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Zooplankton trophic structure in Lake Michigan as revealed by stable carbon and nitrogen isotopes

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ABSTRACT

Within the last few decades Lake Michigan's plankton community has undergone substantial changes. Oligotrophication of the pelagic zone has led to a decrease in zooplankton biomass, while species composition has shifted, with copepod species becoming more dominant. Although these observations have been relatively well documented, their implications for the food web have not been well addressed. To define feeding relationships within the zooplankton community, we measured the stable carbon and nitrogen isotope composition and biomass of major zooplankton species, three seston size classes, and seston collected from three depths in southeastern Lake Michigan. Nitrogen stable isotope ratios suggest a complex plankton food web with zooplankton appearing to occupy at least three distinct trophic positions. The large calanoid copepod *Limnocalanus macrurus* occupied a tertiary consumer trophic position, more than one trophic position above all other zooplankton species sampled. Carbon stable isotopes revealed significant differences among zooplankton species. Though the mechanisms responsible for these differences are not clear, these results suggest that there is significant partitioning of resources at the base of the food web.

Introduction

The Lake Michigan planktonic community has gone through substantial changes over the last few decades. In the late 1980s a major crash was observed for most of the native cladocorean populations. This resulted in a relatively species poor cladoceran community with *Daphnia mendotae* alone maintaining an appreciable population (Barbiero and Tuchman, 2004; Lehman and Caceras, 1993). The introduction of the predatory cladocorean *Bythotrephes longimanus* (hereafter *Bythotrephes*) has been at least partially implicated in this widespread population crash (Barbiero and Tuchman, 2004; Lehman and Caceras, 1993; Pangle et al., 2007; Pichlova-Ptacnikova and Vanderploeg, 2011). Though its effects on the system are less clear, another invasive cladocorean, *Cercopagis pengoi*, was discovered shortly after *Bythotrophes* (Charlebois et al., 2001). It is hypothesized that predation by *C. pengoi* has also impacted the zooplankton community (Witt et al., 2005). Along with these cladocorean predators, another group of Ponto-Caspian invaders was first observed at this time. *Dreissena polymorpha* (zebra mussel) was first discovered in 1989, soon to be followed by the closely related *Dreissena rostriformis bugensis* (quagga mussel) (Nalepa et al., 2006, 2010). These prolific filter feeders rapidly spread, colonizing a large portion of the bottom of Lake Michigan (Nalepa et al., 2010). Like the *cladoceran* invaders before them, the proliferation of *D. bugensis* throughout Lake Michigan coincided with large scale food web changes. Both chlorophyll *a* concentrations and primary productivity decreased significantly, with subsequent increases in water clarity (Barbiero et al., 2009; Fahnenstiel et al., 2010). Along with these changes, total zooplankton biomass declined substantially and the species composition shifted (Vanderploeg et al., 2012). *D. mendotae* and cyclopoid copepods represented a significant portion of this loss of biomass (Barbiero et al., 2012; Vanderploeg et al., 2012) though two calanoid copepods (*Leptodiaptomus minutus* and *Leptodiaptomus ashlandi*) and *Mysis relicta* have also experienced declines (Pothoven et al., 2010; Vanderploeg et al., 2012). Conversely, several species of large calanoid copepods have increased in biomass. *Limnocalanus macrurus* in particular makes up a substantial proportion of the total summer zooplankton biomass in Lake Michigan (Barbiero et al., 2009; Doubek and Lehman, 2011). Other large calanoids including *Leptodiaptomus sicilis* and *Epischura lacustris*, as well as the predatory cladocoran *Bythotrephes* have also recently exhibited more modest population increases (Barbiero et al., 2009; Vanderploeg et al., 2012). Declines in herbivorous cladocerans and increases in copepod taxa reflect a pelagic community with a trophic status more similar to that of Lake Superior (Barbiero et al., 2012).

Although these changes in Lake Michigan's planktonic community are relatively well documented, the implications for the entire pelagic community are still not well understood. Zooplankton represent a critical link between the lower and the upper food web. Changes in the zooplankton community can affect both phytoplankton through top down control as well as energy transfer to higher trophic levels (Carpenter

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et al., 1985; Turschak and Bootsma, This issue). Because zooplankton serve as a conduit of primary production to higher trophic levels, several questions have arisen following major food web changes. For example, could increased biomass of the large calanoid *L. marcurus* provide an important food source for pelagic consumers? Alternatively, could this predatory copepod be putting further strain on planktivorous fishes by feeding on similar food resources? Moreover, how has the shift in zooplankton species composition affected other invasive species? Specifically, could declines in *D. mendotae* have forced *Bythotrephes* to rely more heavily on alternative prey resources? Finally, have energy pathways through the planktonic food web been altered, and to what extent are copepod-dominated energy pathways utilized by planktivorous fishes? More detailed information regarding feeding interactions as well as the overall trophic structure of Lake Michigan's zooplankton food web is necessary to address these and other questions related to Lake Michigan's changing food web.

When attempting to describe food webs, species are often aggregated into functional feeding groups. Though this practice is common, these aggregations are not evenly distributed, and species resolution tends to decrease lower in the food web (Polis, 1991). In models of aquatic food webs, fish are often represented at species specific level while zooplankton tend to be placed into one or two functional feeding groups (Rogers et al., 2014). Although this type of aggregation is common, it may not be valid for the Lake Michigan. In fact, others have suggested that the large number of potential feeding interactions between plankton may result in a relatively high maximum trophic position for plankton food webs (Sprules and Bowerman, 1988). This is especially true in glacial lakes that frequently contain one or more predatory relict species (Sprules and Bowerman, 1988). Furthermore, diverse species specific feeding behaviors have been identified for zooplankton species present in Lake Michigan (Vanderploeg et al., 1988, 1993; Warren, 1985; Wong and Chow-Fraser, 1985). Attempts to elucidate feeding relationships in other aquatic systems have discovered complex trophic structures within zooplankton food webs (Kling et al., 1992; Matthews and Mazumder, 2003a; Ngochera and Bootsma, 2010). Therefore, aggregation of the lower food may mask important ecosystem processes and result in erroneous estimates of basic ecosystem properties including linkage complexity and number of trophic links per species (Abarca-Arenas and Ulanowicz, 2002; Martinez, 1991).

In addition to species aggregation, food webs are often described using results from food preference studies, gut content analysis, and direct observations of feeding. Although these techniques provide necessary information, food webs constructed using these techniques have been criticized as being subjective illustrations, and potentially important trophic interactions may be overlooked (e.g. omnivory and cannibalism; Paine, 1988; Polis, 1991). The analysis of food webs with a higher taxonomic resolution using more objective techniques may provide further insight into the trophic structure of Lake Michigan.

One technique that is increasingly being applied to determine the structure of food webs is the analysis of stable carbon (C^{13}:C^{12}) and nitrogen (N^{15}:N^{14}) isotope ratios. This method relies on making general assumptions about the separation of the heavy and light stable isotopes between trophic transfers. The nitrogen stable isotope is used to infer trophic position by assuming a 3.4‰ increase in consumer tissue relative to their food source (Minagawa and Wada, 1984; Post, 2002; Vander Zanden and Rasmussen, 2001). In contrast, the carbon stable isotope ratios of consumers are similar to their food source since a more conservative increase of approximately 1‰ has been observed between trophic transfers (Hecky and Hesslein, 1995; Vander Zanden and Rasmussen, 1999). The simultaneous analyses of these two isotopes are therefore used to infer both trophic position and dietary sources of consumers.

The objective of this research was to examine feeding interactions and community structure within Lake Michigan's zooplankton community using taxa-specific analysis of stable carbon and nitrogen isotopes.

Methods

Sample collection and processing

On eight dates between June and October 2011, zooplankton and water samples were collected from an offshore site ($z = 50$–70 m) in southwest Lake Michigan near Milwaukee (N 43.0728° and W 87.789°). Samples were collected in zooplankton tow nets with a weighted collection cup (mesh size: 253 μm and 1 mm; mouth opening: 0.75 m and 1 m, respectively). Nets were lowered to approximately 1 m above the lake bottom and then retrieved vertically at a speed of ~1 m s^{-1}. For seston analysis, water samples were collected with a 5-liter Niskin bottle from depths of 15 m and 35 m and pooled.

In the laboratory, water samples were passed through a 210 μm filter to remove most large zooplankton. To isolate seston size classes, the water was passed through a series of Nitex screens to isolate microplankton (64 μm screen), nanoplankton (3 μm) and picoplankton (remaining filtrate). The contents left on the Nitex screens and the filtrate were then rinsed onto separate GF/F (0.7 μm) filters and water was suctioned through at low vacuum, resulting in size classes of 64–210 μm (microplankton), 3–64 μm (nanoplankton), and <3 μm (picoplankton). Non-dietary carbon present in both seston and invertebrate samples has been shown to affect δ^{13}C values resulting in small but significant increases (Carabel et al., 2006; Jaschinski et al., 2008; Mateo et al., 2008). Because of this, acidification of a sample prior to analysis of stable isotope signatures has been recommended (Carabel et al., 2006; Jaschinski et al., 2008; Mateo et al., 2008). However, in addition to affecting the δ^{13}C, strong acids or long exposures to acids have been found to also significantly affect the δ^{15}N of samples (Carabel et al., 2006; Kennedy et al., 2005; Mateo et al., 2008). Therefore, to avoid affecting the δ^{15}N while removing any non-dietary carbon we chose to briefly treat seston samples with a weak 5% HCl followed by a rinse in deionized water directly after filtering. The filter samples were then placed in a desiccator and allowed to dry completely before being packed in aluminum foil disks for stable isotope analysis. While the relative contribution of living plankton and particulate detritus in each of these size classes is uncertain, for pelagic samples from a large lake it is likely that the seston in these size classes is dominated by phytoplankton (Hecky et al., 1993; Hochstädter, 2000), and therefore we feel justified in referring to seston size classes as picoplankton, nanoplankton, and microplankton.

Following collection, zooplankton were left in lake water for several hours to evacuate their gut contents, after which they were narcotized with carbonated water. Using a dissecting scope and a Bogorov counting chamber, major zooplankton species in each sample were identified to the lowest taxonomic level possible, enumerated, and handpicked onto GF/F filters. Copepodites and adults were not separated for analysis. Depending on the size of the zooplankter, 50–200 individuals were placed onto each filter, and the exact number of individuals for each filter was recorded. Due to the time consuming nature of processing these samples, replication for each species at each sample period was limited. However, on a few occasions replicate samples for select species were analyzed from a single net tow, allowing us to assess the degree to which a single sample accurately represents the population. Zooplankton samples were also briefly treated with 5% HCl followed by a rinse with deionized water to remove inorganic carbon that may have been left behind from the carbonated water. Filters were placed in a desiccator to dry and then were packed in aluminum foil disks for stable isotope analysis. Zooplankton counts for both net tows (253 μm and 1 mm) were enumerated in triplicate. For each species, the largest average abundance between the two net tows was reported.

Seston and zooplankton samples were collected again in 2012 between May and November. Prior to collecting water samples for seston, a CTD cast was made (SeaBird SBE25) and the data were viewed to identify the upper and lower boundaries of the metalimnion. On three dates water samples were then collected from the mid-depths of the epilimnion, metalimnion, and hypolimnion using a 5-L Niskin bottle. Samples

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