



Contents lists available at ScienceDirect

Journal of Great Lakes Research

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

The influence of light, substrate, and fish on the habitat preferences of the invasive bloody red shrimp, *Hemimysis anomala*

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ARTICLE INFO

Article history:

Received 9 September 2019

Accepted 5 January 2020

Available online xxxxx

Communicated by Lee Grapentine

Keywords:

Hemimysis

Habitat selection

Predator-prey dynamics

Experiment

Food web

ABSTRACT

The invasive bloody red shrimp, *Hemimysis anomala*, is a novel organism in the Laurentian Great Lakes region that utilizes benthic and open-water habitat. *Hemimysis* is predicted to impact nearshore fish communities in the Northeastern USA where its range is expanding, either negatively through predation of shared zooplankton prey or positively as high-calorie prey. In this experimental study, we examined the factors influencing *Hemimysis*' benthic habitat selection, vertical distribution, and susceptibility to fish predation. In the presence of fish cues, *Hemimysis* preferred cobble over other benthic substrates (*Dreissena* mussels, pebble, or sand) regardless of light conditions; in dark conditions without a fish present, *Hemimysis* preferred open waters with sand habitat. Light and fish cues also interacted to influence the vertical distribution of *Hemimysis*, with the majority of mysids selecting depths that minimized perceived cumulative risk. The mean feeding rates of young-of-year (YOY) alewife (*Alosa pseudoharengus*), adult round goby (*Neogobius melanostomus*), YOY yellow perch (*Perca flavescens*), adult pumpkinseed sunfish (*Lepomis gibbosus*), and YOY lake trout (*Salvelinus namaycush*) varied among species, prey densities, and substrate (range = 0.77–57 mysids/fish/h). In general, feeding rates were highest for alewife, a non-native species in the Great Lakes basin, and in refuge-free conditions for all species, except for non-native round goby, which fed at similar rates regardless of prey refuge availability. Collectively, our results suggest that fish feeding success is contingent upon the interaction of light and *Hemimysis* refuge availability due to behavioral modifications of *Hemimysis* in the presence of fish and adverse light conditions.

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Introduction

Over the past half-century, the Laurentian Great Lakes have experienced substantial ecological change spurred, in part, by the proliferation of over 200 aquatic invasive species and concomitant shifts in community composition, primary and secondary production (Escobar et al., 2018; Mills et al., 2003; Rapai, 2016; Pagnucco et al., 2015). The bloody red shrimp, *Hemimysis anomala* (hereafter *Hemimysis*), is a recent Ponto-Caspian invader now well established in the Great Lakes, the St. Lawrence River, the Erie Canal, and multiple inland lakes of New York State (Brooking et al., 2010; Brown et al., 2012, 2014; Pothoven et al., 2007; Walsh et al., 2010). The absence of native species with a similar niche in nearshore habitats (Marty et al., 2010; Taraborelli et al., 2012) enhances the likelihood of *Hemimysis* shifting food-web

dynamics in recipient lakes, rivers, and canals. *Hemimysis* is positioned in an intraguild, trophic triangle (e.g., Gal et al., 2006; Walsh et al., 2010) with fish predators and shared zooplankton prey; it is both a competitor with fish for zooplankton and a potential prey item for fish. This predator-prey-competitor dynamic confounds a priori predictions of *Hemimysis*' impact on recipient food webs.

The establishment of *Hemimysis* will likely decrease the abundance and diversity of plankton and increase competition for shared food resources, as *Hemimysis* can decimate cladoceran populations in newly invaded systems (Ketelaars et al., 1999; Sinclair et al., 2015). Nearshore, non-native, warm-water mysids and other Ponto-Caspian peracaridan species, including *Hemimysis*, have substantially altered food-web dynamics in recipient systems in Europe and North America (e.g., Arbačiauskas et al., 2010; Chigbu, 2004; Hyatt et al., 2005). *Hemimysis* display higher attack rates, lower prey-handling times, and higher maximum feeding rates on zooplankton when compared with native Great Lakes and

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European glacial-relict analogs, *Mysis diluviana* and *Mysis salemaai*, respectively (Dick et al., 2013; Barrios-O'Neill et al., 2014a). Similar to other nearshore, warmwater mysids, *Hemimysis* may also directly impact fish recruitment by preying on larval fish or eggs of fish (Tornianen and Lehtiniemi, 2008).

Hemimysis may also be an important diet item for fish. In recently invaded systems in Europe, *Hemimysis* are utilized as a food resource by multiple species of fish (e.g., Arbačiauskas et al., 2010; Borcharding et al., 2006; Dumont and Muller, 2010 (Ketelaars et al., 1999). *Hemimysis* are also incorporated into the diet of some Great Lakes planktivores such as yellow perch (*Perca flavescens*) and rock bass (*Ambloplites rupestris*) as well as naturalized, non-native fish such as alewife (*Alosa pseudoharengus*) and round goby (*Neogobius melanostomus*; Geisthardt, 2017; Lantry et al., 2010, 2012; Yuille et al., 2012); however, high variability in percent diet composition (or inferred importance from stable isotopes) among years, sites, and studies restricts predictions of prey utilization and ingestion rates. Estimates from two controlled feeding experiments are limited to *P. fluviatilis* (Borcharding et al., 2007) and three-spined stickleback (*Gasterosteus aculeatus*; Barrios-O'Neill et al., 2014b).

In the Great Lakes, *Hemimysis* overlap spatially with economically- and ecologically-important fish species (Claramunt et al., 2012; Fitzsimons et al., 2012; Janssen and Luebke, 2004; Lane et al., 1996). For example, there is a high degree of overlap between *Hemimysis* and lake trout (*Salvelinus namaycush*) in the uniform, rounded cobble substrate most preferred as nursery grounds for spawning lake trout, which suggests *Hemimysis* could represent an important energy subsidy for developing young-of-year (hereafter YOY) lake trout (Claramunt et al., 2012). Other studies in Lake Michigan and Lake Huron point to *Hemimysis* as a potential prey for developing YOY planktivores in rocky, nearshore habitats (Adams et al., 2013; Geisthardt, 2017; Wang et al., 2012). Increased recruitment of lake trout in Flathead Lake (Idaho) was attributed to the introduction of the North American mysid shrimp, *Mysis diluviana*, due in part to the high-caloric content of the mysid relative to other available prey (Ellis et al., 2011). The same may apply to *Hemimysis* in the Great Lakes region because *Hemimysis* has a higher caloric density than other available zooplankton in nearshore Great Lakes habitats (Walsh et al., 2010) and enhanced growth rates are observed in laboratory studies when fish received a *Hemimysis*-rich diet (Borcharding et al., 2007).

Without more information about the way *Hemimysis* behaviorally, spatially, and temporally interact with fish predators, it remains difficult to predict *Hemimysis*' long-term importance as a prey item that could potentially boost fish growth. We still lack knowledge about how different environmental factors interact to influence the predator-prey dynamics of Great Lakes fish and *Hemimysis*. Here, we present the first controlled experiments to compare how light, substrate type, and potential fish predation influences the habitat preferences of *Hemimysis*. We also document and compare the laboratory-based feeding rates of five potential fish predators, YOY alewife, adult round goby, YOY yellow perch, adult pumpkinseed sunfish (*Lepomis gibbosus*), and YOY lake trout, as a function of light level, refuge availability, and *Hemimysis* density. The five fish predators used in our experiment were selected because of their association with the same type of benthic habitat as *Hemimysis* (Claramunt et al., 2012; Janssen and Luebke, 2004; Lane et al., 1996), their high abundance at our *Hemimysis* collection sites (Boscarino and Brown, unpubl. data) and because of *Hemimysis*' presence or inferred presence in the diet of these fish (Lantry et al., 2010, 2012; Yuille et al., 2012). Specifically, we hypothesize: (1) the benthic substrate preference of *Hemimysis* will depend on the presence of fish cues and ambient light levels; (2) the vertical position of *Hemimysis* in the water column will be dependent on the interaction between light levels and the presence of fish cues;

and (3) the feeding rate of the five potential fish predators of *Hemimysis* will vary among fish species, and depend on prey densities and the presence of a refuge for *Hemimysis*.

Methods

We performed three sets of experiments to investigate the physical and behavioral factors influencing *Hemimysis* habitat selection and vulnerability to fish predation: *Substrate preference experiments*, *Vertical preference experiments*, and *Fish feeding experiments*.

For all experiments, *Hemimysis* were collected at the head of the Seneca-Cayuga canal in Geneva, NY (42° 52' 05.94"N, 76° 56' 24.47"W; z = 2 m) with a plankton net (80-μm mesh, 0.5-m diameter). After collection, mysids were immediately transferred into glass jars and transported to the laboratory where they were held between 16 and 20 °C, the temperature range most preferred by *Hemimysis* (Ioffe et al., 1968; Sun et al., 2013). Mysids were acclimated to laboratory conditions for at least 24 h before being transferred into experimental trials. Mysids were fed ad libitum portions of Cyclop-eez® but fasted in isolation for a minimum of 8 h before being used in any experiment. All laboratory handling and counting of individual mysids were performed in a dimly-lit laboratory to avoid disorienting or stressing organisms. We randomly selected mysids from stock tanks, representing a range of size and age classes (range = 2.62–8.34 mm; 5.64 ± 0.06 mm, reporting convention here and after = mean length \pm SE).

Substrate preference experiments

The *Substrate preference experiments* investigated the influence of light and predator presence on the habitat selection of *Hemimysis* when offered four different types of habitat substrates: cobble, *Dreissena* mussel, pebble, and sand. We based sediment grain size on USGS classification standard nomenclature (Wentworth grade scale; Wentworth, 1922). Round experimental chambers (160-L, 1-m diameter) were divided into four equal wedges (1885 cm²) comprised of each of the four substrate types (Fig. 1). We used round chambers to minimize potential corner effects that might influence prey access (e.g., Coen et al., 1981; Nelson and Coull, 1989). Each of the four sections contained a thin layer of beach sand (<1 mm grain size) that covered the entire bottom of the chamber, on top of which substrate was added.

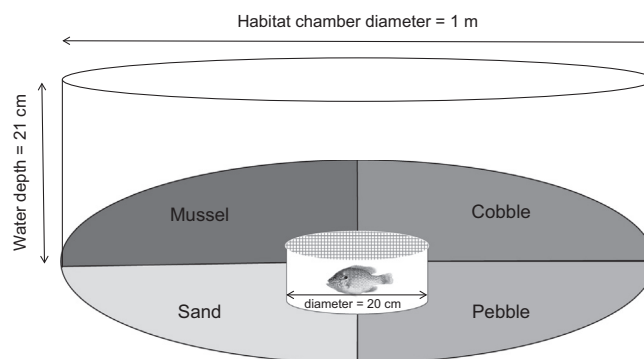


Fig. 1. Schematic of the habitat-choice chambers used in the *Substrate preference experiments*. The order of arrangement of substrate types was consistent across all trials. A Tupperware® container with a mesh top was placed in the center of the chamber; in fish treatments either a live round goby (*Neogobius melanostomus*) or pumpkinseed sunfish (*Lepomis gibbosus*) was placed in this container to allow for the flow of kairomones throughout the chamber while restricting the fish from feeding. Dimensions are not drawn to scale.

The cobble section consisted of a single layer of rounded landscaping rocks (8–10 cm diameter, mean diameter = 9.24 ± 0.81 cm; hereafter cobble), which overlapped to create interstitial space conducive to a refuge for *Hemimysis*. We modeled this habitat type after Claramunt et al. (2012) who reported that these substrate characteristics were most preferred by *Hemimysis* during in situ reef experiments in Lake Michigan. In the *Dreissena* mussel section, mussels were arranged in an overlapping pattern to provide a degree of vertical heterogeneity and accessible refuge spaces between individual mussels (mean mussel length = 2.84 ± 0.23 cm). Mussels were collected from the nearshore region of Seneca Lake, an area with substantially more *D. rostriformis bugensis* than *D. polymorpha*, but no attempt was made to differentiate between species. The pebble sections of the chamber consisted of pebble rocks gathered from Seneca Lake State Park (Geneva, NY), which were arranged in an overlapping pattern to provide close to full coverage of the sand beneath (mean pebble length = 2.56 ± 0.18 cm). This created a pebble habitat that provided a similar degree of interstitial space to the mussel section (similar length and spacing). Finally, the sand section consisted of beach sand only (<1 mm grain size) from Seneca Lake State Park. Beach habitats consisting of pebble and sand are common in the Great Lakes and Finger Lakes. Replicate experimental chambers were consistently arranged so that the mussel bed was opposite of the pebble and the cobble was opposite of the sand (Fig. 1). This was done so that interstitial space and individual substrate diameter descended in equal magnitude away from the rounded cobble to sand-only substrate.

Trials were run in a windowless room either without light (i.e., dark conditions) or at a light level associated with water-column avoidance by both adult and juvenile *Hemimysis* (0.1 mylux, or ~10 lux; Boscarino et al., 2012). We manipulated light conditions by dimming an incandescent bulb and recorded the light level at the beginning of each trial (LX1010B handheld digital lux meter). Trials were run both in the presence of a fish (either round goby or pumpkinseed sunfish) and without a predator present. Round goby were collected via benthic trawl (Lake Ontario) and pumpkinseed sunfish from beach seining (Oneida Lake, NY). Fish were contained in a submerged, 20-cm diameter Tupperware® container and covered with a 1-mm mesh at the top to allow for water and fish kairomone exchange, but prevented fish from escaping into the habitat sections and *Hemimysis* from entering the container (Fig. 1). The container was opaque preventing visual detection by prey or predator.

In total, six independent replicates were run on separate days and with new mysids for each experimental combination of light and fish presence. At the start of a trial, we placed fifty mysids into the center of the chamber. At each hour over an 8-hour period, we placed a molded divider into the chamber to separate each of the four habitat sections. We recorded the relative distribution in each wedge section by taking images with a night vision camera (Sony Digital Handycam®, Model TRV18). Mysids give off distinctive eyeshine and cast a noticeable shadow when imaged with this camera under these light settings (see Boscarino et al., 2007). For the cobble region only, we pulled out each rock from the chamber before taking a photograph to ensure that no mysids were hidden from the camera's view. The rocks were dipped into a separate basin and any mysids were added to the total number photographed in the cobble region. The cobble and any reclaimed mysids were placed back into the experimental chamber once photos had been taken.

Data analysis

The proportion of observations recorded in each region provided a relative index of habitat choice for each replicate trial ($n = 6$). These proportions were averaged across all replicates to arrive at a mean proportion of *Hemimysis* per substrate region for

each combination of light and fish cues. While we were not able to capture each of the original fifty mysids on camera at each hour interval, our photographic counts were reliably within ten individuals of the original fifty for each hour-interval sample.

We used a generalized linear model (GLM) to compare the substrate preferences of *Hemimysis* in treatments with and without light and with and without the presence of fish (round goby or pumpkinseed sunfish) where the dependent variable was the log proportion of *Hemimysis* in each substrate region. Substrate type (i.e., cobble, mussel, pebble, and sand) was used as a repeated measure. Because of a significant interaction among substrate, light conditions, and presence of fish, we examined Bonferroni comparisons within each light and fish combination. As cobble was hypothesized to be the preferred substrate of *Hemimysis* (Claramunt et al., 2012), and the habitat type most commonly selected in our experimental trials, we also compared the proportion of *Hemimysis* in cobble between the two fish treatments (round goby vs. pumpkinseed sunfish) and light levels with a second GLM.

Vertical preference experiments

The Vertical preference experiments investigated how light and fish cues interact to influence the vertical distribution of *Hemimysis*. Experiments were run in 2-m tall, 8-L Plexiglas® cylindrical columns (7.62-cm diameter) held at a constant temperature of 20 °C, as described in detail in Boscarino et al. (2007, 2012). Columns were categorized into four, equal volume regions: Region 1 (0–45 cm; bottom), Region 2 (46–90 cm), Region 3 (91–135 cm), and Region 4 (136–180 cm; top). The bottom 10 cm of Region 1 consisted of 1–3 cm diameter pebble, similar to those used in the Substrate preference experiments.

With the exception of the control trials, which were entirely dark and contained no fish, each replicate consisted of a dark bottom half (Regions 1 and 2) and an illuminated upper half (Regions 3 and 4) at a light level between 10^{-2} and 10^{-3} mylux (~0.1–1 lux; light source was a Kodak Carousel 5200®). These light levels approximate sunset conditions that limit the vertical ascent of adult *Hemimysis* into the water column and suppressed exploratory behavior of adults in both the laboratory and the field (Boscarino et al., 2012). Regions 1 and 2 were shielded from the light with an opaque table and black felt. The felt was also used to cover the walls of the experimental room to minimize reflected light.

Control columns (dark, no fish) and light-only treatments (top half illuminated, no fish) were filled with dechlorinated water from Lake Ontario and then allowed to sit for 24 h to ensure that residual kairomone degraded before experimentation. For the fish treatment, a pumpkinseed sunfish was confined in a 1-mm mesh bag (that also contained a small weighted rock as ballast) and lowered to the bottom of Region 1 where it was held for 1 h before experimentation. For the control and light-only treatments, an identical weighted bag was confined to Region 1 to avoid potentially confounding effects of the physical presence of the mesh bag and rock.

Six replicates were run for each treatment group. Once the mesh bag was lowered into the lower 20 cm of the column, mysids were placed into the bottom half of the columns, then restricted from entering the top of the column while the rest of the column was filled with water by closing a valve located at the 90-cm line (see Boscarino et al., 2007 for full description of the experimental apparatus). After the projector light was turned on, the valve was opened and left undisturbed for 1.3 h, the typical length of time between the beginning of civil twilight and the end of nautical twilight. Throughout the observational period, mysid position was recorded in the same manner as those described in Boscarino et al. (2012) with a Sony Digital Handycam® (Model TRV18). Only

adult *Hemimysis* were used in these experiments to improve detection with our camera.

Data analysis

We compared the vertical position of *Hemimysis* among the treatment groups (control, light only, light plus fish) using a GLM with repeated measures, where the dependent variable was the proportion of *Hemimysis* in each section. The location in the column (Regions 1–4) was the repeated measure. Because of a significant interaction between column region and treatment, we examine Bonferroni comparisons within each treatment.

Fish feeding experiments

In the *Fish feeding experiments*, our objectives were to: (1) derive functional response curves for five fish predators, YOY alewife (*Alosa pseudoharengus*), round goby (*Neogobius melanostomus*), YOY yellow perch (*Perca flavescens*), pumpkinseed sunfish (*Lepomis gibbosus*), and YOY lake trout (*Salvelinus namaycush*) across a range of *Hemimysis* densities experienced in the field during twilight, pelagic conditions; (2) compare the relative feeding success of these five fish predators by examining the proportion of *Hemimysis* consumed across a range of prey densities; and (3) determine the effect of refuge availability for mysids (i.e., cobble substrate) on the feeding rate of each of the five fish predators. Below we subcategorize these: *Effect of prey density trials* (objectives 1 and 2) and *Effect of substrate trials* (objective 3). Before providing specific methods, we describe how fish were collected and maintained for all fish feeding experiments.

Fish collection

The *Fish feeding experiments* were run over the course of four summer and autumn seasons (2015–2018). Fish predators used in our experiments were either caught in the wild (YOY alewife, round goby, YOY yellow perch, and pumpkinseed sunfish) or sourced from local fish hatcheries (YOY yellow perch and YOY lake trout). YOY alewife and pumpkinseed sunfish were captured with a

beach seine (7.62 m × 1.52 m, 2.54 mm stretch mesh) deployed on the western shore of the Hudson River (Highland, NY; Autumn 2015 and 2016). Round goby (Summer 2016 and 2017) and YOY yellow perch (Summer 2018) were collected with a bag seine (7.62 m × 1.82 m, 6.4 mm mesh with 1.82 m × 1.82 m × 1.82 m bag) from the north end of Cayuga Lake, NY. Farmed YOY lake trout and farmed YOY yellow perch were collected from the Bath Fish Hatchery (Bath, NY) and Finger Lakes Aquaculture (Naples, NY), respectively (Summer 2015 and 2016). All collected fish were immediately placed into live wells with source water and maintained during transport at ambient water temperature (18–22 °C for all wild fish and hatchery YOY yellow perch; 13–15 °C for YOY lake trout). In the laboratory, fish were maintained in stock tanks at aforementioned temperatures for at least 48 h before being used in experiments.

Predator sizes (Table 1) and age classes were selected so that all five predator species ranged between 60 and 130 mm (mean = 87 ± 18.4 mm) in total length. There were statistical differences in fish length among species ($F_{4,177} = 124.3$, $p < 0.01$) and experimental year ($F_{3,177} = 350.5$, $p = 0.01$); YOY yellow perch had the greatest mean body length, followed by lake trout, then round goby and pumpkinseed (which were statistically similar), and finally alewife (all pairwise comparisons $p < 0.05$, except round goby and pumpkinseed). Experiments in 2015 used, on average, larger fish than 2016, and experiments in 2018 used, on average, larger fish than all other years; all other comparisons between years were similar. Farmed and wild YOY yellow perch are pooled in our analyses as they had similar feeding rates ($t_{33} = -0.114$, $p = 0.91$; equal variance assumed) and lengths ($t_{12,24} = -0.5$, $p = 0.62$, equal variances assumed).

Effect of prey density trials

The *Effect of prey density trials* were run in 30-L aquaria arranged on an open-air, covered porch. Six to nine replicates were run concurrently for each combination of fish species (YOY alewife, adult round goby, YOY yellow perch, adult pumpkinseed sunfish, and YOY lake trout) and mysid density (1, 2, and 4 mysids/L; Table 1). Prey densities were selected based on low, medium, and high-

Table 1

Experimental conditions for the *Fish feeding experiments* that compared feeding rates of five fish predators: YOY alewife (*Alosa pseudoharengus*), adult round goby (*Neogobius melanostomus*), YOY yellow perch (*Perca flavescens*), adult pumpkinseed sunfish (*Lepomis gibbosus*), and YOY lake trout (*Salvelinus namaycush*). Feeding experiments included trials for the *Effect of prey density* in open aquaria with starting prey densities of 1, 2, or 4 mysids/L (30, 60, or 120 mysids per 30-L aquarium) and trials for the *Effect of substrate* in aquaria with cobble at the bottom (see Methods) at a starting prey density of 2 mysids/L. The number of replicates (n) is the number of trials for each experimental combination of predator species, prey density, and aquarium substrate. There were no statistical differences in feeding rates between farm- and field-sourced yellow perch ($t_{33} = -0.114$, $p = 0.91$; equal variance assumed); thus their data was pooled. See Figs. 4 and 5 and Table 2 for results.

Treatment	Fish Predator	Mysid starting density (/L)	n	Mean temperature (°C ± 1 SE)	Mean fish length (mm ± 1 SE)
<i>Effect of Prey Density</i> Open Aquarium/Pelagic Trials Twilight Light Levels	Alewife	1	6	23.57 ± 0.15	69.33 ± 4.71
		2	6	24.00 ± 0.42	64.17 ± 3.58
		4	6	23.68 ± 0.25	70.67 ± 2.62
	Round goby	1	9	22.92 ± 0.32	65.22 ± 0.62
		2	9	21.26 ± 0.82	74.00 ± 5.16
		4	9	24.16 ± 0.14	64.44 ± 2.54
	Yellow perch	1	6	22.44 ± 0.06	117.58 ± 0.96
		2	6	22.93 ± 0.14	114.33 ± 1.93
		4	6	23.45 ± 0.15	110.58 ± 2.77
	Pumpkinseed	1	6	18.36 ± 0.24	78.17 ± 2.69
		2	6	17.77 ± 0.17	73.83 ± 2.17
		4	6	18.00 ± 0.24	77.67 ± 1.50
<i>Effect of Substrate</i> Cobble Bottom/Benthic trials Twilight Light Levels	Lake trout	1	6	18.73 ± 1.21	98.83 ± 6.20
		2	6	14.90 ± 0.44	93.00 ± 1.42
		4	6	14.98 ± 0.37	99.67 ± 5.01
	Alewife	2	7	22.65 ± 0.24	63.43 ± 4.37
		2	20	22.85 ± 0.43	78.05 ± 3.31
		2	26	22.07 ± 0.21	115.73 ± 1.80
	Round goby	2	12	20.75 ± 0.28	75.33 ± 1.14
		2	12	13.89 ± 0.27	85.5 ± 3.25
		2	12		
	Yellow perch	2			
		2			
		2			

density estimates at our *Hemimysis* collection site (Brown et al., 2012) and represent a range of observed *Hemimysis* densities in the wild (Taraborelli et al., 2012; Walsh et al., 2010). *Hemimysis* were counted and sorted in the same manner as described for mysid prey in Boscarino et al. (2010). Trials were run in open aquaria to approximate pelagic feeding conditions at twilight (i.e., no substrate refuge available in open water). Exploratory trials confirmed that all fish predators consistently swam in the bottom half of the tanks in the absence of prey. Experimental aquaria were held between 17 and 25 °C for all species, except lake trout (due to different overlapping thermal preferences with *Hemimysis*, Table 1). The aquaria were exposed to natural-light conditions to mimic what they would experience in their nearshore habitats. No tank effects with regards to fish behavior were noted among aquaria or trials in preliminary experiments; therefore, each aquarium was considered to be a replicate.

To start each trial, an individual fish predator was indiscriminately chosen from our stock tanks and moved into an experimental aquarium one-half hour before sunset to allow for acclimation prior to the introduction of prey. Mysid prey, at the appropriate predetermined density, were introduced simultaneously to each tank at sunset to coincide with the timing of earliest emergence of *Hemimysis* into the water column (after Borcharding et al., 2006; Boscarino et al., 2012). Fish were allowed to feed from sunset, through civil twilight, to the end of nautical twilight (average experimental duration was 1.3 h). Due to differences in sun position and day length, the duration of civil and nautical twilight was approximately 20 min longer in summer trials (experiments for YOY yellow perch, round goby, and YOY lake trout) than the autumn trials (experiments for YOY alewife and pumpkinseed sunfish; Table 1).

At the end of the feeding period, predators were removed from the aquaria and preserved for later analysis. The remaining water in the aquarium was strained through a 500-μm mesh sieve to collect *Hemimysis* that had not been consumed by fish. We validated our recovery technique by running six controls (two of each mysid density), without any fish predators. In these quality-control trials, we were able to verify that the exact number of *Hemimysis* placed into the tank remained at the end of the feeding trial. This procedure also helped to validate our prey-counting methodology, which also met the mark (with one exception in which we recovered 31 prey items as opposed to the expected 30 which represented an initial error in counting prey).

Effect of substrate trials

At the 2 mysids/L density, we ran a series of similarly designed twilight trials for all five fish species but in aquaria with a cobble refuge (8–10 cm diameter; see above text on *Substrate preference experiments*). Cobble was arranged on the bottom of the aquaria consistent with Claramunt et al.'s (2012) description to mimic benthic interactions between predator and prey when refuge is available to *Hemimysis*.

The experimental procedure was identical to the effect of prey density trials, including the quality-control trials, with one exception. At the end of the twilight feeding period and once the fish predator had been removed from the aquarium, we dipped the rock in a water basin to wash off prey that clung to the cobble. These prey were then added to the final count of prey remaining at the end of the feeding period.

Data analysis

The number of prey consumed during each trial was determined as the difference between the number of individuals originally introduced into the aquarium and those remaining after the

feeding period. We utilize the calculated feeding rates (mysids consumed/fish/h) and proportion consumed (proportion of initial mysid abundance consumed/fish/h) as the basis for comparison among prey density and prey refuge availability.

The *Effect of prey density trials* (no cobble substrate) were used to derive functional response curves for each predator based on the mean feeding rates (mysids consumed/fish/h) at the three initial prey abundances. Our results apply to densities between 1 and 4 mysids/L, which span the range of densities generally reported in the field. We caution that these functional responses not be extrapolated beyond these densities in future predictive models and are best applied to approximate twilight, pelagic feeding rates within the shared, preferred temperature ranges of these fish and *Hemimysis*. Type I functions were based on least-squared regressions forced through the origin and Type II functions were generated using the equation:

$$F = (V_{max}((D)(K_m + D)^{-1}))$$

where F is prey/h; D is the prey density of mysids/L; V_{max} is the asymptotic maximum feeding rate (calculated); K_m is the half-saturation constant (calculated). Calculated coefficients were generated by minimizing the sum of squares with non-linear regression. Selection between functional response models was based on the differences among proportional feeding rates with ANOVA, following the procedures outlined in Hassell (1978), as applied and discussed in Taylor and Collie (2003). A pattern of non-significant proportional mortality rates across prey densities is typical of a density-independent Type I functional response whereas a pattern with significantly higher proportional mortality rates at low prey densities characterizes a Type II functional response (Taylor and Collie, 2003). Finally, a pattern of significantly lower proportional mortality at low prey densities defines a Type III functional response (e.g., Hassell, 1978).

The *Effect of prey density trials* was also compared across fish species and prey densities using the proportion of initial mysid abundance consumed (proportion of mysids/fish/h). Proportional consumption rates were log transformed to satisfy assumptions of normality and analyzed with a mixed GLM to examine the fixed factors of (1) fish predator (YOY alewife, round goby, YOY yellow perch, pumpkinseed sunfish, and YOY lake trout) and (2) prey density (1, 2, and 4 mysids/L), and the random factors of fish length and aquaria temperature. Because there was a significant interaction between fish species and prey density, Bonferroni comparisons among the fish species were examined within prey density groups.

The *Effect of substrate trials* were examined by a second GLM that compared log consumption rates (proportion of mysids consumed/fish/h) among trials conducted with and without cobble at a prey density of 2 mysids/L. There was a significant interaction between fish species and substrate type (open aquaria or cobble substrate), so comparisons between substrate presence or absence were examined within fish species.

Results

Substrate preference experiments

Both light and fish cues influenced the benthic substrate preferences of *Hemimysis* ($F_3 = 40.1$, $p < 0.01$ and $F_6 = 45.4$, $p < 0.01$, respectively) and there was an interaction between light and fish cues by substrate type ($F_6 = 2.4$, $p = 0.03$). Fish cues explained about twice the total variance that light level explained (i.e., higher effect size as eta squared). When a confined fish was present, *Hemimysis* selected for cobble over the other available substrate types ($p < 0.01$ for all comparisons to cobble within fish and light

treatments; Fig. 2). The preference for cobble in the presence of fish was particularly evident under lighted conditions compared to dark conditions ($F_1 = 78.1$, $p < 0.01$; mean proportion = 0.93 ± 0.03 and 0.52 ± 0.03 , respectively) and for pumpkinseed sunfish compared to round goby ($F_1 = 9.63$, $p = 0.01$).

In treatments without fish, *Hemimysis* were more evenly distributed among the substrate types. In dark conditions without fish cues, the proportion of *Hemimysis* was highest in sand compared to all other substrates ($p < 0.01$ for all comparisons to sand within the dark control). While we did not measure swimming speed explicitly, mysid activity was notably higher in dark conditions without fish, relative to all other treatments.

In light conditions without fish, the proportion of *Hemimysis* was lowest in the mussel substrate compared to all other substrates ($p < 0.01$ for all comparisons to mussel within the dark control). Furthermore, without fish present, the proportion of mysids found in cobble under lighted conditions (0.31 ± 0.11 SE) was significantly higher than under dark conditions (0.13 ± 0.06 ; $t_{10} = 3.56$, $p = 0.01$, equal variances assumed) suggesting that *Hemimysis* increasingly sought refuge under light-only conditions relative to dark even without a predator present. All other post-hoc pairwise comparisons within treatments were statistically indistinguishable.

Vertical preference experiments

Mysid vertical position in the water column was strongly dependent on light level and fish presence ($F_6 = 24.15$, $p < 0.01$). Under control conditions (no fish, dark column, Fig. 3A), *Hemimysis* distributed evenly throughout the water column and were consistently observed swimming freely between regions, with no statis-

tical differences among regions (Fig. 3A). In the presence of light without fish, the deepest region of the water column harbored a higher proportion of mysids relative to all other regions (Fig. 3B; mean proportion = 0.71 ± 0.14 SE; Bonferroni comparisons $p < 0.01$). In the presence of light and a live fish, the proportion of mysids in Region 1 dropped by more than half relative to light-only conditions (Fig. 3C; mean proportion = 0.29 ± 0.06 SE). In addition, the proportion of observations in Region 2 was higher than all other regions ($p < 0.01$).

Fish feeding experiments

All five species of fish predators fed on *Hemimysis* with mean twilight feeding rates ranging from 0.77 to 57 mysids/fish/h. However, these were variable by prey density (1–4 mysids/L) and with and without a cobble refuge available to *Hemimysis* (Figs. 4 and 5). Proportional consumption rates were influenced by an interaction among fish species, prey densities, and refuge presence (mixed model GLM, 3-way interaction; $X^2_{12} = 74.08$, $p < 0.01$), with no effect of aquaria temperature ($X^2 = 2.52$, $p = 0.11$) on feeding rates. Predator length was predictive of feeding rates ($X^2 = 5.91$, $p = 0.02$) and was correlated with fish species ($r = 0.36$, $p < 0.01$) and alone explained less than 2% of the variation in feeding rates.

For the *Effect of prey density trials* (no cobble substrate, twilight), a Type I functional response was the best model fit for YOY alewife ($y = 0.125x$, $F_{1,6} = 21.82$, $p = 0.01$), round goby ($y = 0.083x$, $F_{1,19} = 55.83$, $p < 0.01$), pumpkinseed sunfish ($y = 0.013x$, $F_{1,5} = 7.35$, $p = 0.04$), and YOY lake trout ($y = 0.071x$, $F_{1,11} = 41.08$, $p < 0.01$), with increasing feeding rates as mysid density increased (Fig. 4). A Type II functional response, was the best model fit for YOY yellow perch ($V_{\max} = 3.52e^6$ and $K_m = 4.02e^4$), with feeding rates similar at prey densities of 2 and 4 mysids/L.

Fish species displayed differing proportional consumption among the three prey densities (Table 2; interaction term: $F_8 = 3.59$, $p < 0.01$). YOY alewife consistently consumed a larger proportion of prey compared to other fish species. At the lowest prey density (1 mysid/L), YOY alewife fed at significantly higher rates than all other fish species; YOY yellow perch and YOY lake trout fed at higher rates than pumpkinseed sunfish (Table 2A). At the intermediate density (2 mysids/L), YOY alewife numerically fed at a higher rate than all other fish, but only the round goby pairwise comparison with alewife was statistically significant (Table 2B). At the highest prey density (4 mysids/L), YOY alewife again fed at a significantly higher rate than all other fish; round goby, YOY yellow perch, pumpkinseed sunfish and YOY lake trout all had a statistically similar mean feeding rate at this prey density (Table 2C).

For the *Effect of substrate trials* (run at a density of 2 mysids/L, twilight), there was a significant interaction between the fish species and cobble substrate ($F_4 = 7.7$, $p < 0.01$). With cobble available, YOY alewife, round goby, and YOY lake trout had similar feeding rates ($p > 0.05$), which were higher than perch or pumpkinseed (Fig. 5). All other pairwise comparisons in the cobble trials were statistically similar. Notably, all species except round goby consumed double or more *Hemimysis* when there was no cobble substrate (e.g., open aquaria); round goby fed at similar rates with and without cobble.

Discussion

The influence of readily-measured exogenous factors, such as light and temperature, on the distribution of diurnally migrating species is well established (e.g., Forward, 1988; Ringelberg, 2009). Less studied is how these factors interact with predator presence, substrate type, and refuge availability to determine habi-

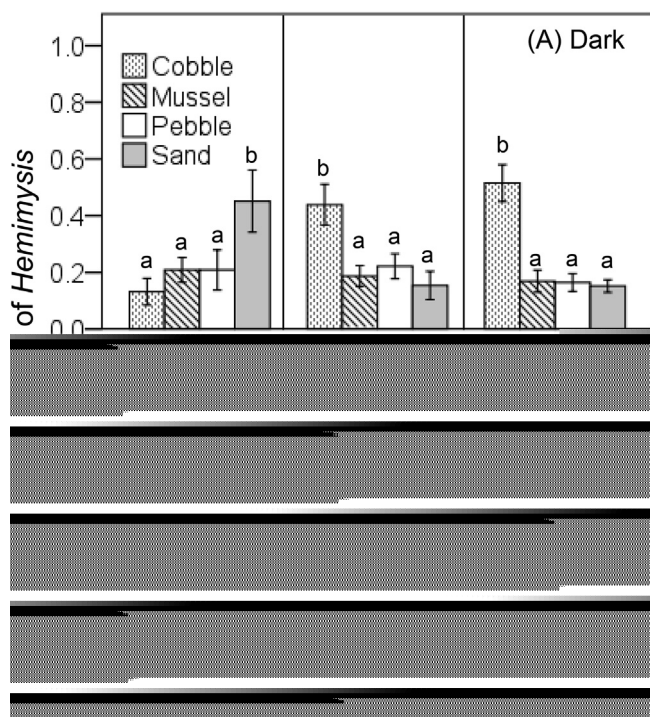


Fig. 2. The mean proportion of *Hemimysis anomala* (± 2 SE) occupying each of four benthic substrates (cobble, *Dreissena* mussels, pebble, and sand only) during the Substrate preference experiments in (A) dark and (B) light conditions (0.1 mylux). Trials were run in the presence and absence of fish predator cues. See Fig. 1 for experimental schematic. Because there were significant interactions among the treatment variables, letter superscripts note when proportions within each light and fish treatment combination (i.e., within panels) were statistically distinct (Bonferroni, $p < 0.01$).

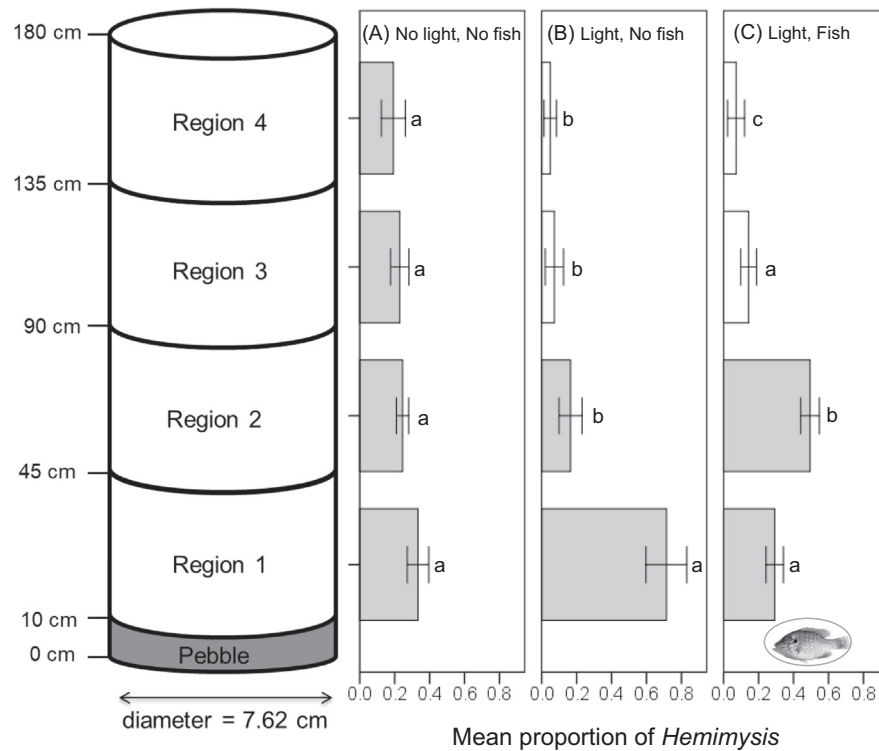


Fig. 3. Schematic of the columns used in the Vertical preference experiments and mean proportion of *Hemimysis anomala* (± 2 SE) occupying each of the four regions during trials: (A) without light or fish (control), (B) with light and no fish, and (C) with light and fish present. The four regions (1–4) were of equal height and volume. Regions 1 and 2 were held dark in experimental trials and Regions 1–4 were held dark in control trials (shaded grey bars). Regions 3 and 4 were illuminated during the light and fish treatments to a light level known to limit the vertical ascent of adult *Hemimysis* (bars not shaded). A weighted mesh bag was placed in the bottom 20 cm of Region 1 of the column for all trials; in the experimental trials with fish, a pumpkinseed sunfish (*Lepomis gibbosus*) was contained in the mesh bag. Because there was a significant interaction between light and fish, post-hoc Bonferroni comparisons were performed within treatments (i.e., within panels) and letters denote statistical significance ($p < 0.05$).

tat selection throughout a diurnal cycle (e.g., Boscarino et al., 2009; Wasserman et al., 2016). Establishing a hierarchy of habitat selection criteria for invasive species can aid in the prediction of how species may disrupt recipient food webs and which systems are the most vulnerable to invasion (Avlijas, 2012; Ricciardi, 2003; Ricciardi et al., 2012; Ricciardi and Rasmussen, 1998). In this study, we focused on the relative influence of light, substrate type, and fish presence on the habitat selection behavior of non-native *Hemimysis* through a series of controlled experiments.

Substrate and vertical preference experiments

Light levels and fish cues modified the substrate selection of *Hemimysis* via their influence on refuge-seeking behavior (Substrate preference experiments). In the presence of a fish predator, *Hemimysis* preferred the highest quality refuge available (i.e., cobble) even in the absence of light. Increasing light intensity enhanced refuge-seeking behavior in the presence of a predator but light alone did not elicit as strong an avoidance response as predator presence alone. The altered behavior and habitat selection of *Hemimysis* in the presence of potential predators may extend to fish beyond those investigated in our study. For example, shelters inhabited by bullhead (*Cottus gobio*) and stone loach (*Nemacheilus barbatula*) remained uncolonized by *Hemimysis* despite large abundances of the mysids in neighboring shelters (Dumont and Muller, 2010).

The behavioral response and habitat selection of *Hemimysis* under various light and fish conditions in the wild likely alters encounter rates with prey items and, by extension, the rate at which *Hemimysis* feeds. Pelagic and littoral mysids display depressed feeding rates in light relative to darkness, due in part

to reduced swimming speeds and, therefore, encounter rates with potential prey (Lindén et al., 2003; Viherluoto, 2001). Lower feeding rates are also observed in the presence of fish cues for at least one zooplanktivorous, migratory mysid, *Mysis mixta*, which can detect a chemical substance released by Baltic herring (Hamrén and Hansson, 1999). This is consistent with our observations of depressed swimming activity (associated with search behavior; e.g., Ramcharan and Sprules, 1986; Takahashi, 2004) in experimental conditions with light and fish present, such that detection of prey by mechanoreception could be compromised (Cooper and Goldman, 1980; Lehtiniemi and Viitasalo, 2001; Viitasalo et al., 1998).

Our Vertical preference experiments provided further evidence that the behavioral responses and habitat selection of *Hemimysis* were influenced by the interaction of light and fish cues. In dark, predator-free conditions, mysids were distributed uniformly throughout the water column and were observed swimming freely between column regions—suggestive that the searching behavior observed in the Substrate preference experiments also has a vertical component. However, mysids were faced with a conflict when presented simultaneously with lighted surface waters and a bottom-confined fish; moving away from the light placed them in proximity to a potential predator and moving away from the predator moved them closer to deterring light levels. Under these circumstances, most mysids chose an intermediate depth (Region 2) indicating that *Hemimysis* can differentiate between adverse directional cues and that the majority of mysids will select an optimal depth that minimizes cumulative, perceived risk. Interestingly, the approximate distance between the illuminated region most selected for by *Hemimysis* in the experimental column and the sunfish's eye was approximately the reaction distance of pumpkinseed

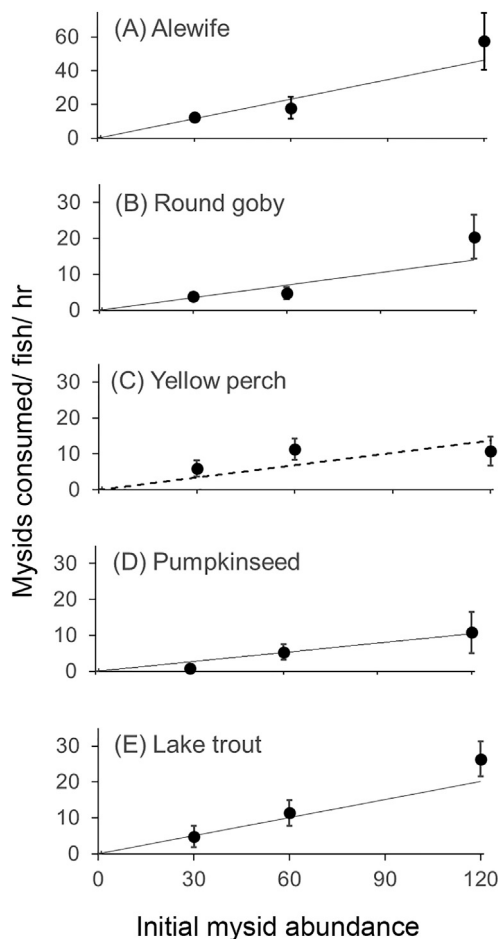


Fig. 4. Mean number of *Hemimysis anomala* (\pm SE) consumed per hour during fish feeding experiments for five fish predators: (A) YOY alewife (note different y-axis scale than other fish), (B) round goby, (C) YOY yellow perch, (D) pumpkinseed sunfish, and (E) YOY lake trout. The *Effect of prey density trials* were conducted in open aquaria (no cobble refuge) at twilight with initial prey abundances of 30, 60, or 120 mysids per aquarium (corresponding to 1, 2, or 4 mysids/L). Solid lines plot a linear Type I functional response (forced through the origin), which was the best model fit for alewife ($y = 0.125^*x$, $F_{1,6} = 21.82$, $p = 0.01$), round goby ($y = 0.083^*x$, $F_{1,19} = 55.83$, $p < 0.01$), pumpkinseed sunfish ($y = 0.013^*x$, $F_{1,5} = 7.35$, $p = 0.04$), and lake trout ($y = 0.071^*x$, $F_{1,11} = 41.08$, $p < 0.01$). Dashed lines plot a Type II functional response (forced through the origin), which was the best model fit for yellow perch ($V_{\max} = 3.52e^6$ and $K_m = 4.02e^4$); see *Methods* for details. Comparisons among fish species were based on the proportion of prey consumed are provided in Table 2.

sunfish on large zooplankton prey (30–40 cm; Confer and Blades, 1975). Given that the majority of mysids selected depths outside the striking range of fish and that mysids display effective escape behavior in the presence of fish predators (e.g., Holbrook et al., 2013; Viitasalo et al., 1998), *Hemimysis* vertical distribution in the water column is likely influenced by optimizing perceived risk-to-reward in a way that is temporally dynamic. Nonetheless, some *Hemimysis* in our experiments selected for depths within the striking distance of fish, demonstrating variation among individuals.

Collectively, our *Substrate preference experiments* and *Vertical preference experiments* are consistent in the hierarchy of cues used by *Hemimysis* for habitat selection. In the presence of either light or fish, *Hemimysis* increasingly chose the highest quality refuge available (i.e., rounded cobble, relative darkness), but the presence of a predator elicits an even stronger refuge-seeking response than light alone. If both light and fish were present, *Hemimysis* overwhelmingly chose refuge. *Hemimysis*' growth rate and its impact on recipient food webs may be influenced by such behavior. For

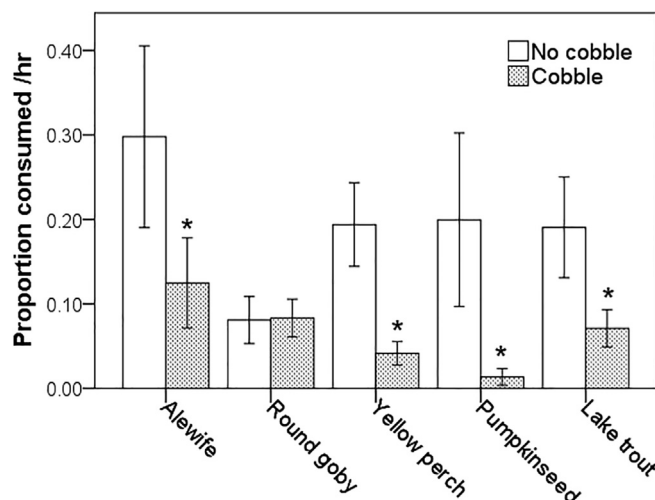


Fig. 5. Mean proportion of *Hemimysis anomala* (\pm SE) consumed per hour during fish feeding experiments with and without a cobble refuge (*Effect of substrate trials*) for five fish predators: alewife, round goby, yellow perch, pumpkinseed sunfish and lake trout. All trials were run at twilight and with a starting prey density of 2 mysids/L. There was a significant interaction between fish species and substrate; post-hoc comparisons within a fish species between cobble and open aquaria conditions were statistically different for all fish (asterisks; $p < 0.02$), except round goby ($p = 0.9$).

example, even if viable habitat conditions exist (i.e., substrate type, salinity, flow rate, prey resources; Marty et al., 2010; Walsh et al., 2012), the establishment and impact of *Hemimysis* might be muted if fish predator densities are high, both as a result of direct predation and modification of mysid feeding behavior that decreases growth potential.

Fish feeding experiments

All five fish predators, YOY alewife, YOY lake trout, YOY yellow perch, adult round goby, and adult pumpkinseed sunfish, accessed and successfully captured *Hemimysis*; but mysid density and substrate type uniquely interacted to influence predator-prey dynamics. In the following subsections, we discuss our results for each of the five predators.

YOY alewife

Alewife, primarily pelagic planktivores, consistently consumed a larger proportion of *Hemimysis* compared to all other fish species. The highest mean feeding rate by YOY alewife on *Hemimysis* in the fish feeding experiments (57 mysids/h) is an order of magnitude greater than those reported for alewife feeding on native *Mysis* in both the laboratory and field (~1–4 mysids/h; Boscarino et al., 2010; Janssen and Brandt, 1980). The lower feeding rates on native *Mysis* may result from alewife-*Mysis* interactions occurring at the upper, leading edge of the mysid migratory layer where prey densities and temperatures are lower than those used in our fish feeding experiments (Boscarino et al., 2010). Alewife likely did not reach satiation levels in our experiments given their Type I functional response and the reports of Lantry et al. (2010) of greater than 800 *Hemimysis* in the stomach of a Lake Ontario alewife.

Alewife may capture *Hemimysis* most successfully during twilight and night when *Hemimysis* emerge into the water column. Alewife display “darting” feeding, a specific attack technique from below that enables alewife to capture evasive prey like mysids in open water (Janssen, 1978). However, this is ineffective near lake bottom and requires alewife to first flush out their prey (Janssen,

Table 2

Mean proportion of mysids consumed per hour and post-hoc Bonferroni pairwise comparisons for the *Fish feeding experiments: Effect of prey density trials* (no cobble substrate). Trials were run at (A) 1 mysid/L, (B) 2 mysids/L, and (C) 4 mysids/L for each of the five fish predators, YOY alewife (*Alosa pseudoharengus*), round goby (*Neogobius melanostomus*), YOY yellow perch (*Perca flavescens*), pumpkinseed sunfish (*Lepomis gibbosus*), and YOY lake trout (*Salvelinus namaycush*). Bold values are statistically significant at $p < 0.05$.

(A) 1 mysid/L	Proportion	SE	Goby	Perch	Pumpkinseed	Lake trout
Alewife	0.410	0.018	<0.01	<0.01	<0.01	<0.01
Goby	0.129	0.020		0.99	0.13	1.00
Perch	0.196	0.038			<0.01	1.00
Pumpkinseed	0.026	0.015				0.04
Trout	0.160	0.046				
(B) 2 mysids/L	Proportion	SE	Goby	Perch	Pumpkinseed	Lake trout
Alewife	0.298	0.054	<0.01	0.40	0.73	0.34
Goby	0.081	0.014		0.14	0.20	0.16
Perch	0.194	0.025			1.00	1.00
Pumpkinseed	0.199	0.051				1.00
Trout	0.191	0.030				
(C) 4 mysids/L	Proportion	SE	Goby	Perch	Pumpkinseed	Lake trout
Alewife	0.477	0.070	<0.01	<0.01	<0.01	<0.01
Goby	0.175	0.025		0.78	1.00	1.00
Perch	0.087	0.017			1.00	0.20
Pumpkinseed	0.094	0.024				0.27
Trout	0.217	0.020				

1978). Alewife feeding rates on *Hemimysis* dropped significantly in our trials with cobble refuge, where this technique may be difficult and energetically costly.

The incorporation of *Hemimysis* into the diet of alewife expands invasive-invasive interactions in Great Lakes food webs. After the establishment of *Bythotrephes longimanus* in Lake Ontario, Mills et al. (1992) reported substantial shifts in alewife diets toward this non-native, predatory cladoceran. Following non-native *Dreissena* spp. establishment in Lake Ontario, alewife further increased their utilization of invasive cladocerans and native *Mysis* (Stewart et al., 2009) due, in part, to *Dreissena*-mediated changes in light level at depths where alewife and mysids interact (Boscarino et al., 2010). The presence of *Hemimysis*, an additional non-native species, could increasingly promote an invasive-rich diet in non-native alewife, especially in the spring when alewife migrate inshore to spawn in habitat that overlaps with *Hemimysis* (Geisthardt, 2017; Klumb et al., 2003; Walsh et al., 2012; this study), and alewife are preferentially selecting for large zooplankton prey (O'Gorman et al., 2000).

YOY lake trout

Feeding rates by YOY lake trout on *Hemimysis* in our *Fish feeding experiments* (mean = 26 mysids/h at highest density treatment) were comparable to those reported for native *Mysis* (21 mysids/h; estimated from Holbrook et al., 2013). YOY lake trout in our experiments may have approached satiation levels and met their energetic needs over the twilight feeding period as similar feeding rates on *Mysis* satisfied lake trout's daily energetic needs even at the low mysid densities and low capture efficiencies reported by Holbrook et al. (2013). However, a Type I response was the best model to explain feeding across the three densities of prey in our experiments, which may reflect the smaller size of *Hemimysis* compared to *Mysis* notwithstanding the caloric and fatty acid differences between *Mysis* and *Hemimysis* (Walsh et al., 2010).

There is a potential benefit to lake trout recruitment given the spatial and behavioral overlap between *Hemimysis* and lake trout in the rocky nursery grounds preferred by lake trout (Claramunt et al., 2012). Lake trout were capable of capturing *Hemimysis*, albeit at reduced rates, even when cobble refuge was available, demonstrating that daytime feeding is possible in areas where the two species overlap. Future work that examines the dynamics between mysids and fish in these cobble nursery grounds will be important to understand the roles of competition (both direct and appar-

ent) and predation among lake trout, *Mysis*, *Hemimysis*, and other zooplankton prey. For example, these dynamics may mirror those highlighted by Schoen et al. (2015) between *Mysis*, lake trout, and other planktivorous fish in Lake Chelan (Washington, USA); the introduction of *Mysis* to the nearshore food web enhanced lake trout density, which subsequently increased lake trout predation risk to other smaller planktivorous fish through apparent competition effects.

Round goby, pumpkinseed sunfish, and YOY yellow perch

Round goby, pumpkinseed sunfish, and YOY yellow perch fed at lower rates than YOY alewife and YOY lake trout, especially at the highest densities of mysid prey. Most field studies also conclude a low utilization of *Hemimysis* by these fish (Brooking et al., 2010; Lantry et al., 2010, 2012; Yuille et al., 2012), which is somewhat surprising given that they are effective predators on native *Mysis* (Pothoven et al., 2000; Walsh et al., 2007) and/or select similar habitat to *Hemimysis* (Claramunt et al., 2012; Janssen and Luebke, 2004; Jude et al., 1995; Lane et al., 1996).

Morphological constraints and inefficient attack strategies may prevent round goby from effectively capturing *Hemimysis*. As facultative molluscivores, the morphological features of round goby are best adapted for feeding on sessile mussels and benthic invertebrates (Fitzsimons et al., 2012). Actively swimming round goby have difficulty capturing highly motile prey like mysids and instead ambush stationary prey (Jude et al., 1995). The sensitivity of *Hemimysis* to round goby kairomones (*Substrate preference experiments*) suggests that individual *Hemimysis* will avoid areas adjacent to a resting goby, thereby lowering the probability of successful prey capture. These factors may inhibit goby feeding success on *Hemimysis* despite a high degree of habitat overlap in their native and invasive range and their potential co-evolution in the Ponto-Caspian region. This is consistent with in situ studies at round goby nesting sites (Fitzsimons et al., 2012; Geisthardt, 2017). For example, fish stomachs rarely contained *Hemimysis* (<4% of round goby caught in gillnets contained *Hemimysis*) despite video evidence suggesting frequent attacks in high-density swarms of *Hemimysis* (Geisthardt, 2017).

Interestingly, round goby was the only species of the five we tested that showed similar feeding rates in open and cobble aquaria. Because of round goby's ability to sense and attack *Hemimysis* in cobble substrate and given its ability to sense moving prey in low-light conditions owing to its lateral line system

(Bergstrom and Mensinger, 2009; Jude et al., 1995), round goby are potentially capable of attacking *Hemimysis* at all times of day. Round goby are also the only true benthic fish of the five predators we studied; they prefer the rocky habitats and cavities also favored by *Hemimysis* (Janssen and Jude, 2001) and were frequently observed inhabiting the interstitial spaces between the overlaying cobble in the *Fish feeding experiments*. Thus, round goby may influence *Hemimysis* population dynamics through indirect processes such as stimulating escape responses that leave *Hemimysis* more exposed to predation by other fish or impact *Hemimysis*' ability to forage effectively (Geisthardt, 2017).

Morphological constraints may also explain the consistently low feeding rates of pumpkinseed sunfish in both open and cobble aquaria. Unlike the related bluegill sunfish, pumpkinseeds are not specially adapted for zooplanktivorous foraging despite being recognized as opportunistic foragers (Copp et al., 2017; García-Berthou and Moreno-Amich, 2000; Wainwright, 1996). Instead, pumpkinseed sunfish undergo an ontogenetic diet shift from primarily littoral micro- and macrocrustaceans to large mollusks (Wainwright, 1996). Changes in the jaw bone and supporting muscle, which typically occurs once fish reach a total length of 50 mm or more (i.e., the size of pumpkinseeds in our study), may restrict their ability to effectively forage on prey as evasive as *Hemimysis*. These restrictions may also explain the lack of *Hemimysis* found in the stomachs of pumpkinseeds in previous gillnet-based studies (e.g., Brooking et al., 2010).

Unlike round goby and pumpkinseed sunfish, yellow perch are morphologically and behaviorally capable of capturing *Hemimysis*. The congener perch species *Perca fluviatilis* incorporates a substantial amount of *Hemimysis* into their diet in invaded systems in the Rhine (Borcherding et al., 2006). Furthermore, *Hemimysis* should be a profitable food item given that growth rates and lipid content of age-0 perch are higher when fed a *Hemimysis*-rich diet (Borcherding et al., 2007). However, YOY yellow perch feeding rates in the *Fish feeding experiments* were among the lowest of all fish species we tested. Most field-based diet studies in North America also indicate low utilization of *Hemimysis* by yellow perch; Lantry et al. (2010, 2012) found *Hemimysis* in the stomachs of <2% of all yellow perch caught in overnight gillnet sets and Brooking et al. (2010) reported the presence of *Hemimysis* in <1% of over 1500 adult and YOY yellow perch.

One possible explanation for the lack of congruence between North American and European field studies is that *Hemimysis* in the Rhine exhibit a rare daytime swarming behavior in open waters in shaded littoral areas (Ketelaars et al., 1999). The added visual advantage conferred to Eurasian perch by feeding on *Hemimysis* during the day in the pelagic realm may explain why *Hemimysis* are incorporated into their diets. North American perch are primarily diurnal predators and are most actively foraging when *Hemimysis* are within the benthic substrate and thus more difficult to access (*Effect of substrate experiments*). Interestingly, recent work by Geisthardt (2017) revealed that *Hemimysis* made up between 30 and 40% of YOY yellow perch diets in an artificial reef in Lake Michigan. The unique construction of the reef provided sheltered "boulder caves" that *Hemimysis* were found swarming in during daytime hours, although swarms were not observed in more exposed pelagic waters (Geisthardt, 2017). YOY yellow perch could therefore potentially be capturing *Hemimysis* within these unique cavities during daytime hours. We only examined feeding rates of YOY yellow perch during twilight conditions when reaction distance and prey capture success is greatly reduced in age-0 perch (Richmond et al., 2004). It may be that the combination of low-light levels, kairomone sensitivity and the effective burst-escape response of mysids (e.g., Holbrook et al., 2013) limits the ability of YOY yellow perch to reliably capture *Hemimysis* during the twilight and night hours even when effectively utilizing their

lateral line sensing. More work is necessary to tease apart the nuances of when and how perch are accessing *Hemimysis* in situ. Experimental and survey design should incorporate microhabitat characteristics, including light level, to investigate the ability of fish to access *Hemimysis* prey during the day on the benthic floor.

Conclusion

Collectively, our results inform the degree to which *Hemimysis* may become established and alter food webs in recipient ecosystems. We provide valuable insight into how environmental factors such as light, kairomones, and refuge characteristics can dynamically influence fish-*Hemimysis* interactions. The functional response curves derived in this study, across a range of *Hemimysis* densities experienced in the field, represent a comparative foundation that future models can build upon. Our *Hemimysis* habitat preference data, when combined with temperature and light-dependent feeding rates and preferences (e.g., Sun et al., 2013; Halpin et al., 2013), may also be used in future bioenergetics models to better understand and predict recruitment dynamics and distribution in spawning and nursery habitats of valued fish species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was financially supported by a Great Lakes Research Consortium Small Grant, a New York State Department of Conservation-funded grant issued through Finger Lakes-Partnership for Regional Invasive Species Management, and by New York Sea Grant project R/CE-28. We thank Dr. Lars Rustam and Bill Thelen of Cornell University for their help and advice on experimental design and the Cornell Biological Field Station for providing the light-controlled facilities used in the *Vertical preference experiments*. We would also like to give special thanks to the Poughkeepsie Day School administration and dedicated interns for providing the institutional support, resources and energy to move this project forward in innovative ways.

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