Seasonal and historical food web relationships between the water flea (*Daphnia mendotae*), the

spiny water flea (*Bythotrephes longimanus*), *Limnocalanus macrurus*, and *Diaptomus* spp. in

Lake Michigan

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Abstract

Limnocalanus macrurus, a large hypolimnetic calanoid copepod, has experienced increased proportional presence in Lake Michigan in recent years. This increase has come at the expense of decreased biomass of many cladoceran species, such as *Daphnia mendotae*. Introduction of the spiny water flea, *Bythotrephes longimanus*, is thought to have played a large role in this dominance reversal. The increase in proportional biomass of *Limnocalanus* is attributed to an increase in overall species abundance, and not an increase in individual body mass of these organisms. What remained unknown was where *Limnocalanus* was positioned in the historical planktonic food web, and how its position changed seasonally. We applied nitrogen isotope spectrometry to historical zooplankton samples from Lake Michigan. We found that *Bythotrephes* was positioned about 1.5 trophic levels higher than *Daphnia*, and that *Limnocalanus* was about one–half trophic level above *Bythotrephes* and thus about two levels above *Daphnia* during the summer. It is unlikely that adult *Limnocalanus* encounter *Bythotrephes* during summer months because of vertical segregation during thermal stratification. *Bythotrephes* became isotopically heavier and *Limnocalanus* became isotopically lighter from May to August. *Limnocalanus* either shifts its diet seasonally to one consisting of more phytoplankton in summer, or its prey (e.g., *Diaptomus* spp.) shifts to a more phytoplankton food base, thus indirectly resulting in decreased trophic status of *Limnocalanus*. This study serves as a historical, foundational basis for zooplankton food web relations in Lake Michigan that complements similar investigation in Lake Huron. Comparing the historical to the recent zooplankton food web may now elucidate how invasive species like *Bythotrephes* and quagga mussels may have altered the Great Lakes zooplankton communities and bioenergetic relationships within the lakes.

Introduction

Lakes Michigan and Huron have experienced a series of lower food web trophic alterations in recent years, the causes of which are active areas of research. The lakes are undergoing oligotrophication (Barbiero et al., 2002; Evans et al., 2011) as a result of actions to reduce phosphorus loading, a key contribution to primary productivity (e.g., Hecky & Kilham, 1988; Elser et al., 1990). There have been consequences of invasive species like the spiny water flea, *Bythotrephes longimanus* (Lehman, 1987; Berg and Garton, 1994; Therriault et al., 2002), and the zebra and quagga mussels, *Dreissena polymorpha* and *D. bugensis* (Ricciardi & Rasmussen, 1998; Stepien et al., 2005). *Bythotrephes* has potentially affected the zooplankton community composition of Lake Huron by causing a dominance shift from cyclopoids and cladocerans to calanoids (Bunnel et al., 2012). Dreissenid mussels have exacerbated oligotrophication of the lakes by filtering phytoplankton from the water column, thereby decreasing lake primary productivity (Fahnenstiel et al., 2010) and by decreasing the deep chlorophyll layer in early summer in Lake Michigan (Pothoven & Fahnenstiel, 2013), a potential food source for many zooplankton species. Furthermore, a decrease in certain planktivorous fish like the alewife and bloater is thought to have contributed to a shift in the lakes' trophic structure (Bunnel et al., 2009). In fact, Barbiero et al. (2012) hypothesize that Lakes Michigan and Huron are converging with Lake Superior, especially at the lower food web level, to such extent that they are all becoming the same lake ecologically.

One zooplankton species noted to have experienced shifts in dominance in recent years is *Limnocalanus macrurus*, a large, hypolimnetic calanoid copepod. *Limnocalanus* occupies all five Laurentian Great Lakes, and has experienced increases in summer biomass in Lake Michigan

since 2004. Barbiero et al. (2009) noted that estimated *Limnocalanus* biomass increased by about 40% in 2004 through 2006 compared to historical years, in both the northern and southern basins of Lake Michigan. The proportional increase in *Limnocalanus* biomass coincided with a decrease in the biomass of cladoceran species, predominately that of *Daphnia mendotae* (Barbiero et al., 2009). In fact, the reported biomass estimates of *Limnocalanus* were underestimated by up to four–fold due to the application of an unsuitable length–weight regression model for another species, *Diaptomus siciloides* (Doubek and Lehman, 2011), and so the actual representation of *Limnocalanus* in the planktonic community is much larger than originally reported.

One remaining key unknown is the historical trophic position of *Limnocalanus* within the zooplankton community. We examined stable isotope composition of archival zooplankton samples collected from May to August in Lake Michigan during 1989 to quantify the historical position of *Limnocalanus* in the zooplankton food chain. *Limnocalanus* is reported to be omnivorous (Bowers and Warren, 1977; Warren, 1983, 1985), so we compared *Limnocalanus* to a known herbivore, *Daphnia mendotae*, and a known predator, *Bythotrephes* to deduce its position in the food web. We also included hypolimnetic *Diaptomus* spp. (mainly *Diaptomus sicilis*) for comparison in the analysis. *Limnocalanus* has high nutritional value for planktivores (Birge and Juday, 1922; Fish, 1960; Price, 1963) and has a narrow tolerance for oxygen and temperature levels (Carter, 1969; Gannon and Beeton, 1971; Kane et al., 2004; Roff, 1973); therefore, *Limnocalanus* is considered to be an indicator species for ecosystem change.

$\delta^{15}N$ levels can be an indicator of relative trophic structure position among organisms that depend on the same primary source of organic matter (Lajtha and Michener, 1994; Griffiths, 1998). Omnivores are isotopically heavier than herbivores, and carnivores are isotopically heavier than omnivores. Therefore, we predicted *a priori* that $\delta^{15}N$ levels for *Limnocalanus*

would be intermediate between the known herbivore, *D. mendotae* and the known carnivore, *Bythotrephes*. A δ^{15}N value of 3.4 ‰ was used to distinguish separate trophic levels, based on previous studies (Minawaga and Wada, 1984). Also, we predicted that *Limnocalanus* would become more herbivorous or less predatory over a season because *Limnocalanus* has been reported to lose access to some zooplankton prey as the lake becomes thermally stratified (Warren, 1983). Therefore, we predicted that the δ^{15}N difference between *Limnocalanus* and *Bythotrephes* would increase from May to August, because *Limnocalanus* would have a larger portion of its diet composed of phytoplankton whereas *Bythotrephes* would remain an obligate predator. To quantify phytoplankton abundance, we examined chlorophyll *a* (chl *a*) concentrations from vertical profiles. We incorporated *Diaptomus* in the analysis to understand where *Daphnia*, *Limnocalanus*, *Bythotrephes* and *Diaptomus* are positioned in the summer food web. *Limnocalanus* and *Bythotrephes* were compared May through August. *Daphnia* were only compared in August, since *Daphnia* were rare in the water column in earlier months. *Diaptomus* were compared in August, as well.

Regarding *Limnocalanus* as an indicator species of ecosystem change, pinpointing its position in the trophic structure can give us a reference for the historical conditions of Lake Michigan, and how trophic relations change seasonally. Contemporary data can then be compared to the historical condition to provide a context for quantifying how zooplankton may be shifting trophic positions as a result of ecosystem changes (Jackson et al., in press).

Methods

Study area and zooplankton sampling

The principal reference station for our analysis (St 2) was located 36 km offshore (100-m depth) of Grand Haven, Michigan (Figure 1). Surveys were conducted from May to October 1st in 1989 (Table 1). Zooplankton were collected by Puget Sound closing nets (Research Nets, Inc.) with a 1–meter diameter mouth, aspect ratio of 5:1, and mesh apertures of either 130 μm or 300 μm. In most cases, three replicate tows with the ship at anchor were split with a Folsom plankton splitter and physically combined for composite counts (Lehman, 1987; Lehman and Caceres, 1993). Specimens were preserved in sucrose-formalin (Haney and Hall, 1973).

Figure 1 about here

Experimental animals

Zooplankton were rinsed repeatedly with reverse osmosis (RO) water to remove sucrose-formalin. *Limnocalanus* and *Bythotrephes* were removed from May through August in 1989 for seasonal $\delta^{15}N$ comparisons. The number of organisms from each species withdrawn from each month varied according their seasonal length–weight regression (Doubek and Lehman, 2011). *Limnocalanus* specimens chosen were of uniform metasomal length of 1.6 mm, +/- 0.1 mm, measured using a Wild M5A stereomicroscope equipped with a calibrated eyepiece micrometer. *Daphnia* were collected only from the August sample since the taxon was rare from May through July. *Diaptomus* samples were included for August. Specimens were further cleaned with watchmaker forceps and insect pins in RO water to remove any phytoplankton or other adherents from their integuments.

Organisms were placed on tared, aluminum boats (Dumont et al., 1975; Edmondson and Winberg, 1971; Makarewicz and Likens, 1979) and dried to constant weight overnight at 60°C (e.g., Burns, 1969; Pace and Orcutt, 1981). After being allowed to cool to room temperature over silica gel in a dessicator, the samples were weighed with a CAHN 29 electrobalance using silica

gel in the chamber to reduce the effect of humidity on the samples (Doubek and Lehman, 2011). Samples were given three minutes to stabilize before measurements were recorded. Mean individual dry weights of each sample were determined by subtracting the initial tare from the final weight and dividing by the number of organisms present in each sample.

NO$_3^-$

If lake nitrate concentrations reach zero, or to extremely low concentrations (i.e., <1 μM), then nitrogen fractionation may not occur since most nitrogen would be assimilated by the organism of study (Waser et al. 1998). Therefore $\delta^{15}N$ values may not be an appropriate tool in measuring trophic structure relations under oligotrophic or nutrient depleted conditions. We included an NO_3^- analysis to ascertain that nitrate levels were not depleted in Lake Michigan at St. 2 during our study period.

Lake water samples were collected by Niskin cast with the vessel at anchor. Filtrate was prepared shipboard using GF/F filters. Samples were refrigerated at 4 °C and nitrate was measured within 48 h by Cd–reduction and analysis for nitrite using a Tecator flow injection analyzer. Mean epilimnetic nitrate concentrations were determined for each month (May–August).

Chl a

Chl *a* concentrations were analyzed in August 1989 to quantify if *Limnocalanus* had access to phytoplankton prey during summer stratification of the lake. Filters for pigment analysis were prepared shipboard by filtering 100–ml replicates of unfiltered lake water through GF/F filters; filters were frozen and stored over silica gel until analysis. Filters were extracted

and macerated in a tissue grinder using 90% v/v acetone. The resulting slurry was filtered

through a GF/D filter and pigment in the filtrate was measured fluorometrically using a Turner

Design TD–700 equipped with 436 nm excitation filter and 680 nm emission filter.

Mass isotope spectrometry

The pellet samples of zooplankton were subjected to CN analysis and mass spectrometry

(Thermo Scientific Delta Plus isotope ratio mass spectrometer) to obtain $\delta^{15}N$ values. We

attempted to attain an aggregate zooplankton mass of 0.5–1 mg for each analytical sample to

optimize detection results from the spectrometer.

Statistical analysis

SYSTAT version 11.0 (SYSTAT Inc., Evanston, IL) was used for one and two-way

analysis of variance with post-hoc Bonferroni contrasts for seasonal comparisons among

zooplankton species. P–values for statistical tests were considered significant at α= 0.05.

Results

Historical summer food web relations

Zooplankton species exhibited significant differences in $\delta^{15}N$ values in August 1989

(ANOVA, F= 196, P< 0.001). Post-hoc tests revealed that all four species were statistically

significant from one another (P< 0.001 in all cases). *Diaptomus* was about one, *Bythotrephes* was

about 1.5 and *Limnocalanus* was about two nominal trophic levels greater than the reference

herbivore *Daphnia*, with mean $\delta^{15}N$ differences with respect to *Daphnia* of 3.3‰, 4.5‰ and

6.6‰, respectively. *Limnocalanus* was almost one nominal level higher than *Bythotrephes* (Figure 2).

Seasonal $\delta^{15}N$ values

From May through August of 1989, a significant difference existed between mean $\delta^{15}N$ of *Limnocalanus* and *Bythotrephes* (P< 0.001 in all cases, Figure 3). *Limnocalanus* was isotopically heavier than *Bythotrephes* in May with a mean $\delta^{15}N$ difference of 6.5‰, almost two nominal trophic levels greater. In June, *Limnocalanus* was situated about 1.5 trophic levels higher than *Bythotrephes*, with a $\delta^{15}N$ difference of about 5.8‰. In July, *Limnocalanus* was almost one trophic level higher than *Bythotrephes*, with a mean $\delta^{15}N$ difference of about 2.7‰. *Limnocalanus* was about one–half trophic level higher than *Bythotrephes* in August.

Vertical distributions of *Limnocalanus* and *Bythotrephes* indicate very limited spatial overlap and hence little prospect that they are potential prey items for one another (Figure 4). Illustrated by a representative summer tow in 1989, the bulk of the *Limnocalanus* population remained deeper than 40–m, whereas the majority of *Bythotrephes* were found in the top ten meters of the water column. Although a portion of the *Limnocalanus* population migrated into shallower water during the night, very little spatial overlap existed overall.

Figure 2 about here

Figure 3 about here

Figure 4 about here

Table 1 about here

NO_3^- analysis

Nitrate levels decreased, on average, seasonally in 1989 as phytoplankton populations assimilated nitrate in cellular processes. However, August nitrate concentrations were just slightly lower than in May (15.8 and 17.3 μM, respectively) and nitrate never reached a concentration low enough to be considered depleted from the water column (Table 1). Therefore, nitrate was always abundant enough for nitrogen isotope fractionation to occur in our 1989 samples.

Chlorophyll a

Chl *a* vertical profiles were analyzed to determine phytoplankton productivity in the summer water column and if *Limnocalanus* had access to hypolimnetic phytoplankton prey. Figure 4 suggests that a deep chlorophyll layer existed in August 1989. A thermocline formed at about 20–m depth, and subsequently, there was a clear distinction between the epilimnion and hypolimnion, as temperatures fell to less than 5 °C below the thermocline. Chl *a* levels (measured as fls) were greatest, on average, above the thermocline, ranging from 1.5 to 2.0 fls. However, a deep chlorophyll layer formed just below the thermocline, with chl *a* levels reaching >2 fls. In addition, the fluorometer detected phytoplankton presence in the hypolimnion, down to the bottom of the water column. *Limnocalanus* had access to ample hypolimnetic phytoplankton prey in the water column in August.

Discussion

Our a priori hypothesis that *Bythotrephes* would occupy a higher trophic level than *Limnocalanus* was not supported. In general, *Bythotrephes* was positioned about one nominal trophic level greater than *Daphnia*, and *Limnocalanus* about one level above *Bythotrephes*, and

two above *Daphnia*, in the historical Lake Michigan zooplankton food chain. Despite the vast proliferation of *Bythotrephes* and their alteration of zooplankton communities in the Great Lakes' food web (e.g., Bunnell et al., 2012), they are only positioned about one trophic level greater than the obligate herbivore. The finding that *Bythotrephes* is about one trophic level above *Daphnia* was also discovered in inland lakes in Ontario, and in Lake Huron (Foster & Sprules, 2010; Jackson et al., in press). *Bythotrephes* became isotopically heavier from May to August, and during August was positioned about 1.5 trophic levels higher than *Daphnia*. The epilimnetic food web in May was composed mainly of naupliar and copepodid diaptomids and cyclopoids as well as a few *Daphnia* and *Bosmina*. More predatory zooplankton like adult and subadult *Diaptomus* became present in the epilimnion in later months (Makarewicz et al., 1998; Bourdeau et al., 2011) giving *Bythotrephes* access to higher trophic status prey. This is the first mention of these historical zooplankton food web relationships in Lake Michigan using nitrogen isotope analysis, that *Limnocalanus* sits higher in the food web than *Bythotrephes* in Lake Michigan, and that the historical hypolimnetic food web was more complex than the epilimnetic food web.

The question remains whether *Bythotrephes* was always approximately one trophic level higher than the obligate herbivore directly after its introduction and spread to the Great Lakes ecosystems, versus years later. *Bythotrephes* has played a large role in the community shift from cladocerans to calanoids in the Great Lakes, including Lake Michigan. Previous studies in the Great Lakes have documented the shift of calanoids, like *Limnocalanus*, becoming more populous in recent years compared to the 1980's when *Bythotrephes* first invaded the lakes (Barbiero et al., 2009; Bunnell et al., 2012). This may be because *Bythotrephes*, an epilimnetic invader, has already decimated epilimentic carnivores, like *Leptodora kindtii* (Branstrator, 1995),

to the point where there is no longer an intermediate trophic level present; there is simply herbivore or omnivore zooplankton and *Bythotrephes*, and other more predatory species like *L. kindtii* are now scarce. Many large calanoids are hypolimnetic and probably do not frequently come into contact with *Bythotrephes*, especially during summer stratification. From our results, *Limnocalanus* remained about one–half trophic level higher than *Bythotrephes* in August, and summer stratification most likely prevented these two species from encountering each other in their respective environments. Therefore, adult hypolimnetic calanoids like *Limnocalanus* and *Senecella* are probably left unaffected from predation by *Bythotrephes*. Decreased representation of cladocerans like *Daphnia* in the epilimnion, along with decreased pressure from fish predation, have probably each contributed to *Limnocalanus*' increased success in Lake Michigan in recent years.

  Limnocalanus became isotopically lighter from May to August. In August, *Limnocalanus* was positioned, on average, two nominal trophic levels higher in the food chain than *Daphnia*, and about one–half level higher than *Bythotrephes*. *Limnocalanus* was also one nominal trophic level higher than *Diaptomus*, another hypolimnetic species. It appears that *Limnocalanus* may be preying upon *Diaptomus*, as well as other organisms present in the hypolimnion, such as cyclopoids or ciliates. Our data suggest two possible mechanisms for why *Limnocalanus* became isotopically lighter over the season. (1) With decreased access to copepod or other zooplankton prey during summer thermal stratification, *Limnocalanus* may have altered its diet to one consisting of more hypolimnetic phytoplankton prey. Summer stratification was accompanied by a deep chlorophyll layer, thus *Limnocalanus* might have taken advantage of this increased primary production and reduced the number of trophic links between itself and the primary food base (Lindemann, 1942). The result would be *Limnocalanus* occupying an overall lower trophic

level. (2) *Diaptomus*, prey for *Limnocalanus*, could be taking advantage of increased access to phytoplankton prey, with a decreased access to smaller copepod prey sources with stratification. The result of *Diaptomus* becoming more omnivorous would result in *Limnocalanus* becoming indirectly isotopically lighter by consuming *Diaptomus* who are feeding lower on the food web. There was no clear way to distinguish which is the leading mechanism in the historical Lake Michigan food web since obligate herbivores are largely absent from the water column in earlier months. Future studies could analyze more species in Lake Michigan or other Laurentian Great Lakes to divulge the reason for *Limnocalanus* becoming isotopically lighter over a season.

Jackson et al. (in press) found similar results in the summer zooplankton food web in Lake Huron from 1993 and 1995. During these time periods, *Limnocalanus* was situated about two nominal trophic levels above *Daphnia* in Lake Huron, which is comparable to the historical relationship in Lake Michigan. The authors found that *Limnocalanus* became more omnivorous from 1993 and 1995 to 2009, either by consuming more hypolimnetic phytoplankton, or consuming *Diaptomus*, which was eating lower on the food chain. It would be valuable to conduct a similar study in Lake Michigan to deduce if *Limnocalanus* is experiencing similar alterations in its trophic position, and to help shed more light on causes for the species' trophic shift over time in these two lakes. It could be that *Limnocalanus* is consuming more phytoplankton in Lake Michigan in recent years. However, recent evidence suggests that phytoplankton productivity and a deep chlorophyll layer have decreased in Lake Michigan due to the invasion of dreissenid mussels (Pothoven & Fahnenstiel, 2013), thereby *Limnocalanus* may not have as much access to summer phytoplankton prey as in the 1980's. Alternatively, *Limnocalanus* may be consuming more omnivorous prey and eating lower on the food chain, such as taking advantage of the abundance of quagga mussels in the lake (Nalepa et al., 2010).

Analyzing contemporary samples and comparing them to the historical condition will help us better quantify how invasive species like *Bythotrephes* and dreissenids have altered the zooplankton community in Lake Michigan.

This study serves as a historical foundation in the status of food web relations in Lake Michigan, shortly after the invasion of *Bythotrephes* and dreissenid mussels, and complements a similar study conducted in Lake Huron (Jackson et al., in press). As Lake Michigan has experienced a number of perturbations in recent years, comparing the historical to the recent zooplankton food web, using *Limnocalanus* as an indicator of ecosystem change, can now elucidate how *Bythotrephes* and dreissenids have altered the Great Lakes zooplankton communities and bioenergetic relationships within the lakes.

Acknowledgements

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