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Stomach contents and stable isotopes analysis indicate *Hemimysis anomala* in Lake Ontario are broadly omnivorous

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ABSTRACT

Hemimysis anomala is a recent invader to North American aquatic ecosystems and is spreading rapidly throughout the Great Lakes region. This is the first littoral mysid in the North American Great Lakes; and, as such, the ecosystem effects are unknown and could be substantial. These effects depend on the role of *Hemimysis* in the food web and, therefore, on its diet. We examined the stomach contents of two life stages of *Hemimysis* from two sites in Lake Ontario during the growing season (May–November 2010). We also report the relationship between zooplankton hard parts and size for a number of potential prey species to allow the back-calculation of prey lengths from stomach contents. Both juvenile (2–5 mm) and adult *Hemimysis* (5–11 mm) were omnivorous, consuming phytoplankton, zooplankton, and benthos when available. However, adults appeared slightly more carnivorous and incorporated larger prey in their diets. *Hemimysis* were able to consume zooplankton prey up to 30% of their own length, including *Bythotrephes longimanus* and *Cercopagis pengoi*. *Daphnia* and *Bosmina* were selected over other prey by both juvenile and adult *Hemimysis* and were most common in stomachs during July and September when their abundances in the zooplankton were highest. Measurements of $\delta^{13}C$ and $\delta^{15}N$ corroborated stomach content materials, indicating an omnivorous diet which included benthic and pelagic sources. Omnivory by *Hemimysis* is typical of mysids in general and makes them less sensitive to seasonal dynamics of preferred prey items.

Introduction

Hemimysis anomala (hereafter *Hemimysis*) is a relatively recent invader in North American aquatic ecosystems, first discovered in the Great Lakes in 2006 (Pothoven et al., 2007; Walsh et al., 2010). By 2009, the species was reported from numerous locations in lakes Michigan and Ontario (Questel et al., 2012) as well as smaller lakes (Brooking et al., 2010). Since then, *Hemimysis* has spread to Lakes Erie and Huron (Marty et al., 2010) as well as adjacent water bodies (Brown et al., 2012, 2014; Kestrup and Ricciardi, 2008) and was recently detected in Lake Superior. *Hemimysis* prefers water temperatures from 21 to 27 °C (maximum: ~32 °C; Sun et al., 2013) and is likely to persist and expand its range (Ricciardi et al., 2012; Brown et al., 2014), especially in response to climatic warming (Penk et al., 2016).

Hemimysis represents a new type of animal in the North American Great Lakes as these systems lacked similar littoral mysids prior to its arrival. The only mysid species in these lakes is the native glacial relict *Mysis diluviana* (formerly *Mysis relicta*; Audzijonyte and Väinolä, 2005), and it is found mainly in cooler (4–12 °C; Rudstam et al., 1999; Boscarino et al., 2007), and hence deeper, water. Littoral mysids are common in some European lakes and rivers and can be very abundant in estuarine environments worldwide (Mauchline, 1980). In addition to *Hemimysis*, several other littoral mysid species are spreading through Europe and are possible new invaders to North American (*Limnomysis benedeni*, and *Katamysis warpachowskyi*; Ricciardi and Rasmussen, 1998; Grigorovich et al., 2003; Borza, 2014). The ecosystem effects of these littoral mysids could be substantial. In Europe, *Hemimysis* invasions have resulted in reductions of zooplankton abundance and diversity in small lakes (Ketelaars et al., 1999). Clearly, we need to understand how *Hemimysis* will affect the existing Great Lakes ecosystem. To do this, diet information is needed to understand how *Hemimysis* fits into the Great Lakes food web and to inform food web models (e.g.

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Stewart and Sprules, 2011; Langseth et al., 2012; Kao et al., 2014) used to predict production available to the fish community as food webs shift.

Mysids are omnivorous, consuming a wide variety of detritus, plants and animals both in the water column and on the bottom (Mauchline, 1980; Rudstam and Johannsson, 2009). *Hemimysis* have been found to feed on both phytoplankton and zooplankton in Europe (Ketelaars et al., 1999). Work in the Great Lakes region has found that *Hemimysis* have highly plastic feeding, able to consume dietary items across multiple trophic levels, but these studies have focused on the St. Lawrence River predominantly near human created structures (e.g., piers; Marty et al., 2012; Ives et al., 2013). An omnivorous diet may allow *Hemimysis* to thrive during periods of low zooplankton abundance and therefore maintain higher population abundances than obligate predators.

Mysids may also change their use of food resources as they increase in size. Several species, including *M. diluviana*, feed more on phytoplankton as juveniles and become more zooplanktivorous as adults (Grossnickle, 1982; Branstrator et al., 2000; Johannsson et al., 2003; O'Malley et al., 2017). Whether *Hemimysis* follow a similar ontogenetic diet shift in the Great Lakes is unknown, in part because only limited information is available on its diet within the Great Lakes region (Ives et al., 2013; Pérez-Fuentetaja and Wuerstle, 2014; Yuille et al., 2012). Studies in Seneca Lake, New York found that adults appeared more carnivorous in laboratory feeding studies, but field work demonstrated similar levels of omnivory in juveniles and adults (Pérez-Fuentetaja and Wuerstle, 2014).

Stomach content analysis allows prey items to be identified and measured, and allows for direct comparisons with prey availability in the environment to calculate prey selectivity. However, stomach content is biased by digestion rates (Stapp, 2002), requires a large number of samples (Cresson et al., 2014), and does not necessarily reflect the nutritional sources supporting growth (i.e., an organism may ingest refractory materials which are not assimilated; Grey et al., 2002; Melville and Connolly, 2003; Post, 2002). In contrast, stable isotopes can be used to estimate the contribution from each food source to an organism's tissue over weeks to months if they are measured in the organisms and its potential food sources (Moore and Semmens, 2008; Phillips and Koch, 2002; Phillips et al., 2014). Combining stomach content with stable isotope analysis draws on the strengths of both methods while minimizing their weaknesses (Grey et al., 2002; Johannsson et al., 2001; Rudnick and Resh, 2005).

We examined the stomach contents and stable isotope ratios of *Hemimysis* adults and juveniles throughout the growing season (May–October) from two locations in Lake Ontario to help determine: (1) what food sources support *Hemimysis*, (2) if adults and juveniles use different food sources, (3) which prey groups are selected, and (4) if carnivory increases seasonally to take advantage of zooplankton increases.

Material and methods

Field sampling

Hemimysis were collected with vertical plankton net hauls (0.5 m diameter, 500 μm-mesh) pulled from the bottom to the surface at multiple depth contours (3, 4, 6, 8, 9, 10, 12, 16, and 20 m) at two locations in eastern Lake Ontario: east of Nine Mile Point (hereafter Sunset Bay [N 43° 32′, W 076° 22′]) and west of Nine Mile Point (hereafter Alcan [N 43′ 30, W 076′ 28]). These two sites were considered replicates as they have similar bottom types (rocky habitat). Samples were collected monthly at night, from May through November 2010 at Sunset Bay and from May through August at Alcan and were preserved in 70% ethanol.

Diet analysis

In the laboratory, all *Hemimysis* in each tow were counted and measured (to the nearest 0.1 mm). Stomachs of individual *Hemimysis* were removed and materials within the stomach were spread onto a glass slide with a drop of water and a coverslip was placed on top. Over 95% of the 156 stomachs analyzed contained at least one prey item. Animals with empty stomachs ($N = 7$) were excluded from the diet analysis. Material within the stomach was identified to the lowest taxonomic level possible with a compound microscope at up to 400× magnification. Where possible, all individual cells or colonies from identified algal species were counted. *Fragilaria* sp. colonies were not included in the total number of diatoms consumed by *Hemimysis*, because they were broken into parts and a precise estimation of their abundance was not possible. Instead, *Fragilaria* sp. was scored as "Absent" if none were observed, as "Few", when 1–10 pieces were counted, as "Common" when between 11 and 50 pieces were counted, and as "Very Common" when >50 pieces were counted. For zooplankton we counted mandibles, postabdominal claws (cladocerans), tail spines (only in *Bosmina*), rostra (only in *Bosmina*), and caudal rami (copepods) to estimate the number consumed. When several parts of one species were observed in the stomach, the minimum possible number of individuals for that species based on unique elements was reported.

We calculated the percent frequency of occurrence for each diet category in juveniles (animals with carapace length ≤ 5 mm) and adults (animals with carapace length > 5 mm in total length) for each month (i.e., the proportion of all *Hemimysis* stomachs with content that contained that item). For July and August samples sizes were large enough to compare sites, in all other months sites were combined.

To determine if *Hemimysis* displayed prey selectivity, zooplankton samples were collected from Sunset Bay with vertical net hauls (0.5 m diameter, 64 μm mesh net) and preserved in 70% ethanol. Zooplankton samples were identified to the lowest possible taxonomic level under a compound microscope. To calculate selectivity, zooplankton tows from depths in which *Hemimysis* were collected (4, 6, 8, 10, 12, 16, and 20 m) were placed into six major groups: (1) *Bythotrephes*, (2) *Cercopagis*, (3) *Leptodora*, (4) Copepods, (5) *Bosmina* and (6) *Daphnia*. Nauplii were not included in the copepod category, as they were not observed in stomach content. Because *Bosmina*/*Daphnia* were not always distinguishable in the stomach, the proportion of known *Bosmina* and *Daphnia* in the stomach was used to estimate the number of each in the diet from the combined group. Feeding selectivity was calculated for adult and juvenile *Hemimysis* using Chesson's selectivity index (α_i):

$$\alpha_i = \frac{r_i}{n_i}\left[\sum_{j=1}^{m}\frac{r_j}{n_j}\right]^{-1}$$

where r is the proportion of the prey group of the ingested food in group i, n is the proportion of prey in the zooplankton community, and m is the number of prey groups considered (Chesson, 1978). Neutral selection is 1/m and therefore varies by the number of food sources, in our data neutral selection varied from 0.17 to 0.33 among months.

Prey size estimation

The relationships between zooplankton lengths and fragment size (e.g., mandible) found in stomachs were developed in one of three ways: (1) zooplankton data from Lake Ontario collected in 1990s (Johannsson et al., 1998), (2) zooplankton data collected in the present study, and (3) published material (Rybock, 1978). *Bosmina* spp., *E. coregoni*, and *D. retrocurva* were collected in 1992 and were measured from the anterior edge of the eye to the base of the mucro (*Bosmina*) or tail spine (*Daphnia*). This measure was less variable than total length from the anterior edge of the head to the base of the tail spine. The mouth parts were measured using a high power compound microscope equipped with a digitizing system. Cladocerans have two mandibles, one of which lays flat (straight) on the microscope slide, and one which lays in a curved position so equations were developed for both structures. At times it is difficult to determine the species from the

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