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Research Article

Enemy release in the invasive New Zealand mud snail in eastern North America

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Abstract

The enemy release hypothesis is one of the best supported hypotheses to explain the success of invasive species. This hypothesis suggests that invaders are successful, in part, because they experience fewer natural enemies (i.e. predators and parasites) in their invaded range compared to their native range. The New Zealand mud snail (NZMS), *Potamopyrgus antipodarum*, is a world-wide invader that is highly infected by digenetic trematodes in its native New Zealand. Here we compared infection prevalence of NZMS from multiple locations in the eastern US to published infection prevalences in the native range, and we also compared the infection prevalences of NZMS to infection prevalences of coexisting native snails where coexisting natives were found. We found no NZMS infected with trematodes at any site. In the two locations with coexisting natives, we found at least some natives infected with trematodes, and in one of the locations, we found both natives and NZMS associated with the annelid, *Chaetogaster limnaei*. *C. limnaei* can exist as a parasite of mollusks in the renal organ, or it can be found in the mantle cavity where it can act as a mutualist, consuming parasites (i.e. miracidia) that may be trying to infect the snail. We found that NZMS were generally less associated with both forms than native snails, but the ectosymbiotic form was more prevalent than the endoparasitic form in NZMS (and most natives). This creates the possibility that the symbiont may be a net benefit to NZMS and could positively influence invasion success.

Key words: *Chaetogaster limnaei*, exotic, introduced, mutualism, parasite, *Potamopyrgus antipodarum*

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Introduction

One of the most prominent hypotheses put forth to explain the success of invasive species is the enemy release hypothesis which states that the reduced pressure by natural biological enemies of non-native species may give them an advantage over their native competitors and increase invasion success (Keane and Crawley 2002; Torchin et al. 2003; Heger et al. 2024). While data from studies testing this hypothesis have been mixed, it appears to be better supported than other major hypotheses to explain invasion success (Jeschke et al. 2012), and it appears to hold especially well in freshwater ecosystems (Prior et al. 2015).

Multiple approaches have been used to assess the enemy release hypothesis (Colautti et al. 2004; Ricciardi et al. 2013). One biogeographical approach is to compare the impact of enemies on the invader in its native versus its introduced range. Here the hypothesis is supported if fewer enemy associations are found in the introduced range. A second community-based approach compares the impact of enemies on the invader to the impact of enemies on native competitors. Here the hypothesis is supported if the invader is less impacted by biological enemies than native competitors. Support for the enemy release hypothesis has been commonly found using biogeographical studies, but the results from community-based studies has been mixed (Colautti et al. 2004).

The New Zealand mud snail (NZMS), *Potamopyrgus antipodarum* Gray 1843, is a world-wide invader found on every continent except Antarctica (Ponder 1988; Bowler 1991; Zaranko et al. 1997; Shamida and Urabe 2003; Kalyoncu et al. 2008; Collado 2014; Taybi et al. 2021). In its native range in New Zealand, it exists in mixed populations of sexual and asexual individuals (clones) (Lively 1987). However, in its introduced range only asexual populations have been found (Proctor et al. 2007; Geist et al. 2022). Multiple negative impacts to native ecosystems have been demonstrated to be caused by NZMS (see reviews by Geist et al. 2022 and Alonso et al. 2023). Numerous traits and factors have been suggested to contribute to the invasion success of this species including its parthenogenetic reproduction (Alonso and Castro-Diez 2008), generalist nature especially with respect to feeding (Dorgelo and Leonards 2001; Liess and Lange 2011; Levri et al. 2017a) (but see Drown et al. 2011), broad environmental tolerances (Winterbourn 1970; Alonso and Castro-Diez 2008; Levri et al. 2023), behavior (Levri and Clark 2015; Levri et al. 2017b, 2019), and enemy release (Emblidge Fromme and Dybdahl 2006; Larson and Krist 2020). To our knowledge, the enemy release hypothesis has only been assessed once before in this species using a relatively broad geographic comparison (Larson and Krist 2020).

Here we examine the enemy release hypothesis in NZMS populations in the eastern United States by exploring the infection prevalences in snails collected from four states. We compared these prevalences to published infection prevalences of NZMS in their native range, and we compared the infection prevalences of NZMS to coexisting native gastropods in locations in Pennsylvania and New Jersey. With these comparisons, we aim to test the enemy release hypothesis and contribute to the understanding of aspects of this globally invasive snail that have been little explored.

Methods

Snail collections and parasite assessment

New Zealand native snail samples were obtained from five locations in the eastern United States in the springs and summers of 2022, 2023, and 2024. Each site was sampled using hand sampling and by passing sieves through aquatic vegetation for at least 30 minutes. If we found at least 5 native snails along with NZMS in the sample during the first 30 minutes, we obtained samples of both NZMS and native snails for comparison, but at only two locations did we find significant populations of other native species of snails with population sizes large enough to compare infection prevalences to NZMS and with populations of snails that were infected with parasites. A total list of sites sampled for NZMS can be found in Suppl. material 1: table S1. At all sites, at least 100 NZMS were assessed for parasitism. At the two sites where significant numbers of snails other than NZMS were found (Millbrook Marsh, Centre County, PA and the Musconetcong River, NJ), we collected at least

100 total snails other than NZMS. Snails were returned to the lab and maintained in 1-liter aerated plastic containers nearly filled with aged tap water treated with Amquel®. Snails were fed with *Spirulina* powder *ad libitum*. We identified snails to the genus level using Peckarsky et al. (1990). NZMS were identified as small (2–6 mm in length), brown to black, operculate snails with elongate, conical, and dextral coiled shells. They typically have five to six whorls. The snails are all female, and most carry a brood of offspring in a brood pouch behind the head (USGS Nonindigenous Aquatic Species Database). Snails were assessed for parasitism by dissection to release cercariae or other parasite stages. Snails were carefully dissected to determine where the individual parasites resided, in or on the snail.

Statistical analyses

To compare the prevalence of infection of NZMS to other species we used a Fisher's exact test analysis using IBM SPSS Statistics statistical software v. 29.0 (2022). We used this test to make pairwise comparisons in infection prevalences between species. Since some infection prevalences were low (0), a Fisher's exact test was preferred.

Results

We found NZMS at only two locations, Millbrook Marsh and the Musconetcong River, coexisting with populations of substantial numbers of other gastropods that were infected with some type of parasite. At all other locations (Gunpowder Falls, MD, Boardman River, MI, and sites in Spring Creek, PA), no infections of NZMS were found. At Millbrook Marsh, NZMS were found to coexist with one other species, *Fontigens nickliniana*, which was found at slightly higher densities than NZMS (in 2024 *Fontigens* 963/m^2 and NZMS 899/m^2; Flanders et al. in prep.). *F. nickliniana* was found to be infected by at least three different unidentified trematodes, an encysting metacercaria and two different cercariae. Details of their life cycles have not been determined. Over the course of seven samples taken over three years (2022–2024), 67.5% of *F. nickliniana* (out of 718 snails) were found to be infected, while no infections of NZMS were found out of 667 snails (see Table 1).

In the three sites in the Musconetcong River in NJ over the course of three years, three native snails were found to be infected by digenetic trematodes out of 689 natives dissected, and no NZMS were found to be infected by trematodes out of 1297 dissected. However, significant infections by the annelid, *Chaetogaster limnaei*, in both native snails and NZMS were found. Confirmation of *Chaetogaster*

Table 1. Infection prevalences by trematodes in native snails and New Zealand mud snails in Millbrook Marsh. All native snails assessed in Millbrook Marsh were *Fontigens nickliniana*.

Collection Dates	# of *F. nickliniana* Sampled	# *F. nickliniana* Infected	% *F. nickliniana* Infected	# of NZMS Sampled	# NZMS Infected	% NZMS Infected
October, 2022	160	114	71.3	40	0	0
May, 2023	573	385	67.2	127	0	0
July, 2023	525	345	65.7	81	0	0
October, 2023	667	441	66.7	152	0	0
May, 2024	76	47	61.8	96	0	0
July, 2024	77	53	68.8	115	0	0
October, 2024	133	108	81.2	56	0	0
Total	2211	1493	67.5	667	0	0

was performed by Ashley Smythe who has studied the worm extensively (e.g. Smythe et al. 2015). *C. limnaei* can exist in mollusks as an endoparasite or as an ectosymbiont that can feed on parasites trying to gain entry into the mollusk (Smythe et al. 2015). Thus, in this paper we will refer to the two forms as the endoparasitic form and the ectosymbiotic form. For infections by *C. limnaei*, we did not distinguish between the endoparasitic and the ectosymbiotic forms in 2022. Thus, we only report data from 2023 and 2024. Also, in 2024, snails were only collected from one site in the river (site 3 – See Suppl. material 1: table S1). *Chaetogaster limnaei* can be positively identified, in part by bifurcate cheatae which can be seen in Figure 1. In 2023 and 2024, we identified *Chaetogaster* as ectosymbiotic if it was found before the snail was removed from its shell, or if after snail removal the worm was found in the mantle cavity. The worm was judged to be endoparasitic if it was found once the visceral mass of the snail was dissected. Ectosymbiotic *Chaetogaster* were found on 12.8% of NZMS over the course of the study, while ectosymbiotic *Chaetogaster* were found on 41.3% of native snails during the same time period (Table 2). However, there was variation between different native species in this association prevalence (proportion of snails of a species with *Chaetogaster*). Endoparasitic *Chaetogaster* were found in 2.2% of NZMS over the course of the study, while endoparasitic *Chaetogaster* were found in 12.5% of native snails during the same time period (Table 2). A breakdown of the prevalences of infection by species can be found in Table 2. The association prevalence between *Chaetogaster* and NZMS was compared to all native snails within each year of collection as well as to each taxon of native snail (Table 3). We use the term "association prevalence" in reference to *Chaetogaster* because the worm is not always parasitic (Smythe et al. 2015). In general, NZMS tended to have a lower overall association prevalence with *Chaetogaster* than native snails, and they also tended to have lower association prevalences with ectosymbiotic forms of the worm as well as endoparasitic forms of the worm compared to natives. However, there were some exceptions, especially in 2024 when there was no difference in endoparasitic prevalences between NZMS and any natives (Tables 2, 3).

NZMS were significantly more likely to house ectosymbiotic *Chaetogaster* than endoparasitic *Chaetogaster* in both years and in data grouped across both years ($P < 0.001$ in all cases). When grouped together, native snails also were significantly more likely to house ectosymbiotic *Chaetogaster* compared to endoparasitic *Chaetogaster* in both years and in data grouped across both years ($P < 0.001$ in all cases). However, in 2023, *P. acuta* housed endoparasitic *Chaetogaster* at

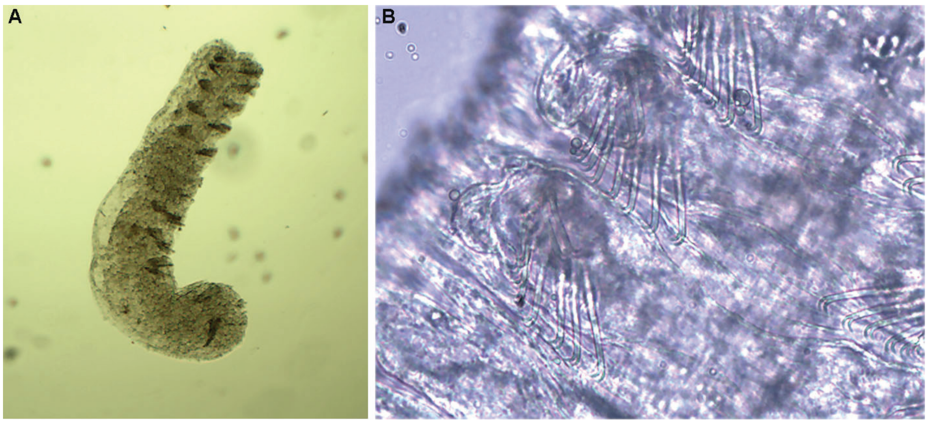

Figure 1. *Chaetogaster limnaei* found in snails collected from the Musconetcong River, NJ at 40× magnification (**A**). A close up of the worm showing the characteristic bifurcate (two-pronged) chaetae at 400× magnification (**B**). Photographs by G. Suter.

Table 2. Association prevalences with *Chaetogaster limnaei* in native snails and New Zealand mud snails in the Musconetcong River in 2023 (A), 2024 (B), and data grouped across both years (C). Total *Chaetogaster* can be less than the sum of those infected with endosymbiotic and ectosymbiotic forms because there were some snails infected with both forms. *Data for *Lymnea* sp. were only from 2023 as it was not found at the site of collection in 2024.

A

2023	Total	# with endoparasitic *C. limnaei*	# with ectosymbiotic *C. limnaei*	Total *C. limnaei*	% endo	% ecto	Total %
Potamopyrgus antipodarum	461	7	64	74	1.5	13.9	16.1
Pleurocera livescens	53	6	12	16	11.3	22.6	30.2
Physa acuta	28	6	0	6	21.4	0	21.4
Physa gyrina	183	17	75	79	9.3	41.0	43.2
Lymnea sp.	25	18	12	21	72.0	48.0	84.0
Total native snails	289	47	99	122	16.3	34.3	42.2

B

2024	Total	# with endoparasitic *C. limnaei*	# with ectosymbiotic *C. limnaei*	Total *C. limnaei*	% endo	% ecto	Total %
Potamopyrgus antipodarum	375	11	43	53	2.9	11.5	14.1
Pleurocera livescens	46	0	24	24	0	52.2	52.2
Physa acuta	17	0	5	5	0	29.4	29.4
Physa gyrina	48	3	37	38	6.3	77.1	79.2
Total native snails	111	3	66	67	2.7	59.5	60.4

C

2023 + 2024	Total	# with endoparasitic *C. limnaei*	# with ectosymbiotic *C. limnaei*	Total *C. limnaei*	% endo	% ecto	Total %
Potamopyrgus antipodarum	836	18	107	127	2.2	12.8	15.2
Pleurocera livescens	99	6	36	40	6.1	36.4	40.4
Physa acuta	45	6	5	11	13.3	11.1	24.4
Physa gyrina	231	20	112	117	8.7	48.5	50.7
Lymnea sp. *	25	18	12	21	72.0	48.0	84.0
Total native snails	400	50	165	189	12.5	41.3	47.3

a higher prevalence than ectosymbiotic forms (P = 0.023), and *Lymnea* sp. (P = 0.148) and *Pleurocera livescens* (P = 0.195) showed no difference in the association prevalences between the two forms. In data grouped across both years, *P. acuta* showed no difference in the association prevalences between the two forms of *Chaetogaster* (P = 0.900). In all other cases, native snails were found to have a higher association prevalence with ectosymbionts compared to ectoparasitic *Chaetogaster* (P < 0.05 in all cases).

Discussion

Discovery of the NZMS in streams in the eastern US has mostly occurred since 2010. The snail was first discovered in the Spring Creek watershed in central PA (which includes Millbrook Marsh) in 2010, the Boardman River, MI in 2016, in the Gunpowder Falls River, MD in 2017, and in the Musconetcong River, NJ in 2018 (USGS Nonindigenous Aquatic Species Database 2025). However, it should be pointed out that all of the populations were found with large populations, and it likely took multiple years for those populations to be discovered once the snail was introduced.

Table 3. P-values, odd ratios, and 95% confidence intervals from the results of Fisher's Exact tests comparing the association prevalence of *Chaetogaster limnaei* in *P. antipodarum* to the prevalence of *C. limnaei* association in native snails for each association type in 2023 (A), 2024 (B), and both years combined (C). Significant p-values (< 0.05) are in bold.

A			
2023	**Endoparasitic *C. limnaei***	**Ectosymbiotic *C. limnaei***	**Total *C. limnaei***
Pleurocera livescens	**= 0.003**; 5.76; 2.00, 16.55	= 0.156; 1.72; 0.86, 3.44	**= 0.008**; 2.39; 1.28, 4.48
Physa acuta	**< 0.001**; 12.30; 4.10, 36.91	= 1.000; 0.89; 0.34, 2.36	= 0.444; 1.38; 0.54, 3.52
Physa gyrina	**< 0.001**; 4.62; 2.07, 10.29	**< 0.001**; 4.08; 2.76, 6.05	**< 0.001**; 3.94; 2.69, 5.76
Lymnea sp.	**< 0.001**; 115.97; 36.60, 339.67	**< 0.001**; 7.48; 3.26, 17.18	**< 0.001**; 58.26; 13.45, 252.28
Total native snails	**< 0.001**; 9.02; 4.48, 18.15	**< 0.001**; 3.13; 2.19, 4.46	**< 0.001**; 3.89; 2.77, 5.45
B			
2024	**Endoparasitic *C. limnaei***	**Ectosymbiotic *C. limnaei***	**Total *C. limnaei***
Pleurocera livescens	= 0.618; 0.97; 0.95, 0.99	**< 0.001**; 8.42; 4.35, 16.30	**< 0.001**; 6.63; 3.47, 12.66
Physa acuta	= 1.000; 0.97; 0.95, 0.99	**< 0.044**; 3.12; 1.05, 9.29	= 0.151; 2.53; .086, 7.48
Physa gyrina	= 0.204; 2.21; 0.59, 8.21	**< 0.001**; 25.97; 12.34, 54.67	**< 0.001**; 23.09; 10.85, 49.11
Total native snails	= 1.000; 0.92; 0.25, 3.35	**< 0.001**; 11.32; 6.91, 18.57	**< 0.001**; 9.25; 5.73, 14.93
C			
2023 + 2024	**Endoparasitic *C. limnaei***	**Ectosymbiotic *C. limnaei***	**Total *C. limnaei***
Pleurocera livescens	**= 0.033**; 2.93; 1.14, 7.57	**< 0.001**; 3.89; 2.47, 6.15	**< 0.001**; 3.79; 2.43, 5.90
Physa acuta	**< 0.001**; 6.99; 2.63, 18.60	= 1.000; 0.85; 0.33, 2.21	= 0.137; 1.81; 0.89, 3.66
Physa gyrina	**< 0.001**; 4.31; 2.24, 8.29	**< 0.001**; 6.41; 4.62, 8.90	**< 0.001**; 5.73; 4.16, 7.89
Lymnea sp.	**< 0.001**; 116.86; 43.42, 314.52	**< 0.001**; 6.29; 2.80, 14.14	**< 0.001**; 29.31; 9.90, 86.81
Total native snails	**< 0.001**; 6.49; 3.73, 11.29	**< 0.001**; 4.78; 3.60, 6.36	**< 0.001**; 4.95; 3.77, 6.50

While NZMS are commonly infected with digenetic trematodes in their native range in New Zealand (Winterbourn 1973; Lively 1987; Levri and Lively 1996; King et al. 2011), the prevalences of infection in the invaded range have been found to be very low, much less than is typically found in New Zealand (Gerard and Le Lannic 2003; Gerard et al. 2003; McKenzie et al. 2003; Adema et al. 2009; Żbikowski and Żbikowska 2009; Alonso and Castro-Diez 2012; Cichy et al. 2017; Larson and Krist 2020). The NZMS is infected by at least 18 species of digenetic trematodes in New Zealand (Hechinger 2012), and infection prevalences in its native range vary widely but are commonly above 5% and can exceed 75% (Winterbourn 1974; Lively 1987; Levri and Lively 1996; King et al. 2011). In this study, NZMS at all sites were free of digenetic trematodes, and the only symbiont that was found was the annelid, *Chaetogaster limnaei*. In that case, the prevalence of the annelid was generally lower in NZMS than coexisting native snails.

The data presented here provide at least some evidence using both the biogeographical and community-based approach supporting the enemy release hypothesis. Biogeographically, the infection prevalence by trematodes found in the introduced range (0%) was less than is typically found in the native range of New Zealand. In some of the locations in this study few or no native snails were found so it is possible that there were no parasites present that could infect NZMS at some locations. In the two locations where substantial numbers of native snails with trematodes were found, NZMS were not infected with trematodes. Thus, while this evidence is limited, it is consistent with biogeographical support for enemy release.

The community approach to assessing enemy release compares the infection prevalence in the invader to the infection prevalence in the same location within native competitors. The conditions to make this comparison were met in two locations, Millbrook Marsh in Pennsylvania and the Musconetcong River in New Jersey. In Millbrook Marsh, the native, *F. nickliniana*, was heavily parasitized with trematodes (67%) (Table 1). In the Musconetcong River, native snails were overall more heavily associated with *Chaetogaster limnaei* than NZMS (Tables 2, 3). Both of these locations provide data that are consistent with enemy release. In the other examination of the enemy release hypothesis in this species, Larson and Krist (2020) examined the association between trematodes and NZMS in the western US. Similar to this study, they found that NZMS had lower prevalences of infection than native snails and were infected by fewer parasite taxa than natives.

To our knowledge, this is the first documentation of the presence of *Chaetogaster limnaei* in NZMS in North America. *Chaetogaster* has been found in NZMS in New Zealand (Winterbourn 1968) and in Europe where Buse (1974) found about 23% of NZMS associated with the worm with association prevalences ranging from 0 to 50% across multiple sites in Wales. McCarthy (1974) also found the worm associated with NZMS in Ireland. *Chaetogaster limnaei* is an annelid symbiont of mollusks found worldwide (Brinkhurst and Jamieson 1971). Interestingly, it can have one of two associations with its host (Smythe et al. 2015). It can exist externally or in the mantle cavity as a mutualist that actively consumes parasites such as trematode miracidia that attempt to penetrate the mollusk (Hopkins et al. 2013), or, alternatively, it can exist as an internal parasite of the mollusk. Thus, its presence can be positive or negative for the host. Some researchers have identified the two lifestyles as different subspecies of *Chaetogaster*, *Chaetogaster limnaei vaghini* (parasite) and *Chaetogaster limnaei limnaei* (mutualist) (Vaghin 1946; Sperber 1948; Gruffydd 1965; Buse 1974). However, more recent molecular evidence suggests that the two lifestyles are explained by phenotypic plasticity (Smythe et al. 2015).

The total association prevalence (endoparasites and ectosymbionts) between *Chaetogaster* and NZMS was lower than native snails in both years with significant differences found between NZMS and all species except for *P. acuta*, but the trend was in the same direction. This could be explained by enemy release, in that the local population of *Chaetogaster* may be locally adapted to the native snails in this area and less adapted to the more recent colonizer. NZMS also were less associated with endoparasitic *Chaetogaster* and ectosymbiotic *Chaetogaster* than native snails in most cases. However, in 2024 no difference was found between the association prevalence in endoparasitic forms between NZMS and any native species.

Because *Chaetogaster* can affect the snails positively or negatively depending upon where it takes up residence in the snail, it could impact the invader in at least two ways. First, if it is an endoparasite, it likely would reduce the fitness of the snail that it inhabits. In this case, endoparasites were more likely to be found in native snails, thus it is likely that NZMS had a net benefit assuming fitness effects of infection did not vary between species of snail. Secondly, as a mutualist ectosymbiont, *Chaetogaster* could provide a benefit to the invader if it is associated with it. In this study we found that the mutualistic ectosymbiotic form of the worm was less likely to be found in NZMS compared to native snails (see Tables 2, 3). Thus, natives may have benefited to a greater degree than NZMS. However, because NZMS were 6 times more likely to be associated with the ectosymbiotic form than the endoparasitic form, the NZMS may have received a net benefit. We do not know the degree of fitness reduction caused by the endoparasitic form or the potential fitness increase caused by the ectosymbiotic form, but the potential exists that the overall association between *Chaetogaster* and NZMS could be a net benefit for the invader. Other studies have also found invasive mollusks associated with *Chaetogaster*. For example, Chinese pond mussels were found associated with *Chaetogaster* in Europe (Cichy et al. 2016), Collado et al. (2019) found that *Chaetogaster* can colonize *Physa acuta* in Chile, and the same snail species harbored the worm in Australia (Mitchell and Leung 2016).

There appeared to be differences in association prevalences between 2023 and 2024 with a greater proportion of ectosymbionts to endoparasites found in 2024 than in 2023 in most snail taxa. The reason for this is unknown, but this suggests that the ratio of benefits from mutualism and costs from parasitism may vary from year to year within and between species. We found that, in most cases, the snails were more likely to be associated with ectosymbiotic forms of *Chaetogaster* than the endoparasitic forms, but there were a few exceptions. Others have discovered variation in the two forms of *Chaetogaster* in their presence in different snail species (e.g. Buse 1974). Mitchell and Leung (2016) found most *Chaetogaster* associated with *Physa acuta* were found as parasites in the renal organ with relatively few ectosymbionts. Hobart et al. (2021) found many more ectosymbionts than endoparasites in *Helisoma* and *Physa*.

Chaetogaster has been found associated with NZMS in New Zealand (Winterbourn 1968); however, it does not appear to be a widespread association as numerous other studies of parasitism in this species in New Zealand have not reported the annelid (Lively 1987; Levri and Lively 1996; King et al. 2011). NZMS appear to be an effective invader without association with *Chaetogaster*, so it is not clear to what extent the worm may enhance or reduce its invasive success. This study found that potentially mutualistic forms are more common in NZMS than the parasitic forms. A mutualistic benefit may exist if, by having ectosymbiotic *Chaetogaster*, NZMS encounter fewer trematode miracidia. The reduction in miracidial encounters may result in significantly lower physiological costs of fighting off infection. The resource and energy savings from reduced parasite encounters, could translate into more resources for reproduction or other traits that could provide other benefits for the snail and could translate into greater invasion success. However, since *Chaetogaster* can act as both a mutualist and a parasite, in order for this association to positively impact invasion success for NZMS, the mutualistic benefits would have to outweigh the parasitic costs which would be related to the ratio of ectosymbionts to endoparasites.

Conclusion

Here we found evidence that the NZMS is released from its enemies in the eastern United States both compared to NZMS in their native range and compared to competing gastropods in its introduced range. The release from parasites that the NZMS appears to have experienced in most of its invaded range may be among the primary reasons that the snail has been found to have the highest secondary productivity of any aquatic invertebrate (Hall et al. 2006) and attain population densities exceeding 500,000 per m^2 (Geist et al. 2022). In streams of the eastern US, invasion by the NZMS is a relatively recent (generally since 2010). Thus, there may not have been sufficient time for many parasitic associations to develop. Continued monitoring of infection prevalence in NZMS in the region is warranted. The snail's association with the mutualist/parasite *Chaetogaster limnaei* in one location also provides an interesting opportunity to study the influence of a potential mutualist on invasion success.

Author contribution

All authors have contributed equally.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary material.

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Supplementary material 1

Locations sampled for NZMS and native snails

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Data type: docx

Explanation note: **table S1.** Locations sampled for NZMS and native snails. Number of NZMS are totaled across sites within location.

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