



Food preference and reproductive plasticity in an invasive freshwater snail*

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Abstract

The freshwater apple snail *Pomacea canaliculata* has become a major crop pest in southeast Asia and Hawai'i and threatens natural wetland habitats in these regions and elsewhere. Deliberately introduced as a potential human food resource, it has also been proposed as a possible biocontrol agent against aquatic weeds. Various factors may facilitate its rapid invasion of new areas; we focus on two: growth rate and food preference. Our field observations and laboratory experiments suggest that in Hawai'i *P. canaliculata* reaches reproductive maturity in 10 months or more, less time than in its native temperate and seasonal Argentina, where it takes 2 years, but longer than in parts of southeast Asia, where it may take as little as 2 months. This increased growth rate, and thence reproductive rate, probably facilitate rapid population growth. Although *P. canaliculata* is usually considered an indiscriminate generalist macrophytophagous feeder, laboratory experiments indicated preferences among the dominant plants at our field site and growth rate differences when constrained to feed only on one of these plants. Water hyacinth (*Eichhornia crassipes*), a major invasive weed, was not preferred in food choice experiments, and snails offered only water hyacinth on which to feed did not differ in growth rate from unfed snails. Another important invasive weed, water lettuce (*Pistia stratiotes*), was also not preferred, but snails fed on it did grow, though not as quickly as those fed on green-leaf lettuce. Among the food plants offered in the experiments the native *Vigna marina* was the most preferred. Therefore, although a generalist, *P. canaliculata* exhibits some discrimination among food plants. We recommend that it not be introduced for use as a biological control agent for aquatic weeds.

Introduction

Human-mediated biological invasions are initiated as a result of either inadvertent transport accompanying unrelated human activities or deliberate, purposeful introduction. Often, in the latter case, and despite much evidence of the negative effects of an invader, people persist in introducing it, either because they do not care about the negative effects or because they consider the perceived positive effects to outweigh the negative

effects (e.g., Cowie, in press a). Organisms perceived as having value as food resources or as biocontrol agents, for example, may continue to be artificially dispersed though they may be ill-suited for these purposes, and, if they become invasive, may threaten conservation or agricultural interests.

A species may become invasive when introduced to a new region because it is released from factors controlling its populations in its native region. The factors may be biological (e.g., predators, disease, competition) or environmental (e.g., seasonality as it constrains breeding cycles and activity patterns). Some

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non-native species may also be pre-adapted to their new environment because of their phylogenetic history. For instance, a temperate species may have evolved from a clade of tropical species such that when released into a tropical environment it remains capable of surviving, or perhaps even of increasing its fitness.

The freshwater snail *Pomacea canaliculata* ranges naturally from temperate South America northwards perhaps as far as the Amazon basin. It is one of several species of the family Ampullariidae commonly called 'apple snails'. Intentional introductions of apple snails as potential food resources have resulted in successful invasions in many regions, particularly southeast Asia (Acosta and Pullin 1991; Naylor 1996). *Pomacea canaliculata* has been reported from Texas (Neck and Schultz 1992), and has recently been discovered in Florida (Thompson 1997) and California (Cerutti 1998). These introductions to the mainland United States are probably via the domestic aquarium trade (e.g., Thompson 1997).

In many parts of its introduced range it has become a serious agricultural pest (Cowie, in press b) and has been implicated in the decline of native freshwater snails (Halwart 1994). In the Philippines, a density of eight snails per m² can decrease rice yields by 90% (Naylor 1996). Climatic modeling (Baker 1998) suggests that major areas of Asia (e.g., central China, India, Bangladesh and Burma) that are heavily dependent on rice as a staple food but that are currently free of introduced apple snails are under serious threat; Australian rice producing areas as well as natural wetlands are similarly threatened.

Pomacea canaliculata has been suggested as a possible aquatic weed control agent in Japan (Okuma et al. 1994; Wada 1997). Other species of ampullariids have been used for this purpose, notably against water lettuce (*Pistia stratiotes*) in the Caribbean, with apparently dramatic effects (Perera and Walls 1996) but also have been implicated in causing decline of native aquatic plants and the native animals that depend on them (Simberloff and Stiling 1996).

Despite this now well-known potential for destruction, *P. canaliculata* continues to spread, often as a result of deliberate introduction by people. It was introduced to the Hawaiian Islands sometime before 1989 as a food resource, probably from the Philippines, and is now the most widely distributed and rapidly spreading of four species of non-native apple snails in the islands (Cowie 1997). In 1992, *P. canaliculata* was known from five sites on O'ahu, three on Maui and two on

Kaua'i (Cowie 1995). By 1995, it was also reported on Lāna'i (Cowie 1996). It has rapidly become the most serious pest of taro (*Colocasia esculenta*), the traditional staple of Hawaiian and other Pacific islanders. Damage to taro has not been quantified, but snail densities in taro fields have been reported as high as 130 snails per m² (Cowie, in press b). A 1998 survey of lowland freshwater systems on O'ahu found that it had spread to 26 bodies of water, including protected areas such as the Campbell National Wildlife Refuge, and Kawaiui Marsh, the largest remaining wetland in the Hawaiian Islands (Lach and Cowie 1999). Nothing is known about its impacts on freshwater communities in Hawai'i but its potential to reach high densities and its voracious appetite suggest that it may pose a threat to the remaining low elevation native aquatic plants and animals.

Pomacea canaliculata exhibits several characteristics that may facilitate its invasive potential: it appears to be a food generalist, feeding on many different kinds of aquatic vegetation (Schnorbach 1995); in many places (e.g., Hawai'i) it has no natural enemies; it is tolerant to a wide range of environmental temperatures (Cowie, in press b) and to high levels of water pollution (L. Lach and R.H. Cowie, unpublished); and it is highly fecund (e.g., Mochida 1991).

A major reason for the extreme invasiveness of *Pomacea canaliculata* in the tropics and subtropics may be the increased potential for growth and reproduction in these areas compared to the temperate regions of its native range. The original introductions to southeast Asia are said to have been from temperate Argentina (Mochida 1991), where growth rate seems strongly linked to ambient temperature and seasonality (Estebenet and Cazzaniga 1992). Thus, release from the cool temperatures and seasonality of its natural range may permit *P. canaliculata* to rapidly achieve high population densities in the tropics (Cowie, in press b).

An additional crucial aspect of its biology that may allow *P. canaliculata* to be so invasive is its apparently very generalist feeding habits. Unlike many freshwater snails that are solely microphagous, eating the periphyton that grows on most submerged surfaces close to the water's surface, apple snails are also macrophytophagous (Estebenet 1995). Cowie (in press b) listed 11 macrophytes that are eaten by *P. canaliculata*. However, laboratory studies of *P. canaliculata* in its native range show that it exhibits preferences among different food plants (Cazzaniga and Estebenet 1984; Estebenet

1995), though nevertheless remaining relatively generalist and indiscriminate (Schnorbach 1995).

We measured growth rates in the field and in the laboratory and we tested food preferences among taro and four species of dominant emergent macrophytes found at the field sites. Our objectives were to determine growth rates and feeding preferences of *P. canaliculata* in Hawai'i in order to better understand the biology and ecology of the snail in its introduced range and thence to provide insights into the potential severity of its ecological impacts and the development of control strategies.

Methods

Growth rate

Laboratory

In May and June 1998, we collected four clutches of *Pomacea canaliculata* eggs that had been laid on emergent vegetation in a drainage pond near the northwest corner of Kawainui Marsh, island of O'ahu, Hawai'i. Each piece of vegetation, with its attached clutch, was placed in a 1-l jar with 300 ml of water such that the eggs were 5–10 cm above the water line. Eggs began to hatch within two weeks of collection; clutches 1 and 2 hatched on 8 June, clutch 3 on 22 June, and clutch 4 on 8 July.

Within 48 h of hatching, hatchlings from each clutch were divided into experimental sets of 15 snails each and each set was placed in a 4-l jar with 1 l of tap water, as follows. We divided each of clutches 1 and 2 into six sets with two sets from each clutch randomly assigned to one of three treatments: unfed, fed on water hyacinth (*Eichhornia crassipes*), fed on store-bought green-leaf lettuce. We divided clutch 3 into four sets randomly assigned to one of four treatments: unfed, fed on water hyacinth, fed on green-leaf lettuce, fed on water lettuce (*Pistia stratiotes*). Clutch 4 was divided into three sets: unfed, fed on green-leaf lettuce, fed on water lettuce. Jars were covered with mesh to prevent escape.

All fed clutches were provided with food ad libitum. Water was changed every 3 days or as necessary to prevent fouling, though occasionally some algal growth occurred on the glass surfaces of the jars between cleaning occasions. Eggs and hatchlings were kept in an air-conditioned room with temperature typically around 23 °C (range 20–28 °C) throughout the experiment.

Until snails were greater than 8.0 mm wide we measured widths under a dissecting microscope using a calibrated graticule. Once snails exceeded 8.0 mm we measured them with calipers, accurate to 0.05 mm. For clutches 1 and 2, we measured snail widths weekly until week 14 and then at weeks 20, 34 and 51. Clutch 3 snails were measured weekly through week 12 and then at weeks 18, 32 and 49. Clutch 4 snails were measured weekly through week 10 and then at weeks 16, 30 and 47.

We used Kruskal–Wallis (non-parametric) tests (with Bonferroni corrections for multiple tests) to compare shell widths among replicates and treatments. For clutches 1 and 2, there was no difference in mean widths between the two replicates of each treatment so the data for two replicates were combined. Treatments were then compared at four times during the course of the experiment, selected a priori, as follows: (i) the start of the experiments (week 0: 'initial'), (ii) the last week, (iii) the last week that all treatments had living snails, and (iv) representative weeks as follows: for clutches 1 and 2, week 14; for clutch 3, week 3; and for clutch 4 week 10. To determine daily growth rate, for each treatment we took the difference in mean widths between consecutive measuring events and divided by the number of days between measuring events for each clutch, and then calculated the mean rate across all clutches.

Field

We studied growth in the field at two sites: an unused stone boat launch in Kawainui Marsh (site 1), and a drainage pond (site 2) approximately 0.5 km NW of site 1. Water hyacinth was the dominant aquatic vegetation at both sites. Site 1 was relatively trash-free, had a silty bottom, and typically had water visibility to a depth of 50–100 cm. Site 2 was highly polluted, containing several pieces of discarded furniture and full trash bags, and with a sludge-like bottom, a thick, often orange and bubbling oily surface sheen, and little visibility below the surface. *Pomacea canaliculata* was far more abundant at site 2.

Because of differences in water quality and snail abundance at each site, we employed different sampling techniques. At site 1, we designated a 5-m² area free of water hyacinth as the collecting area. Approximately 4 m² of this was on a rocky protrusion of the launch that was between 10 and 30 cm below the surface throughout the 3-month collecting period (water levels fluctuated somewhat). The remaining part of the

collecting area was a shallow sand ledge. On each sampling occasion at this site we collected every visible snail that was within the designated collection area. Our first collection date at this site was 26 May 1998 and we collected every 9–10 days until 24 August 1998 for a total of ten collection events.

At site 2 we used a fine mesh rectangular fishing net (15 × 12 cm) to collect snails. We chose three sampling points 2 m apart and 50 cm from shore. From each of these three central points, we also sampled outward every 10 cm for 50 cm in each of eight directions. Thus, each central sampling point had 40 satellite sampling points. At each sampling point, the net was dipped approximately 20 cm, the contents brought to shore and the snails removed. At site 2 we collected every 9–10 days starting on 29 May 1998 and continuing through 14 September 1998, for a total of 12 collection events.

All snails were measured (shell width) and marked with fingernail polish when first captured. For snails greater than 8.5 mm wide, we painted a unique three-digit number on the shell. To allow observation of spiral growth (the amount of shell added in the direction of shell growth) on any subsequent captures, we also marked the leading edge of the shell. Snails that were smaller than 8.5 mm wide were only marked at their leading edge, but their marks were color-coded to allow us to determine original capture dates and recaptures. On each capture occasion, we recorded the identification number of collected marked snails. If growth was apparent, we measured spiral growth and the new shell width and remarked the leading edge. On all but the last capture occasion, captured unmarked snails were all marked. To maximize growth data at site 2, after collecting snails as described above, we also collected all marked snails that we could see in an hour. At both sites, recaptured snails were returned to the point of collection immediately after data were recorded and new marks had dried (within about 10 min). Newly captured snails were distributed throughout the collection area after measuring and marking (within 6 h).

We determined daily growth rates by calculating the difference in width of recaptured snails and dividing by the number of days since the previous capture.

Food preference

In February 1999 we collected approximately 100 adult *Pomacea canaliculata* from three sites: site 1 (above), and roadside ditches in Punalu'u and Hāle'iwa (both also on the island of O'ahu). At site 1, in addition to the

dominant water hyacinth, two other macrophytes were found in abundance: *Ludwigia octovalis* and *Vigna marina*. *L. octovalis* and various grasses were present at both ditch sites. After collection, snails were held in tap water at room temperature ($23 \pm 2^\circ\text{C}$) and starved for a minimum of 24 h before experimentation.

We collected five species of plants for the food-choice experiments: *Eichhornia crassipes* (water hyacinth), *Pistia stratiotes* (water lettuce), *Colocasia esculenta* (taro), *Ludwigia octovalis*, and *Vigna marina*. *E. crassipes*, *P. stratiotes*, and *C. esculenta* are non-native in Hawai'i; *L. octovalis* is pantropical and may have been unintentionally introduced by early Hawaiians, although it may also occur in Hawai'i naturally; *V. marina* is a pantropical coastal species and is assumed to occur in Hawai'i naturally (Wagner et al. 1990). We collected all plant samples from Kawainui Marsh with the exception of taro, which we collected from Kailua Beach Park (O'ahu). Plant specimens were held in plastic bags or unsealed plastic containers. We tested preference for leaves and stems only.

After the starvation period, *P. canaliculata* food preferences were tested in a pairwise fashion. We tested the snails' preferences for each plant species against all other plant species. As controls, we also presented snails a choice between two samples of the same plant species. Food preferences were tested by placing the snail in the center of a 20 × 27 cm aluminum pan filled to approximately 5 cm depth with tap water. The snail was placed equidistant from and not facing either of the two test plants, which were placed at opposite ends of the pan. For each replicate, the test snail was given 15 min to make a choice. We considered a choice had been made and stopped the trial if we observed a snail feeding on a plant or if a snail was in contact with a plant at the end of the 15 min period. On the rare occasions in which the snail did not make a choice within 15 min, we replaced it with a new test snail and repeated the trial. We rinsed the pans with tap water between trials.

We recorded the number of trials in which each plant species was chosen over another. For each set of trials of one plant against another we determined the probability (*P*) of obtaining the observed choices given a null hypothesis of no preference, assuming the data would follow a binomial distribution. We repeated each set of pairwise tests until we observed a significant ($P < 0.01$) preference of one plant over the other ('sequential design' – Cole 1962), or until approximately 30 trials (range 27–43) had been performed with no clear preference observed.

Results

Growth rate

Laboratory

Figures 1A–D show mean widths of surviving snails for each treatment and clutch for the length of the experiment. Figures 2A–D show numbers of snails surviving for each treatment and clutch.

As shown in Figures 1 and 2, unfed snails showed the lowest growth and survival. Thirteen out of 60 unfed snails from clutches 1 and 2 survived through week 20 of the experiment and all were dead by week 51. All of the 30 unfed snails from clutches 3 and 4 were dead by week 4. Occasionally small particles were observed in the digestive tracts of unfed snails during measuring, suggesting that the snails were obtaining some food from surface deposits on the glass jars (algae, etc.).

Snails fed on water hyacinth did not fare much better than unfed snails. Figures 1A–C show that growth rates were almost identical to those of unfed snails and much lower than those of snails fed on green-leaf lettuce. The largest width measured on a snail fed on water hyacinth was 12.3 mm at 34 weeks from clutch 1. Mean widths of snails fed on water hyacinth surviving at the end of the experiment were 9.7 ± 0.7 , 11.3 ± 0.5 , and 6.6 mm (1 snail only) for clutches 1–3, respectively, compared to 23.4 ± 2.8 , 23.4 ± 4.7 , and 23.9 ± 4.1 mm for snails fed on green-leaf lettuce. Dark green and brown particles observed in the digestive tracts of snails fed on water hyacinth suggest that the snails were ingesting parts of the plants and/or surface deposits on the glass jars. However, given that growth rates and mortality were essentially the same as for unfed snails, and that there was no visible damage caused to the water hyacinth by the snails, we conclude that they were eating it little (perhaps detrital material associated with the roots) if at all.

Snails fed on water lettuce grew faster and survived longer than unfed snails (Figures 1C, D, 2C, D) and than snails fed on water hyacinth (Figures 1C, 2C). Clutch 3 snails fed on water lettuce had growth rates approaching those of snails fed on green-leaf lettuce (Figure 1C), but had lower survivorship than the latter (Figure 2C). Clutch 4 snails fed on water lettuce had lower growth rates (Figure 1D) but higher overall survivorship (Figure 2D) than snails fed on green-leaf lettuce. Mean widths of snails fed on water lettuce surviving at the end of the experiment were 23.5 ± 1.3 and 16.2 ± 1.1 mm for clutches 3 and 4, respectively.

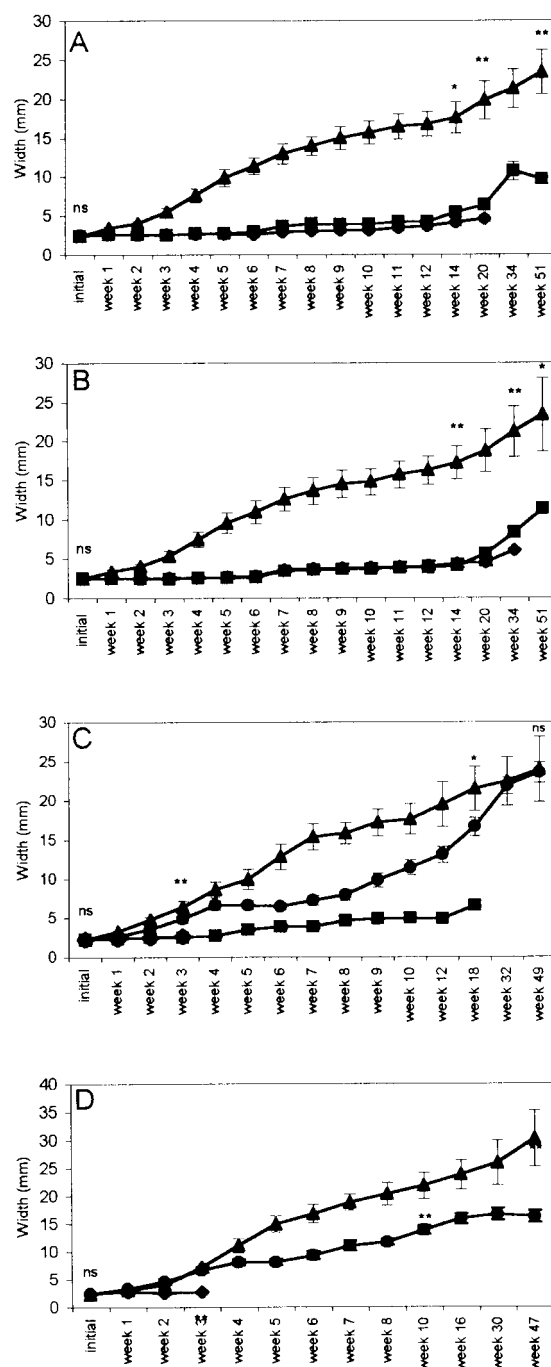


Figure 1. Mean widths (mm) of experimental snails. A – clutch 1 (30 snails per treatment: two jars combined); B – clutch 2 (30 snails per treatment: two jars combined); C – clutch 3 (15 snails per treatment); D – clutch 4 (15 snails per treatment). Diamonds – unfed; squares – fed on water hyacinth; circles – fed on water lettuce; triangles – fed on green-leaf lettuce. Bars represent one standard deviation. Significances in Kruskal–Wallis tests (see methods) are indicated as: ns – not significant; * $P < 0.05$; ** $P < 0.005$.

We provided food *ad libitum*, but did not control for decreased crowding as snails died. It is possible that there was a negative effect of density on growth rate in jars with relatively high survivorship; however if so,

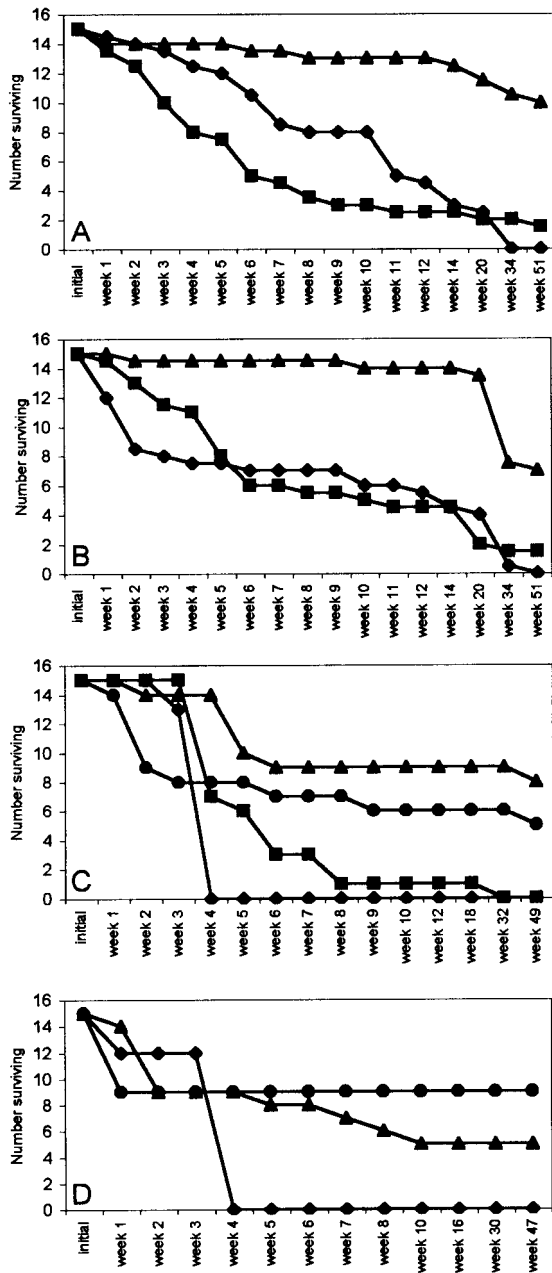


Figure 2. Survival of experimental snails. A – clutch 1 (mean of 2 jars; 15 snails per jar); B – clutch 2 (mean of two jars; 15 snails per jar); C – clutch 3 (one jar; 15 snails); D – clutch 4 (one jar; 15 snails). Symbols as in Figure 1.

it was not enough to reverse the effect of the different foods on growth rate.

Snails fed on green-leaf lettuce were the only snails that reproduced over the course of the experiment. We found three new egg clutches in the jar from clutch 3 at week 44, and one new clutch in the clutch 4 lettuce-fed snail jar at week 43. Adults were separated from egg clutches within a day of laying. All clutches were allowed to hatch and all produced viable snails.

Field

Figure 3 shows the total number of snails captured in each size class by site and Figure 4 shows the proportion of each size class recaptured at least once. At site 1 we never found snails smaller than 15 mm in width, but we did collect more snails that were larger than 21.5 mm than we did at site 2. At site 2 we captured snails of all size classes, though snails smaller than 21.5 mm were more abundant than larger snails. At both sites, the size class with the highest proportion of recaptures was the largest class. At site 1, this was based on recapture of one individual, at site 2 on 25 individuals.

We combined laboratory and field growth data in Figure 5. Using multiple rank tests (with Bonferroni corrections) we compared growth rates between field sites and each laboratory treatment at all size ranges for which there were data; and we compared growth rates between the two field sites in the same way. Growth rate differences among the laboratory treatments have already been demonstrated (above). Snails at site 2 appeared to grow faster than those at site 1 for all age classes that were present at both sites, but these

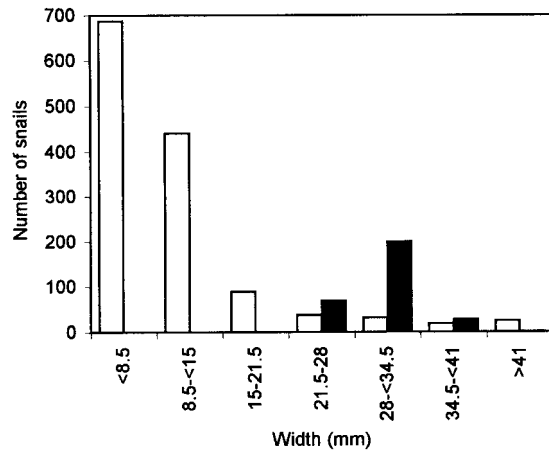


Figure 3. Size-class distribution of *Pomacea canaliculata* captures at site 1 (black bars) and site 2 (open bars).

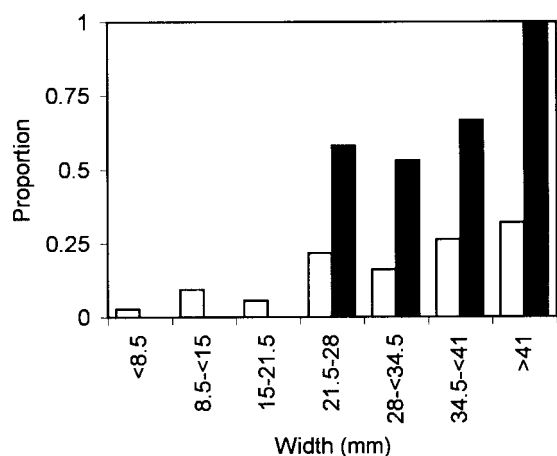


Figure 4. Proportion of *Pomacea canaliculata* recaptured at least once, by size class for site 1 (black) and site 2 (open).

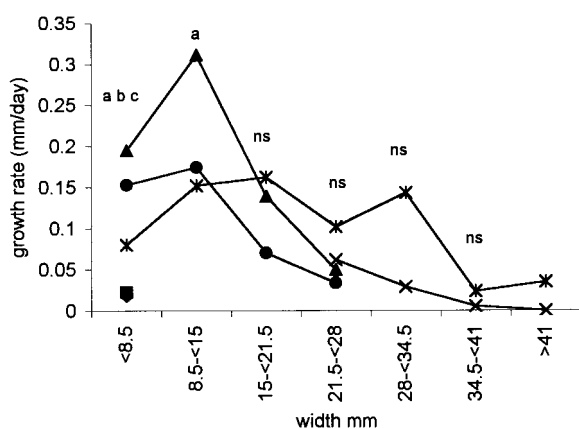


Figure 5. Laboratory and field growth rates by size class. Diamond – unfed (laboratory); square – fed on water hyacinth (laboratory) (note, diamond and square almost coincident on graph); circles – fed on water lettuce (laboratory); triangles – fed on green-leaf lettuce (laboratory); crosses – site 1 (field); asterisks – site 2 (field). Significance in multiple rank comparisons with Bonferroni corrections are indicated as: ns – not significant; significantly different: a – green-leaf lettuce vs. site 2 ($P < 0.05$); b – water hyacinth vs. site 2 ($P < 0.05$); c – unfed vs. site 2 ($P < 0.05$). See text for comparisons tested.

differences were not statistically significant ($P > 0.05$). For snails less than 8.5 mm in width, laboratory snails fed on green-leaf lettuce grew faster than snails in the field (Figure 5) and field snails grew faster than laboratory snails fed on water hyacinth and than unfed snails ($P < 0.05$ in both cases). Snails fed on green-leaf lettuce grew significantly faster than field snails in the 8.5–<15 mm size class, but there was no significant difference in the 15–<21.5 and 21.5–<28 mm classes. Growth rates of field snails and laboratory snails fed

on water lettuce did not differ significantly in any size class.

Food preference

The results of all pairwise trials are summarized in Table 1. The snails clearly preferred the native *Vigna marina* over all other plants ($P < 0.005$ in all cases), except taro, for which the preference was not quite significant ($P = 0.063$). The snails' preference for taro over water hyacinth was also not quite significant ($P = 0.063$). No other significant preferences were exhibited.

Discussion

Pomacea canaliculata occurs naturally in Argentina in regions of temperate climate, extending northwards towards the Amazon basin. It has achieved pest status in much of tropical and subtropical eastern Asia and the Pacific. Increased growth rates as a result of warmer climate may contribute to its rapid spread and establishment.

Our laboratory growth experiment findings are comparable to those of Estebenet and Cazzaniga (1992) who reared *Pomacea canaliculata* at a constant 25 °C and reported successful reproductive activity at 10 months. Our snails were exposed to a temperature of about 23 °C (occasionally ranging from 20 to 28 °C) and also showed reproductive activity at 10 months. In other experiments Estebenet and Cazzaniga (1992) reared snails at seasonally changing temperatures (9–29 °C in Argentina) that led to periods of inactivity, and successful reproduction was only achieved after 25 months. Our snails were never inactive for long periods.

We could not reliably estimate age at reproductive maturity for our field populations in Hawai'i. However, although growth rates in the field for larger snails did not differ significantly from those fed on green-leaf lettuce in the laboratory (the only laboratory snails to reach reproductive maturity), during their early stages these laboratory-reared snails grew faster than the comparable-sized field snails. Therefore our recorded time to reach maturity in the laboratory (10 months) is probably an under-estimate of time to maturity in the field in Hawai'i. In the Philippines, with a warmer climate than Hawai'i, *P. canaliculata* is reported to reach reproductive maturity in 2–3 months (references in Cowie, in press b). However, it also reaches maturity

Table 1. Results of the food preference experiments.

	<i>V. marina</i>	<i>L. octavalis</i>	<i>E. crassipes</i>	<i>P. stratiotes</i>	<i>C. esculenta</i>
<i>Vigna marina</i>	14/14 (50%) ^a <i>P</i> = 0.575 ^b				
<i>Ludwigia octavalis</i>	33/14 (70%) <i>P</i> = 0.004	17/13 (57%) <i>P</i> = 0.292			
<i>Eichhornia crassipes</i> (water hyacinth)	34/11 (76%) <i>P</i> < 0.001	17/20 (46%) <i>P</i> = 0.744	14/17 (45%) <i>P</i> = 0.763		
<i>Pistia stratiotes</i> (water lettuce)	13/2 (87%) <i>P</i> = 0.004	14/19 (42%) <i>P</i> = 0.852	19/14 (58%) <i>P</i> = 0.243	16/19 (46%) <i>P</i> = 0.750	
<i>Colocasia esculenta</i> (taro)	27/16 (63%) <i>P</i> = 0.063	19/14 (58%) <i>P</i> = 0.243	23/13 (64%) <i>P</i> = 0.063	13/14 (48%) <i>P</i> = 0.649	17/15 (53%) <i>P</i> = 0.430

^aThe number preceding the slash is the number of trials in which the plant in the column heading was selected; the number after the slash is the number in which the plant in the row heading was selected. The percentage is the percent of trials in which the plant in the column heading was selected.

^b*P*-values represent the probability of obtaining the observed choices given a null hypothesis of no preference.

in 2 months during the summer in Kyushu, southern Japan (Wada 1997), although summer temperatures in Kyushu approximate those of Hawai'i (mean daily maximum 31–32 °C).

Although the original introductions to southeast Asia were from temperate Argentina, the distribution of *Pomacea canaliculata* extends northwards into the Amazon basin. Thus, it is extremely flexible ecologically and this may be one reason for its success when transported to new environments. Furthermore, the greatest diversity of species in the genus *Pomacea* occurs in tropical south and central America, so that although the original introductions were of snails from a temperate region, the phylogenetic history of *P. canaliculata* may mean that it is evolutionarily preadapted to life in the tropics.

Consistent with expectations for an invasive organism, the snails seem to be able to persist through adverse conditions. *Pomacea canaliculata* can survive buried in mud (normal aestivation behavior) for up to 3 months (Schnorbach 1995), but they have also been reported as able to survive over 7 months without water (Mochida 1991). We found that 39% of unfed snails survived 6 weeks; a few were still alive at 20 weeks; but all were dead by week 51. This finding suggests that in field situations, snails may be able to persist through lengthy periods of low food availability, although whether such starved snails would continue to grow and reproduce is not known.

Diet also plays a role in growth rate. *Pomacea canaliculata* grew poorly on water hyacinth. The snails grew faster on water lettuce, another invasive plant, but not as fast as they did on green-leaf lettuce. We

might expect that *P. canaliculata* would select foods permitting rapid growth. However, our food preference data do not support this expectation. *P. canaliculata* grew much more rapidly on water lettuce than on water hyacinth, yet showed no significant preference between them in the food choice experiment. Our experiments do not account for the possibility that *P. canaliculata* might change its food preferences or growth rates on different food items over the course of its development.

The results from our food preference experiments do confirm Estebenet's (1995) conclusion (using plants collected in Argentina) that *Pomacea canaliculata* actively selects its food and exhibits a preference for certain macrophytes. We tested plants, both native and non-native, that are commonly found with *P. canaliculata* in Hawai'i. *P. canaliculata* prefers *Vigna marina* over all other offered food items, except possibly taro, and may prefer taro to water hyacinth. Although we did not test growth rates on *Vigna marina* or taro, we might expect that *P. canaliculata* would grow most rapidly on these preferred foods. In general, our preference experiments demonstrated little differential pre-contact response to chemicals released by the plants, implying that the differential growth rates (presumably mediated by differential feeding) result from post-contact responses.

Pomacea canaliculata has been proposed as an agent for control of invasive plant species (Cazzaniga 1981; Okuma et al. 1994; Wada 1997). Results from both our growth and food preference experiments indicate that this snail would not be an effective control agent for water hyacinth, which has been considered the world's most important aquatic weed and one which

has spawned an enormous amount of research on biological control (e.g., Harley et al. 1996; Julien et al. 1996). *P. canaliculata* did eat water lettuce, also a major invasive plant (Lach, in press), but its growth when fed on this plant was not as fast as when fed on green-leaf lettuce. Despite exhibiting some clear food preferences, *P. canaliculata* did feed on all offered food items (with the probable exception of water hyacinth) and thus should still be considered a food generalist. In new environments it will be difficult to predict which plant species will be preferred; choices may change as the composition of the plant community changes; and these changes may be mediated directly by human impacts, seasonality, or even snail grazing. Arguments that *P. canaliculata* could be useful in situations where reduction of total aquatic plant biomass is required are dangerous, even if the locality appears circumscribed within relatively unsuitable habitat. *Pomacea canaliculata* has been shown to spread very readily from one body of water to another (Lach and Cowie 1999), probably through a combination of mechanisms involving both snails and their eggs and including deliberate and inadvertent transport by humans, accidental transport by birds, flooding and other unusual meteorological events (e.g., hurricanes). It is extremely unlikely that it would remain confined to the body of water to which it was introduced. *Pomacea canaliculata* should therefore not be introduced to control aquatic weeds, as it may have serious impacts on native aquatic plants and the communities they support, both within the area to which it is introduced and in areas to which it will inevitably spread.

Changes in life history parameters, and perhaps even in feeding habits, in introduced populations of *Pomacea canaliculata*, appear to facilitate the species' invasiveness. Initially, these changes may simply be direct physiological and behavioral responses to a different environment. However, it is also possible that genetic changes may occur over a longer time scale, further facilitating the snails' invasiveness, enhancing their pest status, and emphasizing the need to prevent their introduction and spread in natural ecosystems in the many parts of the world where they would probably thrive.

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References

- Acosta BO and Pullin RSV (1991) Environmental impact of the golden apple snail (*Pomacea* sp.) on rice farming systems in the Philippines. Freshwater Aquaculture Center, Central Luzon State University, Munoz, Nueva Ecija; ICLARM, Manila, vi + 34 pp
- Baker GH (1998) The golden apple snail, *Pomacea canaliculata* (Lamarck) (Mollusca: Ampullariidae), a potential invader of fresh water habitats in Australia. In: Zalucki MP, Drew RAI and White GG (eds) Pest Management – Future Challenges. Proceedings of the Sixth Australasian Applied Entomological Research Conference, Brisbane, Australia, 29 September – 2 October 1998. Volume 2, pp 21–26. University of Queensland Printery, Brisbane
- Cazzaniga NJ (1981) Evaluación preliminar de un gasterópodo para el control de melezas acuáticas su sumergidas. In: C.I.C., II Reunión sobre Malezas Subacuáticas en Canales de Desagüe de CORFO, pp 131–165
- Cazzaniga NJ and Estebenet AL (1984) Revisión y notas sobre los hábitos alimentarios de los Ampullariidae (Gastropoda). *Historia Natural* 4: 213–224
- Cerutti R (1998) An infestation of *Pomacea canaliculata* (Lamarck, 1804) in Lake Miramar, San Diego, California. *The Festivus* 30: 25–27, 29
- Cole LC (1962) A closed sequential test design for toleration experiments. *Ecology* 43: 749–753
- Cowie RH (1995) Identity, distribution and impacts of introduced Ampullariidae and Viviparidae in the Hawaiian Islands. *Journal of Medical and Applied Malacology* 5[for 1993]: 61–67
- Cowie RH (1996) New records of introduced land and freshwater snails in the Hawaiian Islands. *Bishop Museum Occasional Papers* 46: 25–27
- Cowie RH (1997) Catalog and bibliography of the nonindigenous nonmarine snails and slugs of the Hawaiian Islands. *Bishop Museum Occasional Papers* 50: 1–66
- Cowie RH (in press a) Can snails ever be effective and safe biocontrol agents? *International Journal of Pest Management*.
- Cowie RH (in press b) Apple snails as agricultural pests: their biology, impacts, and management. In: Barker GM (ed) *Molluscs as Crop Pests*. CABI, Wallingford
- Estebenet AL (1995) Food and feeding in *Pomacea canaliculata* (Gastropoda: Ampullariidae). *The Veliger* 38: 277–283
- Estebenet AL and Cazzaniga NJ (1992) Growth and demography of *Pomacea canaliculata* (Gastropoda: Ampullariidae) under laboratory conditions. *Malacological Review* 25: 1–12
- Halwart M (1994) The golden apple snail *Pomacea canaliculata* in Asian rice farming systems: present impact and future threat. *International Journal of Pest Management* 40: 199–206
- Harley KLS, Julien MH and Wright AD (1996) Water hyacinth: a tropical worldwide problem and methods for its control. In: Brown H, Cussans GW, Devine MD, Duke SO, Fernandez-Quintanilla C, Helweg A, Labrada RE, Landes M, Kudsk P and

- Streibig JC (eds) Proceedings of the Second International Weed Control Congress, Copenhagen, 25–28 June 1996, Volume II, pp 639–644. Department of Weed Control and Pesticide Ecology, Slagelse, Denmark
- Julien MH, Harley KLS, Wright AD, Cilliers CJ, Hill MP, Center TD, Cordo HA and Cofrancesco AF (1996) International cooperation and linkages in the management of water hyacinth with emphasis on biological control. In: Moran VC and Hoffmann JH (eds) Proceedings of the IX International Symposium on Biological Control of Weeds, 19–26 January 1996, Stellenbosch, South Africa, pp 273–282. University of Capetown, Capetown
- Lach L (in press) Losses from aquatic weeds. In: Pimentel D (ed) Encyclopedia of Pest Management. Marcel Dekker, New York
- Lach L and Cowie RH (1999) The spread of the introduced freshwater apple snail *Pomacea canaliculata* (Lamarck) (Gastropoda: Ampullariidae) on O‘ahu, Hawai‘i. Bishop Museum Occasional Papers 58: 66–71
- Mochida O (1991) Spread of freshwater *Pomacea* snails (Pilidae, Mollusca) from Argentina to Asia. *Micronesica*, Supplement 3: 51–62
- Naylor R (1996) Invasions in agriculture: assessing the cost of the golden apple snail in Asia. *Ambio* 25: 443–448
- Neck RW and Schultz JG (1992) First record of a living channeled applesnail, *Pomacea canaliculata* (Pilidae), from Texas. *Texas Journal of Science* 44: 115–116
- Okuma M, Tanaka K and Sudo S (1994) Weed control method using apple snail (*Pomacea canaliculata*) in paddy fields. *Weed Research, Japan* 39: 114–119
- Perera G and Walls JG (1996) Apple Snails in the Aquarium. T.F.H. Publications, Inc., Neptune City, New Jersey, 121 pp
- Schnorbach H-J (1995) The golden apple snail (*Pomacea canaliculata* Lamarck), an increasingly important pest in rice, and methods of control with Bayluscid. *Pflanzenschutz-Nachrichten Bayer* 48: 313–346
- Simberloff D and Stiling P (1996) Risks of species introduced for biological control. *Biological Conservation* 78: 185–192
- Thompson FG (1997) *Pomacea canaliculata* (Lamarck, 1822) (Gastropoda, Prosobranchia, Pilidae): a freshwater snail introduced to Florida, U.S.A. *Malacological Review* 30: 91
- Wada T (1997) Introduction of the apple snail *Pomacea canaliculata* and its impact on rice agriculture. In: Proceedings. International workshop on biological invasions of ecosystems by pests and beneficial organisms, pp 170–180. National Institute of Agro-Environmental Sciences, Ministry of Agriculture, Forestry and Fisheries, Tsukuba
- Wagner WL, Herbst DR and Sohmer SH (1990) Manual of the flowering plants of Hawai‘i. University of Hawaii Press and Bishop Museum Press, Honolulu, xviii + 1853 pp