Journal of Great Lakes Research 39 (2013) 404–408

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Historical and recent biomass and food web relations of *Limnocalanus* in Lake Huron

Elliot W. Jackson [a], Jonathan P. Doubek [a], Jeffrey S. Schaeffer [b], John T. Lehman [a,*]

[a] *Department of Ecology and Evolutionary Biology, 830N. University Blvd, University of Michigan, Ann Arbor, MI 48109–1048, USA*
[b] *USGS Great Lakes Science Center, 1451 Green Rd., Ann Arbor, MI 48105, USA*

ARTICLE INFO

Article history:
Received 2 October 2012
Accepted 19 April 2013
Available online 30 May 2013

Communicated by Michael Sierszen

Keywords:
Stable isotopes
Trophic structure
Zooplankton

ABSTRACT

Reported population biomass of *Limnocalanus macrurus* in Lake Huron has been underestimated by several-fold owing to application of an inappropriate length–weight regression model. During August and September the underestimates can exceed three-fold, suggesting that secondary production of the species in the lake is greater than previously thought. Increased representation of the species in the plankton community in recent years is associated with a decrease in its trophic level deduced through nitrogen stable isotope analysis of specimens from opportunistic samples obtained in 1993, 1995, and 2009. *Limnocalanus* ^{15}N enrichment relative to primary herbivores appears to have decreased by 1.5‰ over this time period. Similarly, *Diaptomus* ^{15}N enrichment relative to primary herbivores appeared to decrease by 1.1‰ from 1993 to 2009. Our data offer at least two possible explanations for this shift. (1) *Limnocalanus* has adopted a more herbivorous diet in response to the ecological changes in Lake Huron or (2) hypolimnetic *Diaptomus* have adopted a more herbivorous diet and *Limnocalanus* is relying in part on *Diaptomus* as a food source.

Introduction

Sampling by the U.S. EPA, NOAA, and USGS indicates recent changes in the crustacean zooplankton community of Lake Huron compared to years prior to 2003 (Barbiero et al., 2009a,b; Bunnell et al., 2011, 2012). Non-predatory cladoceran biomass decreased by more than 90% between the periods 1998–2002 and 2003–2006, and cyclopoid copepods also declined at unprecedented rates in 2005 to such extent that cyclopoid biomass in 2005 and 2006 was between 6.5% and 15.3% of previous levels (Barbiero et al., 2009b). The mechanisms underlying these changes are hypothesized to be a decline of phytoplankton abundance associated with oligotrophication of the lake and increased invertebrate planktivory (Barbiero et al., 2009a, b; Bunnell et al., 2011). The zooplankton community has reportedly changed in both total biomass and species composition. The decrease in total biomass is a result of dramatic decreases in cladocerans, specifically *Daphnia mendotae* and *Bosmina longirostris,* as well as cyclopoid copepods, while the compositional change is due to the loss of *Daphnia* species and increased representation of *Limnocalanus macrurus.*

However, reported biomass estimates for *L. macrurus* in Lake Huron may greatly underestimate the true change in proportion of these various species. Biomass estimates of *L. macrurus* for Lake Huron were calculated by Barbiero et al. (2009b) using the length–weight relationship for *Diaptomus siciloides* compiled by Downing and Rigler (1984). This relationship applied to *Limnocalanus* has been shown to be inappropriate in the case of Lake Michigan *Limnocalanus* (Doubek and Lehman, 2011), and significantly underestimates its true biomass. Erroneous biomass estimates can lead to misrepresentations of trophic interactions, food web alteration and poorly parameterized bioenergetics modeling.

Limnocalanus macrurus, a calanoid copepod found in all five Laurentian Great Lakes, is a glacial-relict and is hypolimnetic during periods of thermal stratification (Barbiero et al., 2001). Its narrow tolerances for temperature and oxygen variation (Carter, 1969; Gannon and Beeton, 1971; Roff, 1973), its nutritional value for predators (Birge and Juday, 1922; Morsell and Norden, 1968; Price, 1963) and its omnivorous diet (Bowers and Warren, 1977; Warren, 1983, 1985) make *L. macrurus* a potential indicator species of environmental change, trophic relations and possibly changes in other zooplankton recruitment dynamics. Recent studies in Lake Huron suggest that the abundance of this species has exhibited modest increases, and its percent composition in comparison to other zooplankton species has increased greatly, which is concurrent with declines in Cyclopoida. According to Barbiero et al. (2009b), biomass contribution of large-bodied crustaceans (>0.9 mm), mainly *Limnocalanus,* in Lake Huron increased from 18% and 9% in the northern and southern basins during 1998–2002 to 42% and 30% during 2003–2006. In 2007, calanoid copepods (*Limnocalanus macrurus* and others) comprised 73 to 94% of the total zooplankton biomass from May to October (Bunnell et al., 2011). *Limnocalanus* alone accounted for 14.3–37.5% of total zooplankton biomass.

Barbiero et al. (2009a) reported similar dramatic changes in the zooplankton community in Lake Michigan, specifically ascribing *Limnocalanus* increase to both bottom-up and top-down ecological forces. However, currently no studies have quantified whether these

---

* Corresponding author. Tel.: +1 734 763 4680.
E-mail address: jtlehman@umich.edu (J.T. Lehman).

0380-1330/$ – see front matter © 2013 International Association for Great Lakes Research. Published by Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.jglr.2013.05.005

recent changes in the food web are associated with changes in the trophic position of this species within the community.

Based on the current knowledge of *Limnocalanus* from prior studies in Lake Michigan and Lake Huron, we hypothesized that its increased presence in the past decade represents an adaptive response of *Limnocalanus* to habitat change. We hypothesize that stable or modestly increasing *Limnocalanus* biomass in the face of declining biomass of other Crustacea could be caused by a shift in the trophic status of the species in response to recent chemical, physical and ecological changes in Lake Huron (i.e., oligotrophification, dreissenid invasion, and decreased vertebrate predation). We examined opportunistic historical and recent zooplankton samples from Lake Huron to analyze potential dietary shifts by *Limnocalanus* and to offer insight about how the zooplankton community may be responding to a changing lake environment. We applied nitrogen stable isotope analysis of *Limnocalanus* and contemporaneous known herbivores and carnivores to deduce the position of *Limnocalanus* in the trophic structure.

Reproducible differences in $\delta^{15}N$ with trophic level provide a diagnostic measure of relative trophic position among organisms that depend on the same primary source of organic matter (Lajtha and Michener, 1994). Carnivores are isotopically heavier than herbivores, which in turn are isotopically heavier than the algae. Omnivores are isotopically intermediate between herbivores and carnivores. Past studies conclude that an increase of $\delta^{15}N$ values of approximately 3.4‰ indicates a separation between trophic levels (Minawaga and Wada, 1984). Variations in $\delta^{15}N$ trophic fractionation ($\Delta\delta^{15}N$ across trophic levels) have been found to vary by taxon, habitat and diet. By using a recognized herbivore such as *Daphnia* or *Holopedium* as a primary consumer baseline the error variance in trophic position can be reduced to ±0.20‰ (Vander Zanden and Rasmussen, 2001). This use of herbivores as internal standards is particularly important to our study because our opportunistic samples were not collected in the same place every year. Even if they were, water mass movements over time confound the elements of time and space. The $\delta^{15}N$ values of meroplanktonic species have also been found to vary with depth of the water column. Holoplankton, however, do not experience such variations (Sierszen et al., 2006). It is with this knowledge that we applied a priori a Δ3.4‰ $\delta^{15}N$ to distinguish trophic levels within the zooplankton community of Lake Huron.

Use of reference herbivores as internal trophic level standards for isotope analysis is particularly important when sample station locations are not sampled every year, though of course the water masses would differ anyway when stations are separated by a considerable latitude gradient. Different locations may have different blends of nitrate sources which could produce different isotope ratios in phytoplankton and thus differences in the $\delta^{15}N$ values of obligate herbivores.

To further refine our understanding of *Limnocalanus* biomass in Lake Huron, dry mass measurements obtained by Doubek and Lehman (2011) for Lake Michigan were replicated with Lake Huron *Limnocalanus*. Then, following Doubek and Lehman, we compared the actual mass measurements with the length-weight regression model used by Barbiero et al. (2009b) to estimate biomass in Lake Huron.

Methods

Study area and zooplankton sampling

Table 1
Locations and water column depths at sampling stations in Lake Huron.

Station	Latitude (N)	Longitude (W)	Station depth (m)
H12	45° 45.0′	83° 33.0′	108
H8	45° 11.1′	83° 05.2′	100
H4	44° 10.0′	83° 00.0′	60
NC3	46° 2.9′	82° 50.2′	35

Historical and recent zooplankton samples were collected in Jun and Aug of 1993 and 1995, and in Sep 2009. Station locations (Table 1, Fig. 1) were in U.S. waters of central and northern Lake Huron. The net used for 1993 and 1995 collections was a Puget Sound vertical closing net (Research Nets, Inc.) with 1-m mouth diameter, 1:5 aspect ratio and 130 μm mesh aperture. During 2009 we used a zooplankton net with a 1-m mouth, 1:5 aspect ratio and 153 μm mesh aperture. All tows sampled the entire water column towing vertically while the ship lay at anchor. Samples were preserved shipboard with 5% formalin. Formalin fixation is known to cause a 0.5‰ increase in $\delta^{15}N$ values (Edwards et al., 2002; Sarakinos et al., 2002). We acknowledge that our $\delta^{15}N$ results may be increased by this value; however, since all samples were similarly preserved, the effects of formalin are internally consistent for this study. All stations were not sampled every year. We used an internal standard, obligate herbivore, to compare $\delta^{15}N$ results across years. Station H4 and station H8 June samples were only used for biomass estimates and were not included in the isotope analysis because few cladoceran herbivores were present as internal reference standards.

Experimental animals

Zooplankton specimens were copiously rinsed with reverse osmosis (RO) water to remove formalin contamination. Specimens were sorted individually by species, placed in holding containers of RO water with watchmaker forceps, and cleaned of any adhering algae or debris. *Limnocalanus* (C5 and C6 instars) and adult female *Bythotrephes longimanus* f. *cederstroemi* (Berg and Garton, 1994; Therriault et al., 2002) were sorted from all three years. Adult female *Daphnia mendotae* were sorted from 1993 and 1995 collections as a representative herbivore. *Daphnia* spp. were not present in 2009, however, and so adult female *Holopedium gibberum* were sorted instead. In addition, C6 instars of *Epischura lacustris*, *Diaptomus sicilis*, and *Diaptomus oregonensis* were drawn from each sample. Multiple cleaned and like-sized (±2%) specimens for dry mass and isotope analysis were placed in tared aluminum pellets and dried overnight at 60 °C. Dry mass was determined with a CAHN 29 electrobalance using silica gel inside the measuring chamber to maintain low humidity. Dry mass per individual was calculated as the net dry mass of each sample divided by the number of specimens contained in the sample. Pellet samples were subjected to CN analysis and mass spectroscopy (Thermo Scientific Delta Plus isotope ratio mass spectrometer) to obtain $\delta^{15}N$ values.

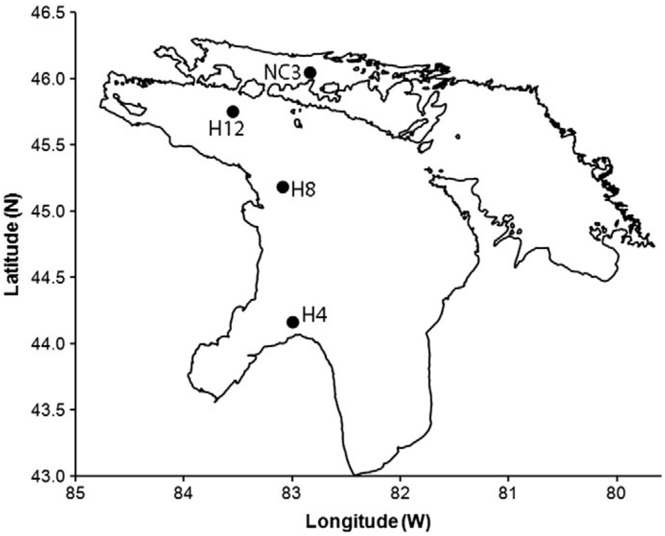

Fig. 1. Map of sampling stations on Lake Huron.