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Research Paper

Changes in Nearshore Zooplankton Associated with Species Invasions and Potential Effects on Larval Lake Whitefish *(Coregonus clupeaformis)*

key words: whitefish, zooplankton, *Dreissena*, *Bythotrephes*, Lake Huron

Abstract

We examined changes in the nearshore zooplankton community of South Bay, Lake Huron before (1982) and after (2002–2005) the invasions of dreissenid mussels and *Bythotrephes longimanus* and found substantial changes including lower cladoceran abundance, particularly Bosminidae, and higher copepod abundance after invasion. We also estimated changes in the energy content of zooplankton potentially available to larval lake whitefish before and after invasion using published values of energy content per unit mass. There were no differences in available zooplankton energy in May, the period when larvae feed inshore based on thermal preferences and surface temperature data. We conclude that changes in nearshore zooplankton communities following these species invasions probably do not affect larval lake whitefish.

1. Introduction

Non-indigenous species are capable of inducing profound ecosystem change when they invade (BARBIERO and TUCHMAN, 2004). These changes may affect industries, such as fishing, upon which local populations depend. The Upper Great Lakes commercial fishing industry employs 75,000 people and generates $4 billion (US) annually (GREAT LAKES FISHERY COMMISSION, 2003). The lake whitefish (*Coregonus clupeaformis*) constitutes a substantial proportion of this industry, contributing nearly 40% of the total commercial catch in Lake Michigan between the years of 1990–98, and averaging 3,305 metric tons per year (POTHOVEN *et al.*, 2001). The population abundance and stability of coregonid fishes is greatly dependent on conditions experienced during their early life history. It has been demonstrated that small changes in their initial growth rate can affect survival rates by 10–30 fold in the first sixty days of life (DAVIS and TODD, 1998). Due to this vulnerability, the introduction of *Bythotrephes longimanus* and dreissenid mussels (the zebra mussel *Dreissena polymorpha* and the quagga mussel, *D. bugensis)* may have significant impacts on the early life history, survivorship, and ultimate sustainability of this economically important species (MCNICKLE *et al.*, 2006).

Bythotrephes is a generalist predator capable of significant alterations to the plankton community. Unlike other predaceous zooplankton, adult *Bythotrephes* have been found to

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prefer larger cladoceran prey (>2.0 mm) in experimental treatments (Schulz and Yurista, 1999). Native to European and Asian waters, *Bythotrephes* was introduced to the Laurentian Great Lakes in 1984, establishing first in Lake Huron and then sequentially in Lakes Erie, Ontario, Michigan and Superior (Bur *et al.*, 1986; Cullis and Johnson, 1988; Evans, 1988; Lange and Cap, 1986; Lehman, 1987). It is generally accepted that they arrived via ballast water during periods of extensive international shipping (Sprules *et al.*, 1990). However, since their introduction, the impact of these animals has likely been severely underestimated (Barbiero and Tuchman, 2004).

Though *Bythotrephes* have been detected in over ninety inland lakes since their establishment in all the Laurentian Great Lakes (Strecker *et al.*, 2006), studies regarding their effects on the zooplankton community have been limited to pelagic waters. Comparisons between the pelagic waters of non-invaded and invaded lakes have demonstrated a 30% decrease in species richness, with severe negative effects on epilimnetic cladocerans (Boudreau and Yan, 2003). It has also been demonstrated that *Bythotrephes* competes with the native planktonic cladoceran *Leptodora kindtii* for several prey species (Garton *et al.*, 1990). The level of disturbance in nearshore plankton communities associated with *Bythotrephes* has not yet been investigated, despite the importance of this habitat for larval fish (Reckahn, 1970).

Dreissena polymorpha was first detected in Lake St. Clair in June 1988, and *D. bugensis* was first observed in the Great Lakes in the mid-1980s (May *et al.*, 2006). Historical studies suggest that dreissenids also entered the Great Lakes via water and sediment in ship ballast (Griffiths *et al.*, 1991). Since their introduction, dreissenid veligers have been noted to constitute a large portion of the zooplankton community (Winkler *et al.*, 2005). Benthic invertebrates, particularly the amphipod *Diporeia*, have declined since the introduction of zebra mussels, forcing adult whitefish to undergo a dietary shift towards less energetic resources (McNickle *et al.*, 2006).

Larval lake whitefish are zooplanktivorous, and thus could be affected by both *B. longimanus* and dreissenid veligers. *Bythotrephes* has been shown to alter both the community composition and size of zooplankton (Barbiero and Tuchman, 2004; Yan *et al.*, 2001), which may impact the availability of certain prey for larval lake whitefish. However, dreissenid veligers represent a possible food source for larval fish (Pothoven *et al.*, 2001). Despite knowledge of community alterations in pelagic waters and benthos and potential effects of these invaders on adult lake whitefish (McNickle *et al.*, 2006), the degree of change in nearshore plankton communities and potential effects on larval whitefish are currently unknown.

In the nearshore zooplankton community, diaptomid copepods and bosminid cladocerans represent a substantial part of larval whitefish stomach contents (Reckahn, 1970). Thus, changes in the distribution and abundance of these particular taxonomic groups might affect the ultimate sustainability of juvenile lake whitefish. The purpose of this study is first to assess the quantitative change in nearshore zooplankton community abundance and composition before and after the invasion of *Bythotrephes longimanus* and *Dreissena polymorpha* in South Bay, Lake Huron, and then to assess the potential bioenergetic impacts of these changes on larval lake whitefish based on data available at the time the study was carried out.

2. Methods

2.1. Collection Site and Methods

The area under study is the nearshore habitat of South Bay, Lake Huron where larval whitefish are typically found (Reckahn, 1970). Ten sampling sites were selected; five located in small embayments and five located on shorelines exposed to the main basin (Fig. 1). All sites sampled were three meters in depth. Zooplankton were collected with a Clarke-Bumpus sampler fitted with 76 µm mesh and the standard internal impeller. An external flow meter was simultaneously deployed so that tow speed-corrected determinations of volume sampled could be made (YENTSCH and DUXBURY, 1956; MCQUEEN and YAN, 1993). Replicate 2-minute tows in opposite directions parallel to the shoreline were taken at a depth of one meter and then combined into a single composite sample at each of the 10 sites. Samples were taken monthly, but actual sampling dates varied across years (Table 1). Sampling was performed by the Ontario Ministry of Natural Resources in 1982 from May to July. Identical procedures were used in 2002 from July to September, in September only for 2003, 2004, and from May to September in 2005. Environmental data (surface temperature, Secchi depth) were also recorded on days that sampling took place. Secchi depth was recorded twice daily in open water of sufficient depth, while surface temperature was recorded at each sampling site. Means are reported in Table 1.

Subsamples of zooplankton were examined microscopically, identified to the lowest possible taxonomic level according to current taxonomic usage (Integrated Taxonomic Information System online database; http://www.cbif.gc.ca/pls/itisca/taxaget?p_ifx=plglt), and densities expressed as number l^{-1}. Body lengths and predicted dry masses (µg) of individual zooplankton were recorded in 2002–2005 using the software Zebra (ALLEN *et al.*, 1994). For analyses of community patterns, zooplankton species were placed into thirteen groups (Table 2) based on body size and feeding ecology (SPRULES, 1984). These thirteen groups were used to represent functional taxonomic niches for zooplankton communities and to facilitate the use of multivariate analysis, providing a reasonable ratio of the number of sites (10 sites in each of three months both before and after invasion = 60 in total) to organism groupings (approximately 5 : 1). These groups were also chosen in order to reduce the potential influence of rare species on multivariate ordinations. Species were then grouped into particular taxonomic categories (copepods, herbivorous cladocerans, *Leptodiaptomus*, bosminid cladocerans) which are frequently found in whitefish diets (RECKHAN, 1970).

Table 1. Physical/biological attributes recorded or estimated during sampling in South Bay, Lake Huron. Mean surface water temperature and Secchi depths are reported from zooplankton sampling events and from archived data. Lake whitefish lengths are estimated from date of zooplankton sampling. *n/a* = not applicable, *n/r* = not reported, *n/s* = not sampled.

Variable		May	June	July	August	September
Sampling dates	1982	14–18	15–16	15	3[1]	*n/s*
	2002	*n/s*	*n/s*	16	12	11
	2003	*n/s*	*n/s*	*n/s*	*n/s*	5–6
	2004	*n/s*	*n/s*	*n/s*	*n/s*	9
	2005	17–18	21	14–15	9–10	12–13
Mean surface Temperature (°C)	1982	8.6	12.3	17.6	19.1	*n/s*
	2002	*n/s*	*n/s*	21.9	23.1	22
	2003	*n/s*	*n/s*	*n/s*	*n/s*	19.4
	2004	*n/s*	*n/s*	*n/s*	*n/s*	18.9
	2005	7.7	18.1	22.2	22.1	19
Mean Secchi depth (m)	1982	6.3*	*n/r*	*n/r*	*n/r*	*n/r*
	2002	*n/s*	*n/s*	8.9	7.1	6.9
	2003	*n/s*	*n/s*	*n/s*	*n/s*	7.3
	2004	*n/s*	*n/s*	*n/s*	*n/s*	6
	2005	8.6	8.6	9.6	7.3	6.9
Estimated larval lake whitefish size (mm)	1982	21.4	46.7	71.2	*n/a*	*n/a*
	2005	22.6	51.3	70.8	*n/a*	*n/a*

[1] Temperature data reported only-zooplankton were collected but never counted or sorted.

* estimated from value reported from May 12, 1983.

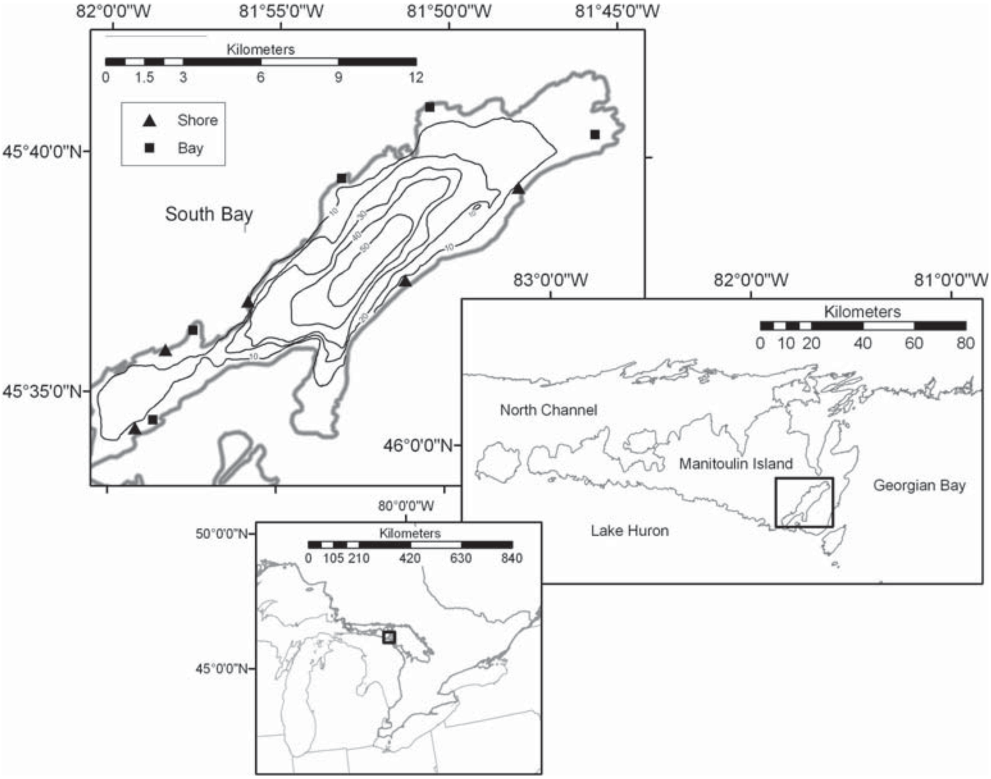

Figure 1. Map of the South Bay, Lake Huron study site. Circles mark embayment sites, and squares mark exposed shoreline sites. Contour intervals are in metres. Data for the maps are from GREAT LAKES BATHYMETRY (2005), UNITED STATES BOUNDARY LAYER (2005), and ONTARIO BOUNDARY LAYER (1992).

B. longimanus was first detected in Lake Huron in 1984 (Bur *et al.*, 1986) and zebra mussels in South Bay in 1997 (McNickle *et al.*, 2006). Quagga mussels were only recently detected in benthic samples collected in 2004 (MDR, unpubl.). Based on their absence from samples collected in the previous two years (McNickle *et al.*, 2006), it is unlikely that *D. bugensis* were present in South Bay before 2004. Accordingly, 1982 and 2005 were contrasted as non-invaded and invaded years respectively, and the four years from 2002 to 2005 were used to assess year-to-year variation in the absence of invasion events. Given the similarities between *D. polymorpha* and *D. bugensis* in the veliger stage, we considered them to be functionally equivalent in the zooplankton community.

2.2. Analysis of Nearshore Zooplankton Community Change

Changes in the zooplankton community associated with the invasion of *B. longimanus* and dreissenid mussels were assessed by comparing May–July samples in a year prior to invasion (1982) and in a year well after invasion (2005). Typical inter-annual variation in zooplankton communities was determined by comparing July–September samples in 2002 and 2005 or September only samples for the four years 2002–2005, times during which no new species invaded South Bay.

Statistical analyses of zooplankton communities were performed on log $(x + 1)$ densities to normalize data (Zar, 1999) and to reduce the influence of rare taxa in multivariate ordinations. Using the

Table 2. Zooplankton taxonomic groups encountered during the study. “y” indicates presence during the time period under study. Association between zooplankton groups and functional group affiliation is shown. Energy density values are reported based on literature values.

Functional grouping and abbreviation	Description	Energy density (j · µg ash-free dry weight^{-1})	Species	1982	2002–2005
Bosminidae, Chydoridae, Sididae and Macrothricidae (Bos_Chy)	Small-bodied cladocerans	0.02331[1]	*Acroperus harpae*	y	y
			Alona spp.	y	y
			Chydorus sphaericus	y	y
			Eubosmina (Eubosmina) coregoni	y	y
			Eurycercus lamellatus	y	y
			Sida crystallina	y	
			Eubosmina (Eubosmina) longispina		y
			Alonella spp.		y
			Macrothrix spp.		y
			Bosmina (Bosmina) longirostris	y	y
Daphnidae (Daph)	Large herbivorous cladocerans	0.02214[2]	*Daphnia (Hyalodaphnia) galeata mendotae*	y	y
			Daphnia (Hyalodaphnia) longiremis	y	y
			Daphnia (Daphnia) retrocurva	y	y
Holopedium (Holop)	Large gelatinous cladoceran	0.02222[3]	*Holopedium* spp.	y	y
Calanoidia (Cal)	Calanoid copepods	0.02461[4]	Calanoid copepodid	y	y
			Leptodiaptomus ashlandi	y	y
			Leptodiaptomus minutus	y	y
			Skistodiaptomus oregonensis	y	y
			Leptodiaptomus sicilis	y	y
Copepod Nauplii (Naup)		0.02461[4]	Calanoid nauplius	y	y
			Cyclopoid nauplius	y	y
Cyclopoida (Cyc)	Cyclopoid copepods	0.02418[5]	Cyclopoid copepodid	y	y
			Diacyclops bicuspidatus thomasi	y	y
			Acanthocyclops vernalis complex		y
			Mesocyclops edax	y	y
			Eucyclops serrulatus		y
			Tropocyclops extensus		y
Senecella calanoides (Sen)	Grazer calanoid copepod	0.02461[4]	*Senecella calanoides*		y
Large copepodid predators (Lim_Epi)		0.02461[4]	*Epischura lacustris*	y	y
			*Limnocalanus macrurus**		y
Dreissenid veligers (Drei)		0.00374[6]	*Dreissena* spp.		y
Leptodora kindtii (Lept)	Predatory cladoceran	0.02207[7]	*Leptodora kindtii*	y	
Ceriodaphnia and *Diaphanosoma* (Cer_Diap)	Mid-sized cladocerans	0.02214[2]	*Ceriodaphnia lacustris*	y	
			Diaphanosoma birgei	y	y
Bythotrephes (Byth)	Predatory cladoceran	0.01674[8]	*Bythotrephes longimanus*		y
Polyhemus pediculus (Pol)	Predatory littoral cladoceran	0.02214[2]	*Polyphemus pediculus*	y	y

[1] Cummins and Wuycheck, 1971. Average of reported value for Bosminidae and Chydoridae.
[2] Cummins and Wuycheck, 1971: Value for Daphnidae.
[3] Cummins and Wuycheck, 1971: Value for general Cladocerans.
[4] Cummins and Wuycheck, 1971: Value for Diaptomidae.
[5] Cummins and Wuycheck, 1971: Value for Cyclopoida.
[6] Madenjian *et al.*, 2006: Estimates of fresh shelled adult mussels converted to shelled dry weight (as per conversions reported in Fisher *et al.*, 1992).
[7] Cummins and Wuycheck, 1971: Value for general Leptodoridae.
[8] Lantry and Stewart, 1993 (but see text).
* Excluded from May energy density estimates based on average size exceeding that of estimated larval lake whitefish gape.

13 functional groupings described in the previous section, we computed ordinations of the sampling sites in taxonomic space using correspondence analysis (CA; Minitab Statistical Software, 2007) to assess community change due both to invasion (May–July 1982 and 2005 data) and annual variability only (July–September 2002 and 2005 data). CA was used because it has been shown to more accurately identify the true underlying community structure compared with other ordination methods, including detrended correspondence analysis (Jackson and Somers, 1991; Hirst and Jackson, 2007).

Because the same sites were sampled between 1982–2005, this permitted the calculation of distance measures for each site between its position in taxonomic space in 1982 with its position in 2005. This distance was interpreted as a measure of each site's community change associated with invasion. Similarly, we computed the distances in site positions between 2002 and 2005 and interpreted them as a measure of each site's variation in taxonomic community composition not associated with species invasion. We used two distance measures to evaluate community change; χ^2 distance, which is the basis for CA, and chord distance (Orlóci, 1967). The χ^2 distance is influenced by the presence of rare taxonomic groups, whereas chord distance treats abundant and rare taxonomic groups equally by emphasizing changes in relative abundance among sites (Legendre and Legendre, 1998). To test the hypothesis that there was no difference in community variation due to invasion versus annual variability, we used a two-sample independent *t*-test to contrast the mean invasion distance with the mean annual variability distance for each distance measure; the test was one-tailed because we expected that differences due to the invasion would be larger than those due to annual change. Because of differences in the months sampled between the invasion (May–July) and annual variability (July–September) data sets which could affect our conclusions regarding nearshore zooplankton change, we also performed a paired *t*-test on only the July samples, which are common to each of the 1982–2005 and 2002–2005 data sets. χ^2 distance was estimated using NT-SYSpc 2.02. Chord distance (D_{cd}) was calculated by first estimating cosine distances between sites in NT-SYSpc, and then applying them to the equation given in Legendre and Legendre (1998):

$$D_{cd} = \sqrt{2 \cdot (1 - \cos \theta)}$$

where Θ is the measure of the angle between site vectors. Sequential Bonferroni corrections to critical *P*-values were made to control for multiple tests (Zar, 1999).

Changes in total zooplankton abundance and abundance of specific combinations of taxa (those important in larval lake whitefish diets, described above) were then evaluated using factorial ANOVAs. ANOVAs testing invasion effects were three-factor fixed-effects models, in which the three factors were "invasion status" (not invaded 1982, invaded 2005), "month" (May, June, July), and "site type" (bay, shoreline). Yearly variation in the absence of invasion was assessed on the July–September 2002 and 2005 data using a similar ANOVA except that year was a random effect. A second test of year-to-year variation was performed on the September 2002–2005 data using a two-factor, mixed model ANOVA with "year" a random effect and "site type" a fixed effect. In all, 15 ANOVAs were performed and a standard Bonferroni correction was made to the critical *P*-value $P = 0.05/15 = 0.0033$) to adjust for multiple tests (Zar, 1999). Although the parametric assumptions of homogeneous variances, normality of residuals and balanced sample sizes (due to loss of one sample) were not met in some ANOVAs, these tests are nevertheless robust (Quinn and Keough, 2002). *Bythotrephes* and dreissenid veliger densities were plotted in post-invasion years to illustrate their relative contributions to post-invasion zooplankton communities.

2.3. Estimating Effects of Community Change on Larval Lake Whitefish

Energy density was estimated for putative zooplankton diets of larval whitefish before invasion (May to July 1982) and after invasion (May to July 2005) by calculating the total energy density of zooplankton consumable by the larvae in each month of the two years. Only species small enough to pass through the mouth gape of whitefish larvae (determined from estimated larval whitefish sizes in Table 1 and a gape-length relationship for lake whitefish spanning larvae to adults, MDR unpubl.) were included in the analyses; only *Limnocalanus* in May samples were excluded on this basis. Lake whitefish size in each sampling period was estimated from data reported in Reckhan (1970) relating Julian day to larval lake whitefish length (relationship over all years, length (mm) = 0.83*(Julian day) –92.4; Table 1). Body mass (dry µg) of individual zooplankton species was only measured in 2002–2005 and was assumed to be the same for 1982. Masses were averaged by each month in 2002–2005 in which each species was detected; average mass was taken from the literature for a few uncommon species which were detected in 1982 only (Downing and Peters, 1980; Guntzel *et al.*, 2003; Ornolfsdottir and Einarsson, 2004; Foster, 2007). Dreissenid veliger mass was estimated by extrapolating a published relationship for adult forms (Bij De Vaate *et al.*, 1992; relationship reported over all locations; values were adjusted to include shell mass as per conversions reported in Fisher *et al.*, 1992). Body mass was then multiplied by numerical abundance to estimate biomass concentration ($\mu g \cdot l^{-1}$) for each taxonomic group.

Total energy content of the zooplankton communities was then estimated by multiplying biomass concentration by published energy values (Table 2) and summing across all species. Where energy density values for a particular species were unavailable we employed the value of a taxonomically similar species or, in some cases, a more general value for the parent taxonomic group (Table 2). For dreissenid veligers, we assumed energy density to be the same as in adults and converted reported energy densities for fresh shelled adults (Madenjian *et al.*, 2006) to energy densities per unit shelled dry mass (using conversions reported in Fisher *et al.*, 1992). For *Bythotrephes*, a general energy value for cladocerans was used (Lantry and Stewart, 1993). To test whether the invasion of dreissenid mussels and *Bythotrephes* affected total zooplankton energy densities, we used a two-factor ANOVA with invasion status (1982 and 2005) and month (May, June, July) as fixed factors. Data were $\log_{10}$-transformed to satisfy assumptions of normality and heterogeneity of variance.

2. Results

Correspondence analysis (CA) indicated clear effects of invasion as reflected by a general lack of overlap between pre- and post-invasion site scores (Fig. 2a). Of the total variation in nearshore zooplankton community composition, 64.4% was explained by the first two axes ($\chi^2 = 68.39$, $df = 708$). The first axis accounted for 50.1% of the total variation alone, and appeared to be related primarily to changes in the bosminid_chydorid zooplankton category (which accounted for 66.7% of the axis 1 community variation, by far the most strongly correlated of all taxonomic groups with this axis). The second axis accounted for an additional 14.3% of the total variation in zooplankton community composition. Dreissenids accounted for 67.4% of this variation, followed by calanoid copepods (15.1%). The sites corresponding to 1982 and 2005 are split primarily along the first axis indicating that pre-invasion communities had greater abundances of bosminid and chydorid cladocerans than post-invasion communities. Daphnids, *Ceriodaphnia, Diaphanosoma* and *Leptodora* also characterized pre-invasion sites (Fig. 2a). Coordinate positions of dreissenids, *Bythotrephes*, *Senecella* and *Leptodora* in Figure 2a should be interpreted cautiously as the first three were only present after invasion and the fourth only before invasion.

Analyses of annual variation in nearshore zooplankton community composition among years during which there were no invasions indicated that 65.4% of this variation was accounted for by canonical axes 1 and 2 (Fig. 2b; $\chi^2 = 85.29$, $df = 580$). Overlap of site scores among years (2002, 2005) was much greater in this comparison than in the invasion CA. Axis 1 accounted for 44.2% of the total variation in zooplankton communities of which 88.5% was due to changes in *Holopedium* abundance. The second axis accounted for an additional 21.2% of zooplankton community variation of which 53.0% was due to changes in dreissenid abundance and a further 23.1% by calanoid copepod abundance. *Ceriodaphnia, Diaphanosoma* and *Polyphemus pediculus* were only detected in 2002 samples, and coordinate positions of these functional groups should be interpreted with caution.

The χ^2 and chord distances between common sites both demonstrated clearly that annual zooplankton community changes during 2002–2005, when no invasions occurred, were significantly smaller than those associated with the invasion of dreissenids and *Bythotrephes* (Table 3). This was true for both the larger dataset in which the months among invasion and annual variability comparisons largely differed, as well as when limiting analyses to the common month of July, despite smaller sample sizes (and therefore lower statistical power) in this reduced dataset.

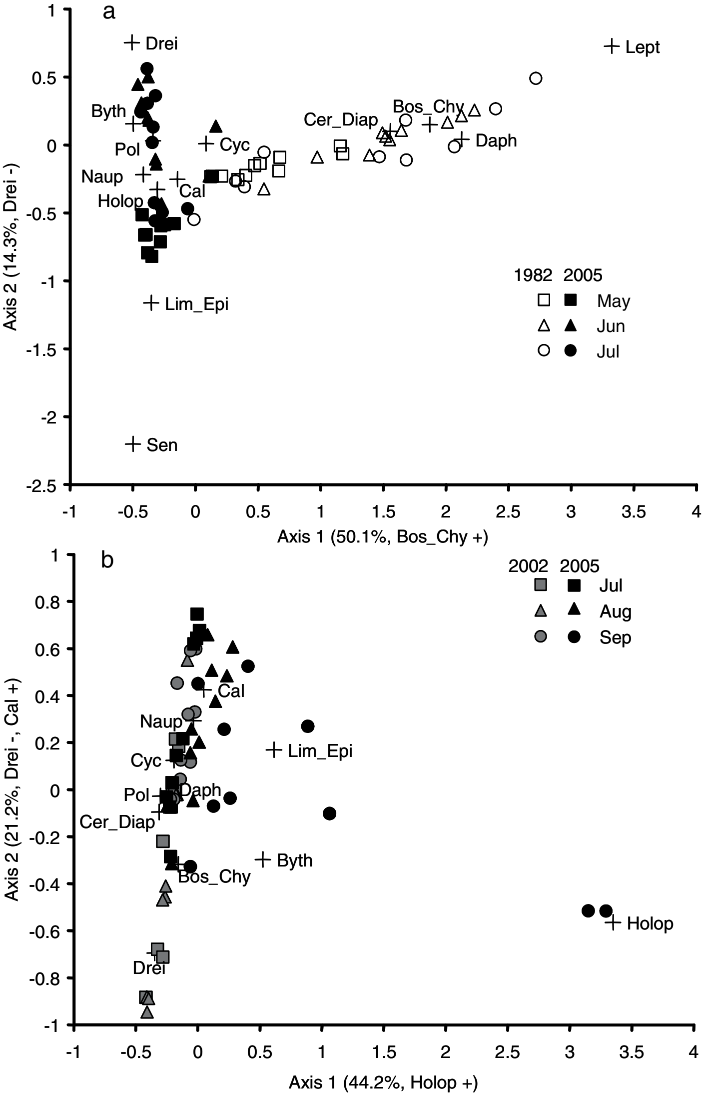

Figure 2. Correspondence analysis showing the change in nearshore zooplankton communities. (a) Changes in nearshore zooplankton community site scores between pre- (1982) and post-invasion (2005) periods. + indicates the coordinate positions of zooplankton functional groups. (b) Correspondence analysis describing the change in nearshore zooplankton communities among years when no invasions occurred (2002–2005). Zooplankton functional group abbreviations are as in Table 2. Proportion of variation explained by each axis and the taxa accounting for the largest proportion of this variation along with signs of the correlation are shown in parentheses.

There were no significant differences in community composition between sample sites in embayments or along open shores (Table 4) so patterns were averaged across sites in the interaction plots that follow. There was a significant difference in total zooplankton densities between pre- and post-invasion communities as well as among months, but this interpretation

Table 3. Student's *t*-tests of distances in taxonomic space among nearshore zooplankton communities affected by dreissenid mussel and *Bythotrephes* invasion (1982, 2005) compared with those subjected to annual variability only (2002, 2005). Community variation measured as χ^2 and chord distances. Degrees of freedom (*df*), *t* statistic (annual minus invasion), one-tailed probabilities of no difference and sequential Bonferroni-corrected critical probabilities are shown. Significance is indicated by an *.

Distance measure	Months used	Test	*df*	*t*	*P* (one-tailed)	P_{crit}
χ^2	Invasion (May–July), annual variability (July–September)	Two-sample *t*-test	57	3.14	0.0013*	0.0167
χ^2	Invasion (July), annual variability (July)	Paired *t*-test	8	3.37	0.0049*	0.025
Chord distance	Invasion (May–July), annual variability (July–September)	Two-sample *t*-test	57	3.39	0.0006*	0.0125
Chord distance	Invasion (July), annual variability (July)	Paired *t*-test	8	1.98	0.0415*	0.05

was confounded by a significant invasion×month interaction (Table 4). Total zooplankton abundance was similar in May but was higher during June and July by roughly an order of magnitude or more after invasion (Fig. 3). Patterns in total copepod densities largely reflected those observed for total abundance, including higher post-invasion densities in June and July (Table 4, Fig. 4). *Leptodiaptomus*, which were by far the dominant copepod group, are more abundant after invasion except July 2002 (Fig. 4). By contrast, herbivorous cladoceran abundance and bosminid abundance were lower after invasion, again with the exception of July 2002 (Fig. 5). There were no significant differences in zooplankton community composition among the post-invasion years (Table 4) further indicating that annual variation in these taxonomic groups is less than that associated with invasion.

Bythotrephes were found in low densities (Fig. 6) compared with total zooplankton abundance in post-invasion years (Fig. 3). In contrast, dreissenid veligers were in low abundance in May samples, but were a large component of the total post-invasion zooplankton community June–August (Fig. 6).

Zooplankton community energy density estimates differed between pre- and post-invasion periods and among months, but there was a significant year × month interaction ($F_{2,54} = 20.12$, $P < 0.0001$, Fig. 7). Tukey's HSD test revealed that post-invasion zooplankton communities were significantly more energy dense than pre-invasion ones in June and July, but not significantly different in May.

4. Discussion

4.1. Changes in the South Bay Nearshore Zooplankton Community

Following the invasion of both *Bythotrephes* and dreissenids in South Bay, the nearshore zooplankton community has undergone significant restructuring. Our analyses indicate that differences in the nearshore zooplankton communities before and after the invasion of *Bythotrephes* and dreissenids are much larger than would be expected based on annual vari-

Table 4. Results of factorial ANOVA tests on concentration of total zooplankton and specific taxonomic groups. * indicates statistical significance after standard Bonferroni correction (critical *P*-value = 0.0033).

Taxonomic Group	Factor	Years and months in comparison					
		Invasion: May–July 1982, 2005		Annual variability: July–September 2002, 2005		Annual variability: September 2002–2005	
		F	*P*	*F*	*P*	*F*	*P*
All zooplankton	Year	77.85	<0.0001*	0.72	0.487	1.21	0.440
	Month	13.28	<0.0001*	1.30	0.434		
	Site type	0.16	0.691	1.76	0.411	0.14	0.735
	Year*Month	20.39	<0.0001*	7.22	1.22		
	Year*Site type	0.13	0.722	1.31	0.371	0.86	0.475
	Month*Site type	0.03	0.966	0.34	0.748		
	Year*Month*Site type	0.24	0.787	0.66	0.523		
All copepods	Year	144.45	<0.0001*	1.06	0.410	2.40	0.245
	Month	8.40	0.001*	0.31	0.762		
	Site type	0.72	0.399	2.05	0.388	0.06	0.827
	Year*Month	29.93	<0.0001*	48.41	0.020		
	Year*Site type	0.12	0.733	1.20	0.387	1.44	0.251
	Month*Site type	0.01	0.992	1.31	0.434		
	Year*Month*Site type	0.24	0.788	0.37	0.693		
Leptodiaptomus spp.	Year	31.56	<0.0001*	3.05	0.223	3.77	0.152
	Month	6.84	0.002*	0.86	0.538		
	Site type	1.16	0.286	4.11	0.292	0.01	0.937
	Year*Month	11.51	<0.0001*	279.23	0.004		
	Year*Site type	0.06	0.810	0.63	0.508	0.29	0.829
	Month*Site type	0.08	0.922	1.95	0.339		
	Year*Month*Site type	0.29	0.749	0.04	0.962		
Herbivorous Cladocera	Year	11.40	0.001*	0.81	0.312	7.93	0.061
	Month	6.43	0.00319*	2.69	0.271		
	Site type	0.23	0.637	7.01	0.230	0.03	0.863
	Year*Month	1.04	0.360	0.83	0.547		
	Year*Site type	0.14	0.706	0.02	0.891	0.66	0.586
	Month*Site type	0.08	0.927	0.20	0.835		
	Year*Month*Site type	0.20	0.816	1.25	0.295		
Bosminid Cladocera	Year	9.69	0.003*	4.57	0.038	4.93	0.111
	Month	4.90	0.012	17.03	0.055		
	Site type	0.00	0.968	1.15	0.478	0.23	0.662
	Year*Month	1.70	0.195	0.15	0.872		
	Year*Site type	0.22	0.643	0.09	0.788	1.68	0.196
	Month*Site type	0.07	0.936	0.41	0.707		
	Year*Month*Site type	0.25	0.779	1.31	0.280		

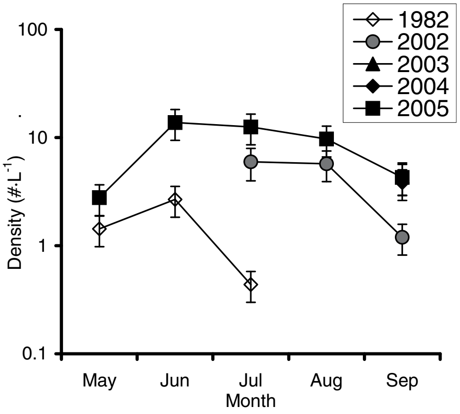

Figure 3. Total zooplankton abundance from May to September for the various years of study. Error bars are ± 1 standard error (*SE*). 2003, 2004 data fall immediately behind 2005 for September.

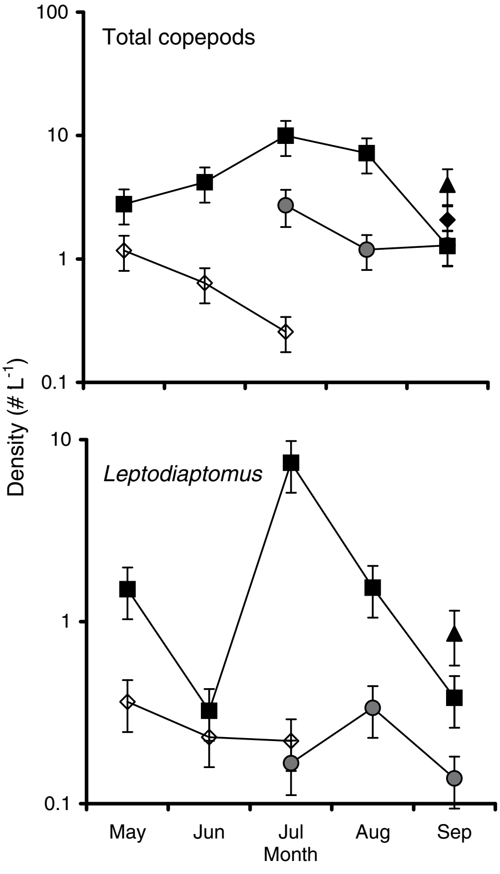

Figure 4. Abundance of total copepods and *Leptodiaptomus* from May to September for the various years of study. Error bars are ± 1 *SE*. Symbols as in Figure 3.

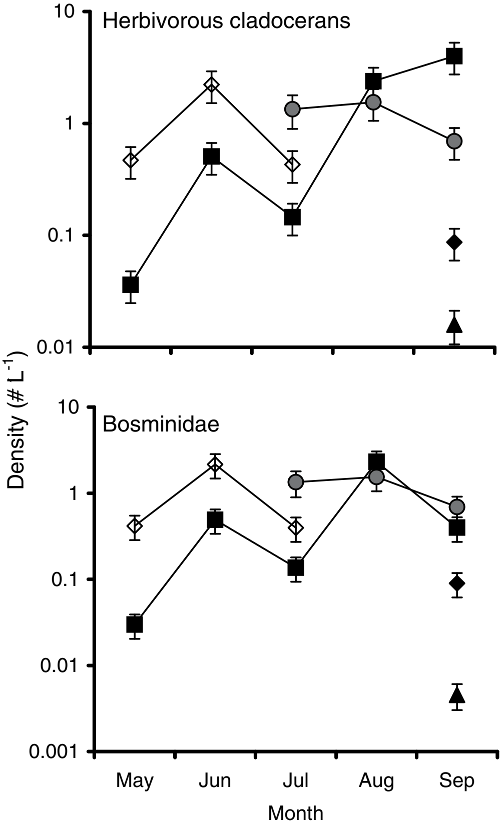

Figure 5. Abundance of herbivorous cladocerans and bosminids from May to September for the various years of study. Error bars are ± 1 *SE*. Symbols as in Figure 3.

ation alone. This was the case despite the influence of two sites with a high abundance of *Holopedium* in September 2005 in the annual variability dataset. Given that our comparisons of distance measures include these outliers, our conclusions about community change are conservative. Given the concordance between results from both χ^2 and chord distance measures, we are confident that changes in the nearshore zooplankton community are real, and cannot be explained by changes in total nearshore zooplankton abundance or the influence of rare taxonomic groups on the ordination solution. We note that zooplankton groups most strongly associated with the pre-invasion time period are cladocerans (daphnids, bosminids, chydorids, *Ceriodaphnia*, *Diaphanosoma*, and *Leptodora*) which are also known to be reduced by *Bythotrephes* invasions into pelagic habitats in inland lakes (YAN and PAWSON, 1997; STRECKER and ARNOTT, 2005; STRECKER *et al.*, 2006) as well as in the Great Lakes (BARBIERO and TUCHMAN, 2004).

It is difficult to argue that the changes we observed in the nearshore zooplankton community are due primarily to environmental differences between 1982 and 2005. Increased abundance of zooplankton, particularly copepods, was associated with higher mean surface temperatures June-September 2005 than 1982, but copepod abundance was also higher in May 2005 when temperatures were lower than 1982. Furthermore, copepods tend to predominate at cooler temperatures (DAVIS and TODD, 1998) so their predominance during the

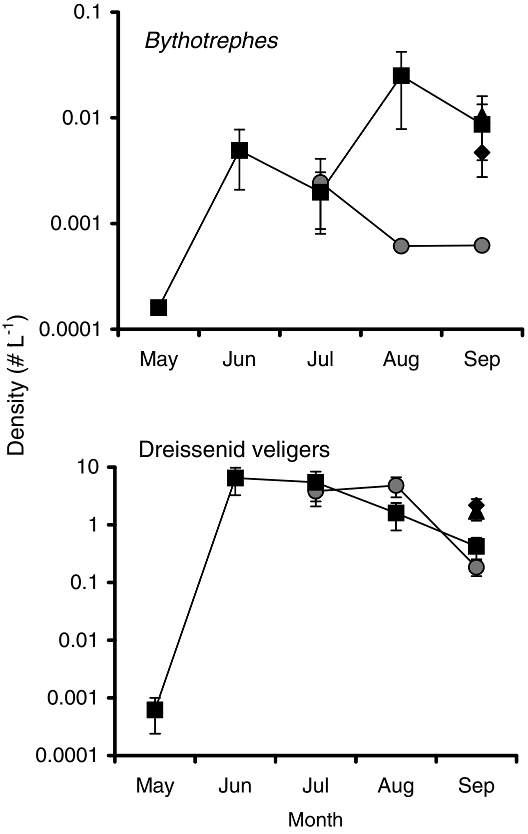

Figure 6. Abundance of *Bythotrephes* and dreissenid veligers from May to September for the various years 2002–2005. Error bars are ± 1 *SE*. Symbols as in Figure 3.

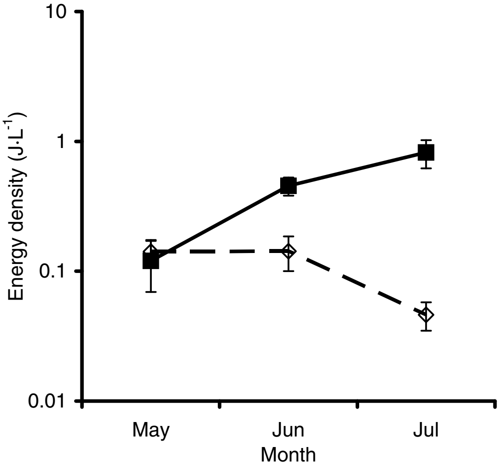

Figure 7. Comparison of zooplankton community energy density available to larval lake whitefish in the pre- (1982, open symbols) and post-invasion (2005, closed symbols) periods, May–July. Error bars are ± 1 *SE*.

warmer summer of 2005 suggests the zooplankton community changes we observe are not likely driven primarily by water temperature.

Though phosphorous data are limited for South Bay over our study period, evidence from other sources suggests that changes in nutrient loading are unlikely. Spring surface phosphorous concentrations in the main basin of Lake Huron ranged between approximately 3 and 6 μg l^{-1} between 1983–2005 (ENVIRONMENT CANADA and US ENVIRONMENTAL PROTECTION AGENCY, 2007). Phosphorous samples collected by the Ontario Ministry of the Environment in Robert's Bay (Southern arm off the inner basin of South Bay) report spring phosphorous concentrations averaging 7.0 and 3.5 μg l^{-1} in 1998 and 2006 respectively, where samples were collected between 8 and 15 m depth. Though these are not surface phosphorous values, they are comparable with those reported for the main basin of Lake Huron. Our Secchi disk water transparency data are limited, especially in 1982, so little can be concluded except to point out that variation in these measures after invasion when zooplankton communities changed very little is comparable to the difference between Secchi depths pre- and post-invasion. Economic development on the shores of South Bay has been negligible since the 1980's (D. ANDERSON, OMNR, personal communication) and the local human population has only increased from 3096 in 1981 to 3683 in 2006. All of this evidence suggests that changes in phosphorous loading to South Bay during the study period are an unlikely explanation for our results. There have also been declines in the abundance of pelagic prey fishes in Lake Huron since 1997 (SCHAEFFER *et al.*, 2006), but such changes in pelagic fish are unlikely to affect the nearshore plankton community we have studied.

Many of the changes we report in the nearshore zooplankton community associated with the invasion of *Bythotrephes* and dreissenids have not been reported. We observed a substantial *increase* in the nearshore community of copepods and their nauplii which is consistent with VANDERPLOEG *et al.*'s (1993) observation that *Bythotrephes* has higher clearance rates and electivity coefficients on cladocerans than faster-swimming copepods in Lake Huron. Our observed increase in *Leptodiaptomus* abundance is also supported by others (YAN and PAWSON, 1997). Though resistance of *Leptodiaptomus* to *Bythotrephes* predation has been accredited to its larger size (YAN and PAWSON, 1997), recent work has shown that *Bythotrephes* has no universal size preference. Instead, it is suggested that *Bythotrephes* predation preferences coincide primarily with size availability, and preferred prey sizes are those in highest density (STRECKER and ARNOTT, 2005). Further, our observation that *Ceriodaphnia* and *Diaphanosoma* densities responded negatively to the presence of *Bythotrephes* also appears to be new. Though *Bythotrephes* are known to feed on *Ceriodaphnia lacustris* in laboratory experiments (LEHMAN and CACERES, 1993; VANDERPLOEG *et al.*, 1993; WAHLSTROM and WESTMAN, 1999), field studies have to this point found no response of these genera to the presence of *Bythotrephes* (BOUDREAU and YAN, 2003).

Species richness of the nearshore cladoceran community in South Bay was stable during post-invasion years despite declines in abundance, contrary to previous open-water assessments. Evaluations of ten invaded lakes reported reductions in cladoceran species richness, diversity, and abundance (STRECKER *et al.*, 2006). Four species of cladocerans (*Sida crystallina, Leptodora kindtii, Diaphanosoma birgei* and *Ceriodaphnia lacustris*) went undetected in post-invasion samples, despite overall higher sampling effort in 2005. However, these species losses were counterbalanced by the appearance *of Macrothrix* spp., *Alonella* spp., and *Eubosmina longispina* in post-invasion years.

In support of previous findings based on open water assessments, both *Leptodora* and *Sida crystallina* were absent from post-invasion samples. *Bythotrephes* and *Leptodora* are often negatively correlated or temporally separated (GARTON *et al.*, 1990), and declines of native *Leptodora kindtii* have been observed elsewhere in the Great Lakes (BARBIERO and TUCHMAN, 2004) and in several inland invaded lakes (FOSTER, 2007). Our study shows that similar patterns are apparent in the nearshore zooplankton community, as *Leptodora kindtii* was not detected in any post-invasion years. Further, the absence of *Sida crystallina* in post-invasion years is supported by STRECKER and ARNOTT (2005) who report declines in their abundance when exposed to *Bythotrephes* in mesocosm experiments.

Holopedium gibberum was the only cladoceran observed not to change between pre- and post-invasion periods. Similar findings of *H. gibberum* resistance to *Bythotrephes* invasion have been attributed to its unique gelatinous sheath and apparent size as a predatory defense in Harp Lake (YAN and PAWSON, 1997). Though *H. gibberum* has been reported to decline over time in open-water Lake Huron surveys (BARBIERO and TUCHMAN, 2004), their study also shows that this species shows a great deal of inter-annual variation, as further demonstrated in differences between our 2002 and 2005 samples in this study.

Surprisingly, we found an overall increase in post-invasion species richness (33) compared with pre-invasion richness (26). BOUDREAU and YAN (2003) found that a decrease in epilimnetic zooplankton abundance and richness is typical of invaded lakes, and largely attributed this to a decline in cladocerans. While our findings confirm a reduction in cladoceran abundance, increases in copepod densities caused a net overall increase in zooplankton abundance, with *Limnocalanus macrurus*, *Senecella calanoides*, *Acanthocyclops vernalis*, *Eucyclops serrulatus* and *Tropocyclops extensus* identified exclusively in post invasion samples. It is possible that this increase in species richness reflects both the greater number of samples taken post-invasion, as well as the increased abundance of copepods sampled. However, it is also possible that the disruption of these nearshore communities has resulted in the opening of ecological niches that may provide occupancy for species typically found in offshore habitats.

There is little evidence in the published literature to suggest that dreissenid veligers have had any affect on the nearshore zooplankton community in South Bay, despite their relatively high abundance during June–September. Recent work has shown that filtering of phytoplankton by dreissenids may positively affect the influence of terrestrial carbon sources in zooplankton (MAGUIRE and GREY, 2006), however, dreissenid veligers have otherwise been reported to have no effect on zooplankton communities despite their high abundance (BARNARD *et al.*, 2006; WINKLER *et al.*, 2005). Bosminid cladocerans declined marginally after invasion, but because of their prevalence in larval whitefish diets this could affect larval withfish growth and survival.

4.2. Implications for Larval Lake Whitefish

Our analysis suggests that larval lake whitefish in 2005 were likely unaffected by the large-scale zooplankton community changes associated with the invasion of *Bythotrephes* and dreissenids because, during May when they are inshore, the available zooplankton energy did not differ between pre- to post-invasion periods. Available prey energy was higher during June and July after invasion but, due to the higher water temperatures and that larval lake whitefish follow the 17 °C isotherm as it deepens (RECKAHN, 1970), it is unlikely they could access this energy source. Observed trends in earlier ice-off dates (JENSEN *et al.*, 2007) and higher water temperatures (AUSTIN and COLMAN, 2007) throughout the Great Lakes region suggest our observations on zooplankton energy availability are probably typical of the post-invasion period.

It is possible that the increase in copepod densities may balance declines in post-invasion bosminid densities with respect to energy available to larval lake whitefish. Although copepods typically have higher energetic content than cladocerans (CUMMINS and WUYCHECK, 1971), they are also more difficult to capture than cladocerans. Given the low densities of dreissenid veligers observed in May, we conclude that they contributed little to larval lake whitefish diets in 2005. Dreissenid veliger energy density is only 15% that of copepods suggesting that their contribution to larval fish diets is small despite their high abundance June–September. Furthermore, evidence from stable isotope studies indicate that fish predation on dreissenid veligers is limited (Barnard *et al.*, 2006). Although our estimation of energy available to larval fish is coarse, we believe it is useful in stimulating studies to better resolve conjectures such as: a) the zooplankton energy base for larval lake whitefish is unaffected by invertebrate invasions, b) increased copepod abundance after invasion may substitute in larval diets for less abundant cladocerans, and c) dreissenid veliger larvae that appear after invasion are unlikely to be a large component of larval lake whitefish diets.

Our study is the first to provide a direct assessment of zooplankton community change in the Great Lakes that is relevant to larval fish in the nearshore, rather than relying on zooplankton community change in pelagic zones (*e.g.*, Barbiero and Tuchman, 2004). Differences between nearshore and pelagic zooplankton communities reported here should caution against using pelagic data to estimate effects on larval fish, such as lake whitefish, that occupy nearshore habitats.

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