Invasiveness and propagule pressure of *Bellemya chinensis* (formerly *Cipangupalinia chinensis*) in northern Wisconsin: a case study

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Abstract

Monitoring and controlling invasion into novel communities by non-indigenous species has been of increasing concern. In recent years, the Chinese mystery snail (*Bellemya chinensis;* formerly *Cipangupalinia chinensis*) has been on the brink of invading portions of the UNDERC property from a portion of Brown Creek south of the culvert near south gate road. I hypothesized that snail movements will be highest in later summer months and that the propagule pressure, or probability of a successful colonization event, will also be high at this time. I employed a removal study at four study sites on Brown Creek to look at recolonization rates in the area just south of the culvert and propagule pressure into the novel habitat area north of the culvert. I found that the rate of snail invasion in the area south of the culvert increased with marginal significance throughout the summer. Snails showed a propensity for the rocky/sandy habitat type, though this preference may be influenced by a number of other variables such as food type and availability, community interactions, and flow rate. Not surprisingly, as rainfall amounts increased throughout the experimental period, so too did current flow rate. Propagule pressure decreased north of the culvert with removal of migrant snails populating the area, while propagule pressure remained high in the densely populated source population south of the culvert. In light of these findings, I suggest modifying the culvert to keep water flow rate high even in times of low current flow and implementing a monitoring and removal program of the area north of the culvert.

Introduction

In 1892, the Chinese mystery snail (*Bellemya chinensis;* formerly *Cipangupalinia chinensis*) was imported for sale in the oriental food markets in the San Francisco Bay area (Bury *et al.* 2007). Since then, the invasive snail has spread to approximately 27 states. In recent years, the University of Notre Dame's UNDERC property has been subject to invasion by the Chinese mystery snail, with a community of snails poised to enter the property from a portion of Brown Creek downstream of the culvert near south gate road (James, pers. observation). A previous study showed that the faster flow rate through the culvert may be the only barrier preventing upstream colonization (Rivera, 2008). Prior to this study, it remained unclear whether the Chinese mystery snails had breached the culvert barrier and colonized novel regions of the creek to the north. Once breached it is unclear how quickly the snails will be able to migrate northward.

As with all invasive species, management of the spread of the invasive Chinese mystery snail has relied on the foresight and action of policy makers, scientists, and community members to assemble well-informed management schemes that target both primary and second invasions (Byers *et al.* 2002; Lodge *et al*. 2006; Zanden and Olden 2008). To be most effective, these efforts must assimilate information on the ability of the snail to invade and its capacity to reach new areas, which co-vary by locale along with a host of interacting factors (Leung and Mandrake 2007). The most important of these factors are propagule pressure and supply of propagules, habitat type and suitability, and interactions with native community assemblages (MacIsaac 2003; Zanden and Olden 2008). Sites that are most vulnerable to invasion and are capable of holding a self-sustaining population must be targeted to prevent further spread. The Brown Creek region north of the culvert at the University of Notre Dame's Environmental Research Center is one such invasion front.

Previous studies have shown that *B. chinensis* distribution is limited primarily to lakes, slow moving streams, and roadside ditches (Bury *et al.* 2007). Other studies have shown that current flow rate may also influence movement and distribution; movement may even be halted by fast moving water (Rivera 2008). Hutchinson et al. reported a 50% decrease in snail activity in areas of high current compared to standing water (Hutchinson 1947). Still other studies have looked at the density dependence of snail movement (Rajasekharan *et al.* 2007). Rajesekhara reported that snails inhabiting areas of high density exhibit a lower dispersal rate when transplanted to a new area of similarly high density, while snails from low density populations transplantation to a high density area responded with a relatively higher dispersal rate. In terms of habitat preference, Chinese mystery snails thrive in silt and mud areas, but are also found in sandy and rocky habitats in smaller numbers, and are typically found in depths ranging from

0.5m to 5m (Wisconsin DNR 2009). Snail density and distribution may also be due in part to food source type. The Chinese mystery snail does not feed on plants and prefers areas with detritus, algae, and phytoplankton. Together these characteristics paint a complex though incomplete picture of the snail's behavior.

In predicting future distributions of the Chinese mystery snail, propagule pressure is an important metric of invasibility. It uses the number of individuals arriving at a new site along an invasion front and the likelihood of one individual successfully establishing to predict the total probability of a successful colonization event (Leung *et al.* 2004). Among the many models used in invasive species ecology, propagule pressure serves as the best predictive tool of the probability of a species invasion (Colautti *et al.* 2006). Propagule size has also been shown to increase the probability of successful establishment by decreasing the reliance on stochastic dispersal events (Simberloff 2009). Drake *et al.* (2005) found that for some species invasions, the interaction of inoculum size and number of introductions, which together combine as a immigration rate, had the greatest affect on propagule pressure by increasing population growth rate and population persistence and decreasing time-to-extinction.

A second factor predicting the geographical course of an invasion, and indeed its long-term success, is habitat suitability. Successful colonization of a new area depends largely on where the invading species' realized niche falls in its fundamental niche (Gallien *et al.* 2010). The realized niche for the invaded area can fall either wholly within both its functional and native realized niche, wholly inside its functional niche but outside its native realized niche, or partially outside its functional niche and wholly outside its native realized niche. By this measure, habitat type and availability interpreted through a niche modeling approach can act as a key predictive tool to determine the geographic course an invasion will follow (Peterson 2003).

A third and final predictor are the biotic and abiotic consequences of interaction with native communities. Little is known about the Chinese mystery snail's community-level effects. Other invasive snail species such as New Zealand's mudsnail have been shown to dominate secondary production by sequestering carbon and nitrogen in river systems, with negative downstream effects on invertebrate production (Hall *et al.* 2003; Hall *et al.* 2006). To date, these types of intertrophic interactions between invertebrate communities and the Chinese mystery snail have not been studied. Other studies have shown that *C. chinensis* does not affect native snail assemblages in the northern Wisconsin lakes (Solomon *et al.* 2010). However, the snails may nevertheless negatively affect individual fitness by reducing available pariphyton and increase the water column N:P ratio (Johnson 2009).

To an extent, the Allee effect—defined as the 'the positive relationship between per-capita growth rate and density when density is low' (Taylor and Hastings 2005)—can also shape the advancement of an invasion front. The Allee effect is most pronounced in small populations and in the initial phases of an invasion when the colonizing population is low (Taylor and Hastings 2005). In some cases, multiple Allee effects can interplay. When only one of these several effects are recognized, estimates of the Allee threshold for a successful invasion can be seriously underestimated, resulting in a poor management outcome (Berec *et al* 2006). For these reasons, it is important to consider the role of the Allee effect in conjunction with propagule pressure, habitat suitability, and community interactions to most accurately model and predict the dynamics of a non-native species invasion (Tobin *et al.* 2007).

In light of these concerns, my study sought to answer two questions: (1) has the culvert holding the snails off property been breached, and (2) what is the probability of invasion—termed propagule pressure—of the snail from the source population south of the Brown Creek culvert into the previously uninhabited regions to the north? A second part of our study also looked at colonization rates of the mystery snail in an unobstructed environment. I hypothesized that snail movement will be greatest during the early summer months because the water temperatures will be lower and oxygen concentrations higher. I also predicted that movement will be equal in both the upstream and downstream directions, that a preference will be shown for muck habitat, and that snail movements will be dependent on current flow rate, as previous literature has indicated (Rivera, 2008). The south end Brown Creek near Palmer Lake was an ideal study site for answering these questions because it contains a gradient of habitat types and environmental factors such as flow rate that can analyzed in conjunction with movement and colonization data.

Materials and Methods

Four sites were selected on the southern end of Brown Creek between the south gate road culvert and Palmer Lake (89.485 W, 46.266 N) (Figure 1). The entire length of Brown Creek stretching from 50m north of the south gate road to Palmer Lake was surveyed for snail populations. In all, over 200m of creek were surveyed. Snails were identified visually using snorkeling techniques. The four experimental sample areas were subsequently chosen based on two criteria: (1) each site of the four sites had to represent a different habitat type along a gradient of differing depths, flow rates, and habitat types, and (2) Chinese mystery snails must have been present during the initial survey.

For convenience, the four sample sites were labeled by location, which we called downstream, south-of-culvert, culvert, and north-of-culvert. Our downstream replicate consisted of a subset of three mucky habitat sites: one 5m from the culvert and two other sites downstream, respectively, all of the mucky and weedy habitat type. The south-of-culvert replicate consisted of an area that measured approximately 2m by 2m and was located south of the westside culvert. This area was sandy and rocky with a moderate flow rate. The culvert replicate was taken from the eastside tunnel. The north-of-culvert was of a rocky habitat type that is bordered by a thick weed bed with a very moderate flow rate.

As a removal study, all efforts were be made to remove the entire population in each of four sampling areas during the collection period. Removal occurred daily during three experimental weeks. In total, samples were collected on 13 days. Snorkeling techniques were used to visually recognize and remove individuals. In this way, the resident Chinese mystery snail population was, to the best of our knowledge, extirpated within the sample area on collection days. We assumed that any new member in the sample area found on subsequent days must have migrated in from the surrounding area.

Snails were counted and measured after collection. Snail size was measured to test if size correlates with number of individuals collected. Measurements were taken from the apex to the bottom of the carapace. No records were taken during non-collection weeks, with gaps of 15 days and 23 days between collection weeks one and two and two and three, respectively.

Two measures of propagule pressure were used to account for varying degrees of Allee effect. One measure assumed no Allee effect, where E is the total probability of establishment, p is the probability of an individual establishing, N is the number of propagules colonizing at location l and time t, and α is a shape coefficient given as $-\ln(1-p)$ (Leung *et al.* 2004) :

$$E\left(N_{l,t}\right) = 1 - e^{-(\alpha N_{l,t})}$$

A second measure of propagule pressure considered the role of Allee effects by the addition of a shape parameter *c* (Leung *et al.* 2004):

$$E(N_{l,t}) = 1 - e^{-(\alpha N_{l,t}{}^{c})}$$

An ANOVA was run to look for a difference in the rate of colonization across sample periods. A repeated measures ANOVA (RM-ANOVA) was used to look at both sizes and counts of snails collected at the south-of-culvert site. A correlation was run to look for interaction between size and count at the south-of-culvert site.

Results

Migration Rates, Size and Count, and Flow Rate

The number of individuals removed from the sandy/rocky habitat type far exceeded the number removed from any other experimental site (Figure 2). An analysis of variance (ANOVA) was used to look for a significant change in recolonization rate at the south-of-culvert site. Results indicated a marginally significant increase in the recolonization rate of the mystery snail as the summer progressed ($F_{2,7} = 4.266$, $P = 0.061$) (Figure 3). Two repeated measures ANOVAs (RM-ANOVA) were used to separately compare both size and counts collected from the south-of-culvert site across the three sample periods. Both size ($F_{1,1} = 18.591$, $p = 0.145$) and count ($F_{1,1} = 0.815$, $p = 0.532$) did not show a significant relationship with sample collection day. A correlation was run to look for an interaction between size and count; no significance was noted ($F_{1,8} = 0.544$, $p = 0.482$, $R^2 = 0.064$). We also looked at the relationship between the change in current flow rate through the eastside culvert and rainfall. Not coincidentally, as local rainfall increased, so did the measurements of current flow through the study area (Figure 4).

Propagule Pressure

Propagule pressure north of the culvert with no Allee effect was decreased from $E(N_{l,t}) = 0.9375$ to $E(N_{l,t}) = 0.0000$ from the first experimental period to the beginning of the second; a similar but more pronounced decrease was observed when considering the Allee effect (Figure 5). Propagule pressure south of the culvert with no Alle effect recorded no decrease from experimental period one through three, remaining at $E(N_{l,t}) = 1.0$. An identical trend was seen when considering the Allee effect.

Discussion

This study sought to better understand and predict the invasion dynamics of the Chinese mystery snail on to the University of Notre Dame's UNDERC property by elucidating the invasiveness and the probability of a new colonization event, which both vary with a number of interrelated factors, including propagule pressure, habitat type and suitability, and interactions with native community assemblages (MacIsaac 2003; Leung and Mandrake 2007; Zanden and Olden 2008). Throughout the duration of the study, I found that the area south of the culvert had a consistently and disproportionately larger number of snails than at any other site on Brown Creek. This high density could be attributed to several factors such as a preference for the moderate flow rate on the fringes of this area which would increase dissolved oxygen, more abundant food and nutrients, or a backlog of individuals as they encounter the sometimes impassible currents in the culvert. Any management effort should focus first on this subpopulation.

Recolonization rates in the south-of-culvert site increased with marginal significance over the three sample periods. Though at first glance this increase could easily be attributed to a better ability to identity and remove snails as the summer went on, two more likely explanations include the effect of reproduction or upstream migration from nearby Palmer Lake to the south. In support of this explanation, there may also have been greater food availability as primary aquatic production increased during the summer months, which in turn would give the snails more energy for upstream migration.

One unforeseen change during our experimental period was a dramatic increase in current flow rate with an increase in precipitation during the second and third experimental periods. Results of this removal study supported the conclusions of Rivera (2008) that current flow rate is the primary deterrent preventing upstream invasion and colonization. By overlaying local rainfall totals with current flow rate (Figure 4), I showed that as rainfall amounts increased, so too did current flow rate. At the culvert invasion front, current effectively acted as a trump card preventing movement upstream. Broadening the discussion of biotic or abiotic determinants as trump cards from our case study to Chinese mystery snail invasion fronts in general, there seems to be one limiting factor that, if breached, could facilitate a novel dispersion event. For Brown Creek, this trump card is flow rate. Overcoming this barrier would require a period of drought. For other sites, this trump card could be a strip of dry land between lakes, a wetland (Bodamer and Bossembroek 2008), or a multitude of other biotic or abiotic determinants. To overcome this barrier, a rare dispersal event would be required to breach the barrier. If Allee effects are present, a series of rare dispersal events would be required until the Allee threshold—or the self-sustaining population threshold level—is reached.

Results of this study indicated a decrease in propagule pressure north of the culvert. These results, however, must be interpreted cautiously because the sample size (n=5) was very low. This can be attributed to the impassibly high current flow rate observed during weeks two and three. Moreover, using only one study site introduces the potential for pseudoreplication. To get a more accurate assessment of the Chinese mystery snail's propagule success, a combination of propagule pressure and the degree to which the population experiences Allee effects would need to be surveyed at a wide range of replicate samples sites on a longer time-scale (Leung *et al*. 2007).

Future studies must also address if and to what degree the Allee effect is exhibited in Chinese mystery snail invasions at low densities. For purposes of this study, equations accounting for both with and without Allee effects were used so as not to wrongly presuppose density dependence or independence in the per capita growth rate. The Allee effect can be visualized by comparing figures 5A and 5B. Note the steeper and more pronounced decline between experimental collection days three (3) and four (4) in the Allee effect graph, which can be explained by a decrease in individual fitness as the density of colonizing snails decreases. As for the snail populations south of the culvert, their higher propagule pressure can be attributed to a combination of the high density of snails surrounding the experimental site and swirling currents and eddies coming from water pouring out of the culverts that may pick snails up and transplant them in areas of low disturbance just adjacent the main area of current flow. This pattern was noted on several collection days. Snails would coalesce where eddies form and in the margins between rocks or in sandy areas just outside the main channel of flow from the culvert.

Equally important to understanding the current invasion dynamics at play in Brown Creek is to create a broader conceptual framework for forecasting future invasions. As shown earlier, short distance dispersal is limited by local constraints. At Brown Creek, this limiting factor is flow rate. Overcoming this would require a period of drought causing the current flow rate to decrease to a traversable speed. However, other stochastic vectors of invasion that would progress in a stepping-stone fashion such as a rare anthropogenic dispersal event or animal dispersal must also be considered (Floerl and Inglis 2005; Floerl *et al.* 2009).

Research in the long-distance spread of the invasive aquatic plants and animals such as the zebra mussel has focused on boating trafficking as a proxy for quantifying the probability of an anthropogenic dispersal event. This type of human-facilitated transport has been largely excluded on the UNDERC property, so any invasion northward must rely first on the propensity and ability of the Chinese mystery snail to disperse northward on its own. For this reason, I believe a period of drought corresponding with a decrease in current flow poses the greatest risk of successful colonization north of the culvert.

However, even if the area north of the culvert is invaded, it may take some time for a population large enough to mount an invasion further north on to UDNERC property lakes because of the effect of lag times in the establishment of invading populations (Crooks 2005). This lag period may be even more pronounced when considered alongside the work of Rajasekharan *et al.* (2007) who showed that dispersal rate decreased in snails coming from densely populated areas. The densely populated source population at the south-of-culvert would suggest a migrating population with lower dispersal rates than snails found in other communities.

Habitat type and availability is also important in invasion dynamics. Wetlands have also been shown to act as barriers in other aquatic invasions including the zebrafish (Bodamer and Bossembroek 2008). A similar tendency might also exist in the Chinese mystery snail, though to date no research has been conducted in this area. Looking to the future, invading north of the culvert would most likely required a rare long-distance dispersal event because the wetland leading northward to Brown Lake would afford little to no favorable habitat. Because long distance dispersal events often are stochastic in frequency and distribution and are rare in a natural setting in the absence of anthropogenic effects (Buchan and Padilla 1999), I predict that colonization north of the culvert would not necessarily result in colonization of Brown Lake to the north on a short timescale. The types of anthropogenic stochastic dispersal mechanisms needed to facilitate a rare dispersal of the snail to other lakes on property are more controlled at UNDERC than sites open to the general public. In sum, predicting the Chinese mystery snail invasion onto the UNDERC property requires consideration of local climate fluctuations vis-à-vis rare long-distance dispersal scenarios.

In addition to propagule pressure and habitat preference, the Chinese mystery snail has some expected and unexpected community-level effects, which in turn can change invasion dynamics. Though the Chinese mystery snail does not appear to change native snail assemblages (Solomon 2010), it may nevertheless be too soon to see noticeable effects on traits such as physiology and fecundity in native snails as dissolved nutrient supplies become depleted by increasing mystery snail populations over many years. Streyer *et al.* (2006) warns that the timescale may be too short to see these kinds of community-wide changes. Heino and Muotka (2006) showed that environmental variables and landscape position affect snail assemblages. As Chinese mystery snail densities continue to rise, we may still see a deleterious effect as environmental variables such as water chemistry change (Johnson 2009)—especially N:P ratios—and native snails are driven from prime habitat areas of lower food quality and available or higher rates of predation. In other systems, the golden apple snail (*Pomacea canaliculata*), another species of invasive snail found in Southeast Asia, has been shown to damage wetland function and integrity at high densities by overgrazing (Carlsson *et al.* 2004). Even though the Chinese mystery snail is does not feed on plants, browsing by the tremendously high densities noted in our study suggests that the Chinese mystery snail may well have similar system-wide effects. Since the area just north of the culvert invasion site is a wetland, future studies should look for a similar effect on wetlands in the Chinese mystery snail by measuring nitrogen and carbon sequestration for mystery snail at different densities. Such a change in ecosystem function could have community-wide effects including changing primary production, altering species assemblages, and stressing or displacing invertebrate communities, among others.

In light of these findings, I suggest modifying the culvert to keep water flow rate high even in times of low water levels and implementing a monitoring and removal program of the area north of the culvert. Future studies should focus on the interplay between changing environmental conditions and propagule pressure, with a specific emphasis on the idea of one or several variables as trumps that prevent the spread of an invading population.

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FIGURES

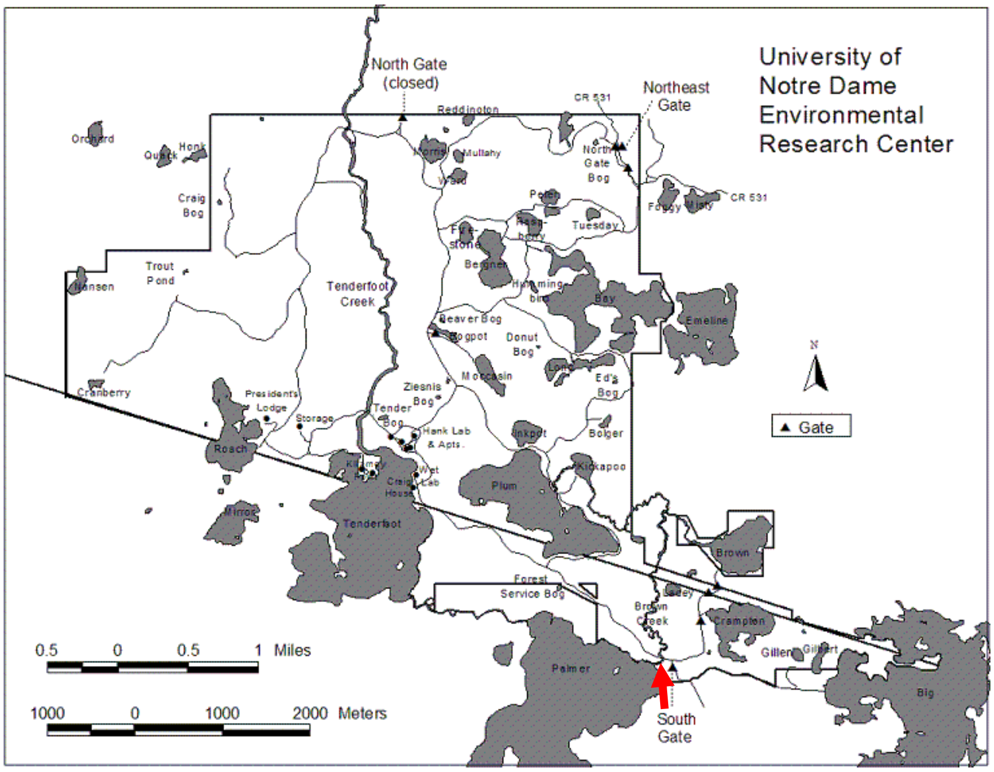


Figure 1. *Map of UNDERC East property*. Snails were removed from three sites on the section of Brown Creek indicated by the arrow.

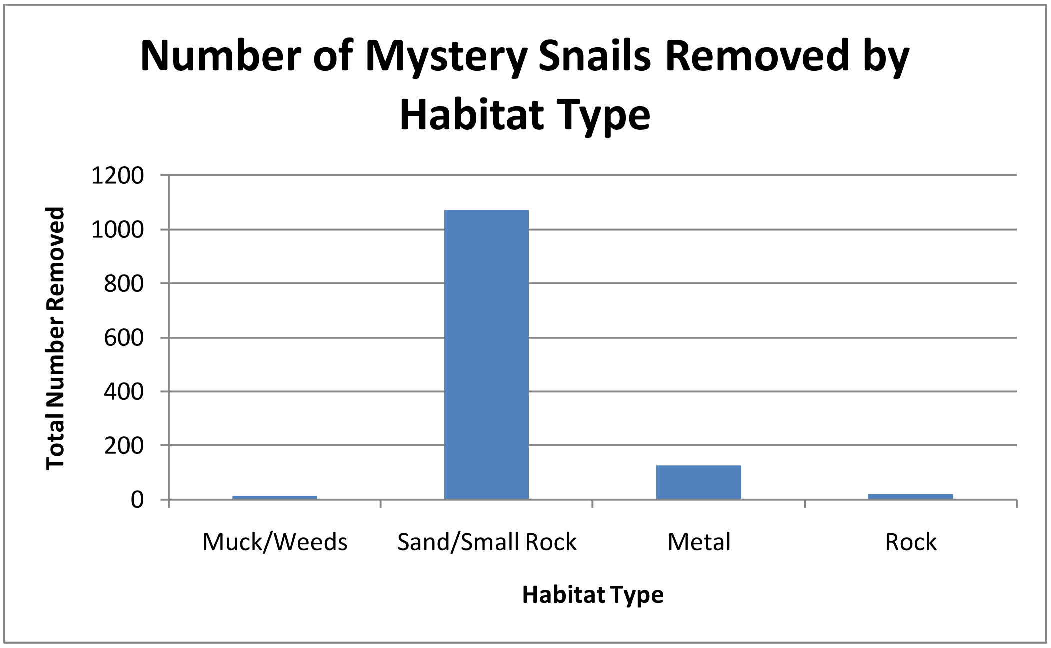


Figure 2. *Total number of mystery snails removed by habitat type.* Snails were found predominantly in the sand/small rock habitat type south of the westside culvert. The rock and metal habitat may also be suitable for the snails as a number of individuals were found there during periods of low current flow rate. However, the higher flow rate in experimental periods two and three blocked dispersion altogether.

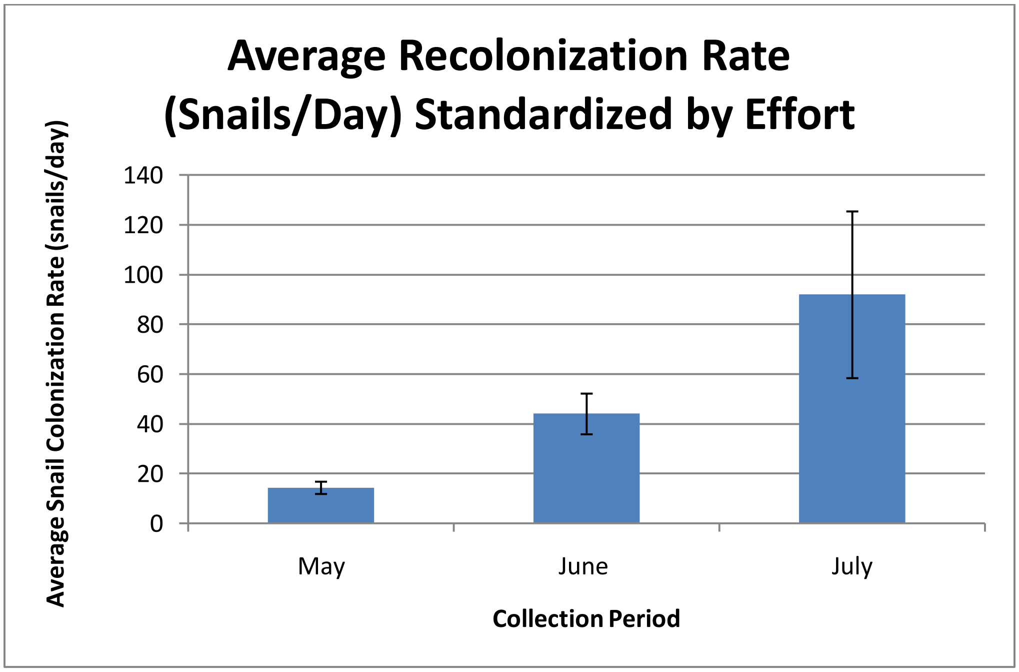


Figure 3. *Average recolonization rates in snails per day standardized by effort.* Samples were collected from the south of culvert site. Results indicate a marginally significant ($F_{2,7} = 4.266$, $P = 0.061$) increase in average recolonization rate across the three experimental weeks.

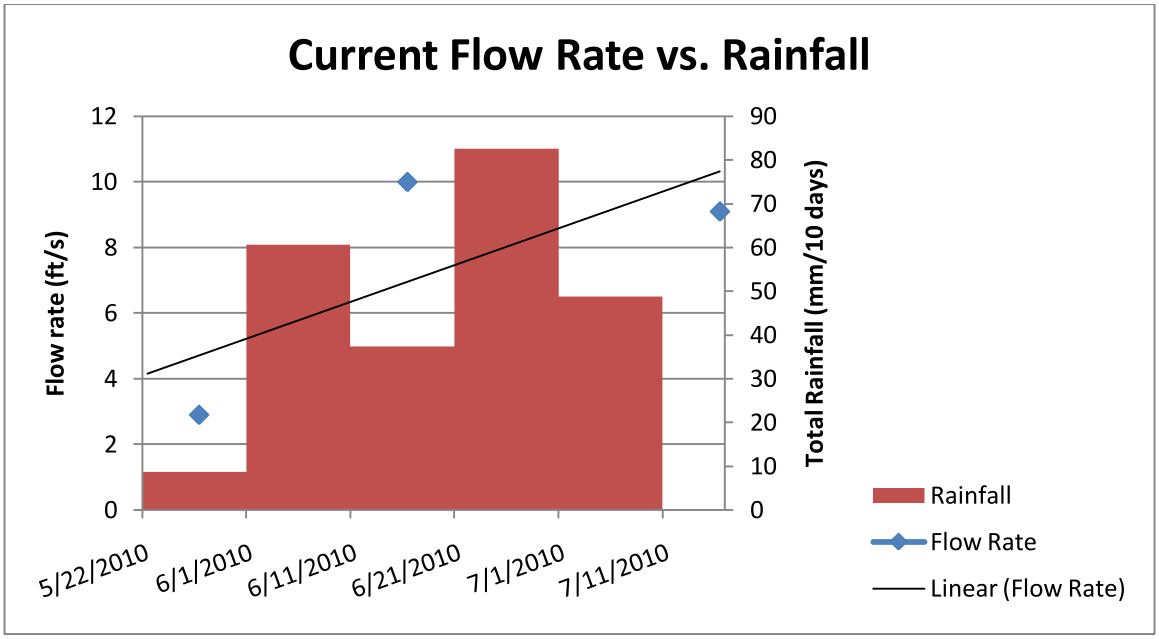
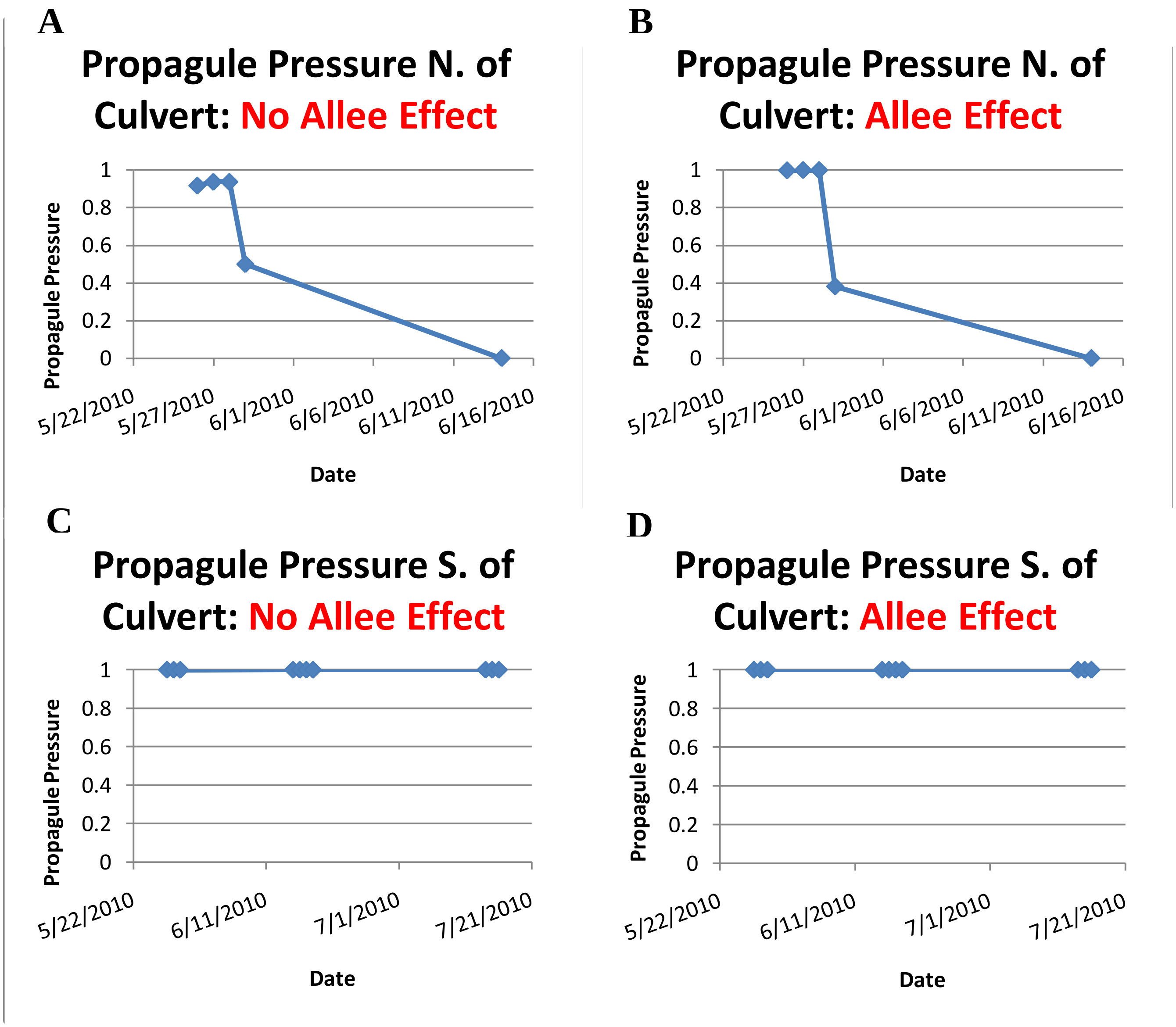


Figure 4. *Average current flow rate versus ten day precipitation totals (mm/10 days).* Average current flow rate (ft/s ± 0.1ft/s) was measured in the eastside culvert on Brown Creek during collection weeks one and two where *Bellamya* had been discovered invading northward during our initial survey. Note the increase in flow rate of 6.7±0.1 ft/s along with a trend of increasing ten day total rainfall amouts that both correlate with an abrupt end to snail upstream invasion.



Propagule Pressure N. of Culvert: No Allee Effect

Propagule Pressure N. of Culvert: Allee Effect

Propagule Pressure S. of Culvert: No Allee Effect

Propagule Pressure S. of Culvert: Allee Effect

Figure 5. *Propagule pressure north and south of the culvert with and without Allee effect.* Propagule pressure north of the culvert with no Allee effect (A) was decreased from 0.9375 to 0.0000 from the first experimental period to the beginning of the second; a similar but more pronounced decrease was observed when considering the Allee effect (B). Propagule pressure south of the culvert with no Alle effect (C) recorded no decrease from experimental period one through three, remaining at 1.0. The same trend was seen when considering the Allee effect.

APPENDIX A — Snail collection data.

Appendix 1A. *Snail collection by location and date.*

Site	**Date**	**Count (#)**	**Average Size (mm)**	**Standard Deviation**	**Units Effort (man hours)**	**Scaled Count (snails/per man hour)**
▨	▨	▨	▨	▨	▨	▨
South of Culvert	5/26/2010	280	32.83	7.51	2.50	112
South of Culvert	5/27/2010	24	35.08	6.85	1.25	19.2
South of Culvert	5/28/2010	13	33.62	4.58	1.00	13
South of Culvert	5/29/2010	11	30.55	5.42	1.00	11
South of Culvert	6/14/2010	163	33.71	6.84	1.00	163
South of Culvert	6/15/2010	73	32.39	6.56	1.25	58.4
South of Culvert	6/16/2010	58	32.76	6.88	1.00	58
South of Culvert	6/17/2010	32	31.53	6.17	1.00	32
South of Culvert	6/18/2010	21	31.29	8.20	0.75	28
South of Culvert	7/13/2010	121	32.84	4.54	1.00	121
South of Culvert	7/14/2010	83	34.26	6.17	1.00	83
South of Culvert	7/15/2010	154	33.25	6.62	1.00	154
South of Culvert	7/16/2010	39	32.63	7.37	1.00	39
▨	▨	▨	▨	▨	▨	▨
North of Culvert	5/26/2010	9	38.16	6.46	2.50	3.6
North of Culvert	5/27/2010	5	43.36	9.29	1.25	4
North of Culvert	5/28/2010	4	33.98	6.19	1.00	4
North of Culvert	5/29/2010	1	26.4	0.00	1.00	1
North of Culvert	6/14/2010	0	0.00	0.00	1.00	0
North of Culvert	6/15/2010	0	0.00	0.00	1.25	0
North of Culvert	6/16/2010	0	0.00	0.00	1.00	0
North of Culvert	6/17/2010	0	0.00	0.00	1.00	0
North of Culvert	6/18/2010	0	0.00	0.00	0.75	0
North of Culvert	7/13/2010	0	0.00	0.00	1.00	0
North of Culvert	7/14/2010	0	0.00	0.00	1.00	0
North of Culvert	7/15/2010	0	0.00	0.00	1.00	0
North of Culvert	7/16/2010	0	0.00	0.00	1.00	0
▨	▨	▨	▨	▨	▨	▨
Right Tunnel	5/26/2010	111	31.61	7.93	2.50	44.4
Right Tunnel	5/27/2010	10	29.65	5.47	1.25	8
Right Tunnel	5/28/2010	5	34.42	6.95	1.00	5
Right Tunnel	5/29/2010	0	0.00	0.00	1.00	0

Right Tunnel	6/14/2010	0	0.00	0.00	1.00	0
Right Tunnel	6/15/2010	0	0.00	0.00	1.25	0
Right Tunnel	6/16/2010	0	0.00	0.00	1.00	0
Right Tunnel	6/17/2010	0	0.00	0.00	1.00	0
Right Tunnel	6/18/2010	0	0.00	0.00	0.75	0
Right Tunnel	7/13/2010	0	0.00	0.00	1.00	0
Right Tunnel	7/14/2010	0	0.00	0.00	1.00	0
Right Tunnel	7/15/2010	0	0.00	0.00	1.00	0
Right Tunnel	7/16/2010	0	0.00	0.00	1.00	0
▨	▨	▨	▨	▨	▨	▨
Downstream	5/26/2010	10	38.46	7.01	2.50	4
Downstream	5/27/2010	0	0.00	0.00	1.25	0
Downstream	5/28/2010	0	0.00	0.00	1.00	0
Downstream	5/29/2010	0	0.00	0.00	1.00	0
Downstream	6/14/2010	2	39.60	5.09	1.00	2
Downstream	6/15/2010	0	0.00	0.00	1.25	0
Downstream	6/16/2010	0	0.00	0.00	1.00	0
Downstream	6/17/2010	0	0.00	0.00	1.00	0
Downstream	6/18/2010	0	0.00	0.00	0.75	0
Downstream	7/13/2010	0	0.00	0.00	1.00	0
Downstream	7/14/2010	0	0.00	0.00	1.00	0
Downstream	7/15/2010	0	0.00	0.00	1.00	0
Downstream	7/16/2010	0	0.00	0.00	1.00	0

Appendix 1B. *Total number of snails collected across all sites per collection day.*

Date	Count (#)	Average Size (mm)	Standard Deviation	Units Effort (man hours)	Scaled Count (snails/per man hour)
5/26/2010	410	35.26	7.23	2.50	164
5/27/2010	39	37.62	7.20	1.25	31.2
5/28/2010	32	34.01	5.91	1.00	32
5/29/2010	12	28.47	5.42	1.00	12
6/14/2010	165	33.78	6.84	1.00	165
6/15/2010	73	32.39	6.56	1.25	58.4
6/16/2010	58	32.76	6.88	1.00	58
6/17/2010	32	31.53	6.17	1.00	32
6/18/2010	21	31.29	8.2	0.75	28
7/13/2010	121	32.84	4.54	1.00	121
7/14/2010	83	34.26	6.17	1.00	83
7/15/2010	154	33.25	6.62	1.00	154
7/16/2010	39	32.63	7.37	1.00	39