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Biotic and abiotic factors influencing zooplankton vertical distribution in Lake Huron

Carly J. Nowicki^{a,*}, David B. Bunnell^b, Patricia M. Armenio^b, David M. Warner^b, Henry A. Vanderploeg^c, Joann F. Cavaletto^c, Christine M. Mayer^a, Jean V. Adams^b

^a University of Toledo, Department of Environmental Science, 2801 West Bancroft Street, Toledo, OH, USA

^b U.S. Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI, USA

^c National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, 4840 S. State Road, Ann Arbor, MI, USA

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ABSTRACT

The vertical distribution of zooplankton can have substantial influence on trophic structure in freshwater systems, particularly by determining spatial overlap for predator/prey dynamics and influencing energy transfer. The zooplankton community in some of the Laurentian Great Lakes has undergone changes in composition and declines in total biomass, especially after 2003. Mechanisms underlying these zooplankton changes remain poorly understood, in part, because few studies have described their vertical distributions during daytime and nighttime conditions or evaluated the extent to which predation, resources, or environmental conditions could explain their distribution patterns. Within multiple 24-h periods during July through October 2012 in Lake Huron, we conducted daytime and nighttime sampling of zooplankton, and measured food (chlorophyll-*a*), temperature, light (Secchi disk depth), and planktivory (biomass of *Bythotrephes longimanus* and *Mysis diluviana*). We used linear mixed models to determine whether the densities for 22 zooplankton taxa varied between day and night in the epi-, meta-, and hypolimnion. For eight taxa, higher epilimnetic densities were observed at night than during the day; general linear models revealed these patterns were best explained by *Mysis diluviana* (four taxa), Secchi disk depth (three taxa), epilimnetic water temperature (three taxa), chlorophyll (one taxon), and biomass of *Bythotrephes longimanus* (one taxon). By investigating the potential effects of both biotic and abiotic variables on the vertical distribution of crustacean zooplankton and rotifers, we provide descriptions of the Lake Huron zooplankton community and discuss how future changes in food web dynamics or climate change may alter zooplankton distribution in freshwater environments.

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Introduction

Within a 24-hour period, zooplankton actively migrates within the water column to alter spatial overlap with their food sources, predators, and other environmental variables (Balcer et al., 1984; Loose and Dawidowicz, 1994; Peacor et al., 2005; Wells, 1960). For example, some cladocerans (e.g., daphnids, bosminids, *Holopedium gibberum*) and cyclopoid copepods (e.g., *Diacyclops thomasi*) have been documented to undergo diel vertical migration (DVM), descending during the day and ascending to surface waters at night (Hutchinson, 1967; Wells, 1960). These migrational patterns can influence trophic dynamics in freshwater systems because zooplankton are vital conduits in the pelagic food web, linking primary producers and higher trophic levels (Carpenter and Kitchell, 1996). The primary mechanism believed to regulate vertical migration is light-mediated predator avoidance (Dodson,

1990; Lampert, 1993), with descent associated with escaping predation under higher light levels, and ascent associated with exploitation of food and warmer water temperatures when the risk of predation is lower. In other words, zooplankton vertical migration is likely driven by a tradeoff between higher predation risk in the surface waters and decreased capacity for growth and reproduction in colder, deeper waters (Loose and Dawidowicz, 1994; Pangle et al., 2007).

The Laurentian Great Lakes offer relatively unique habitat among freshwater lakes, given their deep depths (i.e. exceeding 100 m) and mix of native and nonindigenous planktivores that could influence vertical migration patterns of herbivorous and omnivorous zooplankton species. The vertical migration patterns of predatory invertebrates are somewhat well described. The native invertebrate planktivore, *Mysis diluviana* (opossum shrimp, hereafter called *Mysis*) has demonstrated its own light-mediated pattern of DVM (Beeton and Bowers, 1982; Beeton, 1960; Bowers, 1988), remaining near the bottom of the lake during the day and then moving upward in the water column to feed at night (Beeton, 1960). These movements can influence night-time movements of their prey, driving some zooplankton species further upward towards the surface (Peacor et al., 2005). Alternatively, the

* Corresponding author.

E-mail address: cnowicki@madonna.edu (C.J. Nowicki).

¹ Present address: College of Natural and Social Sciences, Madonna University, 36600 Schoolcraft Road, Livonia, MI 48150, USA.

nonindigenous predatory cladoceran, *Bythotrephes longimanus* Leydig (spiny water flea, hereafter called *Bythotrephes*), is an epilimnetic predator that has also been documented to influence zooplankton vertical position in both the laboratory (Pangle and Peacor, 2006) and in the field (Bourdeau et al., 2011; Bourdeau et al., 2015). In the Great Lakes, *Bythotrephes* occupies the epilimnion during both day and night in the summer months (Lehman and Caceres, 1993; Ptáčnicková et al., 2015), but has been documented to occur ~15–20 m deeper (into the metalimnion) during the day in autumn and then ascend to the epilimnion at night (Lehman and Caceres, 1993). In smaller Canadian lakes, *Bythotrephes* migration was relatively weak, especially in the presence of hypolimnetic planktivores (Young and Yan, 2008).

Other environmental factors beyond planktivore distribution can also vary with vertical depth and influence the vertical distribution of zooplankton in the Great Lakes. For example, several *Daphnia* species will escape to deeper vertical layers to avoid damaging ultraviolet (UV) radiation at the surface during the day (Rhode et al., 2001). Light and water clarity may also be proximate factors for influencing migration associated with the avoidance of visual predators (Bourdeau et al., 2011; Bourdeau et al., 2015). Some species will even synchronize movements and emergence with lunar phases to avoid predation (Rejas et al., 2007). Food and temperature are also significant influential factors driving many zooplankton to ascend to warmer, chlorophyll-rich surface strata at night (Bourdeau et al., 2015; Johnsen and Jakobsen, 1987). Williamson et al. (2011) hypothesized that water transparency plays a key role in regulating these major drivers of zooplankton DVM. Moreover, temperature gradients may be more influential than food on zooplankton vertical distribution (Loose and Dawidowicz, 1994) as colder temperatures in the hypolimnion are less metabolically favorable for many zooplankton species (Bourdeau et al., 2015; Dawidowicz and Loose, 1992) and may cause zooplankton to rise in the water column. Even those species that tend to occupy the relatively warm waters near the interface of the epilimnion and metalimnion, such as *Leptodiatomus ashlandi* and *Leptodiatomus minutus*, exhibit a nighttime migration toward the even warmer surface waters (Balcer et al., 1984). Only by simultaneously measuring both biotic and abiotic characteristics of the food web during both day and night can the factors which influence the vertical distribution of zooplankton species in the Great Lakes during both daytime and nighttime conditions be determined.

Over the last century, most of the Laurentian Great Lakes have undergone substantial anthropogenic disturbances, including proliferation of nonindigenous species, nutrient fluctuations, and changing climate (Bunnell et al., 2014; Gronewold et al., 2013). Lake Huron, the second largest of the Great Lakes in terms of surface area (Beeton, 1984), is unique in that near coincident changes in phytoplankton, zooplankton, and forage fishes occurred around 2003 that have generally persisted to the present. The establishment of dreissenid mussels in Lake Huron in 1989 (Griffiths et al., 1991), along with mandated reductions in phosphorus loading, caused significant reductions in nutrients (Bunnell et al., 2014), declining pelagic primary production (Fahnenstiel et al., 1995a; Fahnenstiel et al., 1995b; Reavie et al., 2014), and increases in water clarity (Bunnell et al., 2014). Total zooplankton biomass declined 70% after 2003, relative to 1998–2002 (Barbiero et al., 2012), and cladoceran and cyclopoid copepods reached record-low biomass (Barbiero et al., 2009). At higher trophic levels, the collapse of alewife and the Chinook salmon fishery around 2003 was due to excessive predation by salmonines (He et al., 2014) and reductions in lower trophic level biomass (Kao et al., 2016). With biological changes occurring at all levels of the ecosystem, Lake Huron provides an appropriate case-study to examine how multiple factors influence food web structure, including vertical distributions of the zooplankton community. One application of the results of this study could be increased knowledge of the extent to which light-dependent planktivores, such as fish larvae or *Bythotrephes*, overlap with rotifers or crustacean zooplankton in the epilimnion and metalimnion during daytime hours.

Although many recent studies in the Great Lakes have described the vertical distribution patterns of crustacean zooplankton during the daytime hours (Bourdeau et al., 2011; Bourdeau et al., 2015), nighttime distribution patterns have been rarely documented. We know of few studies in the Great Lakes that were designed to determine the influence of multiple abiotic factors in conjunction with planktivores on both the diurnal and nocturnal vertical distribution of zooplankton. Furthermore, the description of vertical distribution patterns of rotifers in the Great Lakes is limited. Herein, our objective was to (1) determine the densities of crustacean zooplankton and rotifers in three vertical strata (epilimnion, metalimnion, hypolimnion) during the day and night; (2) within a given stratum, determine which zooplankton species exhibited differences in densities between the day and night; (3) when density differences within a stratum occurred, evaluate how the biomass of invertebrate planktivores (i.e., *Bythotrephes*, *Mysis*), chlorophyll a, water temperature, and Secchi depth could explain the patterns.

Given the importance of non-consumptive (e.g., Pangle et al., 2007) and consumptive (e.g., Bunnell et al., 2011) effects of *Bythotrephes*, we hypothesized that higher *Bythotrephes* densities would cause Lake Huron zooplankton to be more abundant in the epilimnion at night than during the day. Similarly, we hypothesized that higher densities of *Mysis* would induce zooplankton to move up into the epilimnion at night (Peacor et al., 2005). In terms of abiotic factors, we believed clearer water (i.e., deeper Secchi depths) could cause zooplankton to migrate well below the epilimnion during the day, while warmer epilimnetic temperatures may cause some species to move towards the surface at night, and contribute to higher differences in epilimnetic densities between day and night.

Methods

Field survey design

We conducted monthly sampling events from July through October 2012 of zooplankton, *Bythotrephes*, *Mysis*, and water quality parameters. Planktivorous fish were estimated during July and September only, and therefore were not included in our analyses but can be considered present at all sampling sites. Sampling occurred offshore at two ports, Thunder Bay and Hammond Bay, Lake Huron, and at two site depths (46 m and 82 m) at each port (Electronic Supplementary Material (ESM) Fig. S1). These sites were selected as part of ongoing surveys for the Cooperative Science and Monitoring Initiative on Lake Huron. Daytime and nighttime sampling occurred between approximately 0845–2115 h and 2130–0413 h, respectively, avoiding sunrise and sunset by at least one hour. At the start of each sampling event, vertical whole water column profiles of temperature and fluorescence were determined using an instrument equipped with a CTD (conductivity-temperature-depth) sensor (Seabird), and a fluorometer (TurnerScufa Cyclops 7 or WET Labs ECO-AFL/FL). The instrument was acclimated for one minute just below the surface of the water before descent to the substrate surface. Downcasts of temperature and fluorescence profiles (averaged each 1 m) were used to determine the location of vertical strata where zooplankton could be sampled with a closing net; temperature was the primary determination of the vertical strata, as the thermocline was identified and used to define the metalimnion. Three strata (epilimnion, metalimnion, and hypolimnion) were established for the 46 m sites, and four strata (epilimnion, metalimnion, upper hypolimnion, and lower hypolimnion) were established for the 82 m sites, with the exception of Thunder Bay in September where the 82 m site was only sampled at three strata (epilimnion, metalimnion, and hypolimnion). Water clarity was estimated by recording the Secchi disk depth on the shaded side of the research vessel during daytime only. Light was also measured as photosynthetically active radiation at most sampling locations; however, instrumentation varied among sampling events and some measurements were confounded by instrument malfunction. As

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