

# FEEDING RATES OF AN INTRODUCED FRESHWATER GASTROPOD *POMACEA INSULARUM* ON NATIVE AND NONINDIGENOUS AQUATIC PLANTS IN FLORIDA

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## ABSTRACT

*Pomacea insularum* (Gastropoda: Ampullariidae) is a common, nonindigenous species in many parts of the world and an important consumer of aquatic macrophytes. We conducted laboratory trials to quantify the rates of consumption of native and nonindigenous aquatic plants in Florida, where this snail has been introduced. Twenty-two freshwater plant and alga species were presented to naïve *P. insularum* in laboratory trials, using single-snail replicates and simultaneous (no-snail) controls. *Pomacea insularum* damaged >50% of the replicate plants of 16 species; for 14 of these we calculated ash-free dry weight-specific feeding rates of *P. insularum*. The most heavily consumed plants were two native species: *Limnobium spongia* (0.744 g/g/d) and *Chara* sp. (0.478 g/g/d). Nonindigenous *Panicum repens* (0.306 g/g/d), *Hydrilla verticillata* (0.292 g/g/d) and *Ceratophyllum demersum* (0.254 g/g/d); and native *Sagittaria latifolia* (0.257 g/g/d), *Najas guadalupensis* (0.225 g/g/d) and *Vallisneria americana* (0.207 g/g/d) were also heavily consumed. Nonindigenous *Eichhornia crassipes* was consumed at a lower rate (0.053 g/g/d) while nonindigenous *Colocasia esculenta* and *Pistia stratiotes* were not consumed at detectable levels. Our results suggest that *P. insularum* cannot be relied upon as a biological control agent for nonindigenous plants and may heavily impact native macrophytes.

## INTRODUCTION

Apple snails (*Pomacea* species) are native to tropical and subtropical America. Several members of the genus have been introduced to other parts of the world, where they have become serious agricultural pests of important wetland crops such as rice and taro (Cowie, 1995; Naylor, 1996; Cowie, 2002). In some regions introduced *Pomacea* have had a beneficial effect by consuming unwanted plants in rice paddies (Wada, 2006; Luna Maldonado & Nakaji, 2008); for the most part, however, these invaders are regarded as pests (Joshi & Sebastian, 2006). Most introduced *Pomacea* were initially identified as *P. canaliculata* (Lamarck, 1822), but Rawlings *et al.* (2007) and Hayes *et al.* (2008) have recently demonstrated that many—though not all—of these populations are referable to morphologically similar *P. insularum* (d'Orbigny, 1839), sometimes referred to as the island apple snail. Rawlings *et al.* (2007) further argued that, by inference, the ecological impacts of these two biological invaders should be considered comparable.

Florida, USA, contains native *Pomacea paludosa* (Say, 1829) (Thompson, 2000) and at least three nonindigenous congeners: *P. diffusa* Blume, 1957, *P. haustum* (Reeve, 1856) and *P. insularum* (d'Orbigny, 1835) (Rawlings *et al.*, 2007). The most widespread of these invaders in Florida has been identified as the channelled apple snail, *P. canaliculata*, or part of the *P. canaliculata* species complex (Thompson, 1997; Howells *et al.*, 2006), but recent genetic analysis indicates that most of these populations are referable to *P. insularum* (Rawlings *et al.*, 2007). It is unclear when this species arrived in Florida; the earliest occurrence of *P. insularum* that has been taxonomically confirmed by genetic analysis was collected in 2002 (Rawlings *et al.*, 2007), but snails closely resembling this species morphologically have been common in the state since at least 1987 (Thompson, 1997). (In a post-editorial addendum, Rawlings *et al.* [2007] noted that a sample from northeast Florida was genotyped as *P. canaliculata*.)

In addition to their potential to harm agriculture, nonindigenous apple snails also pose significant risks to natural wetland ecosystems (Carlsson, Brönmark & Hansson, 2004; Carlsson & Lacoursière, 2005; Carlsson, 2006). In some invaded wetlands, *Pomacea* (*P. canaliculata* and/or *P. insularum* as per Rawlings *et al.*, 2007) have been associated with a shift from macrophyte-dominated communities to phytoplankton-dominated communities (Carlsson *et al.*, 2004). Modification of wetlands by invasive species may result in loss of biodiversity and ecosystem services (Costanza *et al.*, 1997). If the global ecological impacts attributed to *P. canaliculata* are, in fact, at least partly caused by *P. insularum*, as argued by Rawlings *et al.* (2007), the latter species has the potential to have a large impact on invaded ecosystems in Florida.

The ecosystem impacts of *P. insularum* in Florida have not been resolved (Rawlings *et al.*, 2007; Gettys *et al.*, 2008) and it is also unclear whether this snail may serve as a biocontrol agent for regionally invasive aquatic plants such as *Hydrilla verticillata* (Ajith Kumara, Chandrasekara & Costa, 1999). Previous studies of feeding by *P. insularum* and *P. canaliculata* (reviewed by Howells *et al.*, 2006) suggest that these species eat a wide range of submerged and emergent plants; the only species that appears to be avoided is *Elodea canadensis*; it is unclear, however, owing to taxonomic uncertainties (Rawlings *et al.*, 2007), whether the snails tested for this particular plant were *P. canaliculata* or *P. insularum*. Gettys *et al.* (2008), using non-naïve *P. insularum*, found a preference for *H. verticillata*, *Najas guadalupensis*, and a freshwater alga *Chara*, while *Myriophyllum aquaticum* was consumed only when no other food was available and *Egeria densa* was not consumed at all. An absolute selectivity (yes/no) study by Howells (2002), also using non-naïve *P. insularum* (Howells *et al.*, 2006; Rawlings *et al.*, 2007), found that no macrophyte species was rejected, although neither *E. densa* nor *E. canadensis* was tested.

The above studies were primarily qualitative, but an assessment of the potential impacts of *P. insularum* requires evaluation of consumption rates as well as feeding preferences. The present study assesses the weight-specific feeding rates of *P. insularum* on 22 common aquatic macrophytes in Florida, including eight that are nonindigenous to the state. Inasmuch as the calculation of ash-free dry weights is time-consuming and laboratory-intensive, we also correlated *P. insularum* ash-free dry weights with shell dimensions so that the biomass of *P. insularum* populations can readily be estimated by other field researchers.

## MATERIAL AND METHODS

### *Naïve Pomacea insularum*

Prior exposure to food items can alter the feeding behaviour of herbivorous gastropods (Grantham, Moorhead & Willig, 1993; Kemenes & Benjamin, 1994) so we established a naïve stock of *P. insularum*. *Pomacea insularum* egg clusters were collected from the Withlacoochee River, Florida (28°43.37'N, 82°14.54'W) in October 2006. Eggs and hatchlings were cultured, for the purpose of biological containment, at the University of Florida Whitney Laboratory for Marine Bioscience, St Augustine, Florida. Eggs hatched within 2 weeks and hatchlings were fed terrestrial plants: organically grown lettuce (*Lactuca sativa* variants) and mustard cultivars (*Brassica oleracea* variants). All feeding trials were conducted with single randomly selected snails of 15–30 mm shell length. Neither Estebenet (1995) nor Carlsson & Brönmark (2006) found evidence of an ontogenetic shift in diet in the closely related *P. canaliculata*, so snail size was not included as a factor in feeding response (although size was used when estimating feeding rates). All feeding trials were conducted in the spring to minimize the effects of seasonality (plant maturation) on herbivory response, which have been

reported for other gastropods (Elger, Barrat-Segretain & Willby, 2006).

### *Plant species*

Aquatic plants were collected from the following Florida sources (Table 1), which have never been reported to contain *P. insularum* or *P. canaliculata* and which have had minimal exposure to herbicides and pesticides: research ponds at the University of Florida (29°43.57'N, 82°24.91'W); cultured stocks maintained by the University of Florida Department of Agronomy, Santa Fe River near High Springs (29°51.10'N, 82°36.68'W); and Lake Meta (29°40.14'N, 82°20.15'W). The Santa Fe River site is right below the springs that produce the majority of its flow. None of the other sources had been exposed to herbicides or pesticides in at least the past 12 months. Plants were identified using Smith (1967), Tarver *et al.* (1979) and Baye (2007).

### *Feeding trials*

Macrophytes were cleaned of soil, debris and other species, and dead foliage was removed. The plants that were used were standardized by morphology and weight, and each had a similar amount of handling (typically, one cut stem). Presentation standards for plants are given in Table 1. Apical meristems or whole leaves were included for all taxa except *Typha latifolia*, whose leaves were too large for the experimental unit; for this species 40 cm of leaf, starting from the base (the region mostly likely to be accessible to a benthic gastropod), was used.

Plants were wet-weighed before and after feeding trials. Water droplets were removed from the plant surface by centrifugation in a salad spinner. Each specimen was wetted, spun quickly for 10 rotations and weighed. This was repeated and, if

**Table 1.** Summary of aquatic plants used in feeding trials.

Plant taxon	Common name	Source	Presentation
<i>Alternanthera philoxeroides</i> *	Alligator weed	UF ponds	Leaves, roots, AM
<i>Ceratophyllum demersum</i>	Coontail	Santa Fe R.	Stem, AM
<i>Chara</i> sp.	Musk grass	UF culture	Thallus, apex
<i>Colocasia esculenta</i> *	Taro, elephant ear	UF ponds	Leaf, petiole
<i>Egeria densa</i> *	Common waterweed	UF culture	Stem, AM
<i>Eichhornia crassipes</i> *	Water hyacinth	Santa Fe R.	Leaf, petiole
<i>Hydrilla verticillata</i> *	Hydrilla	UF ponds	Stem, AM
<i>Hydrocotyle umbellata</i>	Water pennywort	UF ponds	Leaves, roots, AM
<i>Limnobium spongia</i>	Frog's bit	UF ponds	Immature plant
<i>Myriophyllum aquaticum</i> *	Parrot feather	UF ponds	Stem, AM
<i>Myriophyllum heterophyllum</i>	Variable-leaf milfoil	UF culture	Stem, AM
<i>Najas guadalupensis</i>	Southern naiad	UF ponds	Stem, AM
<i>Nymphaea odorata</i>	Fragrant water lily	Lake Meta	Leaf, petiole
<i>Panicum repens</i> *	Torpedo grass	UF ponds	Whole leaf blade
<i>Pistia stratiotes</i> *	Water lettuce	UF ponds	Immature plant
<i>Pontederia lanceolata</i>	Pickereel weed	UF ponds	Leaf, petiole
<i>Potamogeton illinoiensis</i>	Curly-leaf pondweed	UF culture	Intact stem
<i>Sagittaria kurziana</i>	Strap-leaf sagittaria	Santa Fe R.	Whole leaf blade
<i>Sagittaria lancifolia</i>	Duck potato	UF ponds	Leaf, petiole
<i>Sagittaria latifolia</i>	Wapato	Santa Fe R.	Leaf, petiole
<i>Typha latifolia</i>	Cattail	UF ponds	Base of leaf blade
<i>Vallisneria spiralis</i>	Tape grass	UF culture	Whole leaf blade

AM, apical meristem; UF, University of Florida; see text for additional details and explanations of the sources.

\*Nonindigenous to Florida

the second measurement was not within 0.01 g of the first, the plant material was spun a third time, and the mean used. The only plant species which was not centrifuged was *T. latifolia*, for which blotting with a paper towel was less damaging.

Plant species that are naturally submersed were fully immersed in the trials. Floating plants were allowed to float in trials, but the action of the air stone (below) kept the plant pressed against one end of the tank, where it could be reached by snails. Emergent plants were placed so that the base was touching the bottom of the tank while the apex was emergent; if the plant tended to float it was wedged into the tank sideways and held in place with the lid.

*Pomacea insularum* were transferred to Gainesville from the Whitney Laboratory culture site and starved for 48 h prior to a feeding trial. An *a priori* power analysis (Zar, 1996) using preliminary results from *Hydrilla verticillatum* with 20 replicates indicated that meaningful results would be obtained with five replicates. In fact 10 replicates were usually used, with an equal number of controls. Feeding trials were conducted in plastic aquaria with snap-lock lids and a hole just large enough to permit a hose for an air stone. Each aquarium contained 10 cm (c. 4 l) of pond water (pH 7.1), filtered through a 25- $\mu$ m mesh. Water from the University of Florida ponds (above) was introduced to the test snails during the starvation period; culture water was diluted 50% with pond water upon arrival at the laboratory and completely replaced with pond water at 24 h.

Feeding trial and control aquaria were placed on a rack in random order with a 12-h day–night light cycle. Temperatures were maintained at 21–22°C. Wet weight of each plant (as above), maximum shell length of each snail and the time the snail entered the aquarium were recorded for each replicate. After c. 24 h, the snails were removed and the precise duration of each feeding trial was noted and converted to a digital day (e.g. 24 h and 36 min = 1.025 day). Remaining aquatic plants were again centrifuged and wet-weighted.

Aquatic plants and snails were examined at the end of feeding trials. Plants were surveyed for apparent feeding damage, which was recorded as +/– for each specimen. The location of *P. insularum* specimens relative to floating plants was noted. In the event that *P. insularum* stopped moving during a feeding trial, the specimen was relocated to a fresh container of water at the end of the trial to observe recovery.

Snails were dissected by severing the columellar muscle using a recurved scalpel (blade no. 12), allowing the tissues to be removed intact. The operculum was removed. Snail tissues and plant tissues were dried at 80°C for 24 h and weighed to the nearest 0.001 g. Tissues were combusted at 500°C for 1 h and re-weighed. Ash-free dry weight was calculated by subtraction of the inorganic ash weight from the dry weight.

### Statistical analyses

The palatability of aquatic plant species was assessed by comparing net changes in weight of plants in test and control treatments. Two-sample *t*-tests (Zar, 1996) were used to test for effects of snail presence on mean net change in wet plant weight. If the null hypothesis of no difference between snail treatments and controls was not rejected at  $\alpha = 0.05$ , a paired-sample *t*-test (Zar, 1996) was used to test the null hypothesis that the control plants did not change weight during the course of the feeding trial. If this null hypothesis was not rejected at  $\alpha = 0.05$ , a one-tailed *t*-test (Zar, 1996) was used to test the hypothesis that the mean net change in plant weight in snail treatments was greater than zero. If the two-sample *t*-test for effects of snail presence on change in wet plant weight was not rejected, the test was repeated using change in plant ash-free dry weight (AFDW). In these tests, beginning AFDW

(AFDW<sub>1</sub>) was estimated from beginning wet weight (WW<sub>1</sub>) using end AFDW (AFDW<sub>2</sub>) as a proportion of end wet weight (WW<sub>2</sub>), as follows:  $AFDW_1 = (AFDW_2 / WW_2) \cdot WW_1$ . The use of AFDW and estimated beginning AFDW reduced variation that might be caused by water absorption or loss by damaged plants during the trial.

Feeding rates were calculated as the mass of plant consumed per unit mass of snail tissue over 24 h, expressed in units of ash-free dry weight. A paired-sample *t*-test (Zar, 1996) was used to determine whether control plants gained or lost mass during the feeding trial. The mean percent change was calculated and applied as a correction factor to the wet weights of plants in the snail treatments. Regression analysis (Zar, 1996) was used to examine the relationship between snail feeding rate and plant organic matter content (ash-free dry weight of plants expressed as a proportion of wet weight).

### Snail length-weight model

We developed a mathematical model of shell dimension versus ash-free dry weight that can be used by field researchers and resource managers who need to estimate weight-specific feeding rates without repeating ash-free drying procedures. In addition to snails from the laboratory, adult *P. insularum* from Nelson Lake and Lake Ann (28°10.68'N, 82°35.15'W) were dissected, dried and combusted as above. Ash-free dry weight of tissues was regressed against shell length to produce a quantitative model that enables prediction of ash-free dry tissue weight.

## RESULTS

### Feeding rates

*Pomacea insularum* significantly consumed 14 of the 22 aquatic plant species (Table 2). Both emergent (six species) and submersed (eight) species were consumed as were both native (nine) and nonindigenous (five) plants. Feeding rate was not related to plant organic content, whether expressed as ash-free dry weight as a per cent of wet weight ( $P = 0.963$ ) or dry organic matter as a per cent of wet weight ( $P = 0.864$ ). When feeding trials for which no feeding was quantitatively detected were assigned a feeding rate of zero and added to the analysis, there was no significant change in the results.

Of the eight aquatic plants that were not significantly consumed, *Nymphaea odorata* and *Typha latifolia* had visible *P. insularum* damage on more than half of the specimens. The damage was too slight, however, statistically to detect a difference in plant weight. Damage was observed on fewer than half of the specimens of the remaining six species.

*Pomacea insularum* was observed crawling towards all of the floating plants (*Hydrocotyle umbellata*, *Limnobium spongia*, *Eichhornia crassipes*, *Pistia stratiotes*) during the trials. At the end of the *H. umbellata* trial, 7 of 10 replicate snails were present on the plant. In the trials of the other three floating plant species, all specimens either had *P. insularum* on them at the end of the trial or exhibited feeding damage.

When presented with *Sagittaria lancifolia*, *P. insularum* stopped crawling and most specimens retreated into their shells by the end of the trial. All snails returned to normal movement within 30 min of being relocated to a fresh container of pond water. No *P. insularum* mortality occurred during the feeding trials and snails did not stop crawling in the presence of any of the remaining plant taxa, including other *Sagittaria* species.

**Table 2.** Results of feeding trails, ranked by consumption rates and, if consumption rates could not be estimated (see text), the proportion of plants that showed apparent *Pomacea insularum* feeding damage (damaged plants).

Plant taxon	P value	Damaged plants	AFDW	Consumption rate
<i>Limnobium spongia</i>	0.00788	90% (9/10)	8.1% (0.9)	0.744 g/g/d (0.127) <i>9.92 g/g/d</i>
<i>Chara</i> sp.	0.00157	100% (6/6)	10.6% (0.5)	0.478 g/g/d (0.091) <i>4.38 g/g/d</i>
<i>Panicum repens</i>	0.000274*	100% (10/10)	21.9% (4.7)	0.369 g/g/d (0.236) <i>2.03 g/g/d</i>
<i>Hydrilla verticillata</i>	0.000484	100% (6/6)	15.4% (5.1)	0.292 g/g/d (0.097) <i>2.50 g/g/d</i>
<i>Sagittaria latifolia</i>	1.08 × 10 <sup>-5</sup> *	100% (10/10)	13.0% (1.6)	0.257 g/g/d (0.073) <i>2.16 g/g/d</i>
<i>Ceratophyllum demersum</i>	0.0105	100% (10/10)	3.8% (0.9)	0.254 g/g/d (0.198) <i>6.51 g/g/d</i>
<i>Najas guadalupensis</i>	0.00192	100% (10/10)	13.8% (3.4)	0.225 g/g/d (0.108) <i>1.96 g/g/d</i>
<i>Vallisneria americana</i>	5.16 × 10 <sup>-9</sup>	100% (12/12)	6.8% (1.2)	0.207 g/g/d (0.062) <i>2.83 g/g/d</i>
<i>Pontederia lanceolata</i>	0.00287	100% (10/10)	8.7% (0.8)	0.161 g/g/d (0.085) <i>2.40 g/g/d</i>
<i>Sagittaria kurziana</i>	0.000536	100% (10/10)	10.4% (1.6)	0.151 g/g/d (0.111) <i>1.73 g/g/d</i>
<i>Myriophyllum heterophyllum</i>	0.0378	100% (10/10)	18.1% (8.0)	0.114 g/g/d (0.074) <i>1.01 g/g/d</i>
<i>Egeria densa</i>	0.0102	80% (8/10)	10.7% (3.5)	0.049 g/g/d (0.047) <i>0.46 g/g/d</i>
<i>Alternanthera philoxeroides</i>	0.0248*	70% (7/10)	11.3% (1.9)	0.045 g/g/d (0.073) <i>0.26 g/g/d</i>
<i>Eichhornia crassipes</i>	0.0122	100% (10/10)	5.9% (1.3)	0.032 g/g/d (0.134) <i>0.45 g/g/d</i>
<i>Nymphaea odorata</i>	0.662	100% (10/10)	11.8% (1.5)	—
<i>Typha latifolia</i>	0.657	70% (7/10)	13.2% (1.8)	—
<i>Potamogeton illinoiensis</i>	0.126	30% (3/10)	9.8% (2.9)	—
<i>Myriophyllum aquaticum</i>	0.359	20% (2/10)	9.7% (1.6)	—
<i>Colocasia esculenta</i>	0.621	10% (1/10)	8.7% (1.1)	—
<i>Hydrocotyle umbellata</i>	0.154	0% (0/10)	8.1% (0.8)	—
<i>Pistia stratiotes</i>	0.209	0% (0/10)	6.2% (1.2)	—
<i>Sagittaria lancifolia</i>	0.442	0% (0/10)	8.7% (0.8)	—

For damaged plants, values in parentheses are the number of plants on which we observed apparent feeding damage out of the total number of replicates. AFDW is ash-free dry weight as a per cent of wet weight; standard deviations are in parentheses. Consumption rate is given as grams of plant material and ash-free dry weight consumed per gram of snail tissue (ash-free dry weight) per day; standard deviations are in parentheses (standard font) and as back-calculated wet weight values (italics).

\*Based on one-tailed t-test vs hypothesized mean of zero: see text.

*Snail length-weight model*

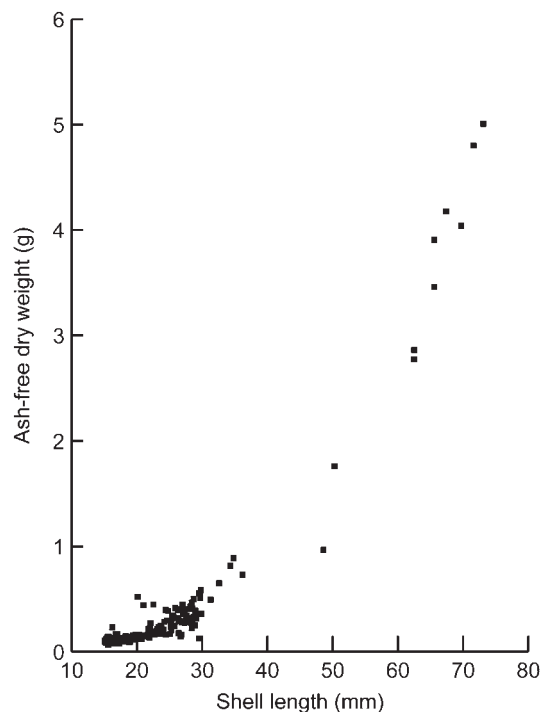
Two hundred and nine specimens of *P. insularum* ranging from 15 to 73 mm shell length were measured, dissected, dried and combusted. The relationship between ash-free dry weight (*y*) and shell length (*x*) was exponential (Fig. 1). Logarithmic transformation yielded a linear relationship:  $\ln y = 2.51 (\ln x) - 4.067$  ( $r^2 = 0.910$ ;  $P < 0.0005$ ).

DISCUSSION

This is the first study to have determined weight-specific feeding rates of *Pomacea* species. This approach was possible because we used cleaned plant fragments; rooted plants could not have been weighed accurately before and after trials. For some plants, however (*Nymphaea odorata*, *Typha latifolia*), even this approach was insufficient to detect the slight feeding damage caused by *P. insularum*; in these instances we were still able to detect qualitative feeding differences between this and other species, because we also recorded the incidence of feeding damage.

If we assume that feeding rate corresponds generally to palatability and preference, we can rank the 22 plant species in order of preference, based on dry weight (both dry and wet weight values are shown in Table 2). The most highly consumed species, *Limnobium spongia*, had relatively thick leaves and stems, while most of the other plants that were consumed to a significant degree had slender leaves or thalli. Organic content of the plants (ash-free dry weight as % of wet weight) had no effect on feeding rate of *P. insularum*.

A high consumption of the fourth-ranked species, *Hydrilla verticillatum*, was also reported by Ajith Kumara *et al.* (1999) for



**Figure 1.** The exponential relationship between ash-free dry weight (*y*) and shell length (*x*) of *Pomacea insularum*. Linear equation:  $\ln y = 2.51 (\ln x) - 4.067$  ( $r^2 = 0.910$ ;  $P < 0.0005$ ).



*P. canaliculata* in Sri Lanka. The effectiveness of *P. insularum* as a biological control for this nonindigenous species, which can attain above-sediment biomass of 1200 g/m<sup>2</sup> (Owens & Madsen, 1998) and an annual production of >1400 g/m<sup>2</sup>/year (Boston, Adams & Madsen, 1989), is countered by the snail's ability to consume native submerged species such as *Vallisneria americana* at comparable levels. Additionally, under optimal feeding conditions (a year-round feeding rate on *H. verticillatum* of 0.292 g/day/g of snail tissue, using ash-free dry weights as calculated in this study), it would require 13.1 g snails/m<sup>2</sup> (ash-free dry weight) to consume the above production for *H. verticillatum*. This quantity, 13.1 g snails/m<sup>2</sup>, is the equivalent of about 82 snails of 20 mm in shell length per square meter, or 14–15 snails 40 mm shell length in the same area (calculated from Fig. 1). Less than optimal feeding conditions or reduced feeding rates by larger snails would increase the density required. In Texas, the densities of snails now known to be *P. insularum* range from under 0.1 to 2.4/m<sup>2</sup> in streams and ponds (Howells *et al.*, 2006; Rawlings *et al.*, 2007), so this snail cannot be relied upon as a biological control agent for *H. verticillatum* except at unusually high densities.

Preferences of *P. insularum* for congeneric plant species were not always similar. For example, *Myriophyllum aquaticum* was not consumed, while *M. heterophyllum* was; the latter is a partial emergent, whereas the vegetative portions of *M. aquaticum* remain submerged. Li, Yu & Yan (2004) reported that another submersed member of the genus, *M. spicatum*, was not preferred by the aquatic pulmonate snail *Radix swinhoei*; those authors attributed the lack of preference to elevated tannin compounds in *M. spicatum*. *Myriophyllum heterophyllum* may reduce the ecological need for secondary compounds by placing a portion of its photosynthetic surface out of the water and, presumably, away from most aquatic grazers. Such a strategy, however, would provide little deterrence to *P. insularum*; even subadults are heavy enough to drag the entire plant under water. These results demonstrate that preference for a given plant species cannot be used to infer preference for congeners and, therefore, that each plant taxon of interest must be tested before inferences can be drawn regarding herbivory. The strong negative reaction by *P. insularum*—cessation of all movement—to *Sagittaria lancifolia* was unique in this study and also unexpected, given that two congeners were measurably consumed.

Invasive species of *Pomacea* apparently share some plant preferences, but not others. Lach *et al.* (2000) studied relative feeding preference and growth rates of *P. canaliculata* in Hawai'i and we tested some of the same macrophytes in the present study. They reported that *P. canaliculata* does not prefer the floating nonindigenous macrophytes *Eichhornia crassipes* or *Pistia stratiotes*, but grows slightly on a diet of the latter and not on the former. In our study (using *P. insularum*) neither *E. crassipes* nor *P. stratiotes* were among the most consumed species (and, by inference, were less preferred), but *E. crassipes* was consumed to a detectable degree while *P. stratiotes* was not—a modest reversal of the results of Lach *et al.* (2000). *Pontederia cordata*, a native congeneric of *E. crassipes*, was also consumed by *P. insularum* in our study. Based on these results, the potential for *P. insularum* to serve as a biological control agent for *E. crassipes* is offset by its ability to consume native *P. cordata*.

The results presented here were obtained using naïve consumers, which avoids the plastic pre-adaptation to a particular prey that has been shown for some other freshwater herbivorous gastropods (Grantham *et al.*, 1993; Kemenes & Benjamin, 1994). This does not preclude the possibility, however, that consumers like *P. insularum* will acclimate to species they would not consume otherwise. For example, *P. insularum* did not favor *Colocasia esculenta* (taro) in this study, whereas *P. canaliculata* is a pest on taro crops in Hawai'i (Howells *et al.*, 2006). The

apparent difference in preference for taro could be specific to the two snail species. Alternatively, *P. canaliculata* in Hawai'i may have learned to consume taro following exposure to artificial monocultures of the crop species.

Our data, together with field estimates of *P. insularum* density and shell length, may assist field researchers in estimating consumption of aquatic plants. Using shell length alone (Fig. 1), a field researcher could use the results presented here to estimate biomass of *P. insularum* for a given snail density, multiply it by weight-specific feeding rates (Table 2), and estimate biomass consumption by *P. insularum* on select species of native and nonindigenous aquatic plants. This method may result in an over-estimate of feeding rates at very high *P. insularum* densities. Two studies report inversely density-dependent feeding by freshwater herbivorous gastropods; if snail density is increased to the point at which snails frequently encounter each other, beyond this they appear to spend more time interacting with each other and less time feeding (Haniffa, 1980; Brown, Carman & Inchausti, 1994). To date, however, densities of *P. insularum* reported in streams and ponds in North America have mostly been in the range of 0.01–2.4/m<sup>2</sup> (Howells *et al.*, 2006), at which incidental encounter rates and hence interactions are presumed to be low.

#### Methodological considerations

Snails >15 mm in shell height were adequate to obtain a measurable feeding response; by using subadult snails (based on estimates of size-at-maturity by Kaneshima, Yamauchi & Higa, 1986) we may have avoided potential problems with the more complex physiology or behaviour of sexually mature adults; other researchers have observed that adult *P. insularum* exhibited highly variable within-trial responses to plant presentations (L. Burlakova and A. Karatayev, personal communication).

A low-speed centrifuge (salad spinner) generally worked well for removing water from plants before and after trials, but some taxa, such as *Chara* sp., often fragmented during centrifugation. The hollow, air-filled petioles of *E. crassipes* presented a challenge to obtaining precise measurements at the end of trials, but not at the beginning; *P. insularum* ate holes through the petiole that let water into the interior and this water did not always spin out efficiently in the centrifuge.

#### Conclusion

In conclusion, subadult *P. insularum* showed a strong feeding response, both in terms of quantity of plants consumed, and in the proportion of the snails that fed. Moreover, there was a wide range in feeding response between plant species, allowing us to make inferences regarding relative preferences. Some native and nonindigenous species were consumed readily, but other nonindigenous species were consumed at a relatively low rate or not at all. The impact of *P. insularum* on monocultures of these species will depend, in part, on growing conditions and productivity of the plants. However, our results show that in 'natural' ecosystems, with both native and nonindigenous plants, *P. insularum* cannot be relied upon as an agent for biological control of nonindigenous species and may heavily impact native aquatic plant species.

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