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RESEARCH ARTICLE

Wetland Restoration and Invasive Species: Apple snail (*Pomacea insularum*) Feeding on Native and Invasive Aquatic Plants

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Abstract

The apple snail *Pomacea insularum* is an aquatic invasive gastropod native to South America that has the potential to cause harm to aquatic ecosystems, wetland restoration, and agriculture. To predict the potential impact of this snail on aquatic ecosystems, we tested the feeding rate of *P. insularum*, under laboratory nonchoice experiments, for 3 species of invasive macrophytes and 13 species of native aquatic plants that are important for wetland restoration and health. High levels of consumption were recorded for four native species (*Ceratophyllum demersum*, *Hymenocallis liriosme*, *Ruppia maritima*, and *Sagittaria lancifolia*) and three invasive species (*Colocasia esculenta*, *Alternanthera philoxeroides*, and *Eichhornia crassipes*). In contrast, less than 10% of the biomass of *Spartina alterniflora*, *Scirpus californicus*, *Thalia dealbata*, and *Typha latifolia* was consumed by *P. insularum* over the test period. The palatability of macrophytes was negatively correlated with dry matter content, making our results generalizable to all regions where this invader may be present. Based on our results, wetland restoration in areas invaded by *P. insularum* should focus on emergent structural species with low palatability. Apple snails should not be considered as agents of biocontrol for invasive plants; although apple snails fed on invasive plants at a high rate, their consumption of many native species was even greater.

Key words: channeled-type apple snail, feeding, invasive, macrophytes, *Pomacea insularum*, restoration, wetlands.

Introduction

Wetlands are among the world's most productive environments and provide tremendous ecological services and economic benefits. They support great biological diversity and provide water purification and groundwater recharge; flood, storm, and hurricane control and protection; retention of pollutants; erosion control; sources of nutrients for aquatic food webs; energy resources; recreation; and tourism opportunities (Mitsch & Gosselink 1993; Barbier et al. 1996). Of the estimated $33 trillion worth of world ecosystems services produced annually, $4.9 trillion is attributed to wetlands (Costanza et al. 1997). These values can only be maintained if the ecological processes of wetlands are allowed to continue functioning. However, wetlands continue to be among the world's most threatened ecosystems (Barbier et al. 1996; Zedler & Kercher 2005). One of the greatest threats to habitat loss in wetland communities is the spread of invasive species (reviewed in Zedler & Kercher 2005; Lacoul & Freedman 2006).

Aquatic plants are the most important components of wetland structure. Thus, herbivores in these systems can have profound impacts on community and ecosystem structure (Sheldon 1987; Lodge 1991; Lodge et al. 1998; Van Donk 1998; Carlsson et al. 2004). Channeled-type apple snails (genus *Pomacea*) are important invaders and agricultural pests of rice and taro in Thailand, Vietnam, parts of Malaysia and Indonesia, China, Taiwan, Japan, Dominican Republic, Hawaii, and in the Philippines (reviewed in Cowie 2002) and are responsible for large economic losses (reviewed in Ranamukhaarachchi & Wickramasinghe 2006). They have fast growth rates (can reach maturity in about 2 months during the summer) and have a large reproductive potential (reviewed in Cowie 2002), facilitating their invasion success.

Because of the massive agricultural damage to crops in Indo-Pacific regions and Hawaii, the U.S. Department of Agriculture prepared a risk analysis of *Pomacea* (Smith & Fowler 2005) and has moved to legally prohibit from interstate movement and transportation of all non-native aquatic snails in the family Ampullariidae (except for

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Pomacea bridgesi [*P. diffusa*; Rawlings et al. 2007], the spiketop apple snail, which consumes microalgae). Because of the potential for environmental damage, Texas Parks and Wildlife Department added Channeled apple snail (*P. canaliculata*) in April 2001 and later all genera and species of the family Ampullariidae including *Pomacea* and *Marisa* (except spiketop apple snail) to its list of legally prohibited harmful and potentially harmful exotic shellfishes. Although nearly all introductions of apple snails in the United States were initially thought to be *P. canaliculata*, recent genetic analyses have shown that introduced snails in Texas are *P. insularum* (Ampullariidae) (Rawlings et al. 2007). Three additional channeled-type apple snail species have been introduced into the southern United States: *P. canaliculata*, *P. diffusa* (identified previously as *P. bridgesi*), and Titan apple snail (*P. haustrum*) (Rawlings et al. 2007). The first confirmed breeding population of *Pomacea* in Texas was found in 1989 (Neck & Schultz 1992), and presently, they are in seven southeastern counties (authors personal data).

Pomacea canaliculata has been demonstrated to consume a variety of aquatic plants in both laboratory and field experiments (Adalla & Morallo-Rejesus 1989; Mochida 1991; Halwart 1994; Estebenet 1995; Lach et al. 2000; Carlsson et al. 2004; Carlsson & Lacoursière 2005). However, much less information exists about the feeding of *P. insularum* and even less is known about plant traits that determine feeding rate, especially whether these snails consume native species or non-natives that are presently spreading in wetlands.

To predict the potential impact of *P. insularum* on aquatic ecosystems, we quantified the feeding rate of this snail under nonchoice experiments for 3 species of invasive macrophytes and 13 species of native aquatic plants that are important for wetland restoration and health. We assessed whether consumption varied with general plant characteristics, especially dry matter content (DMC) and growth habit, which could be used to predict the vulnerability of other aquatic plants important for wetland restoration in other parts of the world invaded by apple snails.

Methods

Snail Size and Consumption

The feeding rates of snails of different sizes were tested to determine if consumption rate depended on the size of snails or was constant on a biomass-specific basis. This information was important for the design of our experimental feeding trials and informative for determining the size of snails that pose the greatest ecological threat to native plant communities. Five size groupings of snails (three snails per group) were tested: 32.0 ± 3.4, 40.7 ± 2.1, 50.1 ± 1.5, 59.3 ± 2.6, and 71.1 ± 1.5 mm.

We used the same experimental chambers and test procedures as for the consumption trials described below, with three replicates of each size group, and Lettuce as the sole test food. The experiment lasted 24 hours. Based on the results of these tests, similar-sized snails were used in all consumption experiments.

Consumption of Invasive Plant Species

Pomacea insularum consumption rates for three species of aquatic plants known to be invasive in North America and elsewhere (Elephant ear [*Colocasia esculenta*], Alligator weed [*Alternanthera philoxeroides*], and Water hyacinth [*Eichhornia crassipes*]) were measured in nonchoice feeding experiments in November of 2004. The plants were collected from southeastern Texas, in Chambers County Golf Course ponds (lat 29°49′N, long 94°38′W), Armand Bayou Nature Center (Pasadena, Harris County, lat 29°35′N, long 95°04′W), and in Lone Star Canal (Chambers County, lat 29°47′N, long 94°38′W). *Pomacea insularum* were collected from ponds at the Chambers County Golf Course. Snails were held under laboratory conditions and fed a diet of Lettuce (*Lactuca sativa*), a known preferred food of *P. insularum* (our data) and *P. canaliculata* (Estebenet & Cazzaniga 1992; Estebenet & Martín 2002), for 20 days before being used in feeding experiments.

This experiment was conducted in a greenhouse under natural light. Four replicate test (with snails) and four control (without snails) plastic chambers (33 × 24 × 15 cm) filled with 8 L of conditioned tap water (a mixture of fresh tap water, held for 24 hours to dechlorinate, and water from aquaria used to hold snails) were used for each of these three test plant species. Each chamber was aerated using Sweetwater regenerative blowers and air diffusers from a Sweetwater Linear Piston Air Pump for 24 hours before and throughout the experiment. Three snails with an average shell height (distance from the apex to the aperture along the axis of coiling) of approximately 45 mm (total wet mass for all three snails approximately 65 g) were randomly chosen from a laboratory population, placed in test chambers, and allowed to acclimate for 24 hours with no food before the beginning of the experiment. Approximately 20 ± 0.1 g (blotted wet weight) of plant material was randomly added to each replicate of test and control chambers. After 96 hours, we measured the total blotted wet mass of plant tissue remaining in each replicate. Water temperature, pH, conductivity, and oxygen saturation were recorded daily in each chamber using a Hanna HI 991300 (HANNA Instruments, Woonsocket, RI, U.S.A). During the feeding trials, the average water temperature was 25.9 ± 0.1°C (average ± SE here and elsewhere), the oxygen saturation was 92.8 ± 0.2%, and the average conductivity and pH were 222 ± 1 μS and 7.8 ± 0.01, respectively.

Consumption of Native Plant Species

Two species of submersed macrophytes, Coontail (*Ceratophyllum demersum*) and Widgeongrass (*Ruppia maritima*), and 11 species of emergent macrophytes, Maraca

amarilla (*Canna glauca*), Spiderlily (*Hymenocallis liriosme*), Maidencane (*Panicum hemitomon*), Pickerelweed (*Pontederia cordata*), Grass-leaf arrowhead (*Sagittaria graminea*), Bulltongue arrowhead (*S. lancifolia*), California bulrush (*Scirpus* (*Schoenoplectus*) *californicus*), Cosmopolitan bulrush (*Sc. maritimus*), Smooth cordgrass (*Spartina alterniflora*), Powdered thalia (*Thalia dealbata*), and Common cattail (*Typha latifolia*), were obtained during the summer 2006 from Armand Bayou Nature Center and the Texas-Genco EcoCenter wetland nursery (Baytown, TX, lat 29°44′N, long 94°58′W).

In this experiment, due to limited space available in the greenhouse, we used aquaria filled with 34 L of dechlorinated water and separated in half by 12.5-mm vinyl mesh (nontoxic to aquatic invertebrates; D. P. Molloy 2005, New York State Museum, Cambridge, NY, personal communication) such that the control for each replicate was under the same conditions as the tested plant. We used five paired replicates (test and control) for each species tested. Due to limited space and material, we were able to test only two species of aquatic plants during each trial. However, each species was tested in two separate independent trials (except for *R. maritima*, *S. graminea*, and *Ty. latifolia*, which were tested only once due to lack of availability). Because the same species were tested in different trials (days), to ensure that snails would feed normally under the experimental conditions, we used a feeding control in all trials: in addition to the two species tested in each trial, we had five replicates with snails that fed Lettuce. This feeding control allowed us to compare the consumption of species tested in different trials (days) by adjusting the consumption of plants relative to the consumption of Lettuce in each trial (see Data Analysis below).

Trials were run from July through September of 2005. Aquaria were kept in an air-conditioned room with the temperature typically around 25°C throughout the experiment. A fiberglass filter circulated and aerated the water in each aquarium. Five snails with an average shell height of approximately 45 mm were randomly chosen from the same laboratory population, placed in test aquaria and allowed to acclimate for 3 days, and were fed Lettuce. At least 24 hours before the beginning of each experiment, all food was removed. At the beginning of each experiment, approximately 25 ± 0.1 g (blotted wet weight of leaves and stems) of plant material was randomly added to the test (with snails) and control (without snails) portions of each aquarium. To ensure that snails had equal access to plant material, all plants tested (emergent and submersed) were cut to equal-sized pieces (approximately 7–10 cm long) and floated on the surface of the water. After 48 hours, we measured the total blotted wet mass of plant tissue remaining in each test and control replicate. The average water temperature in all aquaria was 25.7 ± 0.06°C, the pH was 7.40 ± 0.02, and the conductivity was 203 ± 2 μS.

DMC of each test plant species was calculated as the ratio between their fresh and dry mass. For each species, a minimum of eight replicates of 4–5 g of fresh plant fragments were dried for at least 48 hours at 60°C and then reweighed. Due to limited material, we were unable to measure DMC for the invasive plant species; therefore, we used literature data for these species.

Data Analysis

Due to absorption of water by plants, the amount of plant consumed was calculated with the following equation: $[T_0 \times (C_F/C_0) - T_F]$, where T_0 and T_F were the mass of the plants exposed to snails at the beginning and end of the experiment and C_0 and C_F were the mass of the plants from the paired control chamber at the beginning and end. Because the tests and controls were not paired for the experiments with invasive plants, we used the average of the controls.

To test whether snails consumed a significant amount of plant tissue in the unpaired experiments with invasive plants, we used a two-way model I (fixed-effects) analysis of variance (ANOVA) on the log-transformed difference between the mass of the plants at the beginning and end of the experiment. We tested if snails consumed significant amounts of plant tissue compared to controls and if the consumption among plant species was different. To analyze the consumption of native plant species (all species except *R. maritima*, *S. graminea*, and *Ty. latifolia*, which were tested only once due to lack of availability), we standardized the amount of test plant consumed relative to the feeding control (Lettuce) for each test day: $[(T \times 100\%)/(T_L)]$, where T was the amount of test plant consumed and T_L was the amount of Lettuce consumed. These data were then arcsine transformed and tested if there was a difference in consumption between two replicate trials, with a one-way model II (random effects) ANOVA. Because we found no significant difference between test days ($p = 0.96$, one-way ANOVA), we used these data to test for differences in consumption among species with a one-way model I (fixed-effects) ANOVA.

To determine if there was a relationship between the amount of plant consumed by *P. insularum* and plant DMC, we used a linear regression of the log-transformed amount of plant consumed per gram of *P. insularum* per day and DMC. For all statistical tests, we used the software STATISTICA (version 6; StatSoft, Inc., Tulsa, OK, U.S.A. 2001). Because of recent taxonomic revisions and confusion with common names, we used the Latin and common names of molluscs and plants as found in the Integrated Taxonomic Information System online database (http://www.itis.gov).

Results

Size-Related Consumption

Feeding rate, calculated as the amount of plant consumed per snail wet mass, was significantly different among size groups ($F = 38.7$, $p < 0.001$, ANOVA). There was

a significant negative correlation between snail consumption rate and snail size ($r = -0.73$, $p = 0.002$; Fig. 1). As snail size increased, size-specific consumption rate decreased.

Consumption of Invasive Plant Species

Snails consumed a significant amount of test plant tissue for all invaders ($F = 112.9$, $p << 0.001$, two-way ANOVA), and we did not detect a difference in consumption among replicates for each plant species ($F = 0.17$, $p = 0.84$). There was no significant interaction effect between factors ($F = 2.4$, $p = 0.12$). *Pomacea insularum* consumed from 48 to 76% of available tissue of invasive plants in 96 hours (Table 1).

Consumption of Native Plant Species

The amount of plant tissue consumed by *P. insularum* was different among the tested native macrophyte species (Table 1). Maximum consumption (98.6%) was found for the feeding control, Lettuce (Table 1). Four species of native macrophytes were consumed from 55 to 96%, including submersed *Ceratophyllum demersum* and *Ruppia maritima* and emergent *Hymenocallis liriosme* and *Sagittaria lancifolia*. Five native species (*Canna glauca*, *Panicum hemitomon*, *Pontederia cordata*, *S. graminea*, and *Scirpus maritimus*) were moderately consumed (up to 34%) and less than 10% of *Sc. californicus*, *Spartina alterniflora*, *Thalia dealbata*, and *Typha latifolia* tissue was consumed by snails (Table 1).

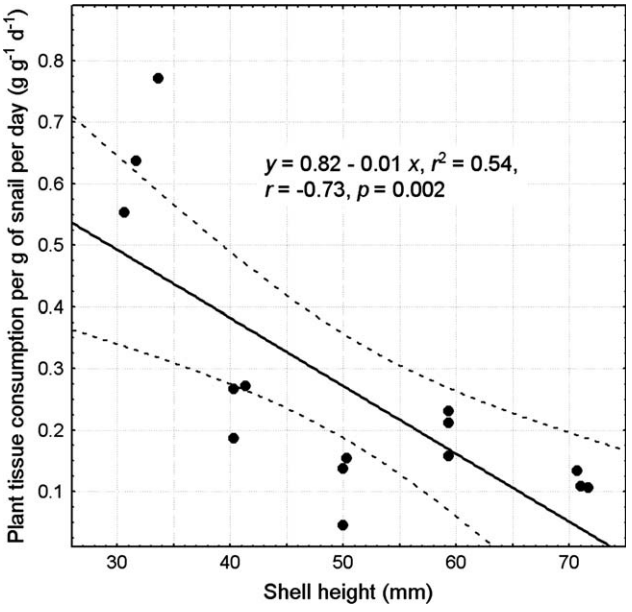


Figure 1. The association between consumption rate of *Lactuca sativa* (gram of plant tissue consumed per gram of snail [both wet weight] per day) for *Pomacea insularum* of different shell height (distance from the apex to the aperture along the axis of coiling).

Pomacea insularum consumption was significantly different among species (plant species: $F = 20.7$, $p < 0.0001$). For species that were tested twice, there was no difference between replicate trials ($F = 0.003$, $p = 0.96$). Consumption of the four most palatable species was not different (*C. demersum*, *H. liriosme*, *R. maritima*, and *S. lancifolia*; $0.68 < p < 0.99$) but was significantly greater than for all other plants ($0.0002 < p < 0.008$, Tukey test; Fig. 2).

We found a significant negative correlation between consumption by *P. insularum* and plant DMC (Fig. 3). This relationship was described by a linear regression: $y = -5.70–1.17x$ ($r = -0.69$, $p = 0.0001$), where y was the amount of plant consumed per gram of snail per day (log transformed) and x was the DMC of the plant (log transformed). Therefore, DMC explained 48% of the variation in snail consumption among different plant species.

Discussion

The rapid loss of wetlands in many parts of the United States and elsewhere in the world has received much attention in recent decades, inspiring various agencies to develop prevention and/or mitigation techniques to offset such losses (Mitsch & Gosselink 1993). One of the greatest threats to wetland communities is the spread of invasive species (Zedler & Kercher 2005; Lacoul & Freedman 2006). Aquatic plants stabilize and are the dominant primary producers in wetland ecosystems. They create diverse and structurally complex habitats, offer refuge and resources for macroinvertebrates and larval fish, and play a key role in nutrient cycling (Mitsch & Gosselink 1993; Barbier et al. 1996). Herbivory by invasive gastropods can influence the structure and abundance of macrophyte communities and, as a result, affect fluxes of nutrients and energy in wetland ecosystems. Carlsson et al. (2004) experimentally demonstrated that invasion by *Pomacea canaliculata* in Asian wetland can dramatically reduce species richness and abundance of macrophytes. Thus, the system may shift from one of clear water and macrophyte dominance to one that is turbid and dominated by planktonic algae (Carlsson et al. 2004). In addition, invasive Channeled apple snails are important agricultural and wetland pests throughout tropical and subtropical regions around the world (reviewed in Joshi & Sebastian 2006). In our experiments, *P. insularum* consumed all the invasive plants tested. The high rate of consumption of the invader *Colocasia esculenta* was expected as a congener, *P. canaliculata*, is known to be a major pest of taro in the Hawaiian Islands (reviewed in Cowie 2002). *Pomacea insularum* consumed greater amounts of three native species than any of the invaders. The average consumption rate across all the native plant species tested ranged from 0 to 90% of initial tissue mass and was not different than that for the invasive plants.

The submersed macrophytes, *Ceratophyllum demersum* and *Ruppia maritima*, were consumed at a significantly

Table 1. Native and invasive plant consumption by *Pomacea insularum*.

Test Date	*Plant Species*	*Adjusted Total Consumption (g)*	*% Consumed*	*Adjusted % Consumed*	*Average Consumption per Gram Snail per Day*	*DMC*
2 May to 6 September 2005	*Lactuca sativa*	28.5 ± 0.6	98.6 ± 2.3		0.119 ± 0.004	0.073 ± 0.008
9 May 2005	*Hymenocallis liriosme*	25.8 ± 0.9	96.2 ± 1.6	88.7 ± 3.2	0.116 ± 0.005	0.053 ± 0.001
20 August 2005	*Ruppia maritima*	24.1 ± 1.3	93.4 ± 3.9	85.3 ± 4.7	0.096 ± 0.005	0.140 ± 0.009
23 May 2005	*Ceratophyllum demersum*	22.6 ± 0.7	95.4 ± 2.4	75.0 ± 2.4	0.100 ± 0.003	0.072 ± 0.010
16 May 2005	*C. demersum*	21.8 ± 1.1	86.3 ± 2.5	75.7 ± 3.8	0.095 ± 0.005	0.101 ± 0.010
7 November 2004	*Colocasia esculenta*	19.4 ± 3.6	75.9 ± 14.4		0.077 ± 0.011	0.121 + 0.023
2 May 2005	*H. liriosme*	19.1 ± 3.9	70.4 ± 14.6	62.1 ± 12.7	0.088 ± 0.018	0.058 ± 0.001
16 May 2005	*Sagittaria lancifolia*	16.9 ± 4.1	56.4 ± 13.8	58.8 ± 14.4	0.075 ± 0.018	0.101 ± 0.006
9 May 2005	*S. lancifolia*	16.8 ± 1.4	55.0 ± 5.2	57.6 ± 4.8	0.075 ± 0.007	0.095 ± 0.001
20 June 2005	*Panicum hemitomon*	14.5 ± 2.4	34.5 ± 5.0	51.8 ± 8.7	0.063 ± 0.011	0.316 ± 0.013
7 November 2004	*Eichhornia crassipes*	14.0 ± 2.7	57.7 ± 10.8		0.052 ± 0.007	0.084 + 0.011
2 May 2005	*S. graminea*	13.1 ± 3.5	42.4 ± 12.5	42.4 ± 11.5	0.060 ± 0.016	0.081 ± 0.001
27 June 2005	*Scirpus maritimus*	12.3 ± 2.9	29.0 ± 6.0	45.8 ± 10.7	0.052 ± 0.012	0.431 ± 0.045
7 November 2004	*Alternanthera philoxeroides*	11.3 ± 1.7	48.2 ± 7.4		0.043 ± 0.005	0.145
20 June 2005	*Canna glauca*	6.9 ± 1.2	23.4 ± 4.2	24.7 ± 4.1	0.029 ± 0.005	0.101 ± 0.016
1 August 2005	*Pa. hemitomon*	6.0 ± 1.6	18.8 ± 5.0	20.7 ± 5.5	0.023 ± 0.006	
27 June 2005	*Pontederia cordata*	6.0 ± 1.2	19.2 ± 4.7	22.2 ± 4.5	0.023 ± 0.006	0.152 ± 0.011
1 August 2005	*Ca. glauca*	5.8 ± 0.7	20.2 ± 2.2	19.9 ± 2.3	0.022 ± 0.003	0.127 ± 0.009
1 August 2005	*Po. cordata*	4.5 ± 1.8	13.5 ± 5.1	16.4 ± 6.7	0.016 ± 0.006	0.151 ± 0.003
23 May 2005	*Sc. californicus*	4.2 ± 2.1	10.1 ± 5.1	13.5 ± 6.8	0.019 ± 0.009	0.206 ± 0.016
6 September 2005	*Spartina alterniflora*	2.2 ± 0.3	7.5 ± 0.9	7.7 ± 0.9	0.009 ± 0.001	0.225 ± 0.008
1 August 2005	*Typha latifolia*	2.2 ± 1.3	6.1 ± 3.7	8.0 ± 4.6	0.008 ± 0.005	0.175 ± 0.005
30 August 2005	*Sp. alterniflora*	1.9 ± 1.0	6.0 ± 3.2	7.4 ± 3.7	0.008 ± 0.004	0.299 ± 0.012
14 June 2005	*Sc. maritimus*	1.7 ± 4.3	2.2 ± 8.1	5.5 ± 13.6	0.006 ± 0.019	0.507 ± 0.031
14 June 2005	*Sc. californicus*	1.1 ± 3.5	0.4 ± 7.7	3.8 ± 11.6	0.005 ± 0.015	0.388 ± 0.010
20 August 2005	*Thalia dealbata*	0.8 ± 1.0	2.4 ± 3.1	3.0 ± 3.7	0.003 ± 0.004	0.226 ± 0.016
30 August 2005	*T. dealbata*	0.0 ± 1.2	−0.3 ± 4.2	−0.1 ± 4.6	0.000 ± 0.005	0.275 ± 0.002

Tests were run over 48 hours for native species and 96 hours for invasive plants. Average (± SE, $n = 5$ for native and $n = 4$ for invasive) wet mass of plant consumed (adjusted for the loss of mass by control plants), percentage of plant consumed, percentage of plant consumed relative to the average consumption of Lettuce in the trial (adjusted % consumed, for native plants), average consumption per gram of snail per day (adjusted total consumption divided by the total snail wet weight and number of trial days), and DMC of the plant are given. DMC data for invasive plants are from published literature (*Co. esculenta* [average of reported values in Devendra & Göhl 1970; Ogle 2006; Oscarssona & Savage 2007], *A. philoxeroides* [Little 1979], and *E. crassipes* [Gunnarsson & Petersen 2007]). *Lactuca sativa* was used in each experiment with native plants as a feeding control to assess day-to-day differences in consumption. Space limitation prevented this same control for the tests involving invasive species.

higher rate than emergent plants. The tissues of submersed macrophytes contain small amounts of lignin and often have higher protein concentrations than emergent plants (Wetzel 1975). In the field, submersed flora may be more accessible to snails and thus more likely to suffer greater damage. Contrary to submersed plants, emergent macrophytes have heavy cell walls and very thick cuticles (Wetzel 1975). The emergent species that were consumed at moderate rate in our experiments, *Canna glauca*, *Hymenocallis liriosme*, *Panicum hemitomon*, *Sagittaria graminea*, and *S. lancifolia*, have broad, succulent leaves and stems allowing easy consumption. They also have a shorter stature than many thin, elongated emergents, which perhaps will allow easier consumption in the field.

We found that the DMC of plants explained almost a half of the variation in snail consumption among different plant species. Plants with a lower DMC were consumed at a much higher rate. Thus, our results can aid with the choice of aquatic plants for restoration in areas inhabited with *P. insularum*; species with a higher DMC will be less affected by this invader and so will be important for initial restoration efforts. Elger and Lemoine (2005) found a similar negative relationship between DMC and consumption of 11 macrophytes by another aquatic snail, *Lymnaea stagnalis*. DMC of plants is primarily affected by cell wall composition and mineral inclusions, and higher DMC may be associated with higher tissue toughness (Elger & Lemoine 2005). Elger and Lemoine (2005) also found that palatability was positively correlated with protein content and low phenolic content.

For three emergent macrophytes (*S. californicus*, *Thalia dealbata*, and *Typha latifolia*), consumption, though statistically significant, was slight and likely not biologically important. In Thailand, Cattail (*Typha* sp.) was found to be unpalatable to *P. canaliculata* (Carlsson et al. 2004). These plants are generally tall, with sturdy stems, thin nonsucculent leaves, and mineralized cell walls that could be difficult for many snails to penetrate with their radulae.

We found a significant negative correlation between snail size and consumption of the control plant Lettuce on

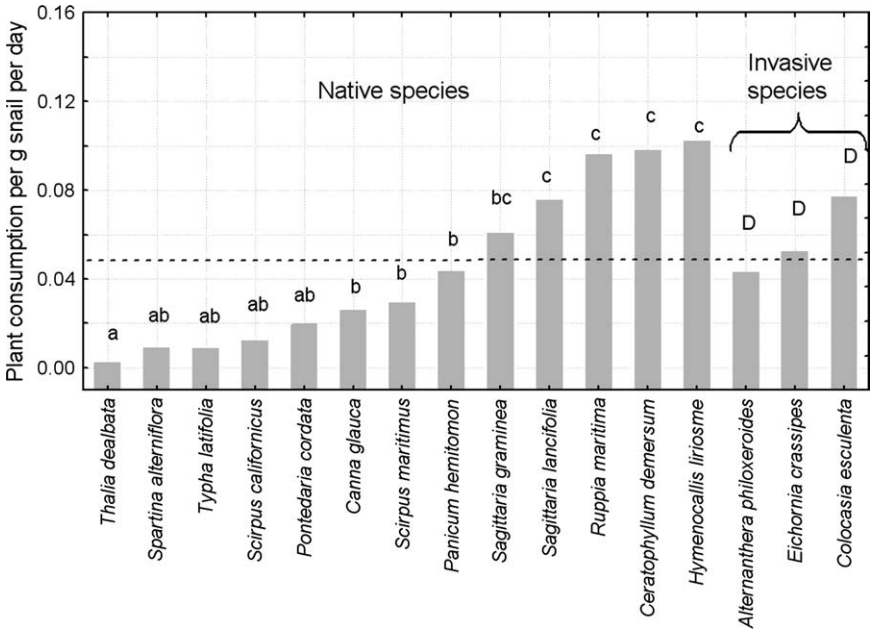


Figure 2. Consumption of native and invasive macrophytes (gram of plant tissue consumed per gram of snail per day, both wet weight) by *Pomacea insularum*. Average consumption ($0.045\ g{\cdot}g^{-1}{\cdot}day^{-1}$) is shown by the dotted line. Different letters above bars indicate significant differences; bars with similar letters were not different (Tukey test). Because of differences in test design, differences in snail consumption of the native (a, b, and c) and invasive species (D) could not be statistically directly compared.

a per mass basis, supporting other work that small snails can have a larger impact on plants. Joshi (2002) found that smaller (40 mm) *P. canaliculata* have the largest negative impact on rice. Because smaller sized *P. insularum* will consume macrophytes at a higher mass-specific rate than the larger snails, controlling the younger life stages is most important for protecting aquatic vegetation from significant damage. However, because larger snails will consume more biomass on an individual basis, it is important to know the size structure and the density of snails to estimate their likely impact.

Conclusions

In our experiments, *Pomacea insularum* consumed substantial amounts of 7 of 13 species that are important for wetland restoration. *Pomacea insularum* is likely to pose the greatest threat to native submersed macrophytes, which generally have a lower DMC (less cellulose and lignin), have higher protein, and are easier to access by snails. Although *Ceratophyllum demersum* is recommended for freshwater wetland restoration, submersed macrophytes are not as common in wetland restoration designs because their propagation is often hindered by turbidity and algal growth in wetland development (Mitsch & Gosselink 1993).

The lowest consumption was found for *Thalia dealbata*, *Spartina alterniflora*, *Typha latifolia*, and *Pontederia cordata*. *Spartina alterniflora* is the primary choice for restoring coastal marshland in the eastern United States (Broome et al. 1988); *Ty. latifolia* and *Po. cordata* are the species recommended to plant in created and restored freshwater marshes (Mitsch & Gosselink 1993). Based on the results of our experiments, they should still be considered important restoration macrophyte species, even in *P. insularum*–infested areas. However, other important species used in restoration were consumed at a high rate by *P. insularum*. Spiderlily (*Hymenocallis*) is

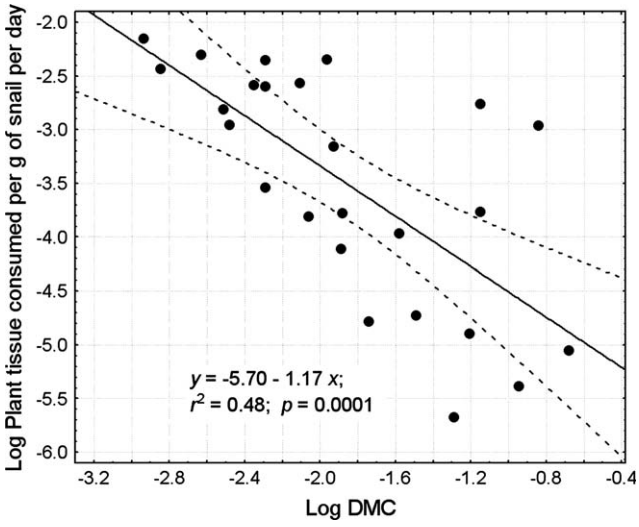


Figure 3. Relationship between the amount of plant tissue consumed per gram of *Pomacea insularum* (both wet weight) per day and plant DMC. Both variables were log transformed for the analysis.

a dominant wetland plant found in the Florida Everglades (Hofstetter 1983). Arrowhead (*Sagittaria*), a broad-leaved monocot, is frequently found as the dominant wetland vegetation in freshwater and coastal marshes (Sasser & Gosselink 1984), and *Sagittaria lancifolia* is generally recommended for wetland restoration and stormwater management (Mitsch & Gosselink 1993). In habitats where apple snails are present, we would recommend starting with emergent flora with a low risk of damage due to snail consumption. Additional experiments should be conducted with other species of invasive apple snails to determine the generality of plant preferences. Although apple snails consumed invasive plants at a high rate, because of their high rates of consumption of many native species, they should not be considered for biocontrol of invasive plants. The impact of apple snails on native vegetation is likely to outweigh any benefits they may provide by consuming invaders.

Implication for Practice

- Wetland restoration in areas with the invasive apple snail, *Pomacea insularum*, should focus on emergent structural species with low palatability. Snail consumption was lowest for *Thalia dealbata*, *Spartina alterniflora*, *Typha latifolia*, and *Scirpus californicus.*
- The palatability of macrophytes was negatively correlated with their DMC. The relationship between palatability and DMC of a plant can be used to estimate the risk of potential damage by apple snails.
- *Pomacea insularum* is likely to pose the greatest threat to native submersed macrophytes, which generally have a lower DMC (less cellulose and lignin), have higher protein, and are easier to access by snails.
- Apple snails should not be considered as biocontrol for invasive plants; although apple snails consumed invasive plants at a high rate, their consumption rates of many native species was even greater.

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