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Effects of food web changes on *Mysis diluviana* diet in Lake Ontario

Brian P. O'Malley [a,*], Lars G. Rudstam [b], James M. Watkins [b], Toby J. Holda [b], Brian C. Weidel [c]

[a] Rubenstein Ecosystem Science Laboratory, University of Vermont, 3 College Street, Burlington, VT 05401, USA
[b] Cornell University Biological Field Station, 900 Shackelton Point Road, Bridgeport, NY 13030, USA
[c] USGS Great Lakes Science Center, Lake Ontario Biological Station, 17 Lake Street, Oswego, NY 13126, USA

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ABSTRACT

Mysids are important benthic-pelagic omnivores in many deep-lake food webs, yet quantitative data on their diet are limited. We explored the trophic role of *Mysis diluviana* in offshore Lake Ontario using samples collected in May, July, and September 2013 with a focus on seasonal and ontogenetic patterns in herbivory and zooplanktivory using two approaches. We hypothesized that *Mysis* diet in 2013 differs from the last investigation in 1995 in response to changes in pelagic prey over 1995 to 2013. Gut fluorescence indicated high grazing by adult and juvenile *Mysis* in May 2013. In July, smaller mysids were more herbivorous than larger individuals, a pattern that was less pronounced in September. Microscopic gut analysis showed copepods, including *Limnocalanus*, were common in diets of both size groups in May. In July, mainly cladocerans were consumed, including *Cercopagis pengoi* which represents a change from a past investigation that preceded *Cercopagis* invasion in the lake. Our results are consistent with earlier observations of a larger proportion of algae in mysid diets in spring, transitioning to relatively more zooplanktivory and use of cladocerans in the summer and fall. Higher chlorophyll content in small mysids in July than in September may be associated with the presence of a deep chlorophyll layer in July that had largely dissipated by September. Overall, *Mysis* in Lake Ontario continues to be a generalist omnivore, incorporating new prey items and exhibiting higher herbivory in spring.

Introduction

Members of the *Mysis relicta* species complex are known to have large ecological impacts on lakes and reservoirs (Lasenby et al., 1986; Nesler and Bergersen, 1991; Rudstam and Johannsson, 2009; Spencer et al., 1991; Walsh et al., 2012). In non-native environments, the introduction of *Mysis diluviana* (formerly *M. relicta*; hereafter *Mysis*) has been linked to declines in zooplankton abundance and alterations in community structure (Goldman et al., 1979; Morgan et al., 1978; Spencer et al., 1991; Ellis et al., 2011). In native environments, such as the Laurentian Great Lakes, *Mysis* can be abundant and an important predator on zooplankton and perhaps benthic amphipods (Bunnell et al., 2011; Gal et al., 2006; Johannsson et al., 2003; Sierszen et al., 2011), as well as an important prey for fish (Isaac et al., 2012; Sierszen et al., 2014; Bunnell et al., 2015). However, the predatory effects of mysids on lower trophic levels have been based on relatively limited empirical diet information (Bunnell et al., 2011; Gal et al., 2006), in particular the degree of herbivory with respect to season or ontogeny (Branstrator et al., 2000; Whall and Lasenby, 2009). Predicting how an omnivore's diet varies in lake food webs is essential to quantify their top-down effects on primary producers (phytoplankton) as well as primary (herbivorous zooplankton) and secondary consumers (predatory zooplankton) that make up planktonic food webs.

The degree of herbivory in *Mysis* varies with season, mysid size, and habitat (Branstrator et al., 2000; Johannsson et al., 2001; France, 2012). The trophic position of *Mysis* can shift from being primarily herbivorous to primarily carnivorous in lakes of different trophic status or food web structure (France, 2012; Whall and Lasenby, 2009). Lake Michigan mysids have been considered primarily herbivores by some authors (McWilliams, 1970; Grossnickle, 1982), primarily predators by others (Bowers and Vanderploeg, 1982; Branstrator and Lehman, 1991), and some combination of both (O'Malley and Bunnell, 2014). In Lake Ontario, grazing on pelagic phytoplankton appears to be an important feeding strategy of *Mysis* during spring when phytoplankton constitutes up to 50% of the overall diet (Johannsson et al., 2001). In summer through fall, Lake Ontario mysids shift towards a greater reliance on zooplankton and rarely feed on phytoplankton (Johannsson et al., 2001). Although spring may be an important grazing period, *Mysis* also feeds on diatoms and other phytoplankton during other seasons, using algae present in the deep chlorophyll layer after the onset of thermal stratification (Bowers and Grossnickle, 1978; Grossnickle, 1979; O'Malley and Bunnell, 2014; Scofield et al., 2017).

A current challenge to studying the diet of *Mysis* is directly quantifying phytoplankton consumption in the field whereby lab-derived clearance rates are often used instead of stomach content analysis (e.g.,

* Corresponding author.
E-mail address: bpomalley89@gmail.com (B.P. O'Malley).

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Bowers and Grossnickle, 1978). The gut fluorescence method (Mackas and Bohrer, 1976) offers an alternative tool to quantify the relative role of phytoplankton in invertebrate diets using field-collected specimens. The technique relies on measuring the total amount of pigments (e.g., chlorophyll, phaeopigment) derived from phytoplankton in a consumer's gut contents. Chlorophyll-a is commonly used in limnological studies as a proxy for phytoplankton biomass in the water column (Wetzel, 2001). Gut fluorescence has been used more frequently in marine zooplankton studies although it has also been applied to herbivorous freshwater invertebrates to determine diel feeding patterns in streams (e.g., mayflies, Cowan and Peckarsky, 1990) and lakes (e.g., copepods, Christoffersen and Jespersen, 1986; amphipods, Gladyshev et al., 2000). In terms of mysids, this technique has generally been used to identify peak feeding times related to diel vertical migration (Grossnickle, 1979; Rudstam et al., 1989; Takahashi et al., 2015). Therefore, while microscopic cell counts of phytoplankton may not be possible because of numerous broken cells, gut fluorescence is an attractive alternative for studying temporal diet shifts in mysids.

The last published data on mysid diets in Lake Ontario are from 1995 (Johannsson et al., 2001, 2003). Since 1995, Lake Ontario's benthic and pelagic habitats have undergone substantial changes in community structure, potentially influencing the diets and energetic pathways of many organisms including *Mysis*. In the benthic zone prior to 1995, the amphipod *Diporeia* spp., a key prey item of native fishes (Owens and Dittman, 2003) and known prey of *Mysis* (Johannsson et al., 2001, 2003), was common at bathymetric depths >50 m but has since declined and is now rare (Birkett et al., 2015; Watkins et al., 2007). At the same time, non-native Quagga mussels (*Dreissena rostriformis bugensis*), first observed in Lake Ontario in 1991 (Mills et al., 1993), became abundant at 30–90 m depths in the late 1990s, then expanded to depths >90 m by the early 2000s, and are now the dominant form of benthic biomass (Birkett et al., 2015; Watkins et al., 2007). In the pelagic zone, large declines in epilimnetic zooplankton and changes in overall community structure have also occurred. Cyclopoid and bosminid densities have declined in the epilimnion and also from whole-water column samples (Barbiero et al., 2014; Rudstam et al., 2017). However, large calanoids (*Limnocalanus macrurus* and *Leptodiaptomus sicilis*), some herbivorous cladocerans (*Daphnia mendotae* and *Holopedium gibberum*), and larger non-native predatory cladocerans (*Bythotrephes longimanus* and *Cercopagis pengoi*), have increased in abundance beginning around the mid-2000s (Barbiero et al., 2014; Rudstam et al., 2017). Although less is known about trends in rotifers across the Great Lakes, rotifer density declined during 1984–2013 from a 100-m deep monitoring site offshore of Rochester, NY (Makarewicz and Lewis, 2015). As a result, the crustacean zooplankton community has undergone an increase in individual body size since the 1990s.

The aim of this study is to update our knowledge of the trophic role of *Mysis* in Lake Ontario through gut fluorescence combined with diet analysis using samples collected in 2013. Because *Mysis* are characterized as opportunistic omnivores (Grossnickle, 1982), and given the changes in community structure that have occurred since diets were last investigated (Barbiero et al., 2014; Rudstam et al., 2017), we hypothesized that *Mysis* diets in 2013 will include higher relative proportions of calanoids and lower proportions of cyclopoids and bosminids than compared to historical observations. *Mysis* may also have increased the proportion of algae in their diets associated with an increase in water clarity that promotes deep chlorophyll layers (Twiss et al., 2012; Watkins et al., 2015). In addition, *Mysis* alter their diet when presented with changes in prey availability by incorporating larger non-native predatory cladocerans (i.e., the fish-hook water flea, *Cercopagis pengoi*, and the spiny water flea, *Bythotrephes longimanus*) in lakes where they occur (Nordin et al., 2008; O'Malley and Bunnell, 2014). In Lake Ontario, *Bytothrephes* was not detected in previous diets despite being recorded in the lake prior to the 1990s, probably because it had remained at low abundances until the 2000s (Barbiero et al., 2014; Rudstam et al., 2015). *Cercopagis* was not recorded in Lake Ontario until 1998 (Makarewicz et al., 2001), but has since become highly abundant in summer months and maintains higher densities than in Lake Michigan (Barbiero et al., 2014; Cavaletto et al., 2010; Rudstam et al., 2015) where it is consumed by *Mysis* (O'Malley and Bunnell, 2014). Therefore, we hypothesized that *Cercopagis*, but not *Bythotrephes*, will be a common prey of *Mysis* in Lake Ontario during 2013 because of the difference in relative abundance between the two species. Because many populations of generalists can actually be composed of specialized individuals, in terms of feeding (Bolnick et al., 2003), we also evaluated the degree of individual specialization exhibited by *Mysis* on zooplankton prey in 2013.

Methods

During 2013, mysids and zooplankton were sampled at night during 21–23 May, 18–22 July, and 9–13 September from sites across Lake Ontario with bottom depths ranging from 47 to 223 m. Sampling took place at least 1 h after sunset and concluded 1 h before sunrise, with only red light used on the back deck of the research vessel for illumination. Samples were collected by vertically towing a 1-m diameter conical net (net mesh 500 μm, tapering to 250 μm with 200 μm cod-end) throughout the entire water column (from 2 to 5 m above bottom to surface). Upon retrieval, contents were rinsed into a jar and preserved in ethanol. Next, an additional tow using the same net was collected from approximately 55–60 m depth to the surface (termed "shallow tow"), or 2–5 m above the bottom to surface at sites <60 m deep. Contents were rinsed into a jar, wrapped in aluminum foil to prevent light penetration, and immediately placed in a freezer to be used for gut fluorescence. We chose 60 m to surface for shallow tows as a tow depth range that targets actively feeding mysids in the metalimnion and upper hypolimnion by towing through peak densities of the *Mysis* layer (~30 m; Boscarino et al., 2009) and through the deep chlorophyll layer in Lake Ontario (Watkins et al., 2015). A subset of mysids from some shallow tows were retained live and placed into 1 L bottles containing filtered lake water (0.2 μm) chilled to <6 °C and held in a dark refrigerator for 24–48 h (at 4–6 °C) to evacuate their gut content before being frozen. At 4 °C gut residence times of 4–6 h have been reported for *Mysis* (Chipps, 1998), therefore we assumed incubating *Mysis* for >24 h would be sufficient to empty their stomachs. These animals were used as controls to test for background fluorescence in animals with empty stomachs.

To measure the average body sizes of available prey, crustacean zooplankton were sampled following *Mysis* sampling with a 0.5-m diameter conical net (150-μm mesh) from 100 m to the surface, or 2 m above the bottom to surface at sites <100 m deep. Contents of the cod end were narcotized with carbonated water and preserved in ethanol. Zooplankton samples were processed by subsampling until at least 200 total individuals were counted and measured from a known volume. Large clumps of predatory cladocerans (i.e., *Cercopagis* and *Bythorephes*) were strained prior to subsampling using a large mesh sieve, and processed separately from remaining zooplankton. All zooplankton counts were performed using a dissecting or compound microscope equipped with a digitizing tablet to record length. Cladocerans and mature copepods were identified to genus or species, while copepodite stages were identified to order. Cladoceran length was measured from top of the head to the base of the carapace; copepod length was from the anterior end of the cephalosome to the posterior end of the caudal rami. Cladoceran and copepod lengths were converted to dry mass (μg) for each individual measured following the Bottrell et al. (1976) pooled equations except for *Holopedium gibberum*, for which we used the Persson and Ekbohm (1980) equation, and predatory cladocerans (equations listed in Watkins et al., 2011). For each sample, we calculated an average individual dry mass (μg) for each zooplankton category identified.

We used gut fluorescence as an index of *Mysis* herbivory by measuring the amount of chlorophyll-a per stomach of up to 10 juvenile and 10

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