BioInvasions Records (2014) Volume 3, Issue 4: 261–267
doi: http://dx.doi.org/10.3391/bir.2014.3.4.07

Research Article

Fifteen miles on the Erie Canal: the spread of *Hemimysis anomala* G.O. Sars, 1907 (bloody red shrimp) in the New York State canal system

Meghan E. Brown[1]*, Brent T. Boscarino[2], Julia Q.G. Roellke[2], Elinor T.K. Stapylton[2] and Amalia R. Driller-Colangelo[2]
[1]*Hobart and William Smith Colleges, Department of Biology, 300 Pulteney Street, Geneva, NY 14456, USA*
[2]*260 Boardman Road, Poughkeepsie Day School, Poughkeepsie, NY 12603, USA*
**Corresponding author*
E-mail: *mbrown@hws.edu*

Received: 23 May 2014 / Accepted: 14 September 2014 / Published online: 20 October 2014
Handling editor: Vadim Panov

Abstract

In Europe and North America, human-made canals and reservoirs have contributed to the spread of non-native species. The mysid shrimp *Hemimysis anomala* G.O. Sars, 1907, which is native to the Ponto-Caspian region of Eurasia, expanded its range through intentional stocking in reservoirs and movement through shipping canals within Europe. The species later invaded the Laurentian Great Lakes, most likely through ballast transport in the early 2000s. Our survey of the New York State canal system (USA) found the species at 10 sites, spanning over 80 km of canal, which confirms the species continues to colonize human-made canal systems and that canals may catalyze its spread. We report two primary geographic areas where *Hemimysis* is present in the New York State canal system—in the Erie Canal east of Oneida Lake and in the Cayuga-Seneca Canal in the Finger Lakes region. Body length was significantly smaller in the western assemblage (Cayuga-Seneca Canal) compared to the assemblage east of Oneida Lake, but within each geographic area there were no significant differences in the proportion of juveniles relative to adults by longitude or the maximum density by longitude. Future studies should examine the role of surface-water flow and recreational boating traffic in the spread of *Hemimysis* as well as to what extent canal ecosystems are impacted by the establishment of this omnivorous crustacean.

Key words: Mysid shrimp, canals, locks, range expansion, invasions

Introduction

Human-manipulated water bodies, such as canals and reservoirs, contribute to the establishment and range expansion of non-native species (e.g., Ricciardi and MacIsaac 2000; Johnson et al. 2008; Moy et al. 2011). The geographic distribution of numerous aquatic species, including *Hemimysis anomala* G.O. Sars, 1907, expanded when shipping canals were built to link the Ponto-Caspian region to Western Europe (e.g., the Rhine-Main-Danube Canal; Ricciardi and MacIsaac 2000 and references within). *Hemimysis* (bloody-red mysid shrimp) was intentionally introduced to reservoirs near the Ponto-Caspian region and Baltic Sea in the 1960s to increase fish production and the species' subsequent spread throughout Europe was aided by commercial shipping traffic transporting organisms in ballast holds (Grigorovich et al. 2002; Pothoven et al. 2007).

Hemimysis has become established in systems that span a wide range of thermal and salinity conditions (Ketelaars et al. 1999) in both lentic and lotic systems (e.g., Walsh et al. 2010; Walsh et al. 2012; Ricciardi et al. 2012). In 2006, *Hemimysis* was detected in the Laurentian Great Lakes and is hypothesized to have been transported to North America from Europe in transoceanic-ship ballasts (Pothoven et al. 2007; Walsh et al.2010). The species quickly became established in neighboring water bodies, including large rivers such as the St. Lawrence River (Kestrup and Ricciardi 2008) and the Cayuga-Seneca Canal (Brown et al. 2012), and inland lakes connected to the Great Lakes via canals such as Oneida Lake, New York (Brooking et al. 2010) and Seneca Lake, New York (Brown et al. 2012). Its non-native range may reflect passive dispersal through water flow and inadvertent transport by humans through boats, fishing equipment and commercial shipping ballast (Dumont 2006; Kestrup and Ricciardi 2008; Wittmann and Ariani 2009; Brown et al. 2012). The morphology of *Hemimysis* is distinct from the only other mysid inhabiting the Great Lakes region, *Mysis diluviana; Hemimysis* has a flattened telson with two sharp spines (Figure 1).

Although canals played an important role in the species' migration from the Ponto-Caspian region to North America, there has been limited study of the canal systems within North America that may aid in the continued range expansion of *Hemimysis*. The New York State canal system connects the formerly distinct Hudson River drainage to the Great Lakes and Finger Lakes watersheds, and many smaller sub-watersheds, via 845 km of human-improved waterways and human-made canals (http://www.canals.ny.gov). We aimed to determine the extent to which *Hemimysis* has spread in the canals of New York State. We surveyed all sections of the New York State canal system except the Champlain Canal (Figure 2), and concentrated on canals that were adjacent to water bodies with known established populations of *Hemimysis* (i.e., Lake Ontario, Oneida Lake, Seneca Lake, and the Cayuga-Seneca Canal). We also examined demographic characteristics of *Hemimysis* at all sites where it was detected.

Methods

Field sampling

Between 17 July and 29 July 2013, 51 sites were sampled in the New York State canal system, including the Erie Canal (the central and eastern sections), the Oswego Canal, the Cayuga-Seneca Canal, the Mohawk River and a small portion of the upper Hudson River drainage basins (see Figure 2 for site locations and Table 1 and supplementary material Table S1 for geo-referencing). All sites had either a permanent cement (or wood) pier or rocky habitat with sufficient interstitial space for *Hemimysis* to inhabit (Claramunt et al. 2012). Sites included New York State transportation locks, private marinas, and public boat launches. Samples from transportation locks were taken both upstream and within the lock, with lock depths ranging from 1 to 11 m.

Sampling was conducted several hours after sunset because the diel migration of *Hemimysis* results in its absence from the water column during daylight hours (Boscarino et al. 2012). Nearly all of our sites were illuminated with artificial lighting, but the proximity of the light to the sampling location varied. Light intensity was measured at all sites east of Oneida Lake during sampling (Sky Quality Meter©, Unihedron) and was below levels that would prevent upward migration of at least the juvenile portion of the population (Boscarino et al. 2012). Red-LED headlamps were used to aid in sampling since *Hemimysis* is not sensitive to red light (Boscarino et al. 2012).

Figure 1. Dorsal view of the statocysts and truncated telson of *Hemimysis anomala* collected from the Erie Canal, New York (Photo: Amalia Driller-Colangelo).

At each site, zooplankton net tows (80 µm mesh, 0.25 m diameter, 1.2 m length) were used to assess the presence of *Hemimysis*. Two oblique tows were conducted by lowering the net to the maximum depth of the site and then slowly pulling the net by hand along the pier for at least 15 m. The two oblique tows covered the same stretch of shoreline and represent replicate tows for a given site. At some sites where *Hemimysis* was detected, a third replicate oblique tow was performed to maximize the number of individuals captured for length and gender analyses. Because the third oblique tow was only at sites where *Hemimysis* was already detected, the additional tow did not impact our overall detection percentages.

Upon collection, samples were visually scanned for the distinctive pigmentation and swimming patterns of *Hemimysis* (Borcherding et al. 2006) before preserving them in ethanol (> 70% final volume). At sites with positive identification, two additional vertical hauls were taken to quantify the density of *Hemimysis* because the volume of water sampled could be determined more precisely than with the oblique tows. The net was lowered to the site depth, held at least 3 seconds on the bottom, and then pulled to the surface (approximately 0.3 m sec^{-1}, after Johannsson et al. 1992). These replicate vertical tows were performed at the same location within the site. Samples were immediately preserved.

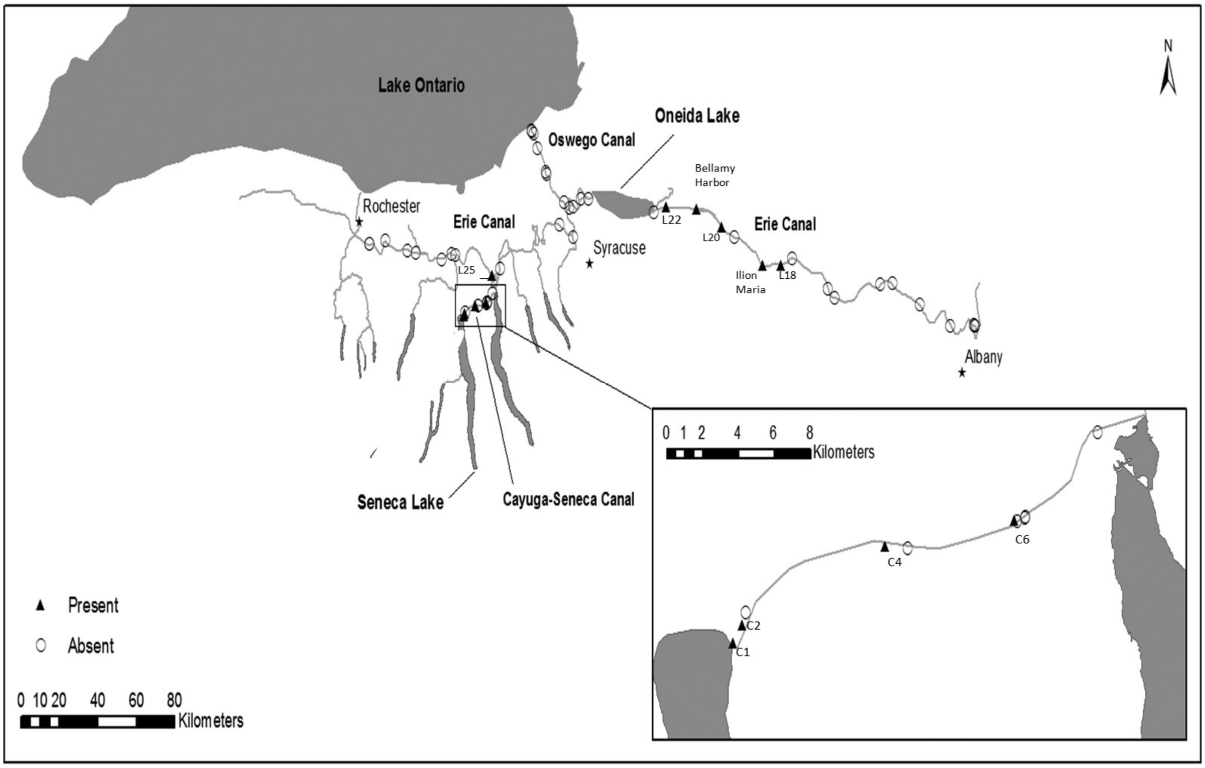

Figure 2. Map of sites sampled for the presence of *Hemimysis anomala* in the New York State canal system. Black triangles are sites where *Hemimysis* was present (site names provided, L = lock) and open circles are sites where *Hemimysis* was not detected. An enlarged view of the Cayuga-Seneca Canal is shown in the lower right corner due to the close geographic proximity of some of these sites. See Table 1 for geo-referencing and attributes of sites where *Hemimysis* was detected. See supplementary material Table S1 for geo-referencing for sites where *Hemimysis* was not detected.

Table 1. Sampling and demographic information for sites where *Hemimysis anomala* was present. Light intensity was only measured at select sites. Peak density is the higher density of the two replicate vertical tows. The percentage of juveniles (J), adult males (M) and adult females (F) for each site was calculated from individuals collected with both vertical and oblique tows. No. gravid is the total number of adult females that were carrying young in vertical and oblique tows. At Lock 25, *Hemimysis* was detected in the oblique tows but none were present in the vertical tows. For locations where *Hemimysis* was not detected see Supplementary material Table S1.

Site Name	Date (yr-mo-day)	Time	Latitude	Long.	Light intensity (candela m^{-2})	Peak density (ind. m^{-3})	Replicate tow (ind. m^{-3})	% J	% M	% F	No. gravid
Western assemblage											
C1	13-07-18	00:03	42.8682	-76.9402	-	626.2	453.3	64	23	13	1
C2	13-07-18	23:55	42.8747	-76.9354	-	5.1	5.1	90	0	10	0
C4 (Lock CS4)	13-07-18	23:37	42.9011	-76.8640	-	18.5	12.9	70	26	4	0
C6	13-07-18	23:07	42.9099	-76.7992	-	64.5	32.5	16	26	58	2
Lock 25	13-07-18	22:15	42.9988	-76.7618	0.02000	0.0	0.0	100	0	0	0
Eastern assemblage											
Lock 22	13-07-18	00:10	43.2095	-75.6449	0.00170	24.8	3.5	75	8	17	0
Bellamy Harbor	13-07-17	23:00	43.2017	-75.4520	0.00006	4.7	0.0	0	100	0	0
Lock 20	13-07-17	22:17	43.1428	-75.2912	0.00005	72.8	0.0	6	82	13	0
Ilion Marina	13-07-26	00:20	43.0204	-75.0300	0.00180	56.6	21.2	36	29	35	0
Lock 18	13-07-26	00:00	43.0162	-74.9169	0.00060	31.8	7.1	11	56	33	0

Laboratory processing and analysis

All collected samples were filtered through a 63 µm-mesh sieve to separate *Hemimysis* from other plankton and debris, and then counted in entirety for *Hemimysis*. Individuals were identified microscopically (Leica MZ 12.5, 10–20x) as juvenile, adult male, gravid adult female and non-gravid adult female. Adults and juveniles were differentiated based on body length (juveniles < 4.5 mm; Halpin et al. 2013). Sex was confirmed by the presence of the fourth pleopod (males) or oostegytes (female; Pothoven et al. 2007). The length and gender of 15 individuals (or all individuals when $n < 15$) at each site was measured from still images (Leica DFC 320 or Ken-A-Vision network camera 3.0) using Motic© 2.0 imaging software by measuring the distance between the anterior tip of the carapace to the end of the telson (Pothoven et al. 2007).

Statistical analyses

The proportion of juveniles and the maximum density of *Hemimysis* found in the vertical tows (both square root transformed to normalize the data) were regressed across longitude using simple linear models. These regressions were examined for demographic gradients that might indicate a progressive establishment in the canals. Separate regressions were performed within each of two geographic areas (western and eastern sites) where *Hemimysis* was detected (see *Results*). Maximum density was used as the comparative statistic to minimize bias due to variability between replicate vertical hauls, as the distribution of *Hemimysis* is patchy even within a small sampling area and individuals tend to congregate in dense swarms (e.g., de Lafontaine et al. 2012). Densities can be high within the swarm and minimal to zero only a few meters away (Walsh et al. 2010).

Light is the primary cue initiating *Hemimysis* diel migration and juvenile *Hemimysis* display less sensitivity to light and will inhabit brighter waters than adults (Boscarino et al. 2012). To assess if light intensity impacted the maximum density of *Hemimysis* or the proportion of juveniles in vertical net tows, a simple linear regression was performed for all sites east of Oneida Lake. These were the only sites where light intensity was measured.

Finally, to compare the demographic characteristics of *Hemimysis* inhabiting the two geographic areas (see *Results*), we used *t*-tests to examine the proportion of juveniles, maximum density and body length between the two geographic areas.

Results

Hemimysis was found at 10 of 51 sites (Figure 2, Table 1), with two major invasion areas: a 50-km stretch of the Erie Canal between the cities of Rome and Herkimer (Lock 22, Bellamy Harbor Park, Ilion Marina, and Lock 18) and a 30-km stretch of the Cayuga-Seneca Canal (C1, C2, C4 [Lock CS4], C6, and Lock 25). This is the first report of *Hemimysis* in the Erie Canal. There was high variability between density estimates of *Hemimysis* obtained with vertical net tows at most sites where it was detected (Table 1); therefore, we analyzed maximum detected density as an indicator of establishment at a given site. Hereafter, we will refer to the newly reported *Hemimysis* found in the Erie Canal east of Oneida Lake as the eastern assemblage, and those found in the Cayuga-Seneca canal region (including Lock 25 on the Erie Canal) as the western assemblage.

Eastern assemblage

The highest density in the eastern assemblage was reported at Lock 20 in the town of Whitesboro (72.8 ind. m^{-3}). There were no gravid females detected at any of the sites east of Oneida Lake. There was no statistical relationship between longitude and the proportion of juveniles ($F_{1,3}$ = 0.11; p = 0.76) or longitude and the maximum density ($F_{1,3}$ = 0.69; p = 0.47), although the easternmost site consisted of only juvenile *Hemimysis*. Light intensity did not predict the maximum density ($F_{1,3}$ = 0.02; p = 0.91) or mean body length of *Hemimysis* ($F_{1,3}$ = 1.53; p = 0.30).

Western assemblage

The highest density in the western assemblage was at the head of the Cayuga-Seneca canal where it originates from Seneca Lake (626 ind. m^{-3}); this was much greater than the density observed at any other site in the eastern or western assemblage. Gravid females were present at this site and at the farthest downstream site on the Cayuga-Seneca Canal where *Hemimysis* was detected. Longitude did not predict the proportion of juveniles ($F_{1,3}$ = 0.14; p = 0.73) or the maximum density of *Hemimysis* ($F_{1,3}$ = 1.19; p = 0.36).

Comparison of eastern and western assemblages

Mean body length of individuals in the western assemblage (mean = 4.54 mm, SE = 0.37, n = 52) was significantly lower (t = 2.03; p = 0.02) than in the eastern assemblage (mean = 5.43 mm, SE = 0.22, n = 66; Table 1), but the proportion of juveniles was only marginally different between the two assemblages ($t_{5,5}$ = 2.12; p = 0.07). There were no significant differences between the maximum densities (after square root transformation to normalize variance) found in the eastern and western assemblages ($t_{5,5}$ = 0.47; p = 0.66).

Discussion

Hemimysis has expanded its range into two areas of the New York State canal system, an assemblage in the Erie Canal (east of Oneida Lake) and a western assemblage in the Cayuga-Seneca Canal (west and downstream of Seneca Lake; Figure 2). *Hemimysis* was not detected in the Oswego Canal or the western section of the Erie Canal, likely because the species has not yet established in these locations. We predict that *Hemimysis* will continue to spread in the New York State canal system given that *Hemimysis* is broadly tolerant to physical and chemical conditions (Ketelaars et al. 1999) and sites where we did not detect the species have similar habitat to sites where *Hemimysis* was detected.

Our results represent a conservative distribution of the species as it is possible that the density of *Hemimysis* at some sites was below detection or that the tow location within a site did not intersect with a *Hemimysis* swarm. The high variability in density estimates between replicate vertical tows in this study (and others) indicate the inherent difficulty in ascertaining precise density estimates at a given invasion site. *Hemimysis* distributions can be patchy and densities can show a high level of variability even within a small sampling area (Walsh et al. 2010; de Lafontaine et al. 2012). Further, since we concentrated our sampling at transportation locks, no sites were located between Cayuga Lake and Onondaga Lake in the central portion of the Erie Canal.

The western assemblage is well-established based on high densities, the presence of reproductive females and juveniles (Table 1) and its repeated detection at all but the most downstream site since 2010 (Brown et al. 2012). The absence of reproductive females in the eastern assemblage may have resulted from the low density or absence of gravid females during our mid-summer sampling dates, which is consistent with the temporal reproduction patterns of *Hemimysis* in the region (Brown et al. 2012) and its punctuated reproduction elsewhere (Dumont and Muller 2010). As juveniles — and very small juveniles — were present in the eastern assemblage, we hypothesize that the species is established and reproducing in the eastern section of the Erie Canal as well.

The greater maximum densities and detection of reproductive females in the western assemblage may indicate a more established population of *Hemimysis* there than in the eastern assemblage. We examined several attributes of the two assemblages for clues about the establishment and spread of the species but found no consistent relationship between the proportion of juveniles or maximum densities and geographic location (between or within the two geographic areas). Given that light is an important proximate cue for upward movement of *Hemimysis* and that light sensitivity has an ontogenetic component, we also tested whether light influenced maximum density or size distribution of *Hemimysis*; however, our results suggest that light levels present at our sites did not significantly impact our demographic analyses. Finally, the demographic differences between the eastern and western assemblages (i.e., confirmed reproduction and smaller mean body length in the western assemblage) may be due to the limited snapshot we attained in our survey. A sampling regime with greater temporal coverage and more variables should be employed to study demographic and ecological differences among locations. For example, flow rate appeared to vary among sites and among locations at individual locks, but water velocity was not measured, and this may influence spatial distribution and detection.

Our study does not address how *Hemimysis* is moving in the canal system, but the geographic pattern and known flow directions suggest that passive dispersal through surface-water flow and human-assisted transport (e.g., anglers and boaters moving *Hemimysis* in bait buckets or bilge water) are potential vectors. The spread of *Hemimysis* in the Seneca-Cayuga canal follows downstream flow from Seneca Lake and could be the product of natural drift (Brown et al. 2012). The spread of *Hemimysis* east of Oneida Lake is against the direction of flow (Goebel 2001) and thus represents a range expansion that may be aided by boating and angling traffic. Further, *Hemimysis* was not detected in the Oswego Canal (the outflow of

Oneida Lake), which is directly connected to two lakes where the species is established (Oneida Lake, Brooking et al. 2010, and Lake Ontario, Walsh et al. 2010); thus, vectors beyond hydrological connections must be considered in range expansion. As the New York State canal system is principally used for recreational boating versus commercial transport, the spread of *Hemimysis* here might be different in method and rate than that of its spread in Europe where commercial shipping and ballast movement have been implicated. Regardless of the vectors moving *Hemimysis*, if the initial inland lake invasions (i.e., Oneida Lake and Seneca Lake) are serving as hubs of spread to the canals it is spreading at a rate of 10–15 km per year or more, a large distance for an invader less than 10 mm in length, and reminiscent of Thomas Allen's 1905 folk song (Low Bridge, Everybody Down) that chronicles 15 miles on the Erie Canal.

Given the wide and rapid spread of *Hemimysis* reported here and elsewhere (e.g., Borcherding et al. 2006; Wittmann and Ariani 2009; Brooking et al. 2010), the ecological impact of the species on recipient canal ecosystems remains an important question. *Hemimysis* is an omnivore with a post-invasion history that predicts food web effects (Ketelaars et al. 1999; Borcherding et al. 2006; Stich et al. 2009; Ricciardi et al. 2012). In lakes, competition for zooplankton prey between *Hemimysis* and native predators is of concern because *Hemimysis* has high feeding rates (Dick et al. 2013). In canal systems, prey assemblages, possible competitors, and ecological interactions, such as predator-prey migration patterns, are likely different than in lakes and require further study. The ultimate impact of *Hemimysis* will depend on its feeding ecology in the physical environment of the New York State canal systems and the structure of the canal's food web, which are both poorly studied and likely variable. Ives and colleagues (2013) found that *Hemimysis* relied on pelagic and benthic nutrient production at both lotic and lentic sites. Thus, the diet flexibility of the species will likely lead to an impact on several prey groups and trophic levels, the extent to which will depend on the site-specific niche of *Hemimysis* (Ives et al. 2013). Further, the degree of reliance on pelagic and benthic nutrients differs among locations (Ives et al. 2013), which implies that food web impacts in canals may be different than those found in lakes.

In summary, *Hemimysis* was detected in over 80 km of the New York State canal system, which provides an additional example of range expansion of non-native species that may be aided by human-manipulated water bodies. The canal system provides additional habitat for *Hemimysis* and may accelerate the species' movement to inland lakes and rivers. Johnson and colleagues (2008) concluded that non-native species are up to 300 times more likely to establish in reservoirs created by human-constructed dams compared to natural lakes and natural lakes near impoundments have a greater invasion risk than those more distant. Canal systems may provide a similar catalyst as reservoirs, and the range expansion of *Hemimysis* in the New York State canal systems represents an opportunity to learn about how human-improved waterways foster invasions and how they can be managed to reduce the risk of spread and impacts of non-native species.

Acknowledgements

Funding for this work was provided to Meghan Brown, Brent Boscarino, and the Finger Lakes Institute from the Great Lakes Restoration Initiative from the US Fish and Wildlife Service, which is coordinated by the New York State Department of Environmental Conservation and the Finger Lakes-Lake Ontario Watershed Protection Alliance. We thank Shannon Beston and Matthew Paufve from Hobart and William Smith Colleges for their help sampling. Shannon Beston also assisted with Figure 2. We also thank Karina Lambert, Joe Widay, David Mandra, and Usama Hosain for help with field sampling and laboratory processing. Two anonymous reviewers provided recommendations on an earlier version of this paper that improved its content and clarity.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Sampling information for sites where *Hemimysis anomala* was not detected.

This material is available as part of online article from:
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