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Notes

Historical trophic position of *Limnocalanus macrurus* in Lake Michigan

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ABSTRACT

In Lake Michigan, oligotrophication and invasive species proliferation have led to dramatic changes in the planktonic food web. *Limnocalanus macrurus* is a native, glacial relict predatory copepod whose trophic role within the zooplankton community may help us better understand the dynamics behind those changes. We applied nitrogen isotope spectrometry to zooplankton from Lake Michigan to quantify the yearly and seasonal position of *Limnocalanus* and other taxa in the historical Lake Michigan planktonic food web. We found that *Limnocalanus* was positioned about one-half trophic level above *Bythotrephes* and about two levels above *Daphnia* during the summer in 1989, 1993, 1995 and 1997. It was unlikely that adult *Limnocalanus* encountered *Bythotrephes* during summer months because of vertical segregation during thermal stratification. Instead, *Limnocalanus* probably had greater access to copepod prey such as *Diaptomus* and *Epischura*. *Limnocalanus* became isotopically lighter seasonally in relation to *Daphnia* and either shifted its diet to one consisting of more phytoplankton, or its prey (e.g., *Diaptomus*) shifted 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 such as *Bythotrephes* and quagga mussels have altered zooplankton communities and bioenergetic relationships within the Great Lakes.

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Introduction

Lakes Michigan and Huron have experienced a series of lower food web trophic alterations in recent years. The lakes are undergoing oligotrophication (Barbiero et al., 2002; Evans et al., 2011) ascribed to reduced phosphorus loading, a key contribution to primary productivity (e.g., Elser et al., 1990; Hecky and Kilham, 1988). During the mid to late 1980s, there were species invasions by the spiny water flea, *Bythotrephes longimanus* (Berg and Garton, 1994; Lehman, 1987; Therriault et al., 2002), and the zebra and quagga mussels, *Dreissena polymorpha* and *Dreissena bugensis* (Ricciardi and Rasmussen, 1998; Stepien et al., 2005). *Bythotrephes* has affected the zooplankton community composition of Lake Huron by causing a dominance shift from cyclopoids and cladocerans to calanoids (Bunnell et al., 2012). Dreissenid mussels have exacerbated oligotrophication of the lakes by filtering phytoplankton from the water column, thereby decreasing lake primary production (Fahnenstiel et al., 2010) and by decreasing the deep chlorophyll layer in early summer in Lake Michigan (Pothoven and Fahnenstiel, 2013), a potential food source for many zooplankton species. Furthermore, decreases in planktivorous fish such as the alewife and bloater may have contributed to the trophic changes (Bunnell et al., 2009). Barbiero et al. (2012) argue that the lower food webs of Lakes Michigan and Huron are now converging with and becoming similar to that of Lake Superior.

Limnocalanus macrurus is a native, glacial relict predatory copepod whose trophic role within the zooplankton community may provide a functional indicator of food web changes within the planktonic community of Lake Michigan. One key unknown is the trophic position of *Limnocalanus*, especially with respect to its relationships with invasive zooplankton. We examined stable isotope composition of archival zooplankton samples collected in Lake Michigan during 1989, 1993, 1995 and 1997 to quantify the historical position of *Limnocalanus* in the zooplankton food web. *Limnocalanus* is reported to be omnivorous (Bowers and Warren, 1977; Warren, 1983, 1985), so we used a reference known herbivore, *Daphnia mendotae*, and a reference known predator, *Bythotrephes*, to deduce its position in the food web. We also included hypolimnetic *Diaptomus* spp. (mainly *Diaptomus sicilis*) and *Epischura lacustris* for comparison.

δ^{15}N can indicate relative trophic position among organisms that depend on the same primary source of organic matter (Griffiths, 1998; Lajtha and Michener, 1994). Omnivores are isotopically heavier than herbivores, and carnivores are isotopically heavier than omnivores. Therefore, we predicted a priori that δ^{15}N levels for *Limnocalanus* would be intermediate between the known herbivore, *D. mendotae* and the known carnivore, *Bythotrephes*. A nominal δ^{15}N difference of 3.4‰ was used to distinguish separate trophic levels, based on previous studies (Minawaga and Wada, 1984). For seasonal comparisons,

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Limnocalanus and *Bythotrephes* were compared May through August in 1989. *Daphnia* were only compared in July and August, since *Daphnia* were rare in the water column in earlier months. *Diaptomus* were also compared in August. We predicted that *Limnocalanus* would become more herbivorous from spring to summer because *Limnocalanus* has been reported to lose access to some zooplankton prey during thermal stratification (Warren, 1983). We thus expected the δ^{15}N difference between *Limnocalanus* and *Daphnia* to decrease from July to August, but the δ^{15}N difference between *Bythotrephes* and *Daphnia* to remain the same as obligate predator and herbivore.

In addition to seasonal trophic comparisons, we examined interannual variability by comparing δ^{15}N values of the aforementioned four taxa, plus *Epischura*, from August of 1989, 1993, 1995, and 1997. Jackson et al. (2013) found that *Limnocalanus* had a decreased trophic position in Lake Huron in 1995 compared to 1993. We therefore predicted that *Limnocalanus* would either have no isotope signature change or would become more herbivorous (lower δ^{15}N difference compared to obligate herbivore) from 1989 to the 1990s, if Lake Michigan had started to experience zooplankton trophic alterations by that time.

Limnocalanus has high nutritional value for planktivores (Birge and Juday, 1922; Fish, 1960; Price, 1963) and narrow tolerance for oxygen and temperature levels (Carter, 1969; Gannon and Beeton, 1971; Kane et al., 2004; Roff, 1973); therefore, *Limnocalanus* may be an indicator species for ecosystem change. It is thus important to quantify its historical trophic position so that modern data can be collected and compared to learn if and how zooplankton trophic positions are shifting as a result of recent ecosystem changes (Jackson et al., 2013).

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 (Fig. 1). Surveys were conducted from May through early fall in 1989, 1993, 1995 and 1997, but isotope data collection focused on August to match the season interval of recent historical *Limnocalanus* studies in Lake Michigan (Barbiero et al., 2009; Doubek and Lehman, 2011). Zooplankton were collected by Puget Sound closing nets (Research Nets, Inc.) with a 1-meter diameter mouth, an aspect ratio of 5:1, and mesh apertures of 130 μm. In most cases, three replicate tows from 90 m to the surface with the ship at anchor were split with a Folsom plankton splitter and ¼ of each was physically combined for composite samples (Lehman, 1987; Lehman and Caceres, 1993). Zooplankton drawn from these composite samples were used for the isotope analyses. Specimens were preserved in sucrose-formalin (Haney and Hall, 1973). Vertical distributions of zooplankton in 1989 were determined by using the Puget Sound closing net to sample depth intervals of 90–40 m, 40–30 m, 30–20 m, 20–10 m, and 10 m to surface.

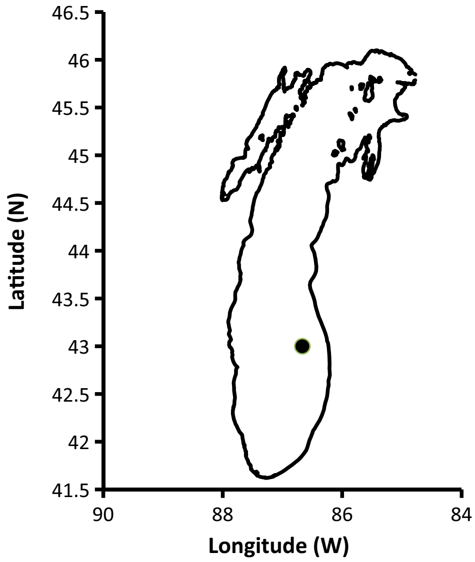

Fig. 1. The principal sampling station for zooplankton tows in 1989, 1993, 1995 and 1997 (St 2). Station 2 was located about 36 km offshore of Grand Haven, Michigan. Exact coordinates were 43° N 86° 40′ W.

Chl *a* and temperature profiles

Chl *a* was analyzed in August 1989 in conjunction with vertical distribution studies to quantify if *Limnocalanus* had access to phytoplankton prey during summer stratification of the lake. Chlorophyll fluorescence was measured with a SeaTech in vivo fluorometer mounted on a Seabird 9/11 CTD profiling from the surface to ca. 95 m. Temperature profiles were also measured with each CTD cast.

For pigment analyses, lake water was collected by Niskin casts and 100 mL replicates were filtered 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.

Experimental animals

Zooplankton were rinsed repeatedly with reverse osmosis (RO) water to remove sucrose-formalin. For seasonal δ^{15}N comparisons, *Limnocalanus* and *Bythotrephes* were removed from May through August in 1989. *Daphnia* were collected only from July and August since the taxon was rare in earlier months. *Diaptomus* were included for August. All four taxa plus *Epischura* were also collected for August in 1993, 1995 and 1997 (Table 1). The number of organisms of each species drawn from each sample varied according their seasonal weights (Doubek and Lehman, 2011). *Limnocalanus* specimens chosen were of

Table 1
Mean δ^{15}N and SE for zooplankton analyzed in 1989, 1993, 1995 and 1997 from Station 2 (tow 90 m to surface) in Lake Michigan. Mean δ^{15}N and SE, with CIs, were also calculated for each taxa in reference to the obligate herbivore, *Daphnia* (in bold).

Year	Month	Taxon	*N*	δ^{15}N	SE	δ^{15}N vs. herbivore	SE	95% CI
1989	May	*Bythotrephes*	3	5.2	0.11			
		Limnocalanus	4	11.7	0.11			
	June	*Bythotrephes*	3	4.2	0.16			
		Limnocalanus	4	10.0	0.07			
	July	***Daphnia***	3	2.4	0.06			
		Bythotrephes	3	6.9	0.02	4.6	0.06	4.4–4.8
		Limnocalanus	4	9.6	0.17	7.2	0.18	6.8–7.6
	August	***Daphnia***	4	4.0	0.16			
		Diaptomus	3	7.3	0.07	3.3	0.18	2.9–3.7
		Bythotrephes	3	8.5	0.14	4.6	0.21	4.0–5.0
		Limnocalanus	4	10.5	0.11	6.5	0.19	6.0–7.0
1993	August	***Daphnia***	2	2.0	0.13			
		Epischura	3	5.9	0.30	3.9	0.33	3.0–4.8
		Diaptomus	3	7.3	0.12	5.3	0.18	4.8–5.8
		Bythotrephes	3	6.1	0.23	4.1	0.26	3.4–4.8
		Limnocalanus	1	9.7	NA	7.7	NA	NA
1995	August	***Daphnia***	3	1.8	0.07			
		Epischura	2	6.8	0.44	5.0	0.45	3.8–6.2
		Diaptomus	3	7.3	0.07	5.5	0.10	5.3–5.8
		Bythotrephes	3	7.5	0.33	5.7	0.34	4.8–6.6
		Limnocalanus	3	10.9	0.08	9.0	0.11	8.8–9.4
1997	August	***Daphnia***	1	1.7	NA		NA	NA
		Epischura	1	4.6	NA	2.9	NA	NA
		Diaptomus	3	5.3	1.4	3.6	NA	NA
		Bythotrephes	1	6.8	NA	5.1	NA	NA
		Limnocalanus	2	8.2	0.37	6.5	NA	NA

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