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Feeding and growth of native, invasive and non-invasive alien apple snails (Ampullariidae) in the United States: Invasives eat more and grow more

Wendy E. Morrison · Mark E. Hay

Abstract The United States hosts one native and five non-native species of aquatic apple snails (Ampullariidae). All are currently found in or around the Everglades in Florida. Two of these introduced species have devastated wetlands in Southeast Asia, but little is known about how they may impact the Everglades. To evaluate potential impacts of introduced apple snails relative to the native species, we investigated plant species preference, consumption rates, growth rates, and growth efficiencies in five introduced and the single native species across eight native macrophytes common in the Everglades. Three of the non-native snails are invasive, one has shown no tendency to expand, and one appears to have minimal direct impact on macrophytes due to its diet. All snails exhibited similar feeding preferences, with *Utricularia* sp. being the most preferred, *Bacopa caroliniana*, *Sagittaria latifolia*, and *Nymphaea odorata* being of intermediate preference, and *Eleocharis cellulosa*, *Pontederia cordata*, *Panicum hemitomon* and *Typha* sp. being least preferred (avoided as foods). Consumption and growth was minimal for *P. diffusa* on all macrophytes. On *Utricularia* sp. and *Bacopa caroliniana*, the invasive species *Pomacea insularum* and *P. canaliculata* tended to eat more, grow more, and have higher conversion efficiencies than the native *P. paludosa* or the non-invasive *P. haustrum*. These contrasts were more often significant for *P. insularum* than for *P. canaliculata*. The greater rates of expansion by the invasive species may derive from their enhanced feeding and growth rates.

Keywords Aquatic · Consumption rates · Exotic species · Macrophyte · Food choice

Introduction

Some 50,000 non-native species have been introduced to the United States, resulting in an estimated economic cost of $120 billion per year (Pimentel et al. 2005). About 50% of imperiled native species are at risk due to competition with or predation by non-native species (Wilcove et al. 1998). Invasive species impact all habitat types (Parker et al. 1999), but appear to have stronger impacts on freshwater than on terrestrial ecosystems (Sala et al. 2000). Not all introduced species have strong negative impacts on native ecosystems, necessitating an improved understanding of which species are most threatening and under what circumstances (Parker et al. 1999).

Apple snail (Ampullariidae) introductions have caused negative economic and ecological impacts in many regions (Cowie 2002; Joshi and Sebastian

W. E. Morrison · M. E. Hay (✉)
Georgia Institute of Technology, School of Biology,
310 Ferst Drive, Atlanta, GA 30332, USA
e-mail: mark.hay@biology.gatech.edu

2006). Their introduction to Taiwan cost US$30 million in lost rice farming revenue in 1986 alone (Mochida 1991). Their impacts on other commercial crops, such as taro, water spinach, water chestnut, and lotus are also considerable (Cowie 2002; Carlsson 2006). The introduction of *Pomacea canaliculata* to Thailand changed aquatic ecosystems from clear, macrophyte dominated systems into turbid, plankton dominated ones (Carlsson et al. 2004). Due to this history, *P. canaliculata* is currently listed as among "*100 of the World's Worst Invasive Alien Species*" (Lowe et al. 2000). However, there has been historical confusion in identification between *P. canaliculata* and *P. insularum* with recent genetic studies suggesting that *P. insularum* may also have caused considerable damage in SE Asia (Rawlings et al. 2007; Hayes et al. 2008).

Five species of non-native apple snails have been introduced to the southern United States, to California, Texas, Arizona, Georgia, and Florida (Rawlings et al. 2007). All five currently occur in and around the Everglades in Florida (Rawlings et al. 2007; T. Rawlings pers. comm.). Only one species of apple snail, *Pomacea paludosa*, is native to North America, with native populations in Florida, Alabama and Georgia (Rawlings et al. 2007). The native species is an important component of South Florida ecosystems and serves as a critical, almost exclusive, prey for the endangered Everglades Kite (Bennetts et al. 1994). Of the five introduced species, three (*Pomacea insularum*, *Pomacea canaliculata*, and *Marisa cornuarietis*) are invasive pests, one (*Pomacea haustrum*) appears non-invasive because it has been in the United States probably for over 30 years without spreading (Rawlings et al. 2007), and the fifth species (*Pomacea diffusa*; often referrred to as *P. bridgesii* in previous literature) consumes primarily algae and has little direct impact on aquatic macrophytes (Howells 2002, but see Aditya and Raut 2001).

Due to the potential impact of introduced apple snails on commercial crops and native vegetation, the U. S. Department of Agriculture has banned movement of apple snails (except *P. diffusa*) across state lines without a permit and requires all facilities housing the snails to implement proper precautions to prevent escape. Given these circumstances, field determination of impacts of the introduced apple snails on native vegetation is difficult. We thus conducted a laboratory study to determine the feeding

preferences, feeding rates, growth rates, and growth efficiencies of native and non-native apple snails in the U.S., specifically as they relate to the possible effects of non-native introductions around the Everglades National Park and similar habitats.

Materials and methods

Animals and plants used

Pomacea paludosa and *P. insularum* were collected as eggs; *P. insularum* from Lake Lure in Georgia (N 31° 33.210′ W 82° 28.947′) and both species from Lake Tohopekaliga in Florida (N 28° 13.033 W 81° 22.533). Adult *P. canaliculata* were obtained from Neighborhood Fish Farm in Miami, Florida. *Pomacea diffusa*, *P. haustrum*, and *Marisa cornuarietis* were obtained from Paradise Aquatics in Winterhaven, Florida. All species produced eggs that hatched in the lab; juveniles hatched from eggs were used for all experiments. All species were identified according to characteristics of their eggs (Rawlings et al. 2007), and because juveniles are difficult to identify, the species were held in separate tanks. Each snail was used in only one experiment and then euthanized. All snails used hatched between 2 June and 29 July 2008.

Since we wanted to estimate how alien snail species might impact habitats supporting the native species, and because a recent meta-analysis indicated that non-native consumers selectively impact native plants (Parker et al. 2006) we focused on native aquatic macrophytes that are important in the Everglades ecosystem, that is, they were listed as common native species by two books describing the ecosystems of the Everglades (Gunderson 1994; Lodge 2005). The exception was *Typha* sp., which was listed only by Lodge (2005) but was included because of its increasing abundance in disturbed aquatic habitats (C. Guerra, Miami Audubon pers. comm.). *Nymphaea odorata*, *Panicum hemitomon*, *Typha* sp., *Pontederia cordata*, and *Utricularia* sp. were collected at various locations in Georgia. *Sagittaria latifolia*, *Bacopa caroliniana*, and *Eleocharis cellulosa* were purchased from Biosphere Consulting Inc, a plant nursery that guaranteed no pesticides were used on the plants. All plants were planted in 72 L tubs and grown in a greenhouse to be harvested as needed for experiments.

Experimental procedure

Choice assays

Snails were simultaneously offered small pieces of eight plant species (*Bacopa caroliniana*, *Eleocharis cellulosa*, *Nymphaea odorata*, *Panicum hemitomon*, *Pontederia cordata*, *Sagittaria latifolia*, *Typha* sp., and *Utricularia* sp.) in replicate ($N = 16$ for each snail species, with each individual receiving all eight plant species) 739 ml containers and allowed to feed for 3 days (water level was 3–4 cm deep, 2–5 times the height of the snails). Snails encountered plants by crawling across the bottom of the container or floating across the surface of the water. Plant mass was not equivalent across plant species as we standardized for herbivore encounter rate, offering approximately equivalent surface area of each plant species in each container. Since *Utricularia* sp. is so filamentous, a very small mass provides a large surface area ensuring a high encounter rate. To remove this bias and have a sufficient mass to allow for measurements, we bundled a larger amount of this plant together using a small piece of wire. Similarly, small pieces of *Typha* sp. and *Panicum hemitomon* were also joined together using wire. This caused these species to sink while the other species floated. However, as the *Utricularia* sp. was eaten first and the *Panicum hemitomon* and *Typha* sp. not eaten at all (see results), and because the snails were raised on lettuce, which both floated on top of the water and sank to the bottom, such that the snails were accustomed to looking in both areas for food, the location of the plants on the surface vs. bottom probably did not impact the results. Assays were spatially grouped into 16 blocks, with each block including one replicate of every snail species plus one control to monitor autogenic changes in plant mass unrelated to feeding (Roa 1992). Within each block, all pieces were cut from the same plant when possible, and no individual plant was used in more than one block. We adjusted the number of snails per replicate (1–13) so that the total mass of snails in each replicate within a block was similar. Among blocks, mean snail mass ranged between 0.4 and 1.5 grams/replicate. There was no significant difference among snail species in the number or weight of snails used ($F = 0.14$, $P = 0.98$; $F = 0.11$ $P = 0.99$, respectively). Assays were checked every 4–8 h to visually estimate the percentage of each plant consumed. At the end of 3 days, all snails were removed from the assays, the remaining plant material blotted, and wet mass determined. Plant starting mass was corrected for autogenic change according to the formula (Stachowicz and Hay 1996): $T_i \ x \ (C_f/C_i)$, where T_i is the initial mass of plant available for consumption by the snails and C_i and C_f are the initial and final masses of the plants from the matching controls.

Growth

We measured snail growth when fed different plants by placing individual snails ($N = 16$ for each snail species by plant species combination) into 296 ml plastic cups and feeding them ad libitum one of the plant species. Snails were kept at a constant temperature of 25°C. To keep replicates to a manageable number we used six of the eight plant species used in the choice assays (*Utricularia* sp., *Bacopa caroliniana*, *Eleocharis cellulosa*, *Nymphaea odorata*, *Panicum hemitomon*, and *Pontederia cordata*), excluding one low and one high preference species; snails included all species but *M. cornuarietis*, many of which died in the lab prior to this assay. Each of 16 blocks consisted of 33 cups randomly assigned to a location within the block. *Pomacea diffusa* was offered only four species of plants due to its dislike of macrophytes (see results of choice experiments). For each snail species, a control snail was included in each block to measure changes in mass when starved (i.e. no food was provided). Snail mass was measured blind relative to treatment at the beginning and end of the experiment. Cups were checked every 3 days to add water and food as needed. Once a week, half of the water and all of the food was replaced. Originally cups were filled to approximately 2 cm from the top and covered with aluminum foil with holes. The snails experienced some mortality with this methodology, necessitating replacement of the dead snails and modification of the tops from aluminum to screen mesh. All snails that died during the first week of the growth experiment were replaced and the date of replacement noted. After the first week, dead snails were not replaced. Growth was corrected for actual days of growth at the end of the experiment (24–31 days). Snails ranged between 0.05 and 1.7 g wet mass at the start of the experiment. Ideally, all

snails would be the same starting size; however, we were unable to find 528 snails across 5 species that matched in size. Therefore, we matched all snail sizes within a block. The experiment was initiated with no significant difference in sizes among snail species. However, smaller *P. paludosa* experienced considerable mortality the first week of the experiment and were replaced with slightly larger snails, leading to a significantly larger size for *P. paludosa* after the new snails were added to replace the dead ones at the end of week one (mean mass = 0.54 g) compared to the rest of the species (mean mass ranged from 0.24 to 0.31 g) ($F = 12.6$, $P < 0.001$). For the snails added after week one, growth at the end of the experiments was adjusted to account for the shorter total time that these snails had for growth. To correct for different starting sizes, snail mass was entered as a covariate in all subsequent statistical analyses. If snail mass was not significant, we removed it from the analysis and ran an analysis of variance (ANOVA). Analysis of covariance (ANCOVA) was only necessary for three analyses: percent growth of *P. paludosa* grown on different plants, and differences in growth among snail species when grown on *Utricularia* sp. and on *Bacopa caroliniana*.

During the last 3 days of the growth experiment, mass eaten by each snail was measured. As with the choice assays, for each replicate, food pieces were cut from the same individual plant and a control piece set aside to measure changes in plant mass unrelated to grazing. At the end of 3 days the leftover plant pieces were weighed and corrected according to changes in mass of the control specific for that block. Feeding was assessed as mass of plant consumed per mass of snail. Growth efficiency was calculated as the daily growth of the snail in grams/daily consumption in grams. Since growth was measured over 1 month, but consumption only quantified for the last 3 days, we assumed that the consumption in the last 3 days represented average consumption/g snail throughout the month. We removed data points when snail growth or consumption was less than or equal to zero because calculating efficiencies with these numbers creates biologically unrealistic values.

Statistical analyses

Choice assays were analyzed using a modified Friedman's test to account for non-independence among the plant species within each replicate (Conover and Iman 1981; Roa 1992). Because of this non-independence, Friedman's test requires dependent variables (i.e. consumption) to be ranked within each replicate. However, instead of running the comparison using chi-squared (the usual Friedman's statistic, Conover 1999) we used two-way analysis of variance (with replicate and treatment as the independent variables) as this is more reliable with larger matrixes (Conover and Iman 1981). Tukey's pairwise comparisons were performed on the rank data. The no-choice feeding assays, growth assays, and efficiencies were analyzed using Analysis of Covariance (ANCOVA) on ranked transformations with snail mass as the covariate. Non-parametric rank transformations were used since the data did not meet the assumptions of homogeneous variance and no other transformations adequately fixed this problem. Tukey's adjustment was used on all pairwise comparisons to minimize Type I error. When the results of the ANCOVA suggested the covariate (snail mass) was not significant, pairwise comparisons were performed on the results from the one way Analysis of Variance (ANOVA). To determine if individual results differed significantly from zero, *t*-tests were completed with the significance level (α) corrected by dividing by the number of comparisons completed per graph. Chi-squared contingency tables were used to evaluate differences in mortality across snail species and plant diet. Due to small sample sizes and the lack of variance measurements, analyses tested for the occurrence of any differences among snail species or plant species, but no pairwise comparisons could be reliably computed.

Results

All snail species showed crudely similar patterns of preference when offered a choice among the eight macrophytes (Fig. 1). *Utricularia.* sp. was readily consumed by all species with *Sagittaria latifolia* also being heavily consumed by *Pomacea canaliculata* and *P. insularum*. *Bacopa caroliniana* and *Nymphaea odorata* were consumed at intermediate rates by most snail species, with *Panicum hemitomon*, *Pontedaria cordata*, *Eleocharis cellulosa*, and *Typha* sp. being largely avoided. *Pomacea diffusa* consumed so little of any plant that there were no significant differences in its feeding among plants. However, the response of
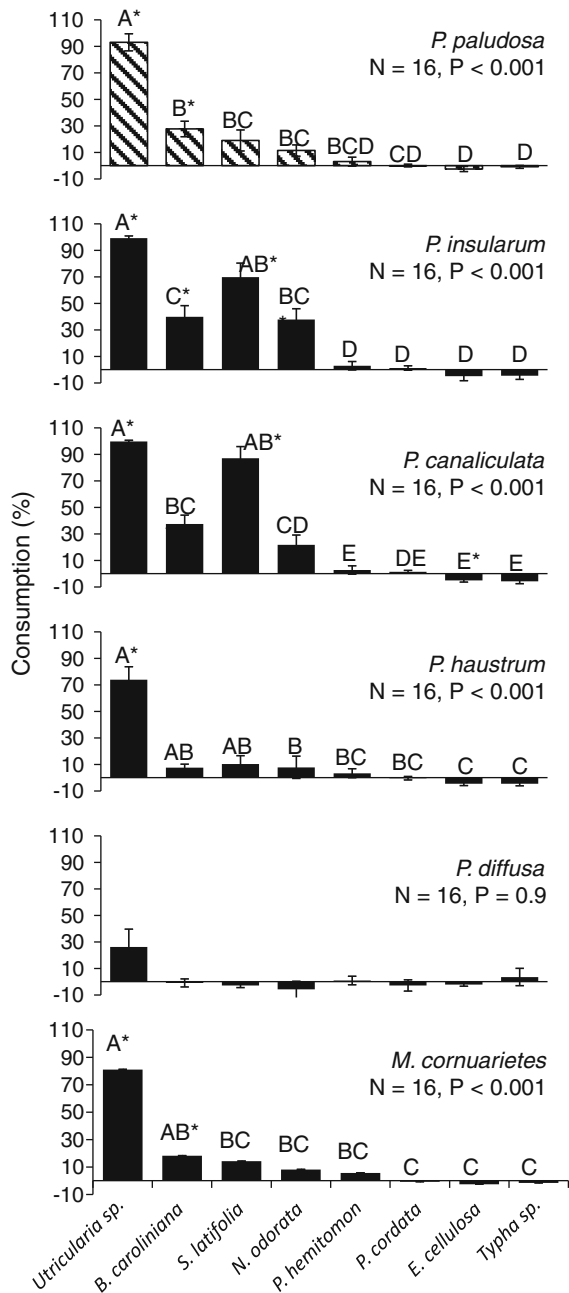
Fig. 1 Snail consumption of plants (mean ± SE) during the choice assays. *P*-values are from ANOVA. *Different letters* represent significant differences using Tukey's multiple comparison tests on ranked data. *Asterisks* indicate consumption is significantly different from zero using *T*-tests with α corrected to 0.006 for multiple comparisons

Fig. 2 Total grams of plant consumed across all plant species per gram of snail per day (mean ± SE) during the choice assays. *Statistical tests* and symbols as in Fig. 1, except that the data were not ranked and block was entered as a covariate to account for differences among blocks in snail weight used

over time suggested that all snail species consumed *Utricularia* sp. first. The consumption of the second, third and fourth choices varied somewhat among snail species (Fig. 1).

When we summed all feeding on all plant species in each replicate to evaluate how total consumption rates varied among snail species, *P. insularum* and *P. canaliculata* were statistically indistinguishable and consumed about 190 mg of plant/g snail/day (Fig. 2). *Marisa cornuarietis* and *P. haustrum* consumed significantly less at about 70–115 mg/g snail/day. *Pomacea diffusa* consumed less than all other species, and could not be demonstrated to be feeding because the mean mass eaten did not differ significantly from zero ($N = 16$, $P = 0.88$). The native snail *P. paludosa* fed at an intermediate rate of about 140 mg of plant/g snail/day; this was significantly more feeding than *P. haustrum* and *P. diffusa*, but did not differ significantly from other species.

When constrained to feeding on a single plant species, *Pomacea paludosa*, *P. canaliculata* and *P. insularum* consumed significantly more *Utricularia* sp. and *Bacopa caroliniana* than any other species (Fig. 3). *Pomacea haustrum* showed a similar pattern but its consumption of *Utricularia* sp. did not differ significantly from its consumption of *Nymphaea odorata*. As in the choice assays, *P. diffusa* could not be demonstrated to feed on any plant. *Marisa cornuarietis* was not tested. All five of the snail species tested consumed very little (0–45 mg/g snail/day) of *Nymphaea odorata*, *Eleocharis cellulosa*,

P. diffusa to *Utricularia* was bimodal; 44% of replicates showed no consumption, while 31% consumed >80%. Visual estimates of plant consumption
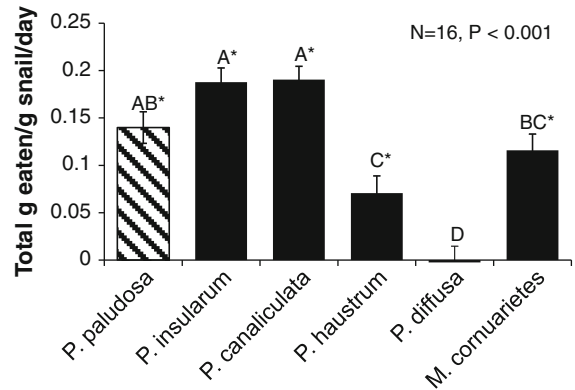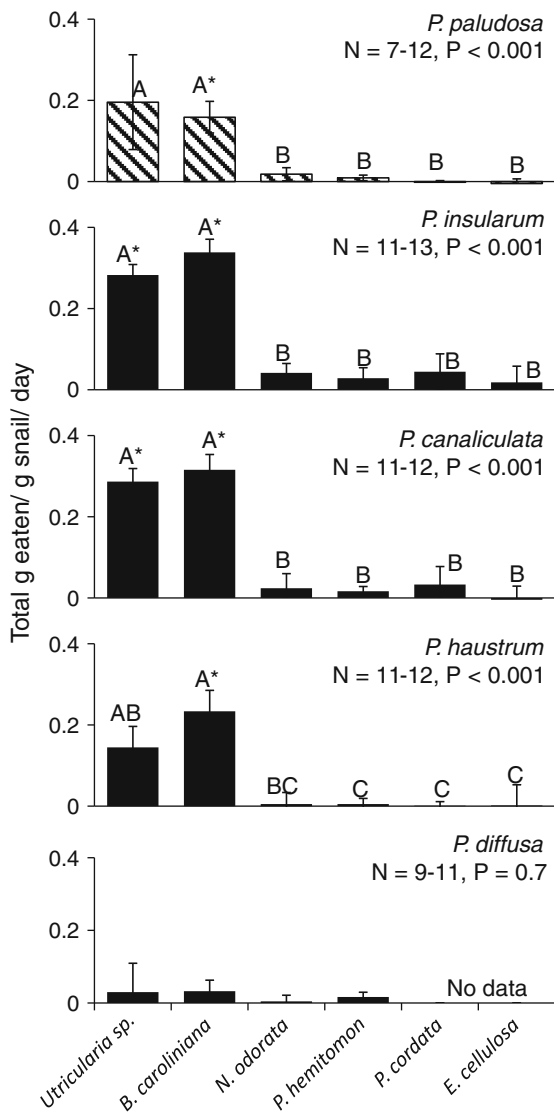
Fig. 3 Grams of plant consumed per gram of snail per day (mean ± SE) during the no-choice assays. *P*-values are from ANOVA, except for *P. paludosa* which was run with snail weight as a covariate. Statistical symbols as in Fig. 1

Pontederia cordata, and *Panicum hemitomon*. Regarding the two plant species most readily consumed, *P. insularum* and *P. canaliculata* consumed more *Utricularia* sp. than *P. diffusa*, while *P. paludosa* and *P. haustrum* consumed intermediate amounts that did not differ significantly from the amounts eaten by the other species (Table 1). Similarly, *P. insularum* and *P. canaliculata* consumed more *Bacopa caroliniana* than either *P. paludosa* or *P. diffusa*, with *P.haustrum* being intermediate (Table 1).

Table 1 Grams of plant consumed per gram of snail per day (mean + SE) during the no-choice assays

	Utricularia sp.	*B. caroliniana*
P. insularum	0.28 ± 0.03	0.34 ± 0.03
P. canaliculata	0.29 ± 0.03	0.32 ± 0.04
P. haustrum	0.14 ± 0.05	0.23 ± 0.05
P. paludosa	0.2 ± 0.12	0.16 ± 0.04
P. diffusa	0.03 ± 0.08	0.03 ± 0.03

Overlapping lines depict non-significant statistical differences using Tukey's multiple comparison tests on ranked data analyzed with ANOVA

Diet strongly affected growth ($P < 0.001$) of all snail species (Fig. 4). All grew on *Utricularia* sp. (20–266%/month) and *Bacopa caroliniana* (6–101%), with the difference between the two plants not significant. Only *P. insularum* achieved positive growth on *Nymphaea odorata*. Growth in all other snail-plant combinations did not differ significantly from zero. *Pomacea diffusa* did not exhibit significant positive growth on any plant species; *P. haustrum* had positive growth only on *Utricularia* sp.; *P. paludosa* and *P. canaliculata* had positive growth on *Utricularia* sp. and *Bacopa caroliniana*; and *P. insularum* had positive growth on *Utricularia* sp., *Bacopa caroliniana* and *Nymphaea odorata*.

On the three plant species on which positive growth was achieved, the introduced species *P. insularum* always grew significantly more than the native *P. paludosa*, while the introduced species *P. canaliculata* showed a similar trend but this was significant only for *Utricularia* sp. (Table 2). Growth efficiencies ranged between zero and 0.13 across all snail and plant combinations (Fig. 5). There were no significant differences among snail species in efficiencies on *Bacopa caroliniana* or *Nymphaea odorata*, but on *Utricularia* sp. *P. insularum* had significantly higher efficiency than *P. diffusa* and the native *P. paludosa*.

When summed across all diets, there were differences among snail species in total mortality ($\chi^2 = 21.7$ $P = 0.0002$). *Pomacea diffusa* and *P. paludosa* experienced the greatest mortality (~20%) while the other three species suffered much less (4–8%). When all snail species were summed across a specific diet, there were significant differences among plant species in survivorship of snails confined to those plants ($\chi^2 = 18.0$ $P = 0.006$). Snails
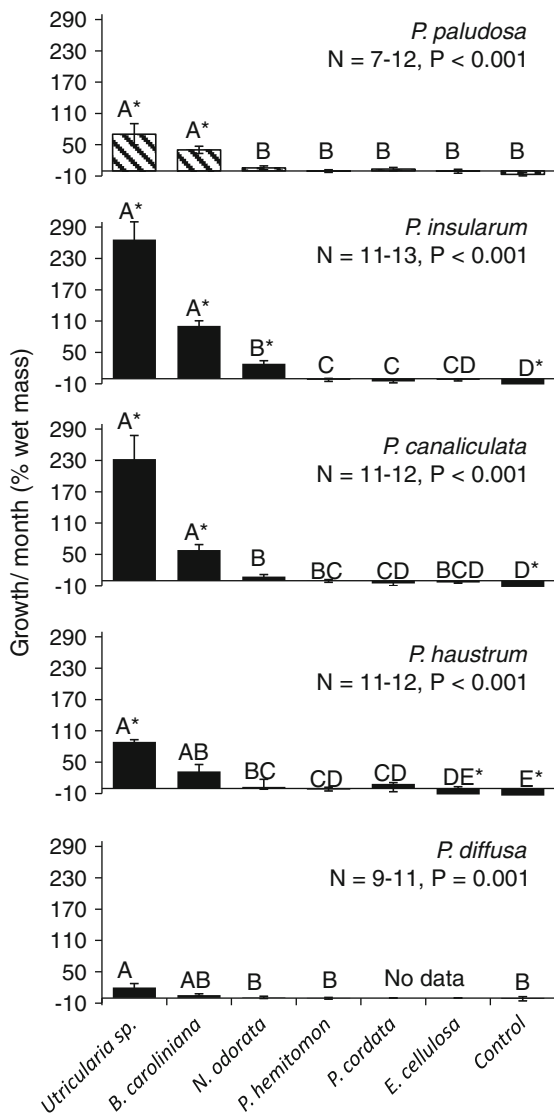
Fig. 4 Percent (±SE) growth in snail mass when feeding on different single-species diets. *P*-values are from ANOVA. Statistical symbols as in Fig. 1. "Controls" represent starved snails
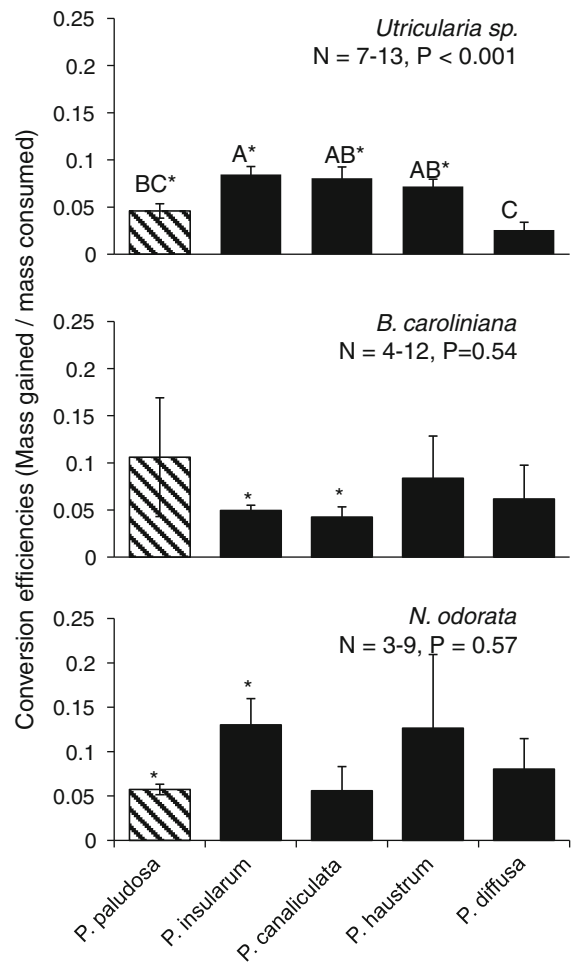

Fig. 5 Growth efficiency of snails (±SE) when feeding on each of the three plant species that supported positive growth. *P*-values are from ANOVA. Statistical symbols as in Fig. 1

confined to *Utricularia* sp. and *Bacopa caroliniana* survived well (2–3% mortality), while those feeding on other plant diets experienced 10–15% mortality, with starved snails suffering 22% mortality (Fig. 6).

Table 2 Percent (+SE) growth in snail mass when feeding on one of the three plant species that supported positive growth over the month long experiment

	Utricularia sp.	*B. caroliniana*	*N. odorata*
P. insularum	266 ± 34	101 ± 10	28 ± 6
P. canaliculata	233 ± 45	59 ± 10	8 ± 4
P. paludosa	70 ± 20	40 ± 7	6 ± 4
P. haustrum	89 ± 13	33 ± 14	3 ± 5
P. diffusa	20 ± 8	6 ± 2	1 ± 2

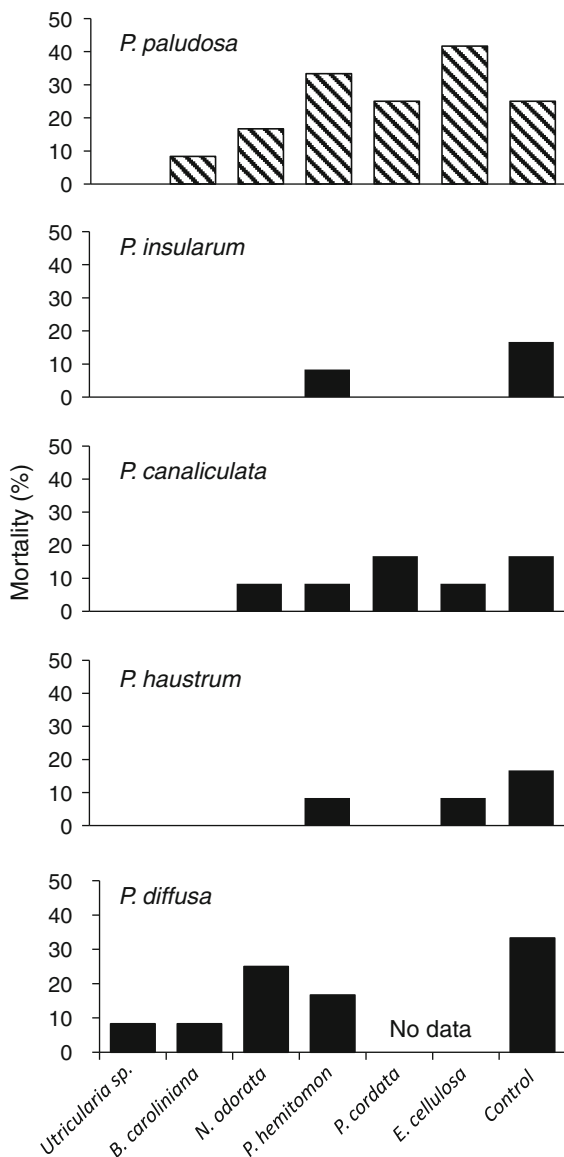Statistics as in Table 1, except analyses included snail weight as covariate

Fig. 6 Snail mortality during the one-month feeding experiment. "Controls" represent starved snails

Discussion

Food preferences were crudely similar across all species. *Utricularia* sp. was always a preferred food, and *Panicum hemitomon*, *Pontederia cordata*, *Typha* sp., and *Eleocharis cellulosa* were always avoided. *Bacopa caroliniana*, *Sagittaria latifolia* and *Nymphaea odorata* were consumed at intermediate rates by all species with the exception of *P. diffusa*, which fed at low rates, if at all, on all macrophytes (Fig. 2).

Regarding *Pomacea diffusa*, our findings differ from those of Aditya and Raut (2001), whose snails "devoured completely" both macrophyte species offered (*Eichhornia crassipes* and *Cabomba* sp.). They also reported that *P. diffusa* preferred animal to plant tissue, consuming live worms, mollusk eggs, and dead animals. In our study, *Utricularia* sp. was consumed by 31% of the *P. diffusa*, but all other macrophytes were almost completely avoided. Howells (2002), however, found similar results to ours, with none of the 18 macrophytes offered to the snails consumed except for "slight nibble on leaf tips" of *Cabomba caroliniana*. We are surprised by the results of Aditya and Raut (2001), especially the consumption of *Eichhornia crassipes*. *Pomacea haustrum*, a species that showed a higher propensity to eat macrophytes, completely avoided *Eichhornia crassipes*, consuming on average only 3% after 4 days (Morrison 2010). We wonder if strains of *P. diffusa* differ in food preferences (see Sotka and Hay 2002 for a marine example) or whether Aditya and Raut (2001) may have used a hybrid between *P. diffusa* and another *Pomacea* species. Nonetheless, even though our results suggest that *P. diffusa* would have a minimal direct impact on macrophytes, consumption of epiphytes and or invertebrate eggs could lead to indirect ecosystem impacts.

Food preferences in *P. canaliculata* and *P. insularum* have been assessed previously (Estebenet 1995; Lach et al. 2000; Carlsson et al. 2004; Carlsson and Lacoursière 2005; Gettys et al. 2008; Boland et al. 2008; Burlakova et al. 2009, Baker et al. 2010). Carlsson et al. (2004) recorded absence of almost all aquatic plants after introduction of *P. canaliculata* in Thailand, demonstrating a willingness by the snails to eat all plants except *Typha* sp. The low consumption of *Typha* species is similar across all studies (Carlsson et al. 2004; Burlakova et al. 2009; Baker et al. 2010, this study), but snail preferences among other plants has been less consistent. For example, *Pistia stratiotes* and *Sagittaria lancifolia* were completely rejected in one study (Baker et al. 2010) but consumed in others (Carlsson et al. 2004; Burlakova et al. 2009). Similarly, our snails rejected *Panicum hemitomon* and *Pontederia cordata* but these species were consumed in another study (Burlakova et al. 2009). It appears that there may be considerable among-population variance in the palatability of the plants, the feeding preferences of the snails, or both.

Growth of all apple snails was low on all macrophytes except *Utricularia* sp. and *Bacopa caroliniana*, on which mass increased 20–266% and 6–101%, respectively (Fig. 4; Table 2). Sharfstein and Steinman (2001) measured mass increases in *P. paludosa* (water temperature 20°C) that were an order of magnitude higher. However, their *Utricularia* sp. and *Eleocharis* sp. included associated periphyton (detritus, algae, and microbes), which could be an additional food source, while our plants did not support any obvious periphyton. Estebenet (1995) measured growth in *P. canaliculata* at room temperature over 4 months. Growth over the second month of her experiment (when snail size matched ours; mean shell height 10 mm) was similar to the growth we measured. This suggests that our measures of growth are reliable for snails fed individual macrophyte species, but that a diverse diet including detritus and algae allows for higher growth.

Mean consumption measured in the choice and no choice assays was 0–0.19 and 0–0.34 grams of plant per gram of snail per day, respectively. Carlsson and Brönmark (2006) reported consumption of 0.25 grams of plant per gram of snail per day in newly hatched *P. canaliculata*. Rigorous comparisons with other studies are not possible as consumption rate changes with snail size (Boland et al. 2008) and snail sizes and macrophyte species used differed among studies. Also, comparisons are difficult because of uncertainty regarding the correct identification of the snails in many earlier studies (Cowie et al. 2006). Growth efficiency of the invasive and native snails was similar for all combinations except that *P. insularum* exhibited significantly greater efficiency than the native *P. paludosa* when fed *Utricularia* sp. (Fig. 5). Growth efficiencies for *P. canaliculata* in our study (4–8%) were lower than the conversion efficiencies of 10–20% measured by Tamburi and Martin (2009), but this may be because these authors fed their snails cultivated lettuce and we fed ours field collected *Utricularia* sp. When pooled across all diets, mortality tended to be higher for the native *P. paludosa* than for the non-native species (Fig. 6).

Apple snail species differ in many life history characteristics. The invasive *P. insularum* can be up to four times heavier than the native *P. paludosa* (Conner et al. 2008). Clultch size is highly variable among species; native *P. paludosa* have on average 30 eggs per clutch (maximum 141) (Rawlings et al. 2007), *P. canaliculata* has approximately 150 eggs per clutch (Boland et al. 2008) while *P. insularum* can have over 1000 eggs per clutch (Rawlings et al. 2007; Boland et al. 2008), with some clutches containing over 4,500 eggs (Barnes et al. 2008). If the snails produce an estimated 22 clutches per year (Cowie 2002), this translates into a large difference in number of offspring. Native snail densities are 0–3 snails per square meter in Florida (Darby et al. 2004). Densities of *P. insularum* in stable, permanently wet invaded habitats were similar to native densities and averaged less than 2 snails per square meter but in seasonal agricultural systems could reach as high as 130 snails per square meter (Burlakova et al. 2010).

Even though the *Pomacea* species we assessed exhibited similar food preferences, the differences in feeding rates, growth, efficiencies, and mortality when combined with differences in size and fecundity suggest that a change in *Pomacea* species could impact aquatic habitats of South Florida. However, our results suggest that complete denudation of the flora would not occur as all species rejected *Panicum hemitomon*, *Eleocharis cellulosa*, and *Pontederia cordata*, even when provided no other choice (but see Burlakova et al. 2009 for different results regarding *Panicum hemitomon*). Our study suggests that *Utricularia* sp. would be one of the first plants impacted. In Georgia, *P. insularum* occurs just 29 km from the Okefenokee Swamp (pers. comm. Chad Sexton, Georgia DNR). Introduction of *P. insularum* could impact the Swamp due to the high prevalence of *Utricularia* sp. there (Greening and Gerritsen 1987). Invasive species often have a large impact if they fill a novel function in the new habitat (Parker et al. 1999). Introducing invasive apple snails into areas without native apple snails may lead to a larger impact as plant species in this area may not be able to resist or tolerate the voracious appetite of non-native apple snails with which they have not evolved (Parker et al. 2006).

In conclusion, even though the gross morphology of the species in our study was similar, the invasive *P. insularum* exhibited greater growth, greater efficiency, and lower mortality than the native *P. paludosa* even though its consumption of various plants was similar (Table 2; Figs. 5, 6). The invasive *P. canaliculata* exhibited similar values to those of *P. insularum*, although *P. canaliculata* grew significantly more than the native *P. paludosa* only on *Utricularia* sp.

Comparatively, the non-invasive *Pomacea haustrum* exhibited lower growth and efficiency than the invasive *P. insularum*, having values similar to those of the native *P. paludosa* (Figs. 5, 6). This might explain why *P. insularum* is expanding its range while *P. haustrum* is not (Rawlings et al. 2007), with *P. insularum* currently replacing *P. haustrum* in some areas in Florida (pers. comm. Timothy Collins, Florida International University). The similarity in the results for *P. insularum* and *P. canaliculata* was not surprising as these species are closely related (Rawlings et al. 2007; Hayes et al. 2008), but *P. insularum* was consistently higher than *P. canaliculata* on growth, and conversion efficiencies and lower on mortality. *Pomacea canaliculata* is listed as one of the world's 100 worst invasive species (Lowe et al. 2000) but *P. insularum* may be capable of causing similar damage, especially as fecundity is higher in *P. insularum* (Rawlings et al. 2007; Boland et al. 2008). Overall, the invasive species in our study feed faster and grow more than both the native and the non-invasive species. The invasive and non-invasive alien species from this study are similar in morphology, fecundity, and size, but differ in their propensity to expand into new areas. We were able to document differences in growth and efficiency between these species suggesting one mechanism for why the faster growing and more efficient species is invasive while its relative is not. Given the limited number of apple snails available for study, more studies comparing characteristics of other groups of related invasive and non-invasive aliens are needed to determine if this is a general trend for invasive versus non-invasive alien species.

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