

Home-field advantage: native signal crayfish (*Pacifastacus leniusculus*) out consume newly introduced crayfishes for invasive Chinese mystery snail (*Bellamya chinensis*)

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Abstract The introduction of non-indigenous plants, animals and pathogens is one of today's most pressing environmental challenges. Freshwater ecologists are challenged to predict the potential consequences of species invasions because many ecosystems increasingly support novel assemblages of native and non-native species that are likely to interact in complex ways. In this study we evaluated how native signal crayfish (*Pacifastacus leniusculus*) and non-native red swamp crayfish (*Procambarus clarkii*) and northern crayfish (*Orconectes virilis*) utilize a novel prey resource: the non-native Chinese mystery snail (*Bellamya chinensis*). All species are widespread in the United States, as well as globally, and recent surveys have discovered them co-occurring in lakes of Washington State. A series of mesocosm experiments revealed that crayfish are able to consume *B. chinensis*, despite the snail's large size, thick outer shell and trapdoor defense behaviour. Crayfish exhibited size-selective predation whereby consumption levels decreased with increasing snail size; a common pattern among decapod predators. Comparison of prey profitability curves—defined as the yield of food (weight of snail tissue) per second of feeding time (the time taken to crack the shell and consume the contents)—suggests that small and very large snails may represent

the most profitable prey choice. By contrast, previous studies have reported the opposite pattern for crayfish consumption on thin-shelled snails. For all snail size classes, we found that native *P. leniusculus* and invasive *O. virilis* consumed greater numbers of snails than invasive *P. clarkii*. Moreover, *P. leniusculus* consistently handled and consumed snails at a faster pace compared to both invasive crayfishes across the range of snail sizes examined in our study. These results suggest not only that *B. chinensis* is a suitable food source for crayfish, but also that native *P. leniusculus* may ultimately out-consume invasive crayfishes for this new prey resource.

Keywords *Procambarus clarkii* · *Orconectes virilis* · *Cipangopaludina chinensis* · Exotic species · Invasional meltdown · Predator–prey interactions

Introduction

The introduction of non-indigenous plants, animals and pathogens is one of today's most pressing global environmental challenges (Mack et al. 2000). Although only a fraction of introduced species become established and even fewer have any appreciable effect on their new ecosystems, many others exert significant ecological, evolutionary and economic impacts. The magnitude of this problem has been

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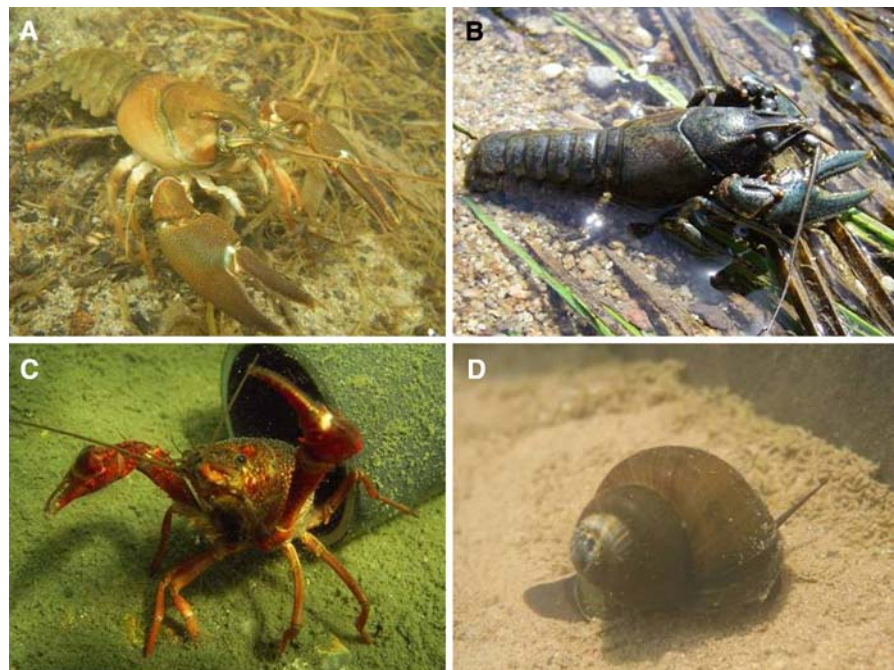
recognized in recent decades, and government agencies have responded by designing and implementing management strategies aimed at reducing the negative effects of invasive species (Lodge et al. 2006).

Despite recent efforts, our ability to forecast the impact of aquatic invasive species on recipient ecosystems is still limited (Vander Zanden and Olden 2008). Perhaps the most fundamental challenge in predicting the undesired consequences of invasive species is that many aquatic ecosystems increasingly support multiple non-indigenous species. Complex interactions among multiple invaders can lead to a range of outcomes for native species and ecosystems, many of which are difficult to predict a priori (Byers et al. 2002; Bruno et al. 2005). Recent studies have demonstrated that invasive species can mediate the ecological effects of one another through competition and/or predation, have no effect on each other, or exhibit facilitative interactions (e.g., Grosholz 2005; Griffen et al. 2008). Because of the potentially complex interrelations among invasive species and their native and non-native prey, experimental studies may be particularly suited for comparative studies of common resource utilization by native and non-native species (Parker et al. 1999).

Invasive species are of significant concern in the northwest United States because of the large network

of freshwater lakes and rivers that support a rich diversity of biological life (Sanderson et al. 2009). The last decade has witnessed the successful establishment of two non-native crayfish species—red swamp crayfish (*Procambarus clarkii*) and northern crayfish (*Orconectes virilis*)—in lakes of Washington, USA (Fig. 1a, b); both species have a history of invasiveness and have demonstrated ecological impacts throughout their invaded global ranges. Crayfish are important polytrophic consumers in temperate freshwater environments and play a central ecological role by providing a direct link from primary production and detrital-based food webs to fish and terrestrial predators (Nyström et al. 1996). Small-scale experiments and field studies have demonstrated significant ecological impacts of *P. clarkii* and *O. virilis* on detritus, macrophytes, benthic insects, snails, crayfishes and fish in lotic and lentic waters (e.g., Chambers et al. 1990; Geiger et al. 2005; Gherardi 2006; Gherardi and Acquistapace 2007). These species have only recently been documented in Washington (Mueller 2001; Larson and Olden 2008) and are invading a freshwater landscape occupied by a single native crayfish species—the signal crayfish (*Pacifastacus leniusculus*) (Fig. 1c). Interestingly, *P. leniusculus* is a formidable invasive species in its own right, causing significant ecological harm where it has been introduced in

Fig. 1 Organisms examined in our study: **a** *Pacifastacus leniusculus* (signal crayfish), **b** *Orconectes virilis* (northern crayfish), **c** *Procambarus clarkii* (red swamp crayfish), and **d** *Bellamya chinensis* (Chinese mystery snail). Photo credits: Jeff Benca (a), Julian Olden (b, d) and Karl Mueller (c)



Europe and Asia (Söderbäck 1995; Nyström and Pérez 1998; Holdich 2002; Usio et al. 2007). Taken together, *P. clarkii*, *P. leniusculus* and *O. virilis* are the three most globally invasive crayfish species, respectively (Hobbs et al. 1989), and therefore Washington lakes provide both a unique research opportunity and a difficult management challenge.

Washington lake ecosystems, like those in many other regions of the world, have a complex invasion history involving the simultaneous introduction of numerous plants and animals. Chinese mystery snail (*Bellamya chinensis*) (Fig. 1d) was first observed in Washington over 40 years ago and is now broadly distributed in hundreds of lakes that supported relatively few native snails. Likely first introduced into Washington by aquarium hobbyists releasing unwanted individuals into local waterbodies, *B. chinensis* is the second largest snail in North America (second only to the invasive apple snail, *Pomacea paludosa*) and is native to eastern and southeastern Asia. A thick outer shell and a hard operculum flap or trapdoor covering the shell opening (aperture) affords *B. chinensis* with a high degree of protection from predators and unfavourable environmental conditions. Although little is known about its ecological impacts (but see Johnson et al. 2009), once introduced these snails can achieve very high densities (Bury et al. 2007), and were reportedly removed from the Great Lakes by the metric ton during the 1960s. *B. chinensis* is widespread throughout Washington State, and the lack of shared evolutionary history between *B. chinensis* and all three species of crayfish provides the opportunity for novel species interactions.

Crayfishes are voracious consumers of freshwater gastropods (Alexander and Covich 1991), and a number of studies have demonstrated that the distribution and species composition of snail assemblages are structured by crayfish predation (e.g., Chambers et al. 1990; Lodge and Lorman 1987; Lodge et al. 1994; Nyström et al. 1996; McCarthy et al. 2006). The shell of freshwater snails is a conspicuous morphological defense that impedes shell-damaging predators, and a body of literature has shown that many snail species with thicker shells are often less susceptible to crayfish predation (e.g., Brown 1998; Krist 2002). Most freshwater gastropods, including those native to Washington, have thin outer shells, relatively wide apertures and no opercula. Previous research has shown that

crayfish typically chip away the aperture margin of the shell using their maxillipeds (mouth parts) and first pair of walking legs to gain access to edible snail tissue (DeWitt et al. 2000) in a similar mechanism used by crabs consuming marine snails. Despite the fact that *B. chinensis* are now a common component of benthic communities in lakes, information regarding predation on this species by crayfish is non-existent. By virtue of the relatively thicker shell of *B. chinensis* compared to most native snails (Johnson et al. 2009) and the ability to close their trapdoor, we might expect that crayfish will not be able to utilize this novel prey item throughout its invaded range in Washington.

The purpose of this study was to provide the first investigation of whether the invasive snail *B. chinensis* represents a new prey resource for crayfish, and if so, whether they are differentially-utilized by native and invasive crayfish. We performed two complementary experiments to quantify the use of *B. chinensis* as prey by *P. leniusculus*, *O. virilis* and *P. clarkii*. In the first series of mesocosm experiments, we estimated levels of consumption on different size classes of snails for each crayfish species. Increasing snail size is associated with thicker shells (Lewis and Magnuson 1999), and thus crayfish may exhibit strong selectivity for smaller, thinner-shelled individuals (Brown 1998). The second experiment addressed the mechanism underlying patterns of consumption by examining differential handling time of *B. chinensis* by crayfish species needed to crush and consume snail tissue. Results from this experiment allowed for comparisons of prey profitability for different snail size classes across crayfish species. Together, our study uses an experimental approach to provide insight into potentially novel crayfish-snail interactions between native and non-native crayfishes and a seemingly ubiquitous non-native snail in lake ecosystems of Washington, USA.

Methods

Study species

The signal crayfish (*P. leniusculus*) is a large crayfish native to the Pacific Northwest region of the United States and Canada, and has been widely introduced in

western North America, Japan and over 20 countries in Europe (Hobbs et al. 1989; Holdich 2002; Usio et al. 2007). While usually introduced with the intent of establishing recreational or commercial fisheries, *P. leniusculus* has instead severely impacted aquatic ecosystems by displacing native crayfish (Usio et al. 2001), competing with native fish (Light 2005), and reducing densities of other aquatic invertebrates and macrophytes (Nyström and Pérez 1998; Nyström et al. 1999; Nilsson et al. 2000).

The red swamp crayfish (*P. clarkii*) is the most widespread invasive crayfish in the United States and the world, expanding from its native range in north-eastern Mexico and south-central United States to at least 19 US states and all continents except Antarctica and Australia (Hobbs et al. 1989). The highly aggressive behavior, potential for rapid population increase, and omnivorous feeding habits of *P. clarkii* have resulted in numerous ecological impacts manifested across entire lake food webs (e.g., Geiger et al. 2005; Gherardi 2006; Gherardi and Acquista-pace 2007). *P. clarkii* was first recorded in Washington in the summer of 2000 (Mueller 2001).

The northern crayfish (*O. virilis*) has a broad natural distribution across central North America (Pflieger 1996), and has been widely introduced both within the United States as well as occasionally in Europe (Hobbs et al. 1989). Although its impacts are poorly studied relative to other invasive crayfishes, *O. virilis* has been found to reduce macrophyte biomass and diversity (Chambers et al. 1990) and impact native fishes (Carpenter 2005). *O. virilis* was only recently detected in western Washington (Larson and Olden 2008).

The Chinese mystery snail (*Bellamya* [= *Cipangopaludina*] *chinensis*) is a large (>60 mm maximum shell height) viviparid snail native to eastern and southeastern Asia that was first documented in the United States in Chinese markets of San Francisco (Wood 1892). *B. chinensis* was almost certainly introduced to the US multiple times through the aquarium trade, water gardening industry or for culinary purposes (Mackie 1999), and is now widely distributed in lakes and slow-moving rivers across North America, including at least 27 US states and all of the Laurentian Great Lakes (Jokinen 1982; Bury et al. 2007). Due to its wide distribution and high densities in Washington lakes (J.D. Olden, unpublished data), *B. chinensis* may have significant impacts in invaded systems (also see Johnson et al. 2009).

Experimental animals

Study animals were collected from lakes in western Washington. We sampled crayfish from littoral zone habitats using modified Gee minnow traps baited with dry dog food, and *B. chinensis* were gathered by snorkeling. Crayfish species were collected from separate lakes containing no other crayfish species but all supporting populations of *B. chinensis*: *P. leniusculus* (Martha Lake: 48°13'N, 122°72'W), *O. virilis* (Lake Ballinger: 47°59'N, 122°32'W), and *P. clarkii* (Silver Lake: 48°00'N, 122°24'W). Therefore, all crayfish have a prior history with *B. chinensis*, although the length of exposure is unknown. *B. chinensis* were collected from Pine Lake (47°35'N, 122°12'W), which contains *P. leniusculus* and *P. clarkii*, and therefore had prior experience with crayfish predators. Crayfish were taken to the School of Aquatic and Fishery Science's hatchery at the University of Washington, and housed separated by species in six aerated indoor tanks (bottom area = 0.8 m²: two tanks per species) with a constant flow-through of fresh water from nearby Lake Washington. All tanks contained cinderblocks to provide shelter, and crayfish were fed canned tuna daily until 72 h prior to commencing the consumption experiment and 24 h prior to the handling time experiment. We determined the sex of all crayfish, measured carapace length (CL) from the anterior tip of the rostrum to the posterior edge of the carapace, and measured the length and width of the right chela with digital calipers (accuracy 0.1 mm). Only intermolt animals with intact chelae and walking legs were used in the experiments. Shell height of *B. chinensis* was measured from the apex to the basal inflection of the aperture.

Consumption experiment

We conducted an experiment to quantify the magnitude of snail consumption of different size classes by crayfish. The experiment was conducted in mid-August 2008 using indoor mesocosms (90-L, 0.18 m²; mesocosm size selected to ensure high encounter rates of all snails), under ambient photo-period (L:D = 14:10) and water temperature (20.7–21.1°C). Mesocosms were covered with 5 kg of coarse gravel (0.5–2.0 cm in diameter, 3 cm depth) and filled with water directly from Lake Washington (including constant

flow-through) to a depth of 5 cm from the gravel surface. To each mesocosm we added 17 individuals of *B. chinensis* in each of four size classes as follows: 10 small (10.0–14.9 mm), 5 medium (15.0–22.9 mm), 1 large (23.0–29.9 mm) and 1 extra-large (30.0–39.9 mm); a size distribution that is representative of lake populations in its invaded range. We randomly assigned each mesocosm to one of the following treatments: no crayfish, one *P. leniusculus*, one *O. virilis*, one *P. clarkii*; including eight replicates per treatment (seven males and one female per species; sex ratio based on crayfish availability). Crayfish were added to the mesocosm 1 h after snail addition, and a fixed-time experiment of 40 h duration was conducted. This duration was chosen, based on feeding rates in preliminary trials, to minimize the probability that a size class would be eliminated. Length statistics of the experimental crayfish are as follows: *P. leniusculus* (mean CL = 61.4 mm, range = 50.4–66.5 mm), *O. virilis* (mean CL = 49.1 mm, range = 42.0–50.4 mm) and *P. clarkii* (mean CL = 54.8 mm, range = 42.8–61.4 mm). At the end of the experiment, we drained the water from each mesocosm and enumerated and measured all snails for height and mass.

The appropriate statistical analysis for multiple-choice experiments remains a target of much discussion and debate in the literature (e.g., Lockwood 1998; Raffa et al. 2002; Prince et al. 2004). Unfortunately, most methodologies are only applicable for experiments where a consumer is given the choice between equal amounts of different food types. Our experiment intentionally used unequal amounts of snails in each size class in order to more accurately reflect the relative abundance of snails available to crayfish in nature. Consequently, we tested for differences in the proportion of snails (to control for unequal initial numbers) consumed across size classes among crayfish treatments using an 50-50 multivariate analysis of variance (MANOVA), a modified variant of the classic MANOVA for collinear responses (Langsrud 2002). 50-50 MANOVA was developed to handle several collinear responses (in the case of our study referring to within-treatment correlations between snail size classes) by reducing the dimensionality of the data using principal component (PC) decompositions in combination with general linear modeling. Briefly, this approach first uses PC analysis to project the data onto multivariate

space defined by orthogonal axes that most efficiently describe the dominant gradients of variation. Next, the classic MANOVA is applied on the ratio between the mean model error explained by the first k PCs (explaining at least 50% of the variability in the original data) and the mean model error of the last 25% of PCs (explaining the least amount of the variability in the original data). We refer the reader to Langsrud (2002) and Langsrud et al. (2007) for more details. After confirming the significance of the 50-50 MANOVA we applied separate analyzes of covariance (ANCOVA) for each snail size class to test for differences in the proportion of snails consumed across crayfish species, with either CL, chela length or chela width entered as a covariate. We found no significant effects of the covariates ($P > 0.05$), therefore the results from ANOVAs and Fisher's LSD post-hoc comparison tests are presented. Furthermore, consumption values for the female crayfishes were within the range of values for male crayfishes (results not shown). Proportion data was arcsine square-root transformed to meet assumptions of normality.

Handling time experiment

Handling time of different size classes of *B. chinensis* was quantified using direct observation under red light between the hours of 20:00 and 1:00 (September 15–18, 2008). Using 38-L aquaria we offered a single snail from each size class to a single crayfish of each species, and calculated the total time the crayfish spent cracking the shell and consuming the tissue. We ran each experiment for a maximum of 120 min, after which no outcome was recorded if the crayfish had not consumed the snail. We conducted ten replicate trials for each crayfish-size class combination. Trials were conducted in the order small-medium-large-extra large, and crayfish were reused in each trial. Trials were separated by a 24 h interval in which crayfish were fasted so that satiation was not expected to interfere with handling time or snail consumption. Because all crayfish had been collected from lakes with populations of *B. chinensis*, we anticipated that crayfish had prior experience with *B. chinensis* and did not acquire significant new expertise over the course of our experiment. Length statistics and sex of the experimental crayfish (used in all size class sizes)

are as follows: *P. leniusculus* (CL mean = 57.5 mm, range = 49.7–65.2 mm, six males and four females; sex ratio based on crayfish availability), *O. virilis* (CL mean = 48.9 mm, range = 42.7–54.8 mm, ten males) and *P. clarkii* (CL mean = 55.0 mm, range = 46.9–61.2 mm, ten males).

For those trials in which snails were consumed we calculated handling time (h) and snail prey value (v) as dry weight of consumed snail tissue per second of handling time: $v = M/h$; where M is tissue dry mass. Shell free dry tissue mass was calculated from a derived length-shell free dry mass regression [mass (g) = 0.0001 length^{2.5606}, $r^2 = 0.967$, $P < 0.001$, $n = 30$]. The frequency of consumption based on these experiments also provides additional insight into snail size selectivity examined in the first experiment. 50-50 MANOVA was applied to test for differences in handling time across size classes among crayfish treatments. After confirming the significance of the 50-50 MANOVA separate ANCOVAs for each snail size class were used to test for differences in handling time across crayfish species, with either CL, chela length or chela width entered as a covariate. We found no significant effects of the covariates ($P > 0.05$), therefore the results from ANOVAs and Fisher's LSD post-hoc comparison tests are presented. Furthermore, there was no significant difference in handling time between male and female *P. leniusculus* (results based on T -tests) for the small size class ($T_{3,5} = 0.97$, $P = 0.368$) and medium size class ($T_{2,4} = -0.48$, $P = 0.656$) (sample size not adequate for large and extra-large size classes). The relationships between snail length (L) and handling time were fitted according to the function: $h = bL^c$ (representing the expected relationship based on previous snail-size preference experiments). Both linear and non-linear functions (logarithmic, power, and polynomial) were tested for the relationship between snail length and prey value. The most reliable model was inferred by adjusted R-squared values and statistical significance. In all cases, the normality of residuals was checked and confirmed not to be violated.

Results

Crayfish species showed strong size selectivity in their consumption behavior of *B. chinensis* across snail size classes (50-50 MANOVA: $P < 0.001$). Experimental

animals consumed on average 51% and 21% of the small and medium snail class, respectively, but only preyed upon 9% of the large size class and 17% of the extra-large size class. We found significant differences in species' consumption of the small size class (ANOVA: $F_{3,28} = 8.33$, $P < 0.001$), where all crayfish species consumed more than natural mortality in the predator-free treatment (0% mortality for all size classes), and *P. leniusculus* and *O. virilis* consumed twice the number of snails compared to *P. clarkii* (Fig. 2a). Similar patterns were observed for the medium size class (ANOVA: $F_{3,28} = 5.01$, $P = 0.007$), where *O. virilis*, *P. leniusculus*, and *P. clarkii* consumed 35%, 18% and 10% of the available snails, respectively (Fig. 2b). No significant treatment effects were found for large (ANOVA: $F_{3,28} = 2.33$, $P = 0.096$) and extra-large snail treatments (ANOVA: $F_{3,28} = 1.56$, $P = 0.222$), although *P. leniusculus* and *O. virilis* did consume snails from these larger size classes (Fig. 4c, d). *P. clarkii* always rejected large and extra-large snail across all trials.

Observations made during the handling time experiment showed that crayfish manipulated *B. chinensis* using their first pair of walking legs (and chelae in the case of larger snails) and crushed the shell at the aperture using their maxillipeds and mandibles. Pieces of snail tissue were ripped and ingested, and fragments of shell were always observed. In some cases, crayfish crushed the body whorl or spire of the shell of large and extra-large snails using their chelae. The proportion of snails from different size classes that were handled (and consumed) corresponded closely with the results from the consumption experiment; in all cases crayfish handled smaller snails more often (Fig. 3). The one exception was that *P. leniusculus* handled and consumed snails in the large size class in 50% of the trials, whereas this size class experienced 0% mortality in the consumption experiment.

Handling time across species ranged from 2 min for the smallest snail (10.9 mm) to 55 min for the largest snail (38.7 mm); both consumed by *P. leniusculus*. Mean handling time ($\pm 1SD$) for the snail size classes was 8.4 ± 6.8 min (small), 17.1 ± 10.9 min (medium), 31.9 ± 15.3 min (large), and 40.5 ± 20.5 min (extra-large). Crayfish species showed strong differences in their handling times of *B. chinensis* across snail size classes (50-50 MANOVA: $P < 0.001$). Handling time of the small size

Fig. 2 Snail mortality (proportion of *B. chinensis* consumed) of the four size classes subjected to different experimental treatments. Significantly different means are shown using common letters over bars in panel (a) and (b) based on Fisher’s LSD post-hoc tests (overall ANOVA was not statistically significant for panels c and d). Means (bars) and standard deviations (whiskers) are presented

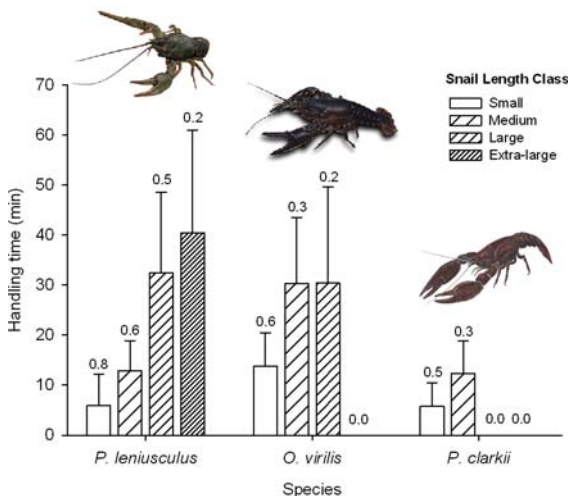
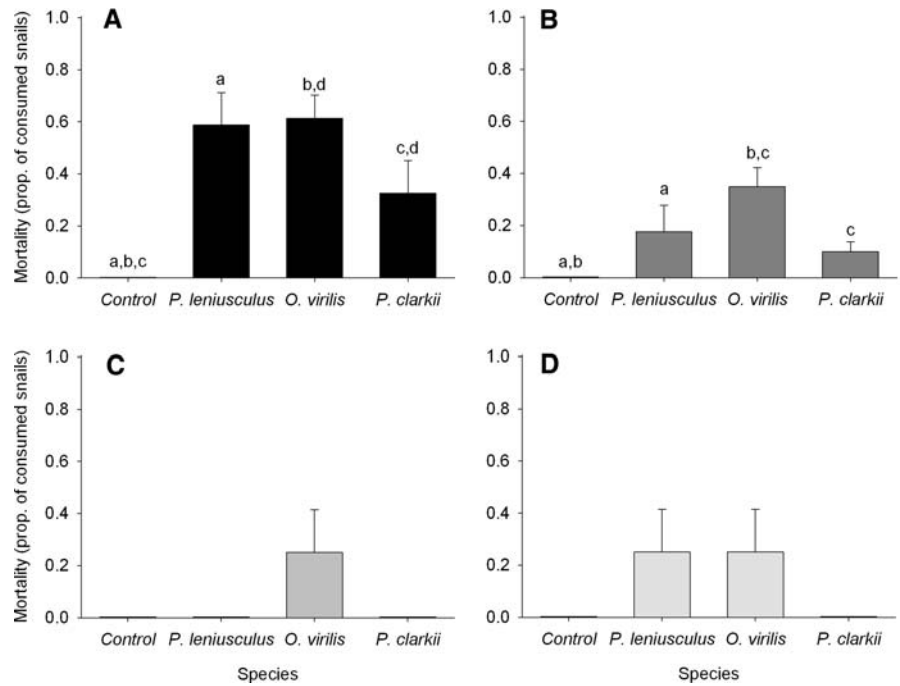


Fig. 3 Snail handling time (minutes) of the four size classes consumed by *P. leniusculus*, *O. virilis* and *P. clarkii*. The proportion of individuals ($n = 10$) consumed are indicated. Means (bars) and standard deviations (whiskers) are presented

class differed significantly among crayfish treatments (ANOVA: $F_{2,16} = 3.61$, $P = 0.050$); mean time to handle and consume was significantly lower for *P. leniusculus* (LSD post-hoc test: $P = 0.026$) and *P. clarkii* ($P = 0.042$) compared to *O. virilis* (Fig. 3). Similarly, snails in the medium size class were handled for different amounts of time across species

(ANOVA: $F_{2,9} = 5.11$, $P = 0.033$); again with *P. leniusculus* (LSD post-hoc test: $P = 0.015$) and *P. clarkii* ($P = 0.026$) handling snails for significantly less time compared to *O. virilis*. No significant difference in handling time between *P. leniusculus* and *O. virilis* was observed for the large size class (Student’s t -test: $t_5 = 0.14$, $P = 0.897$), and *P. clarkii* never handled snails in this size class (Fig. 3).

Handling time increased non-linearly with snail size for *P. leniusculus* ($h = 0.215L^{0.473}$, $R^2 = 0.61$, $F_{1,19} = 29.25$, $P < 0.001$) and *O. virilis* ($h = 1.502L^{0.937}$, $R^2 = 0.38$, $F_{1,9} = 5.48$, $P = 0.044$), but showed a non-significant relationship for *P. clarkii* ($h = 0.298L^{1.256}$, $R^2 = 0.21$, $F_{1,6} = 1.59$, $P = 0.254$) (Fig. 4). *P. leniusculus* handled (and consumed) small snails more quickly compared to *O. virilis* (e.g., for a 15 mm snail, the handling time of *O. virilis* was almost twice that of *P. leniusculus*), but this difference diminished with increasing snail size and both species had equal handling times when snails approached 30–35 mm in length.

Prey value (i.e., dry weight of consumed snail tissue per second of handling time) differed between size classes (Fig. 5); the small and extra-large size classes had the highest prey values for *P. leniusculus* (ANOVA: $F_{3,17} = 2.69$, $P = 0.078$), whereas prey value was highest for the large size class for *O. virilis*

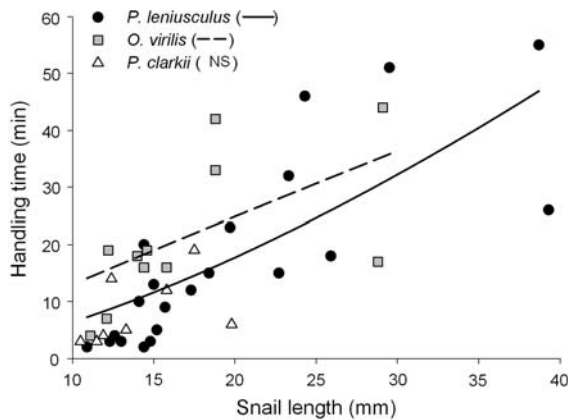


Fig. 4 Snail handling time (*minutes*) as a function of *B. chinensis* length (mm). Power functions are plotted for statistically significant relationships, which included *P. leniusculus* (circles and solid line) and *O. virilis* (squares and dashed line). The proportion of individuals consumed is reported in Fig. 3

(ANOVA: $F_{2,8} = 7.09$, $P = 0.017$). No differences between small and medium size classes were observed for *P. clarkii* (Student's t -test: $t_6 = -0.66$, $P = 0.536$). Prey profitability varied substantially with snail length, and showed a consistent relationship across crayfish species. It was generally the case that the smallest and largest snails were more profitable (Fig. 6), resulting in strong-fitting polynomial relationships for *P. leniusculus* ($v = 0.921 - 0.062L + 0.001L^2$, $R^2 = 0.27$, $F_{1,18} = 3.32$, $P = 0.085$), *O. virilis* ($v = 0.642 - 0.066L + 0.002L^2$, $R^2 = 0.64$, $F_{1,8} = 7.13$, $P = 0.028$) and *P. clarkii* ($v = 2.746 - 0.368L + 0.013L^2$, $R^2 = 0.67$, $F_{1,5} = 5.08$, $P = 0.074$). These regression models provided a significantly better statistical fit to the data compared to linear and power functions (*results not shown*). Notably, small snails were more profitable to native *P. leniusculus* compared to the invasive *O. virilis* and *P. clarkii* (Fig. 6).

Discussion

Human-induced environmental change has caused the re-shuffling of native and non-native species into assemblages that are compositionally unlike any found previously (Hobbs et al. 2006). Newly emerging ecosystems that contain unique mixtures of species will give rise to fundamental changes in key biological interactions and processes, yet the ultimate

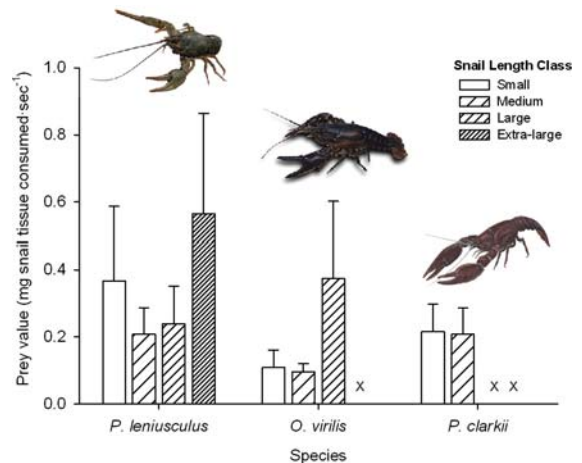


Fig. 5 Prey value (mg of dry tissue consumed \times second $^{-1}$) of the four size classes consumed by *P. leniusculus*, *O. virilis* and *P. clarkii*. "X" indicates that no individuals were consumed (see Fig. 3). Means (bars) and standard deviations (whiskers) are presented. The proportion of individuals consumed is reported in Fig. 3

nature of these novel linkages remains unknown (Bruno et al. 2005). Our study suggests that the invasive Chinese mystery snail (*B. chinensis*) represents a novel prey resource for both native and non-native crayfishes despite its large size, thick outer shell and trapdoor defense behaviour. Although shell thickness plays a central role in crayfish preference for gastropods (Brown 1998), *B. chinensis* still appears to be vulnerable to predation by adult crayfishes of the species examined in our study. Given that *B. chinensis* is now a common component of benthic communities in many lakes in Washington (and elsewhere), this species may augment the food resources for both native and non-native crayfish. Previous studies have shown that non-native species in the classes Gastropoda and Bivalvia may constitute a new prey source and energetic pathway in freshwater ecosystems. For example, experimental studies have shown that invasive zebra mussels (*Dreissena polymorpha*) and Asian clam (*Corbicula fluminea*) are preyed upon by crayfishes (e.g. MacIsaac 1994; Martin and Corkum 1994) and fishes (e.g., Robinson and Wellborn 1988; Magoulick and Lewis 2002), and can increase the diversity and abundance of invertebrate prey for benthivorous fishes (e.g., Thayer et al. 1997). Vinson and Baker (2008) found that rainbow trout (*Oncorhynchus mykiss*) consume non-native New Zealand mud snail (*Potamopyrgus antipodarum*)

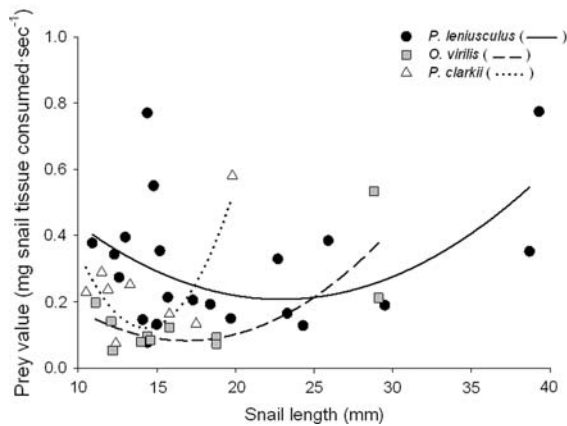


Fig. 6 Profitability curves representing the relationship between snail length of *B. chinensis* (mm) and prey value (mg snail tissue consumed \times second $^{-1}$). Non-linear regression models (second-order polynomial) are plotted for statistically significant relationships, which included *P. leniusculus* (circles and solid line), *O. virilis* (squares and dashed line) and *P. clarkii* (triangles and dotted lines). The proportion of individuals consumed is reported in Fig. 3

in the field, although experimental trials showed that mud snails may be energetically-insufficient to support metabolic requirements. Similarly, native common carp (*Cyprinus carpio*) was found to be an effective predator of invasive golden apple snails in rice field experiments in Malaysia (Sin 2006).

Crayfish were found to consume most size classes of *B. chinensis* by either crushing the shell or chipping away the margin of the opening to gain access to tissue. Our results based on the consumption and handling time experiments suggest that all crayfish species exhibited size-selective predation, where consumption levels decreased with increasing snail size. This pattern is common among decapod predators (Juanes 1992). Theoretically, crayfishes should select sizes of snail for which prey profitability—defined as the yield of food (weight of snail tissue) per second of feeding time (the time taken to crack the shell and consume the contents)—approaches a maximum. Results from our handling experiments suggest that small and very large size classes may represent the most profitable prey choice. The reason behind this bimodal profitability curve is that although tissue mass increases exponentially with snail length, we found no such relationship between snail length and handling time. Therefore, the increase in time needed to crack open larger snails

is more than compensated by the enhanced pay-off of gaining access to greater tissue mass. These results contrast findings from previous studies examining the behaviour of crayfish feeding on thin-shelled gastropods. Warner (1996) found that snail handling time by *P. leniusculus* and tissue mass of common pond snail (*Lymnaea stagnalis*) increased exponentially with snail size, which resulted in a strong preference for consuming medium-sized snails according to Warner et al. (1995). Similarly, Nyström and Pérez (1998) found that intermediate sizes of *L. stagnalis* were preferentially consumed and were the most energetically profitable for *P. leniusculus*. These studies hypothesized that small-sized prey were not profitable because of low flesh weight and handling difficulties, whereas large-sized prey were sub-optimal because increasing shell thickness made them very time-consuming to crack open.

For all snail size classes, we found that native *P. leniusculus* and invasive *O. virilis* consumed greater numbers of snails compared to invasive *P. clarkii*. Moreover, *P. leniusculus* consistently handled and consumed snails at a fast pace compared to *O. virilis* across the range of snail sizes examined in our study. These results suggest that *B. chinensis* is not only a suitable food source for all crayfish species, but native *P. leniusculus* may more quickly handle this prey item compared to invasive crayfishes. Whether this ultimately translates into *P. leniusculus* having a competitive advantage over invasive crayfish in a natural setting remains unknown. Regardless, it is clear that depending on snail density and size distribution, native crayfish predation by *P. leniusculus* has the potential to affect local population densities of *B. chinensis*. Does the presence of native crayfishes enhance the biotic resistance of lakes to snail invasions? The answer to this question is unclear. At the local scale, we suspect that *P. leniusculus* does exert significant predation pressure on *B. chinensis*, and that snail densities may be depressed compared to crayfish-free habitats. However, at the lake-scale, we find little evidence that lakes containing *P. leniusculus* are less likely to support populations of *B. chinensis*. Based on a regional survey of 58 lakes (J.D. Olden, unpublished data) observed patterns of species co-occurrence were not significantly different from random expectations ($\chi^2 = 0.14$, $P = 0.70$). In fact, in those lakes containing *P. leniusculus* we found *B. chinensis* to be present in more than half (57% of lakes).

In contrast to the resistance of snail invasions by native crayfish predation, we might also expect that lakes containing *B. chinensis* may facilitate the establishment of invasive crayfish by providing an abundant prey resource (i.e., invasional meltdown). We believe this may be particularly relevant in Washington which supports a relatively species-poor native snail fauna compared to other regions of North America (<http://www.natureserve.org/>). Consequently, the widespread distribution and often high densities of *B. chinensis* in Washington lakes may serve to exacerbate the establishment success and ecological impacts of invasive crayfish. Unfortunately this hypothesis is very difficult to test, especially at the landscape scale, because the timing of introduction and establishment of *P. clarkii*, *O. virilis* and *B. chinensis* is unknown. The lack of data chronicling the time course of species invasions is a common knowledge gap. We suspect that well-designed manipulative experiments or long-term observational studies will be required to elucidate the relative roles of positive and negative interactions in shaping species invasions (e.g., Stachowicz et al. 1999, France and Duffy 2006).

Food choice depends on several factors, including resource preference, prey availability, and life-history stage (Sih and Christensen 2001). Despite the many advantages of using laboratory experiments to assess predator–prey interactions, it is important to recognize potential limitations associated with each of these factors. First, crayfish were only offered a single prey item (*B. chinensis*) and were not provided a wider choice of potential food, including numerous low value items such as detritus and plant material, as well as other snail species. For example, previous studies on the trophic ecology of *P. clarkii* have suggested that, in spite of its opportunistic habits, this species may feed selectively on macrophytes and aquatic insects (reviewed in Correia 2003). This may explain the relatively low consumption of *B. chinensis* by *P. clarkii* compared to the other species. Furthermore, previous studies have showed that crayfish can exhibit strong selectivity for snail species, where thin-shelled species are commonly selected over hard-shelled species (e.g., Saffran and Barton 1993; Brown 1998; Johnson et al. 2009). While these are both plausible explanations, it is also possible that differences in chelae gap size (distance between fingers) may explain differences in

consumption and handling rates (however, chela length and width were not significant covariates in the ANCOVAs). Second, prey availability is an important factor influencing prey choice by crayfish. For this reason we carefully considered the size of the mesocosm prior to the experiments to ensure that snail choice was not an experimental artifact of incomplete knowledge and differences in encounter rates across snail size classes. Despite this, we recognize that predator–prey interactions between crayfish and snails are dependent on the size of the experimental arena (Dickey and McCarthy 2007), although we expect these effects to be consistent across species. Third, stomach and stable isotope studies suggest that crayfish undergo ontogenetic shifts in their diet, whereby juvenile crayfish are primarily carnivorous and adults are omnivorous (e.g., Correia 2003; Bondar et al. 2005). The results from our study are representative of snail consumption by adult crayfish.

In conclusion, quantifying the ecological impacts of invasive species is a complex and challenging endeavor (Parker et al. 1999; Strayer et al. 2006). Currently, we know comparatively little about how the effects of individual invaders may be attenuated or amplified as a result of novel species interactions making the net consequences of biological invasions difficult to predict (Bruno et al. 2005). Results from our mesocosm experiments demonstrate that the Chinese mystery snail (*B. chinensis*) represents a novel prey resource for both native and non-native crayfishes despite its thick outer shell and trapdoor defense behaviour. Given the common occurrence of multiple invaders within many freshwater ecosystems, there is greater need for future research exploring newly emerging interactions among native and non-native species.

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