in the northern and southern basins of Lake Huron. Groups in each panel include: (a) calanoid copepods, (b) cyclopoid copepods, (c) herbivorous cladocerans.

Discussion

Comparisons of seasonal biomass for broad taxonomic groupings between 1984 and 2007 in Lake Huron revealed a marked shift towards a greater proportion of calanoid copepods and lower proportions of cyclopoid copepods and herbivorous cladocerans. This result was consistent with a long-term (i.e., 1984–2006) analysis of Lake Huron data collected in August by USEPA (Barbiero et al., 2009a), where the biomass of cladocerans and cyclopoids in 2003–2006 was significantly lower than in earlier time periods (i.e., 1984–1986, 1987–1990, 1998–2002). When we directly compared species-specific abundance estimates between 1983–1984 and 2007, we found a result consistent with the proportional biomass comparisons for all four cyclopoid taxa: higher seasonal abundance in 1983–1984 than in 2007. For cladocerans and calanoid copepods, however, the seasonal abundance results by taxa were more complex and sometimes less consistent with the trends in proportional biomass. For cladocerans, abundance of *D. galeata mendotae* was actually greater in 2007 than in 1983–1984 and abundance of *H. gibberum* did not differ between time periods. Only *Bosmina* spp. revealed the expected pattern of higher abundance in 1983–1984 than in 2007. For calanoid copepods, although their proportion of the biomass increased in 2007 relative to 1984, we found that only *E. lacustris* had a higher seasonal abundance in 2007 than in 1984. Overall, our results generally supported the changes in zooplankton community composition reported by Barbiero et al. (2009a), although we did find that seasonal abundance estimates for some cladoceran and calanoid species did not result in the differences that would have been predicted.

Descriptions of monthly or seasonal zooplankton dynamics are relatively rare for Lake Huron. Beyond those reported herein, we know of two other studies with seasonal sampling. Watson and Carpenter (1974) reported monthly abundance estimates across 14 sites between April and November 1971. Direct comparisons to the 1984 and 2007 data would be unfair because the net hauls were limited to 50 m in depth. Relative to the whole-water derived estimates from 1983 to

1984 and 2007, the calanoid copepod densities in 1971 would be biased low because many of these species occur in the hypolimnion during the day. On the other hand, estimates of cladocerans and cyclopoid copepods in 1971 would likely be biased high because the amount of water sampled would be less than our whole-water tows. With these caveats in mind, the zooplankton community that Watson and Carpenter (1974) described in 1971 had a far greater percentage of cyclopoids (40% of the total zooplankton community, by number) than we observed in 2007. Evans (1986) was the only other seasonal zooplankton study from Lake Huron that we found, but it was also not comparable to our data because only the top 25 m of the water column was sampled.

Why the proportional biomass of calanoid and cyclopoid copepods and herbivorous cladocerans shifted between 1984 and 2007 is a complex question to answer. Of further complication is that between 1984 and 2007 several other perturbations occurred within the offshore of the Lake Huron food web. Concentrations of total phosphorus in spring have declined slowly through time (Barbiero et al., 2009a), resulting in a more oligotrophic system. Beginning in 2003, the spring phytoplankton bloom and chlorophyll a concentrations declined markedly, and summer chlorophyll concentrations also declined in 2005–2006 (Barbiero et al., 2011). It is conceivable that invasive dreissenid mussels could have contributed to the decline in spring phytoplankton (when the water column is not stratified; Fahnenstiel et al., 2010), but this explanation deserves additional scrutiny because of the relatively low dreissenid densities in the offshore of Lake Huron (Barbiero et al., 2011; Nalepa et al., 2007). Invasive *Bythotrephes* have also become established since 1984 and may have led to declines in abundance for several herbivorous cladoceran species (e.g., *D. pulicaria*, *D. retrocurva*, *Eubosmina coregoni*, Barbiero and Tuchman, 2004; Makarewicz et al., 1995) both directly via predation (Bunnell et al., 2011; Lehman, 1991; Lehman and Cáceres, 1993) and indirectly by inducing these species to occupy cooler waters (to avoid predation), which negatively influences their production (Pangle and Peacor, 2006; Pangle et al., 2007). Finally, densities of planktivorous prey fishes

Table 3

Aikaike's Information Criterion (AIC) values estimated from generalized additive models that sought to explain variation in seasonal abundance ($\#/m^3$) of 15 different zooplankton taxa in Lake Huron in 1983–1984 (pooled as 1 year in the model) and 2007. Order of taxa below is cladocerans, cyclopoid copepods, and calanoid copepods (and alphabetical within each). Model 1 included the explanatory variables “day of the year” (DOY, smoothed), basin (B), year (Y), and $DOY \times Y$ and $DOY \times B$ interaction terms. Model 2 included all of the above variables except those that included Y. Models with AIC values that are at least 2 less than the other model are in bold and were considered to be more parsimonious. When ΔAIC values were <2 , the models were indistinguishable; we interpreted this to mean that the difference in abundance between years was insignificant. When ΔAIC values were >2 , we reported the P-value to test whether the main effect of Y was significant ($\alpha = 0.05$), and if so, the far-right column indicated which years had a higher overall abundance.

	Model 1	Model 2	ΔAIC	P-value for main Y effect	Direction of main Y effect
<i>Bosmina</i> spp.	125.30	128.68	3.38	0.026	1983–1984 > 2007
<i>Daphnia galeata mendotae</i>	197.34	207.39	10.05	0.015	2007 > 1983–1984
<i>Holopedium gibberum</i>	170.44	171.14	0.70		
Cyclopoid copepodites	116.45	151.05	34.6	<0.001	1983–1984 > 2007
<i>Diacyclops thomasi</i>	136.37	148.45	12.08	0.005	1983–1984 > 2007
<i>Mesocyclops edax</i>	136.93	177.39	40.46	<0.001	1983–1984 > 2007
<i>Tropocyclops prasinus mexicanus</i>	120.24	145.71	25.47	<0.001	1983–1984 > 2007
Calanoid copepodites	92.90	105.27	12.37	0.758	
<i>Epischura lacustris</i>	124.14	129.99	5.85	0.014	2007 > 1983–1984
<i>Leptodiaptomus ashlandi</i>	132.04	134.88	2.84	0.051	
<i>Leptodiaptomus minutus</i>	180.57	183.79	3.22	0.069	
<i>Leptodiaptomus sicilis</i>	139.12	141.48	2.36	0.319	
<i>Limnocalanus macrurus</i>	131.32	141.92	10.60	0.066	
<i>Senecella calanoides</i>	130.73	156.52	25.79	0.181	
<i>Skistodiaptomus oregonensis</i>	180.32	187.33	7.01	0.224	

were significantly lower in 2007 relative to 1984, including the near extirpation of alewife *Alosa pseudoharengus* around 2003 (Riley et al., 2008). Owing to near relatively simultaneous changes happening at multiple trophic levels, several different mechanisms could conceivably be underlying the shifts in zooplankton community composition in Lake Huron. Below, we explore the extent to which the proportional declines in cyclopoid and cladoceran biomass and reductions in species richness of cladocerans could be explained by either “top–down” (excessive planktivory) or “bottom–up” (limiting resources) forces.

The simplest explanation for the decline of cyclopoid copepods between the early 1980s and 2007 is that Lake Huron has been moving towards a more oligotrophic system since the mid-1970s (Barbiero et al., 2009a), and that cyclopoid copepods are generally outcompeted by calanoid copepods in oligotrophic conditions (Soto and Hurlbert, 1991). Calanoid copepod nauplii and adults have lower food thresholds and metabolism than cyclopoid copepods and are able to depress food available to cyclopoid nauplii (i.e., phytoplankton) and adults (i.e., microzooplankton) in low food conditions (Adrian, 1997; Sommer and Stibor, 2002; Soto and Hurlbert, 1991). Further, cyclopoid copepods generally are more abundant at higher nutrient concentrations because of the corresponding increased availability of their microzooplankton prey (Pace, 1986). Since 2003, the rate of oligotrophication in Lake Huron has increased at an even faster rate (Barbiero et al., 2009a, 2011), suggesting that densities of rotifers and other microzooplankton prey were concomitantly declining. Surprisingly, total rotifer densities in Lake Huron exhibited no downward trend between 1984 and 2006, as some genera have declined (i.e., *Keratella*, *Kellicottia*, *Polyarthra* spp.) while *Conochilus* spp. has markedly increased (Barbiero and Warren, 2011). Although these shifts in rotifer community composition are consistent with oligotrophication (Barbiero and Warren, 2011), it remains unclear as to whether these changes in rotifer community composition have negatively affected cyclopoid production and biomass.

Not only did proportional biomass of herbivorous cladocerans decline between 1984 and 2007, species diversity also dropped considerably given that several species were abundant in 1984 but rare in 2007 (*D. longiremis*, *D. pulicaria*, *D. retrocurva*, and *Eubosmina* spp.). Barbiero and Tuchman (2004) argued that the *Bythotrephes* invasion in the late 1980s drove the decline in cladoceran diversity. Interestingly, *D. galeata mendotae* has actually increased in seasonal abundance between 1983–1984 and 2007. Previous work has found abundance of *D. galeata mendotae* to remain unchanged in Lakes Huron and Michigan following the invasion of *Bythotrephes* (Barbiero and

Tuchman, 2004; Lehman, 1991). How *D. galeata mendotae* has managed to coexist with *Bythotrephes* (while *D. retrocurva* and *D. pulicaria* have not) is not clear. Initially, the large helmet and spine of *D. galeata mendotae* was believed to be important (Lehman, 1991), but later studies demonstrated that *Bythotrephes* were able to consume helmeted *D. galeata mendotae* (Schulz and Yurista, 1999). Recent studies argue *D. galeata mendotae* was able to adapt to the invasion of *Bythotrephes* by undergoing deeper “diel vertical migration” (DVM) during the day (Barbiero and Tuchman, 2004; Schulz and Yurista, 1999), largely based on a field study pre- and post-*Bythotrephes* invasion (Lehman and Cáceres, 1993). Curiously, however, *D. pulicaria* exhibited a similar adaptation to undergo deeper DVM during the day (Lehman and Cáceres, 1993), but this was apparently insufficient to permit their coexistence. Finally, alewife have been reported to control densities of the relatively large *D. galeata mendotae* (Brooks and Dodson, 1965; Wells, 1970), and the steep decline in alewife in Lake Huron since 2003 could also have contributed to a resurgence in *D. galeata mendotae*.

The decline of *Bosmina* also can be explained by multiple mechanisms. First, *Bythotrephes* could have a negative impact through both direct (i.e., planktivory) and indirect (i.e., inducing them to occupy cooler less productive waters) means. Second, higher densities of *D. galeata mendotae* could outcompete smaller cladocerans such as bosminids (Brooks and Dodson, 1965), although this may not necessarily be the case (Dodson et al., 1976). Lastly, Barbiero et al. (2011) documented a decline of spring chlorophyll and phytoplankton in Lake Huron between 2003 and 2006 and argued that these bottom–up forces could negatively impact cladocerans. Possible mechanisms theorized by Barbiero et al. (2011) included heightened planktivory pressure from *Mysis relicta* (which historically had relied on phytoplankton for as much as 50% of their diet during spring (Johannsson et al., 2001)) and lower production as a result of declining phytoplankton availability (Threlkeld et al., 1980).

Researchers trying to understand changes in the Lake Michigan cladoceran community have also struggled with the relative importance of top–down versus bottom–up factors. From the 1970s through 1990s, they largely converged on the hypothesis that observed declines in herbivorous daphnid species richness or biomass were due to planktivory – in particular from alewife – but also from non-native *Bythotrephes* as it became established in the late 1980s (Lehman, 1991; Lehman and Cáceres, 1993; Makarewicz et al., 1995; Scavia et al., 1988; Wells, 1970; but see Evans, 1992). Recent bioenergetic modeling in northern Lake Huron indicated that planktivory by prey

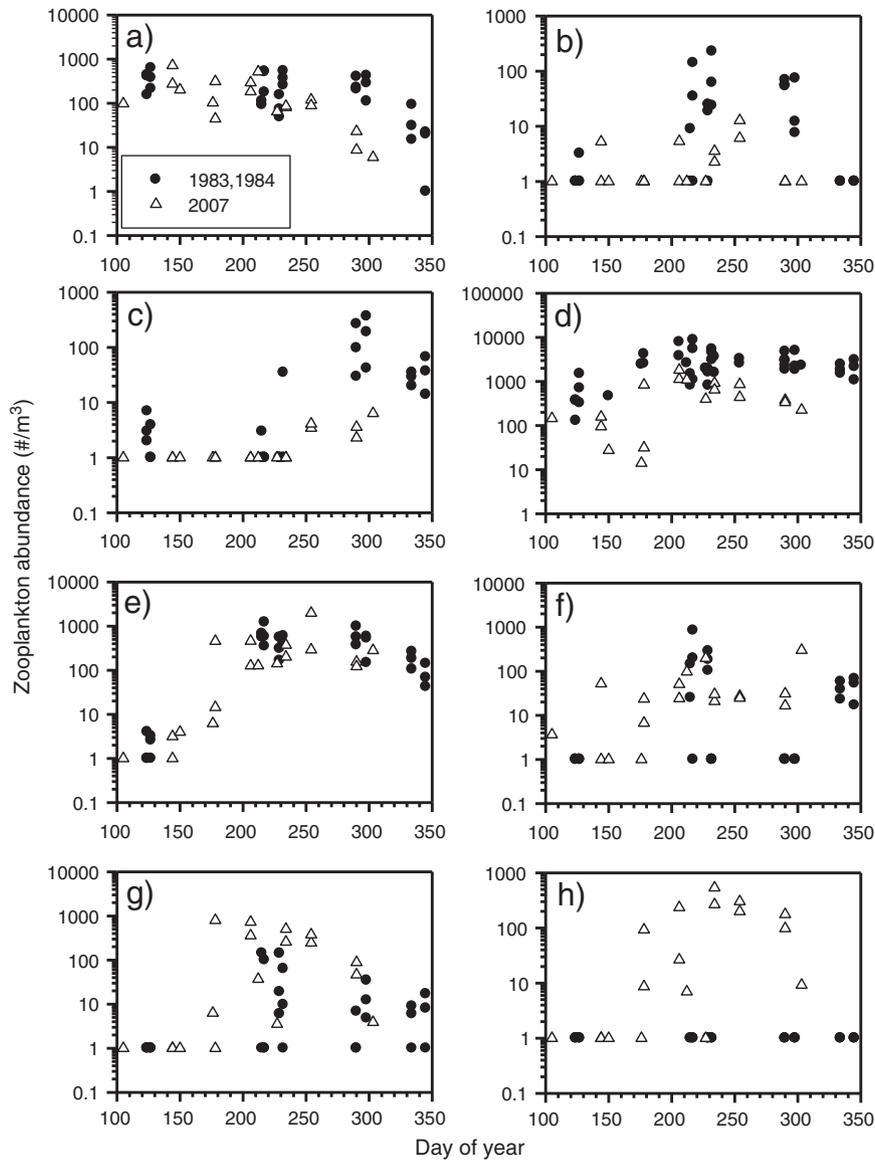


Fig. 3. Abundance ($\#/m^3$) of cyclopoid copepod and cladoceran taxa as a function of day of year in 1983–1984 (filled circles) and 2007 (open triangles), sampled with whole-water column, 153- μm mesh zooplankton nets in the northern and southern basins of Lake Huron. Taxa in each panel include: (a) *Diacyclops thomasi*, (b) *Mesocyclops edax*, (c) *Tropocyclops prasinus mexicanus*, (d) cyclopoid copepodites, (e) *Bosmina* spp., (f) *Daphnia galeata mendotae*, (g) *Holopedium gibberum*, (h) *Bythotrephes longimanus*. For clarity of presentation, the Y-axis is on the log-10 scale, and we added 1 to all values so that abundance = 0 would be visible.

fish, which have been at or near record-low levels since 2003 (Riley et al., 2008), was likely insufficient to induce the declines in cladocerans or even cyclopoids (Bunnell et al., 2011). This same bioenergetic modeling approach, however, revealed that *Bythotrephes* consumption could well be large enough to cause declines in zooplankton biomass. Whether *Bythotrephes* consumption could have directly led to the decline of their preferred daphnid and bosminid prey depends on spatial overlap during the day, when *Bythotrephes* feeding occurs. In light of the uncertainty of the mechanisms for both top-down and bottom-up drivers of declining cladoceran biomass, we cannot conclusively state that one mechanism is more important than another with our current understanding.

In this paper, we followed up on the Bunnell et al. (2011) analyses by determining the extent of spatial overlap between *Bythotrephes* and their prey, and compared *Bythotrephes* consumption to production of overlapping prey in the top 20 m of water in October. As in Bunnell et al. (2011), consumption by *Bythotrephes* could exceed production of zooplankton, even if *Bythotrephes* were not feeding under optimal conditions (i.e., even the GE method resulted in excessive predation on one

site). This work, however, revealed that the bulk of prey available to *Bythotrephes* in the top 20 m of water in October was calanoid copepodites and copepod nauplii. Previous diet analyses of *Bythotrephes* have revealed the presence of copepods, presumably copepodites and nauplii (Dumitru et al., 2001; Schulz and Yurista, 1995), and our modeling suggested that any top-down control of zooplankton by *Bythotrephes* would largely be restricted to copepods occupying the epi- or metalimnion given their putative spatial overlap with this prey. As found in previous studies (Lehman and Cáceres, 1993; Pangle and Peacor, 2006; Pangle et al., 2007), daphnids and bosminids occupied deeper waters (at least greater than 20 m) in October when *Bythotrephes* were abundant, suggesting that *Bythotrephes* could not be exerting direct top-down control on these herbivorous cladocerans in these waters. Rather, *Bythotrephes* [and even other epilimnetic fish planktivores (Dodson, 1988)] could be indirectly reducing cladoceran production by inducing them to occupy deeper, colder waters (sensu Pangle and Peacor, 2006; Pangle et al., 2007). We also cannot discount the possibility that the absence of these herbivorous cladocerans in the top 20 m was due to excessive predation by *Bythotrephes*. A second

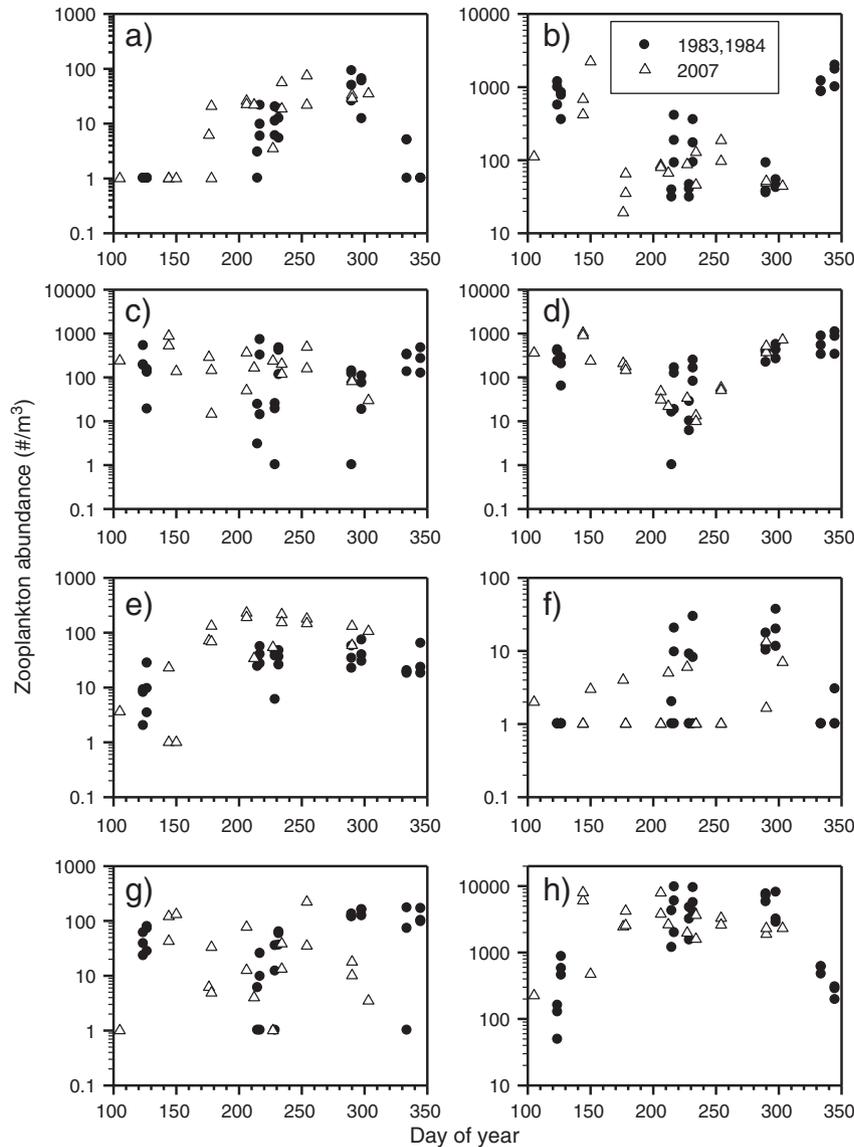


Fig. 4. Abundance ($\#/m^3$) of calanoid copepod taxa as a function of day of year in 1984 (filled circles) and 2007 (open triangles), sampled with whole-water column, 153- μm mesh zooplankton nets in the northern and southern basins of Lake Huron. Taxa in each panel include: (a) *Epischnura lacustris*, (b) *Leptodiaptomus ashlandi*, (c) *L. minutus*, (d) *L. sicilis*, (e) *Limnocalanus macrurus*, (f) *Senecella calanoides*, (g) *Skistodiaptomus oregonensis*, (h) calanoid copepodites. For clarity of presentation, the Y-axis is on the log-10 scale, and we added 1 to all values so that abundance = 0 would be visible.

alternative explanation could be that cladocerans were altering their vertical distribution in response to changes in phytoplankton composition, biomass, and vertical distribution (sensu Fahnenstiel et al., 2010).

Analyses of the proportion of *Bythotrephes* in the top 20 m of water revealed a decline from 70% in June and July (at dusk), to 58% in August and September (at night) to only 41% during October (at daytime). Previous research has indicated that *Bythotrephes* remains epi- and metalimnetic during both the day and night (Lehman and Cáceres, 1993; Pangle et al., 2007; Young and Yan, 2008), likely because they cannot effectively feed at lower light levels at deeper depths during the day (Pangle and Peacor, 2009). When the depth of the metalimnion was considered, our results were largely consistent with previous studies. Our top 20-m tows did not capture the metalimnion during August through October; hence it is not surprising that a considerable proportion of the *Bythotrephes* population was found in depths greater than 20 m.

In summary, our analyses of monthly and seasonal zooplankton trends largely support the findings of Barbiero et al. (2009a) that the Lake Huron zooplankton community has undergone a dramatic shift between 1983–1984 and 2007. The proportion of the community composed of calanoid copepods increased, while the proportion composed of cyclopoid copepods and herbivorous cladocerans declined. Fully disentangling competing “top–down” versus “bottom–up” mechanisms to explain these community shifts is not possible with current understanding, and both may well be contributing to the changes we have observed. Ongoing oligotrophication and declining phytoplankton biomass are likely influencing zooplankton community composition by competitive interactions that favor calanoid over cyclopoid copepods (McNaught, 1975; Richman and Dodson, 1983; Senter, 1994; Soto and Hurlbert, 1991). Planktivores also could be influencing community composition, despite most planktivorous fish species declining in abundance since 1994 (Riley et al., 2008). Through bioenergetic modeling, Bunnell et al. (2011) revealed *Bythotrephes* as the dominant planktivore

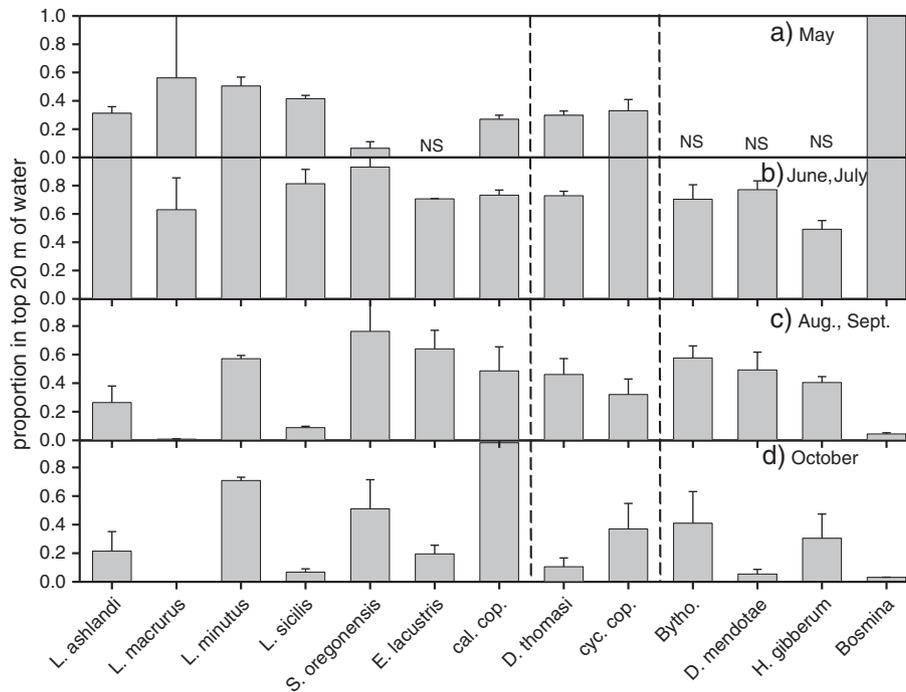


Fig. 5. The mean proportion (\pm standard error) of individuals sampled from a given taxa in the top 20 m of the water column. The species are ordered by calanoids, cyclopoids, and cladocerans (with dashed line dividers) from left to right. The top row depicts the mean proportion sampled during May, when the temperature was isothermal and samples were collected at dusk or at night. The second row depicts the mean proportion sampled in June–July, when the entire epilimnion and metalimnion was sampled at dusk. The third row depicts the mean proportion sampled in August–September, when ~85% of epilimnion was sampled at night. The bottom row depicts the mean proportion in October, when ~60% of the epilimnion was sampled during the day.

in northern Lake Huron in 2007. Analyses herein revealed minimal spatial overlap (at least in the top 20 m) between *Bythotrephes* and cyclopoid copepods and herbivorous cladocerans, suggesting that the

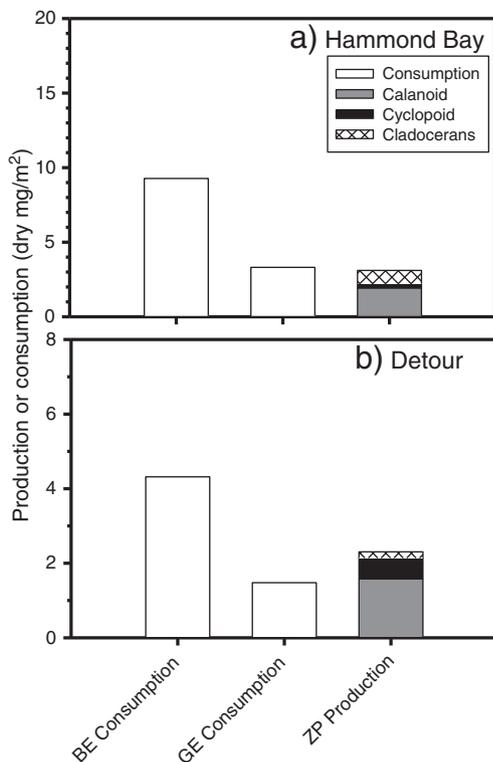


Fig. 6. Comparison of consumption by *Bythotrephes longimanus* by two different methods (BE: bioenergetic; GE: growth efficiency) relative to production of crustacean zooplankton in the top 20 m of the water column during the day in October offshore of (a) Hammond Bay, and (b) Detour, Michigan. Zooplankton (ZP) production is separated into coarse categories of herbivorous cladoceran or cyclopoid or calanoid copepod categories.

negative effect of *Bythotrephes* on these taxa was more likely via indirect effects, as demonstrated by Pangle et al. (2007). For *Bythotrephes* to be the primary driver, however, an unbiased time series of *Bythotrephes* abundance revealing an increase in the early 2000s, just prior to the shift in community composition, would be needed. Unfortunately, no such time series exists to evaluate this hypothesis. One could speculate, however, that because alewife densities had dropped to nearly zero by autumn 2003, and alewife consumption of *Bythotrephes* has been demonstrated to exceed *Bythotrephes* production in nearshore Lake Michigan waters (Pothoven et al., 2007), *Bythotrephes* densities may have increased following the alewife collapse. Note, however, that similar zooplankton community composition changes have occurred in Lake Michigan without a collapse of the alewife population (Barbiero et al., 2009b; Barbiero et al., 2012; Vanderploeg et al., 2012). Clearly, greater understanding of these putative bottom-up and top-down mechanisms is required for ecologists and managers in the Great Lakes to have some level of certainty regarding whether these changes in the Lake Huron zooplankton community are indicative of a new regime or are a shorter-term response to the multiple perturbations within the food web.

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