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BIOLOGY, ECOLOGY AND CONTROL OF THE INVASIVE
CHANNELED APPLE SNAIL, *POMACEA CANALICULATA*

by

CHRISTINA M. TREXLER
B.S. University of Central Florida, 2005

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology
in the College of Sciences
at the University of Central Florida
Orlando, Florida

Summer Term
2011

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ABSTRACT

Invasive species are detrimental to native biotas worldwide. Recently, Florida was invaded by a freshwater snail (*Pomacea canaliculata*) native to Argentina. This snail is a serious pest of rice crops in Asia, but little is known about its interactions within Florida ecosystems. Possible competitive exclusion of the native congener (*P. paludosa*) is a concern because it is the almost exclusive prey of the federally endangered Everglades snail kite (*Rostrhamus sociabilis*).

My research consisted of three parts. First, to identify possible methods to control *P. canaliculata* in the egg stage, I experimentally evaluated the effects of photoperiod, substrate availability, and food type and availability on hatching success and hatchling survival. None of these factors significantly affected hatching or survival, suggesting that *P. canaliculata* could invade many water bodies. Second, I used a randomized block design to assess the separate and combined effects of population density and food availability on growth and spawning of *P. canaliculata*. Food availability but not density significantly affected growth; snails fed less food grew less, but neither factor affected spawning. Third, I used a replacement series design to assess competition between *P. canaliculata* and *P. paludosa* under food limitation. For both species, snails fed less grew significantly less, and snails exposed to greater congener densities spawned less than when exposed to conspecifics only. While my results predict that *P. paludosa* should exclude *P. canaliculata*, previous literature and current invasions suggest that the exotic snail may co-exist with its North American congener.

ACKNOWLEDGMENTS

I thank my committee members, Dr. John Osborne, Dr. John Fauth and Dr. David Jenkins for providing a strong foundation on which to begin a thesis. I thank Gloria Eby for help collecting snails from Lake Brantley, and undergraduate assistants James Kraver, Julia Sackheim and Stacy Zubkousky for help with experiment management. I thank the UCF Biology Graduate students for all the assistance and reviews, namely Rachel Morgan, Katie Windes and Annie Weiler-Weeks, as well as my family and friends for support. This project was supported by a grant from the Seminole County Stormwater Division and scholarships from the Astronaut Trail Shell Club.

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INTRODUCTION

Invasive species negatively affect ecological systems worldwide (Mooney and Cleland 2001), may outcompete native species (Brown and Wilson 1956; Porter and Savignano 1990; Holway 1999; Brown and Mitchell 2001; Mooney and Cleland 2001) and can cause detrimental changes in native systems (Wyckoff and Webb 1996; Human and Gordon 1997; Vander Zanden et al. 1999; Levin et al. 2006). In turn, these changes can homogenize biotas, destabilize ecosystems and reduce ecosystem services (Vitousek 1990; see Lodge 1993 for review; McKinney and Lockwood 1999; Olden et al. 2004). Effects of invasions in freshwater ecosystems can be difficult to predict because many factors determine invasibility (Moyle and Light 1996). The extent and severity of each invasion differs and management agencies must prioritize which to fight and then develop efficient control tactics (Kaiser 1999; Mack et al. 2000; Gurevitch and Padilla 2004). Florida has been invaded by numerous species, including plants, fishes, reptiles and birds (Frank and McCoy 1995). Of the 31 exotic freshwater mollusk species established in the US and Great Lakes region (Keller et al. 2007), 11 are in Florida (unpublished data, USGS online non-indigenous species database).

One recent freshwater invader and the subject of this thesis, *Pomacea canaliculata* (channeled or golden apple snail), is indigenous to South America and currently inhabits >100 water bodies in Florida, ranging from roadside ditches to major lakes and rivers (Dana Denson, Florida Department of Environmental Protection, *personal communication*). *Pomacea canaliculata* exhibits qualities typical of invasive herbivores: a large appetite for native plants (Lach et al. 2000; Boland et al. 2008; Gloria Eby, Seminole County Stormwater division, *personal communication*), tolerance of extreme conditions (Oya et al. 1987; Halwart 1994),

niche generalism (Naylor 1996; Cazzangia 2002), high potential reproductive output and long lifespan (Naylor 1996). After its introduction to Asian rice paddies as a food source in the 1980s, *P. canaliculata* spread, causing millions of dollars of damage (Halwart 1994; Naylor 1996). Ecologically, *P. canaliculata* converted the Asian wetland flora from aquatic plant-based to an undesirable algae-based condition (Carlsson et al. 2004). In Lake Brantley, Florida, *P. canaliculata* contributed to a biota shift from native to invasive plants after its arrival, likely through the aquarium trade (Gloria Eby, Seminole County Stormwater division, *personal communication*). In addition, *P. canaliculata* can eutrophy water bodies through its high rates of herbivory, defecation and subsequent nutrient release (Carlsson et al. 2004a; Carlsson and Lacoursiere 2005).

Pomacea canaliculata may indirectly threaten the endangered snail kite (*Rostrhamus sociabilis*) by displacing its main food source, the native Florida apple snail *P. paludosa* (Sykes 1987). Consumption of *P. canaliculata* by the kite has not been evaluated. Peripheral habitats of the snail kite (Takekawa and Beissinger 1989) are currently being invaded by *P. canaliculata* (Figure 1), but competition between the snails has not been evaluated in a Florida ecosystem. Both species share biological features (eggs oviposited out of water, lungoid organ, aestivation) that make them likely competitors. Adults of *P. canaliculata* are generalists that eat large amounts of most aquatic vegetation, some detritus (Estebenet and Martin 2002) and even prey on eggs and hatchlings of the tropical snail, *Biomphalaria peregrine* (Cazzangia 1990a). *Pomacea canaliculata* (Figure 2) is extremely fecund; females reach reproductive maturity at 2-3 mo (Estebenet and Martin 2002; Estoy et al. 2002a,b) and lay an average of 8700 eggs/y over a lifespan of 3-4 y (Naylor 1996). Fecundity of *P. paludosa* is lower because of its shorter lifespan

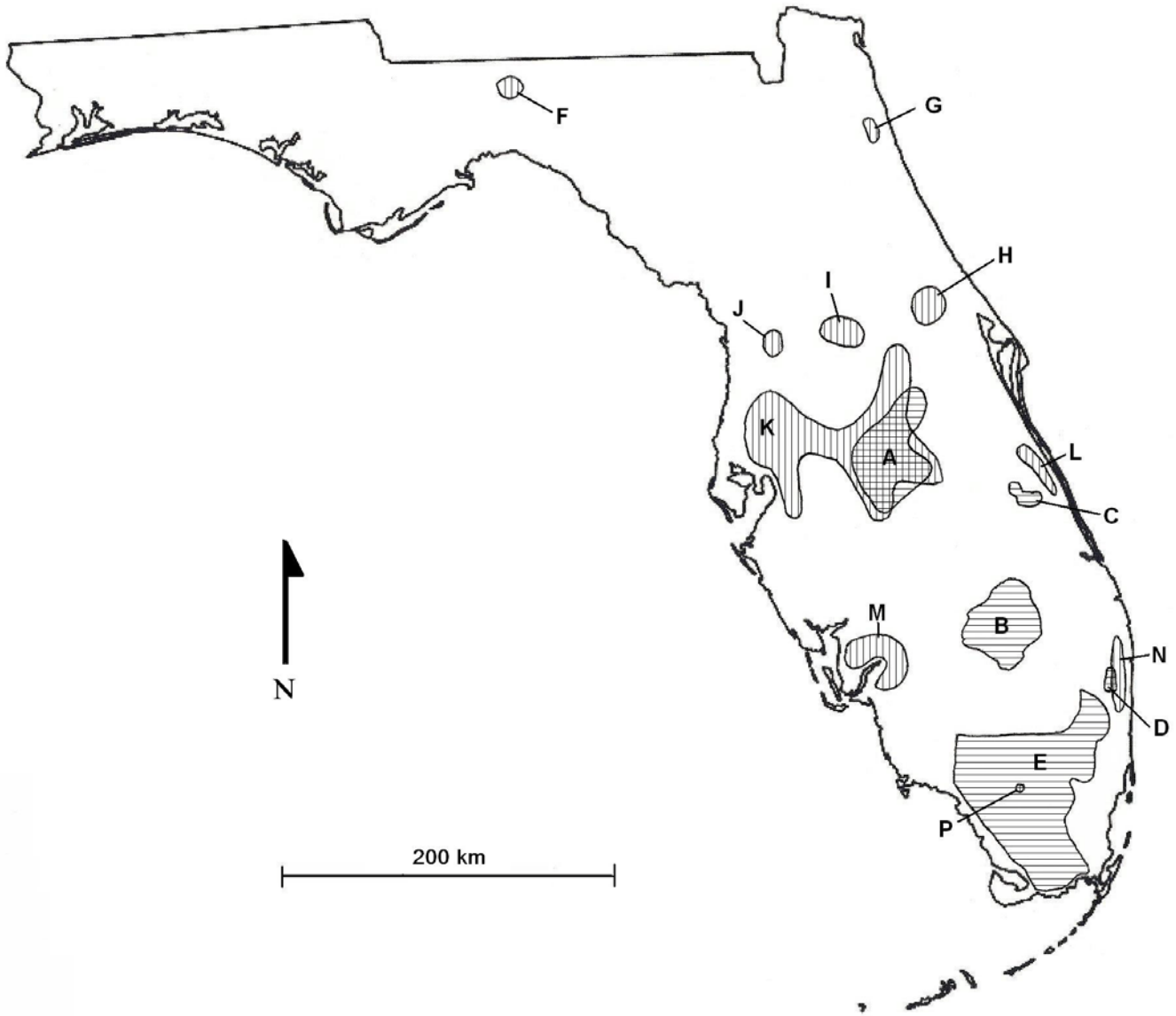


Figure 1. Distribution of the channeled apple snail, *Pomacea canaliculata* (vertically shaded polygons adapted from Dana Denson, Florida Department of Environmental protection, *personal communication*) and the snail kite, *Rostrhamus sociabilis*, (horizontally shaded polygons adapted from Takekawa and Beissinger 1989). A = Kissimmee chain of lakes, B = Lake Okeechobee, C = St. Johns Marsh, D = Loxahatchee Slough, E = Everglades wetlands, F = various water bodies around Tallahassee, G = upper St. Johns River and tributaries, H = Volusia County water bodies

in and around the St. Johns River, I = Lake County water bodies in residential areas near Eustis, J = Withlacoochee River, K = Area including the Kissimmee chain of lakes, Tampa Bay tributaries and associated water bodies in-between, L = residential water bodies east of the St. Johns Marsh, M = Water bodies near the northeastern tributary to San Carlos Bay, N = residential water bodies east of the Loxahatchee natural area, P = single report within Everglades National Park.

(1-2 y) and smaller clutches (Darby et al. 2003). Moreover, displacement of *P. paludosa* may be accelerated by the snail kite because selective predators that eat native species facilitate dominance of invasive congeners (Garvey et al. 1994).

My study investigates the reproductive biology of *P. canaliculata* in Florida and the strength of competitive interactions with the native *P. paludosa*. I aim to provide wildlife managers with information that leads to control methods. Evaluating species interactions (e.g., competition) can improve understanding of mechanisms that facilitate species invasions (Osenberg 1989; Taylor and Aarssen 1989) and help identify the best invasion-management strategy. Optimal control theory, which often is applied in an agricultural setting (Zimdahl 1988), uses life history knowledge of weed and crop plants to determine the critical period for weed removal – the time when weeds most negatively affect crop plants and when crop plants are least affected by the control mechanism (Zimdahl 1988). This strategy minimizes the management resources needed and increases crop yield, and can be applied to *P. canaliculata* to determine control methods once information about ontogeny is acquired, including its life cycle (Figure 2).

Understanding factors that inhibit growth, spawning, hatching and hatchling survival is beneficial for developing controls for egg-laying invasive species (Cowie 2002). Three factors I investigated could affect survival and hatching: food type available at hatching, photoperiod during clutch maturation and population density. If available food is not edible to hatchlings, survival can be lower (Halwart 1994; Albrecht et al. 1999; Lach et al. 2000). Day length, as a part of seasonality, can affect egg maturation (Halwart 1994). Thus, management should be

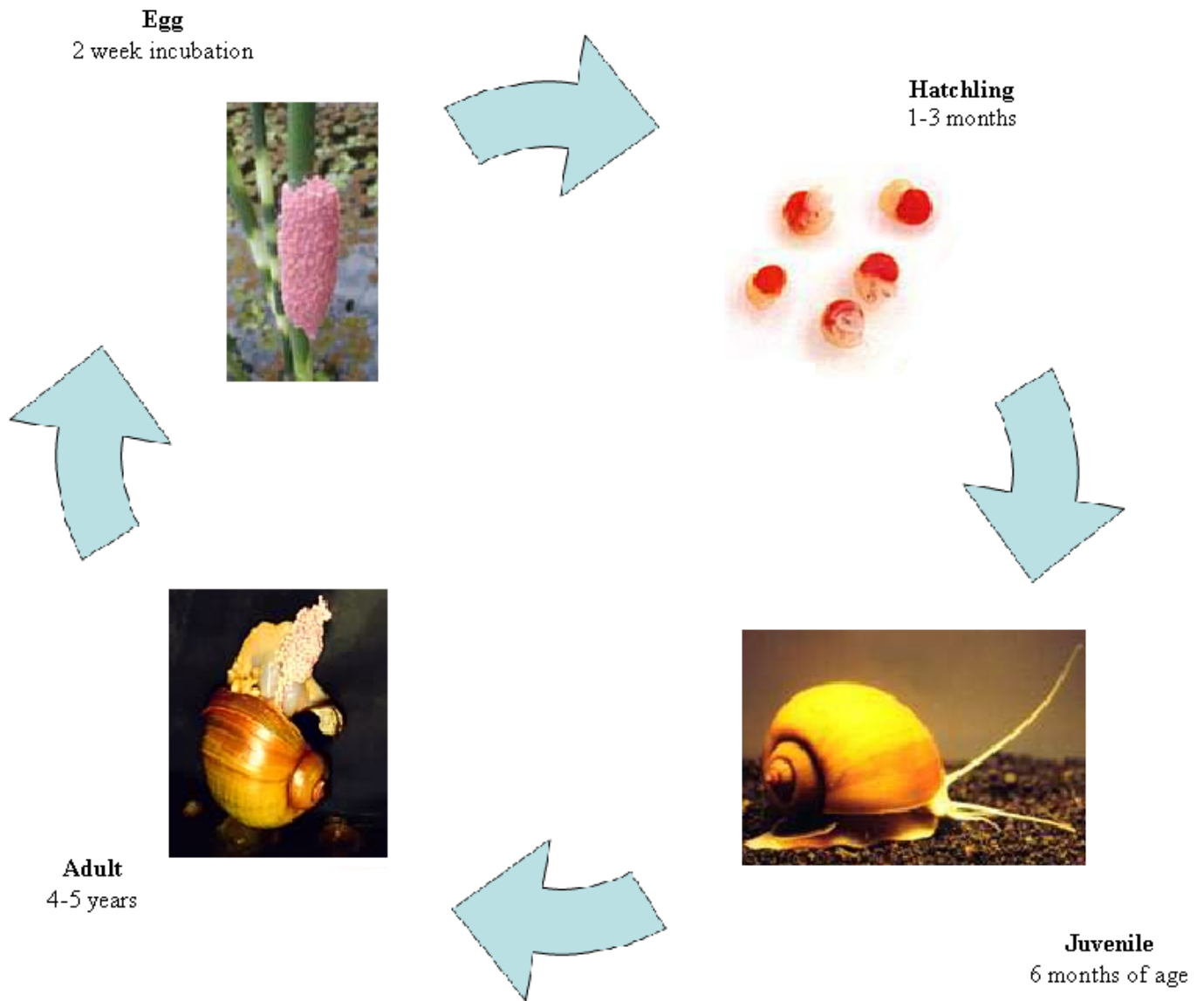


Figure 2. Life cycle of *Pomacea canaliculata*.www.applesnail.net.

more aggressive in invasion sites with preferred hatchling food during photoperiods when clutches have a greater hatching rate. Population density can affect reproduction and fecundity (Gill 1972a, Levitan 1991; Muthiga and Jaccarini 2005) and plays a role in understanding competitive interactions (Law and Watkinson 1987). These in turn enable understanding of ecosystem invasibility and effects on native species (Thomas and Benjamin 1974; Tilman 1980; Dyer and Rice 1999; Brown and Mitchell 2001). In some studies of *P. canaliculata*, frequency of reproduction depended on population density (Tanaka et al. 1999), while in others it was limited by food availability (Albrecht et al. 1999; Estoy et al. 2002b).

My thesis uses laboratory and field experiments to evaluate aspects of the reproductive biology of *P. canaliculata* and its interaction with *P. paludosa*. I concentrated on three topics: 1) identifying factors affecting hatchling survival of *P. canaliculata*, 2) quantifying the independent effects of food availability and population density on its growth and reproduction, and 3) observing competitive interactions between *P. canaliculata* and *P. paludosa*. Results of my research will give wildlife managers information to help control *P. canaliculata* in central Florida waters.

METHODS and MATERIALS

I evaluated the biology of *P. canaliculata* in three separate experiments. Experiment 1 tested specific factors that may affect success or survival, Experiment 2 determined the effects of density and food availability on growth and spawning, and Experiment 3 used a density replacement series to quantify competitive effects on the native *P. paludosa*.

Experiment 1: Factors affecting survival of hatchling *Pomacea canaliculata*

Experiment 1 was a series of similar experiments that tested four factors that could affect hatching and survival of young *P. canaliculata*: food type and availability, photoperiod, and sediment availability. I tested the null hypothesis that each factor had no effect on hatchability or survival of this invasive snail.

I collected clutches spawned by adults obtained from Lake Brantley, Florida, and held under laboratory conditions at the University of Central Florida (UCF) Biological Field Station. I used 25-30 snails in approximately a 50:50 sex ratio as a breeding group and held them in a 150 L aquarium with cycled pond water. Snails were provided unlimited food (*Hydrilla*) and oxygen using air bubblers, and I cleaned the tank as needed by siphoning debris from the bottom. Snails intermittently laid clutches along the tank sides. I carefully removed clutches, divided them in half and immediately placed them onto small pieces of plastic to recement. To reduce handling, I first weighed the plastic without the clutch, then weighed the clutch after placement on plastic and determined clutch mass by subtraction. I allowed the clutch to re-cement to the plastic on a

horizontal axis for ≤ 12 h before hanging it vertically and subjecting it to experimental treatments.

I randomly assigned one-half of each clutch to control conditions and the other to treatment conditions. Treatments were carried out in a random order when clutches were available. Control conditions consisted of unlimited food (both *Hydrilla* and *Spirulina*), a 12:12 photoperiod, dissolved oxygen distributed by an aquarium bubbler, no sediment on the bottom substrate and ambient temperature of approximately 25° C. Treatment conditions were: summer photoperiod (14:10) and winter photoperiod (10:14); a 'pond bottom' consisting of pond sediment and degraded plant matter; *Hydrilla* only; *Spirulina* only; and no food. While one variable was tested, all other variables were held under control conditions, and each treatment was replicated five times. Testing occurred between October 2006 and June 2009.

The treatment arena consisted of a 3.75 L glass jar filled with approximately 800 ml of pond water. I attached the plastic sheets containing clutches to the rim of the jar using clothespins. I subjected clutches to treatments no later than 4 d after oviposition and checked them every 2-3 d for signs of hatching, then allowed hatchling snails to remain under the experimental condition for four weeks. I assessed hatching success (snails hatched as a percentage of clutch mass) and hatchling survival (snails alive as a percentage of those hatched). I first analyzed the effect of treatment with the raw data using paired t-tests. Any pairs of clutches where survival in the control half was zero were considered 'duds' and were removed from this analysis. To test for other sources of variation, I then used linear regression to check for influences of hatching date, number hatched, clutch mass, relative humidity and temperature. Paired t-tests were performed on residuals of these regressions to determine treatment effects.

Post hoc power analysis was completed to determine sample sizes necessary to capture an effect for factors that were not statistically significant.

Experiment 2: Separate and combined effects of food availability and population density on *Pomacea canaliculata*

Experiment 2 tested responses to reduced food and increased population density on reproduction (clutch frequency and clutch size) and growth of snails nearing reproductive age. I tested the null hypothesis that density and food availability did not affect growth or reproduction against the alternative hypothesis, that food, density or both significantly affected growth, reproduction or both.

I used *P. canaliculata* raised from eggs spawned by adults from Lake Brantley, Florida and hatched under laboratory conditions at the UCF Biological Field Station. I fed hatchling snails live *Hydrilla* harvested from UCF experimental ponds and dried *Spirulina, ad libitum*. Juvenile and adult snails were fed live *Hydrilla, ad libitum*. I kept snails in 37 L (10 gallon) aquaria containing pond water from UCF experimental ponds and changed water as needed. I reared hatchlings under laboratory conditions until they reached sexual maturity at approximately 25 mm shell height (Tanaka et al. 1999).

I placed large (420 L, 1 m² surface area) tanks outside near the UCF experimental ponds (Figure 3) and changed water as needed. Sides of the tanks provided egg-laying substrate (10-12 cm from water surface) as they were not filled to the brim. I monitored clutches bi-weekly, recorded their sizes and allowed eggs to hatch.

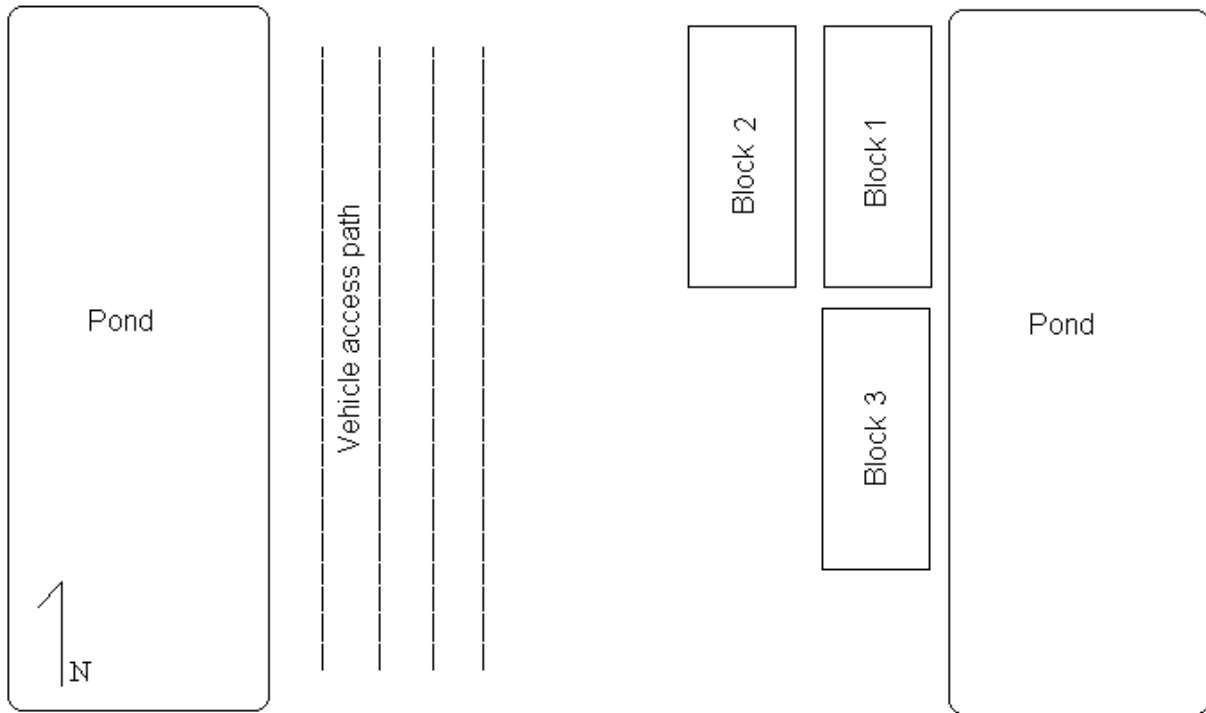


Figure 3. Layout of tanks at UCF experimental ponds for Experiment 2 (not to scale).

Invasive snail sex was determined using the shell height:aperture width ratio method (Cazzangia 1990b). I assigned juvenile *P. canaliculata* to tanks at densities of 2, 4, or 8 snails/m² while maintaining a 1:1 sex ratio. Snail densities in Florida have not been measured but my experimental densities are similar to those of invasive populations in Asian rice paddies: 1-5 snails/m² (Halwart 1994) to 6.5-9.5 snails/m² (Carlsson and Lacoursiere 2004). Snail densities were crossed with three food availabilities: high (*ad libitum*), medium (approximately 50% of maximal food needs) or low (approximately 25% of maximal food needs). I estimated maximum need for *Hydrilla* as 0.499 g/g snail mass/day (Appendix A).

Each food/density combination was completed three times and tanks were arranged in a randomized block design to control for any potential gradient caused by proximity to the experimental pond shoreline and the vehicle access path. The exception was Block 3 which was placed south of Block 1 to accommodate limitations in water pumping equipment. To deter snails from escaping or being eaten by other species, I covered tanks with 2 cm heavy wire mesh. I fed snails bi-weekly and measured tank water temperature, dissolved oxygen, specific conductivity and pH monthly. I assessed size, mass and survival of the initial snails at the end of the experiment, 3 mo after it began. I analyzed results using a three-way fixed model (food x density x block) ANCOVA with number of females per tank (as females grow faster and larger than males; Estebenet and Martin 2002) and mean tank temperature (to control for the known effect of temperature on growth; Albrecht et al. 1999; Estebenet and Martin 2002) as covariates for growth. I analyzed spawning using a three-way fixed model ANOVA. I performed Sidak's *post hoc* test on all appropriate data. Final snail masses and shell heights did not include snails that died during the experiment. Change in mean snail mass and shell height was used rather

than total change to exclude dead snails. As external sexing methods could not be 100% accurate, dissections were completed to verify the number of males and females. Spawning was assessed as eggs laid per female.

Experiment 3: Interactions between invasive *Pomacea canaliculata* and native Florida *P. paludosa*

I conducted a replacement series experiment to determine the effects of the two snail species on each other under multiple density ratios. I tested the null hypothesis that each species had no effect on the other's survival, growth or reproduction (i.e., they were not competitors). I evaluated this hypothesis by estimating parameters of Lotka-Volterra competition models and assessing its predicted outcome (May 1973, Tilman 1980).

The replacement series had a total density of eight snails/tank (m^2) and I substituted each species in multiples of two (0, 2, 4, 6 or 8 individuals) at each of two food availabilities: high (*ad libitum*) and moderate (40% of required food needs). A 1:1 sex ratio was maintained for each species. Snail sex was determined using shell height:aperture width ratio (Cazzangia 1990b) for invasive snails and the morphological method (Hanning 1979) for native snails. As external sexing methods were not 100% accurate, I verified the number of males and females by dissection at the end of the experiment. Spawning was assessed as eggs laid per female.

I completed three replicates of each food/density combination with tanks arranged in a randomized block design to control for any potential gradient caused by proximity to the experimental pond shoreline and the vehicle access path. In contrast to experiment 2, Block 3 was placed west of Block 2 after modifications were made to the water pumping equipment. I

estimated maximum food needs for *P. paludosa* through preliminary trials as 0.354 g *Hydrilla*/g snail/day (Appendix A).

Husbandry techniques, experiment arena management and monitoring were the same as described in Experiment 2. *Pomacea paludosa* was difficult to rear in the laboratory, so I collected snails from UCF experimental ponds, held and fed in the same manner as *P. canaliculata* above, until placing them into a total of 30 outdoor tanks for the experiment near UCF experimental ponds (Figure 4). I analyzed results using a three-way fixed model (food x density x block) ANCOVA. The covariate for invasive snail growth was temperature; for invasive snail spawning covariates were temperature, invasive snail shell height increase and proportion of invasive females. Shell height increase has an inverse relationship with spawning (Albrecht et al. 1999) and proportion of females controlled for the effect of sperm competition and sperm storage (Catalan et al. 2002; Estebenet and Martin 2002; Estoy et al. 2002). Mean water temperature was the covariate for native snail growth and spawning. I performed Sidak's *post hoc* test on all appropriate data. I used equation systems from Lotka-Volterra competition modeling to estimate the effect of interspecies competition (Chesson 2000). Carrying capacity (K) and interspecific competition coefficients (α_{ij}) were estimated from food requirements per mean final snail mass for individuals fed *ad libitum* food and reproduction, respectively.

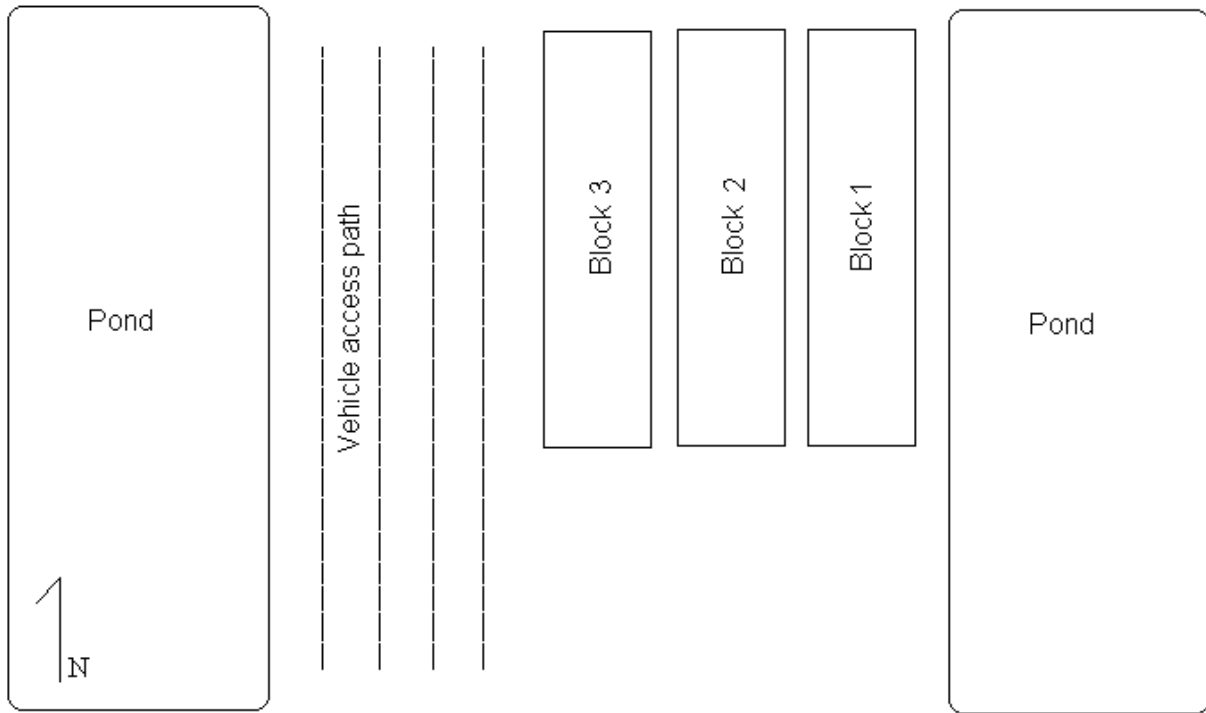


Figure 4. Layout of tanks at UCF experimental ponds for Experiment 3 (not to scale).

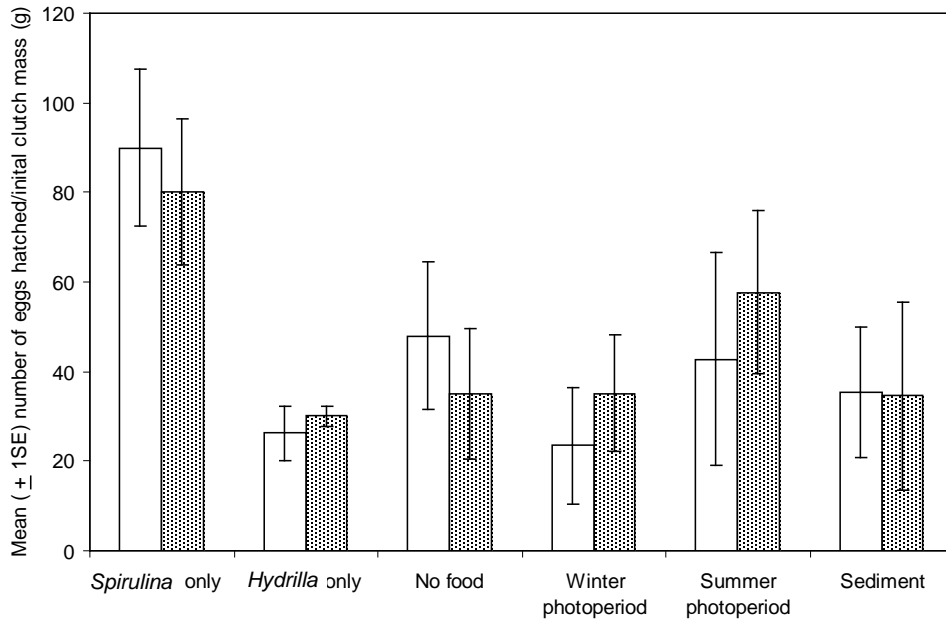
RESULTS

Experiment 1: Factors affecting survival of hatchling *Pomacea canaliculata*

None of the treatments significantly affected hatching of eggs or survival of hatchlings at the $\alpha = 0.05$ level (Table B1). Means were extremely variable with an overall hatching rate of 44.9 snails/g clutch and 15% overall survival (Figure 5). *Post hoc* power analysis revealed that all but one factor required a sample size of 23 or more to detect an effect at $\alpha = 0.05$ given the observed means and variances. Detecting a statistically significant effect of summer photoperiod response on survival would have required a sample size of twelve, compared to the five that I used (Table B1).

When clutches were pooled to identify relationships with other possible factors, the combined effect of mean temperature, mean relative humidity, date hatched and overall clutch mass explained 9.7% of hatching variation among clutches and none of the factors were statistically significant (Table 1). Mean temperature, mean relative humidity, date hatched, overall clutch mass and number hatched explained 36.5% of the variation in survival, with temperature and relative humidity (RH) statistically significant factors (Table 2). Survival increased with increasing temperature and decreased with increasing RH. Temperature ranged between 62-83F (mean 72.7) and RH between 59.8-77.1 (mean 69.3). T-tests performed on unstandardized residuals from these regressions did not indicate any significant treatment effects and all treatments yielded test power of 23% or less (Table B2).

a)



b)

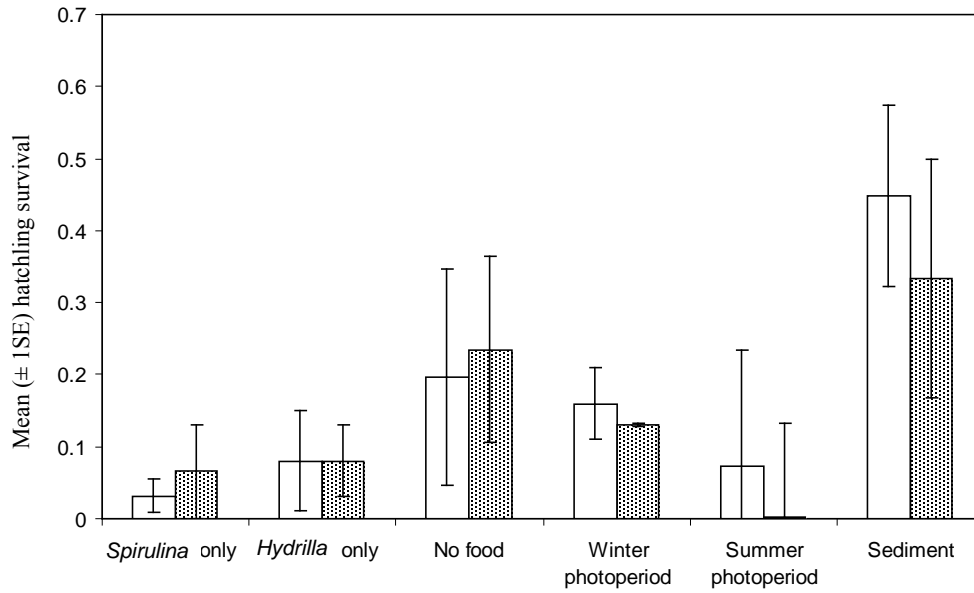


Figure 5. Mean (± 1 SE) a) hatching success and b) survival of *Pomacea canaliculata* in Experiment 1. Control means are unshaded bars, treatment means are light shaded bars.

Table 1. Statistical results of linear regression in Experiment 1: hatchability. Overall model: $R^2 = 0.097$, $n = 44$, $p = 0.393$.

Factor	Beta	t	p
Clutch mass	-0.761	-0.401	0.691
Mean temp	2.784	1.814	0.077
Mean RH	-2.097	-1.368	0.179
Date hatched	-0.001	-0.147	0.884

Table 2. Statistical results of linear regression in Experiment 1: survival. Overall model: $R^2 = 0.365$, $n = 44$, $p = 0.003$, * indicates significant F-ratio at $\alpha = 0.05$.

Factor	Beta	t	p
Snails hatched	<0.001	-1.641	0.109
Mean temp	-0.034	-3.655	0.001*
Mean RH	0.035	3.822	<0.001*
Clutch mass	0.010	0.858	0.396
Date hatched	<0.001	-1.641	0.109

Experiment 2: Separate and combined effects of food availability and population density on

Pomacea canaliculata

Only three snails died and, on average, surviving snails increased in mass by 153% and in shell height by 33% during the 3 mo experiment. Mass and shell height differed significantly among food treatments (Tables 3, 4). Snails fed *ad libitum* food had the greatest increase in mass (215%) and shell height (41%), which was significantly greater than the only 94% increase in mass and 23% increase in shell height by the snails fed the 25% food ration (Figure 6).

Mean eggs laid in all tanks was 1,150 eggs per female. Upon dissection, seventeen tanks did not contain a 1:1 sex ratio. Eight tanks had either no males or no females and were excluded from analysis because spawning was impossible. No factor or interaction was statistically significant (Table 5).

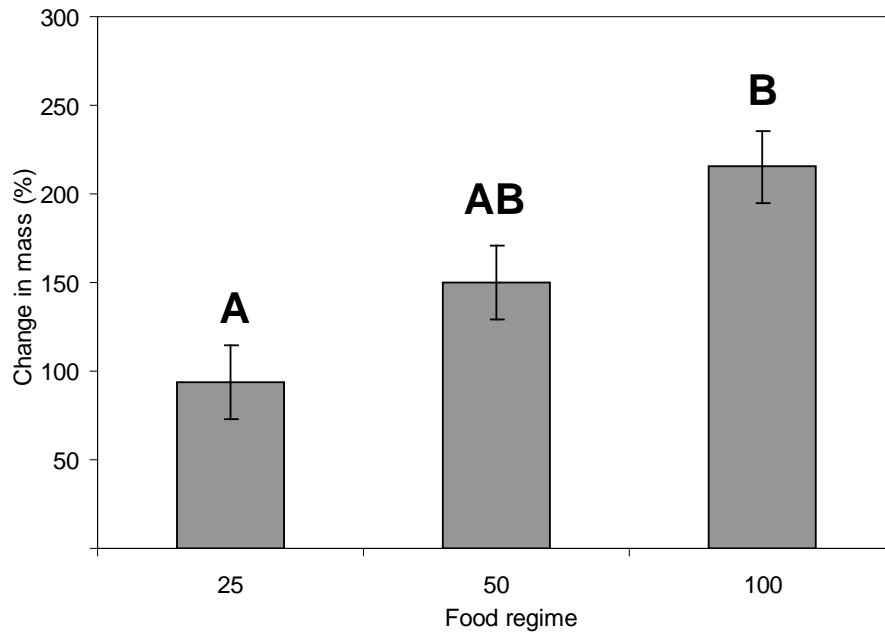
Table 3: Model I (fixed factor) ANOVA for Experiment 2, effect on snail mass. Overall model: $R^2 = 0.944$. Factor = variable tested, df = degrees of freedom and SS = sum of squares, * indicates significant F-ratio at $\alpha = 0.05$.

Factor	df	SS	F-ratio	p-value
Food	2	41779	9.997	0.012*
Density	2	1347	0.322	0.736
Block	2	11322	2.709	0.145
Food x Block	4	26163	3.130	0.103
Food x Density	4	11978	1.433	0.330
Density x Block	4	16416	1.964	0.219
Mean water temp	1	6125	2.931	0.138
Number of females	1	8053	3.854	0.097
Error	6	12538		
Total	26	855446		

Table 4: Model I (fixed factor) ANOVA for Experiment 2, effect on snail shell height. Overall model: $R^2 = 0.922$. Factor = variable tested, df = degrees of freedom and SS = sum of squares, * indicates significant F-ratio at $\alpha = 0.05$.

Factor	df	SS	F-ratio	p-value
Food	2	1000	8.089	0.020*
Density	2	11	0.088	0.917
Block	2	114	0.923	0.447
Food x Block	4	262	1.060	0.451
Food x Density	4	372	1.504	0.312
Density x Block	4	147	0.592	0.681
Mean water temp	1	21	0.347	0.577
Number of females	1	43	0.687	0.439
Error	6	371		
Total	26	4784		

a)



b)

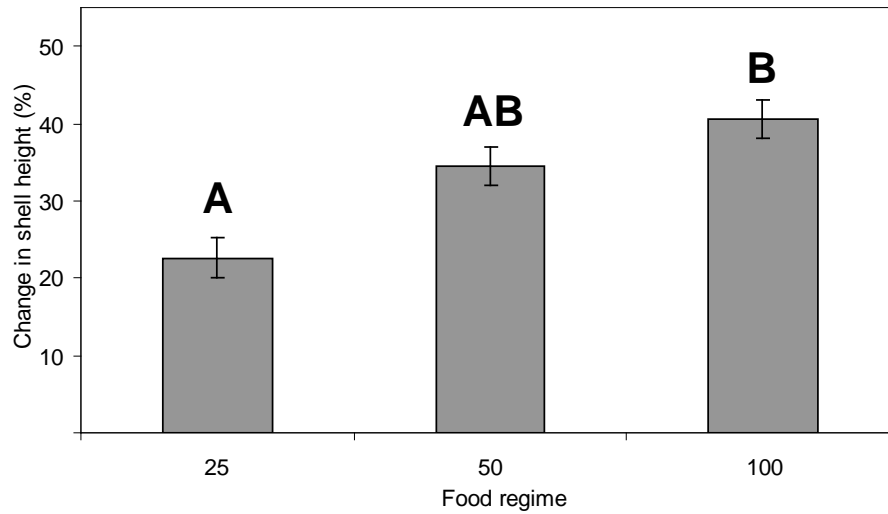


Figure 6. Mean (± 1 SE) change in a) mass and b) shell height for *Pomacea canaliculata* in Experiment 2 as a function of food regime. 25% and 50% food regimes were not significantly different; 50% and *ad libitum* were not significantly different (Sidak's test).

Table 5: Model I (fixed factor) ANOVA for Experiment 2, effect on spawning. Overall model:

$R^2 = 0.963$. Factor = variable tested, df = degrees of freedom and SS = sum of squares.

Factor	df	SS	F-ratio	p-value
Food	2	9446590	3.499	0.222
Density	2	7842900	2.905	0.256
Block	2	8408879	3.114	0.243
Food x Block	4	22145679	4.101	0.206
Food x Density	3	1170737	0.289	0.834
Density x Block	3	12296443	3.036	0.258
Error	2	2700134		
Total	18	93059400		

Experiment 3: Interactions between invasive *Pomacea canaliculata* and native Florida *P.*

paludosa

Overall, five invasive and 26 native snails died. Mean mass of native snails increased by 27.9% and mean shell height by 13.1%, but these responses were not significantly affected by any factor (Tables 6, 7). Mean mass of invasive snails increased by 418% and their mean shell height by 70.2%. Food significantly increased mean mass (Table 8) and shell height (Table 9) of invasive snails; snails fed *ad libitum* food gained the most mass (567%) and shell height (91%). This was much greater than the only 270% increase in mass and 49% increase in shell height by snails fed 40% food (Figure 7). Density ratio and its interactions had no statistically significant effect on either mass or shell height (Tables 8, 9).

One tank did not contain both sexes of the native snail and was excluded from the analysis because spawning was impossible. Mean spawning for *P. paludosa* was 150 eggs per female for the experiment. Food significantly affected spawning (Table 10); snails in the *ad libitum* food regime laid almost three times as many eggs per female as those in the 40% food regime (Figure 8). Density combination also affected spawning; native snails laid more eggs per female in tanks with a larger proportion of conspecific females. Tanks with eight native snails and no invasive snails laid 278 eggs per female, much more than the 89 eggs per female laid by native snails in tanks with six invasive snails (Figure 9). Native snails in the 2, 4 and 6 conspecific treatments laid approximately 40%, 50% and 60% of the eggs laid by snails in the 8 conspecific tanks, respectively (Figure 10).

Two tanks did not contain both sexes of the invasive snail and were excluded from the analysis because spawning was impossible. *Pomacea canaliculata* laid a mean of 1314 eggs per

Table 6. Model I (fixed factor) ANOVA for Experiment 3, effect on native snail mass increase.

Overall model: $R^2 = 0.841$. Factor = variable tested, df = degrees of freedom and SS = sum of squares.

Factor	df	SS	F-ratio	p-value
Food	1	1132	0.673	0.449
Density Combination (DC)	3	9511	1.885	0.250
Block	2	6430	1.911	0.242
Food x Block	2	8365	2.487	0.178
Food x DC	3	14194	2.813	0.147
DC x Block	6	12185	1.207	0.427
Mean water temp	1	2902	1.725	0.246
Error	5	8410		
Total	23	71775		

Table 7. Model I (fixed factor) ANOVA for Experiment 3, effect on native snail shell height.

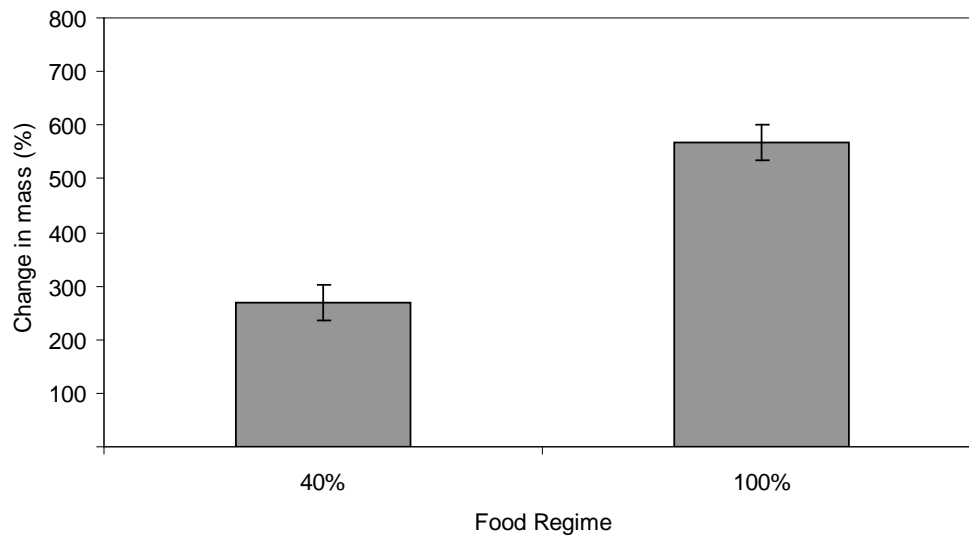
Overall model: $R^2 = 0.770$. Factor = variable tested, df = degrees of freedom and SS = sum of squares.

Factor	df	SS	F-ratio	p-value
Food	1	77	1.075	0.347
Density Combination (DC)	3	20	1.218	0.394
Block	2	264	0.141	0.872
Food x Block	2	105	0.728	0.528
Food x DC	3	50	0.230	0.872
DC x Block	6	552	1.275	0.404
Mean water temp	1	80	1.110	0.340
Error	5	361		
Total	23	5695		

Table 8. Model I (fixed factor) ANOVA for Experiment 3, effect on invasive snail mass. Overall model: $R^2 = 0.952$. Factor = variable tested, df = degrees of freedom and SS = sum of squares, * indicates significant F-ratio at $\alpha = 0.05$.

Factor	df	SS	F-ratio	p-value
Food	1	415037	31.046	0.003*
Density Combination (DC)	3	17186	0.429	0.742
Block	2	92821	3.472	0.113
Food x Block	2	115223	4.309	0.082
Food x DC	3	33548	0.836	0.529
DC x Block	6	219976	2.742	0.144
Mean water temp	1	14525	1.086	0.345
Error	5	62679		
Total	24	55752709		

a)



b)

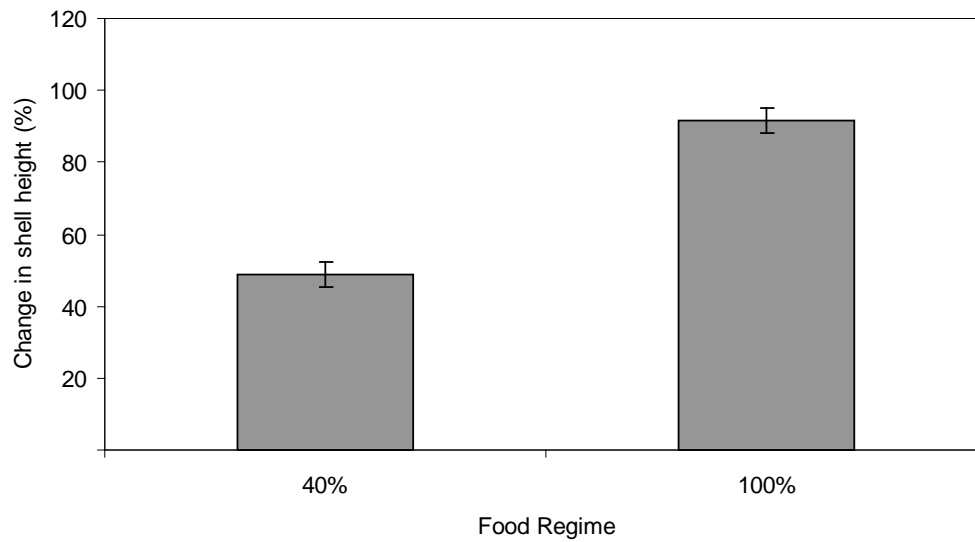


Figure 7. Mean (± 1 SE) change in a) mass and b) shell height for *Pomacea canaliculata* in Experiment 3 as a function of food regime.

Table 9. Model I (fixed factor) ANOVA for Experiment 3, effect on invasive snail shell height.

Overall model: $R^2 = 0.973$. Factor = variable tested, df = degrees of freedom and SS = sum of squares, * indicates significant F-ratio at $\alpha = 0.05$.

Factor	df	SS	F-ratio	p-value
Food	1	8407	104.230	<0.001*
Density Combination (DC)	3	675	2.790	0.279
Block	2	425	2.634	0.223
Food x Block	2	132	0.815	0.553
Food x DC	3	429	1.774	0.361
DC x Block	6	478	0.988	0.633
Mean water temp	1	493	6.107	0.129
Error	4	403		
Total	24	133118		

Table 10. Model I (fixed factor) ANOVA for Experiment 3, effect on native snail spawning.

Overall model: $R^2 = 0.929$. Factor = variable tested, df = degrees of freedom and SS = sum of squares, * indicates significant F-ratio at $\alpha = 0.05$.

Factor	df	SS	F-ratio	p-value
Food	1	135026	24.417	0.004*
Density Combination (DC)	3	90596	5.461	0.049*
Block	2	5664	0.512	0.628
Food x Block	2	41613	3.762	0.101
Food x DC	3	4827	0.291	0.831
DC x Block	6	64202	1.935	0.243
Mean water temp	1	5065	0.916	0.383
Error	5	27650		
Total	23	927733		

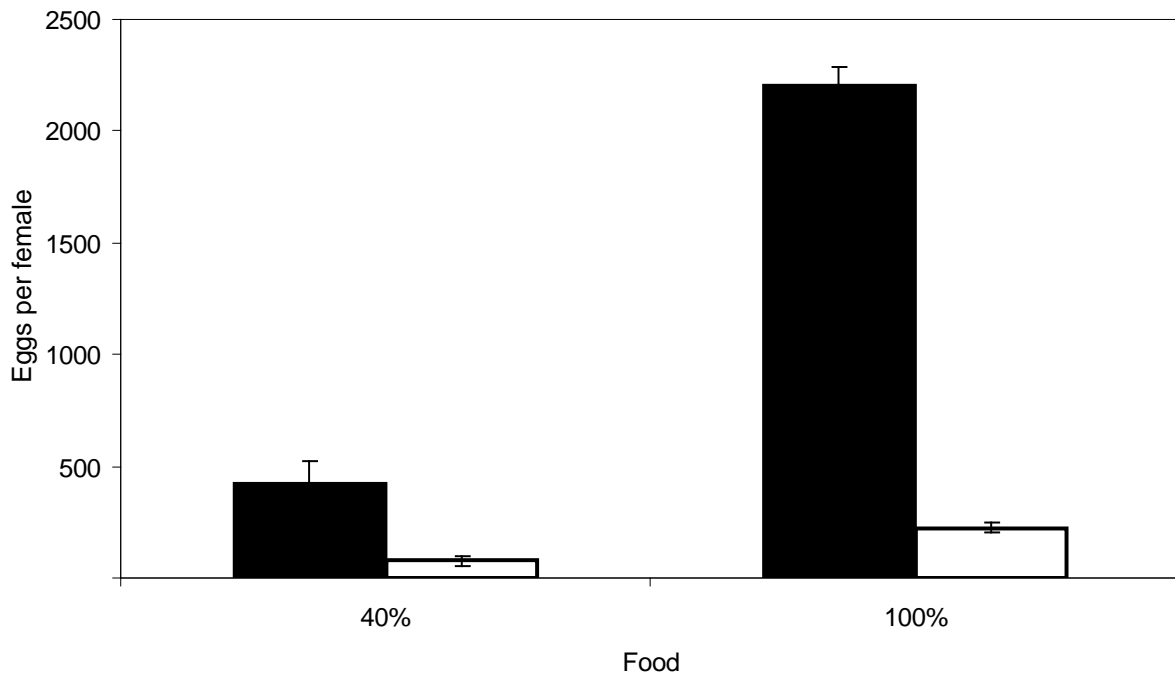


Figure 8. Mean (± 1 SE) eggs per female of invasive *Pomacea canaliculata* (black bars) and native *P. paludosa* (open bars) in Experiment 3.

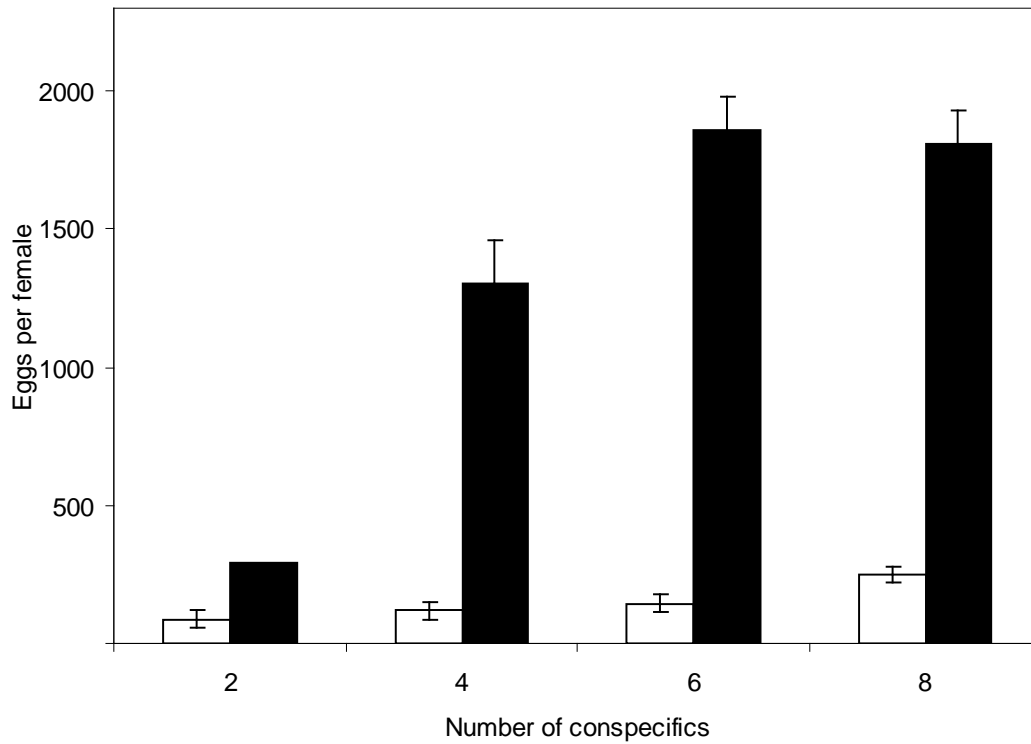


Figure 9. Mean (± 1 SE) eggs laid of *Pomacea canaliculata* (black bars) and *P. paludosa* (clear bars) in Experiment 3 as a function of density combination. No density combination was significantly different from the others (Sidak's test).

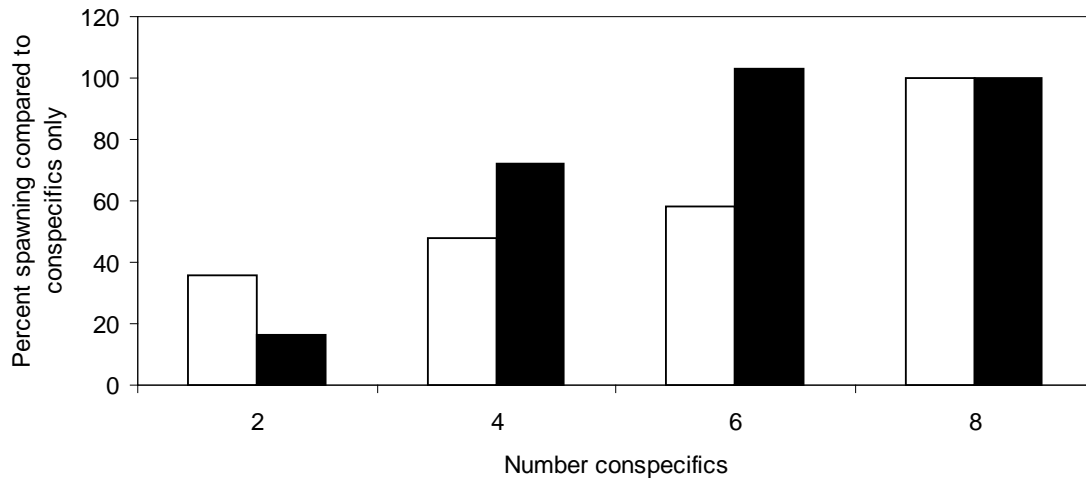


Figure 10. Percentage eggs laid per female of *Pomacea canaliculata* (black bars) and *P. paludosa* (clear bars) in Experiment 3 using the conspecific only treatment as a baseline (100%)

Table 11. Model I (fixed factor) ANOVA for Experiment 3, effect on invasive snail spawning.

Overall model: $R^2 = 0.997$. Factor = variable tested, df = degrees of freedom and SS = sum of squares, * indicates significant F-ratio at $\alpha = 0.05$.

Factor	df	SS	F-ratio	p-value
Food	1	504312	7.428	0.112
Density Combination (DC)	3	5906289	28.997	0.034*
Block	2	1463914	10.781	0.085
Food x Block	2	1209989	8.911	0.101
Food x DC	3	2618473	12.855	0.073
DC x Block	6	1472387	3.614	0.233
Mean water temp	1	100341	1.478	0.348
Proportion of females	1	178992	2.636	0.246
Shell height	1	57070	0.841	0.456
Error	2	135792		
Total	22	84562589		

female for the experiment. Density combination was significant (Table 11); eggs laid per female increased significantly with larger proportions of invasive snails. Invasive snails in tanks with two *P. canaliculata* laid a mean of 294 eggs per female while those with eight laid 1806 eggs per female (Figure 9). Invasive snails in the 2, 4 and 6 conspecific treatments laid approximately 20%, 70% and 105% of the eggs laid by snails in the 8 conspecific tanks, respectively (Figure 10). For both species, when exposed to 6 conspecifics and spawning was possible, individuals did not spawn until the last month of the experiment, if at all.

Population growth of *P. canaliculata* when faced with competition from *P. paludosa* can be modeled as

$$dN_c/dt = r_c N_c (K_c - N_c - \alpha_{cp} N_p) / K_c$$

and population growth of *P. paludosa* when faced with competition from *P. canaliculata* was modeled as

$$dN_p/dt = r_p N_p (K_p - N_p - \alpha_{pc} N_c) / K_p$$

where N = population size, K = carrying capacity, α = interspecies competition coefficient, r is the rate of increase, c refers to *P. canaliculata* and p refers to *P. paludosa*. Because intrinsic rates of increase could not be determined from survival over multiple generations, it was estimated from

$$r = \ln(s)/t$$

where s = reproductive output (eggs) per female and t = generation time in months. I used mean eggs laid per female from tanks that were not exposed to competition and fed unlimited food and I used generation times of 6 mo. for *P. canaliculata* (assuming optimal conditions, Estebenet and Martin 2002) and 12 mo. for *P. paludosa* (Darby et al. 2008) which resulted in r values of

$$r_p = \ln(333.44)/12 = 0.484 \text{ and } r_c = \ln(2970.99)/6 = 1.3328$$

The snail species affected the others' reproduction unequally. Mean snail spawning taken from snails fed *ad libitum* food and not exposed to competition were 2970.99 eggs/female for *P. canaliculata* and 333.44 eggs/female for *P. paludosa*. Each conspecific density was compared to the 8 conspecific treatment to determine the relative proportion of eggs laid. The linear regression slope of these proportions from 2, 4 and 6 conspecific densities yielded the competition coefficients:

$$\alpha_{cp} = 0.511 \text{ and } \alpha_{pc} = 0.0788$$

Pomacea canaliculata requires 0.499 g *Hydrilla*/g snail and *P. paludosa* requires 0.354 g *Hydrilla*/g snail. Multiplied to their respective mean masses to obtain food requirements per individual snail, and using a hypothetical availability of 100 g *Hydrilla*/m², this yielded carrying capacities of

$$K_p = 23.680 \text{ and } K_c = 4.577$$

When estimated values of K and α were used to create isoclines based on Lotka-Volterra modeling, *P. paludosa* was predicted to competitively exclude *P. canaliculata* (Figure 11).

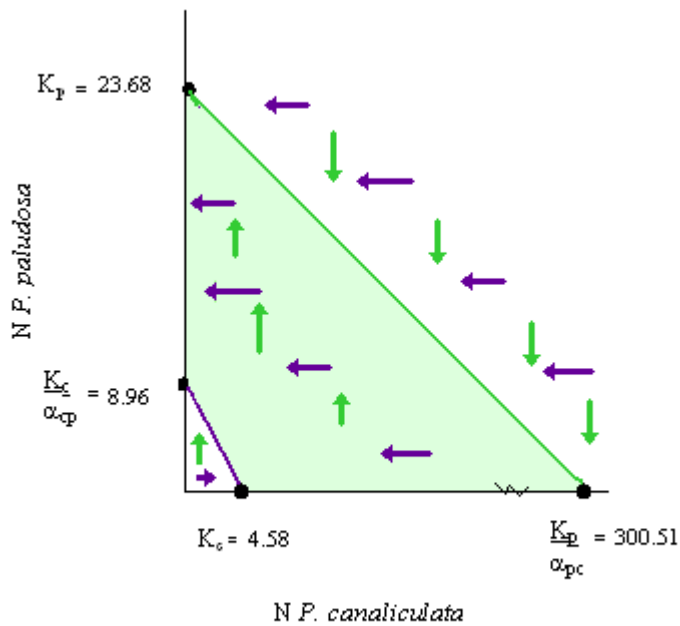


Figure 11. Predicted outcome of competition between *Pomacea canaliculata* and *P. paludosa* based on Lotka-Volterra modeling. *P. canaliculata* is represented with green, *P. paludosa* with purple. Purple and green arrows represent changes in population density for *P. canaliculata* and *P. paludosa*, respectively. N = population size, K = carrying capacity and α = interspecies competition coefficient. The combined effect of each species on the other is $K_p/\alpha_{pc} > K_c$ and $K_c/\alpha_{cp} < K_p$, resulting in exclusion of the invasive snail, *P. canaliculata*.

DISCUSSION

Exotic invasive species have tremendous negative effects on agriculture and the environment in the United States (Pimentel et al. 2005). Exotic mollusks contribute to declines of freshwater systems, aquaculture (Schloesser 1996; Martin et al. 2007) and agricultural economies (Joshi 2005). *Pomacea canaliculata* may potentially compete with the native congener *P. paludosa* but its effects are unknown in Florida's natural systems. To accurately understand and anticipate the severity of the invasion of *P. canaliculata* in Florida, we must first understand its biology and interactions with Florida systems.

There are few studies regarding clutch biology of *P. canaliculata*. Sex ratios per clutch are extremely variable and not attributed to common environmental factors such as temperature, food availability or habitat size (Yusa, 2004). Instead, variability was attributed to genetic effects. In my study, hatching and survival were highly variable and not significantly affected by tested factors. While temperature and relative humidity significantly correlated with survival, they only explained a small proportion of the variance.

Food type and availability did not significantly affect survival, suggesting that *P. canaliculata* hatchlings either obtained very little nutrients from or possibly did not consume food resources available during my study. Temperature directly correlated and relative humidity (RH) inversely correlated with survival, suggesting that hatchlings were susceptible to these differences. Seasonal differences in spawning were observed (Albrecht et al. 1999) but the separate effects of photoperiod and temperature have not been evaluated for hatching or survival. *Pomacea canaliculata* can establish in diverse conditions (Cazzaniga 2006). Current infestations

in rice paddies throughout Southeast Asia and the Pacific islands (Halwart 1994), in cold winter habitats such as north Japan (Ito 2002; Wada and Matsukura 2007) and multiple sites in the U.S. (Howells and Smith 2002) provide examples of thermal tolerance. All invasions of the snail in Florida should be taken seriously, and areas currently not invaded should be monitored closely.

Overall, individual mass generally declines with increasing population density (White et al. 2007). My research on these two freshwater mollusks did not detect statistically significant effects of density on growth or reproduction and instead revealed that food significantly affected growth with a significant difference between low (25% of food requirements) and unlimited food levels. This supports previous findings that populations of *P. canaliculata* are limited by food availability, not their inherent numbers (Albrecht et al. 1999; Estoy et al. 2002b) and follows the common view that food is a major limiting resource driving intraspecies competition (Gill 1972a; Haven 1973; Creese and Underwood 1982). In other mollusks, high densities reduced growth, clutch sizes (Cameron and Carter 1979, Baur 1988) and feeding activity even when food was available (Dan and Bailey 1982). This provides insight for snail control; limiting dense *Hydrilla* would indirectly control *P. canaliculata* by limiting its food resources.

Lack of inherent limitation by population densities indicates that *P. canaliculata* may achieve particularly large densities in invaded areas where sufficient food is available. Observations of *P. canaliculata* densities range between 1 to 9.5 snails/m² (Halwart 1994; Carlsson and Lacoursiere 2004), much larger than *P. paludosa* densities in Florida at less than 1 snail/m² (Darby et al. 1999; Karunaratne et al. 2006). No factor in Experiment 2 had a statistically significant effect on snail spawning, thus I cannot provide insight to conflicting findings (Tanaka et al. 1999; Albrecht et al. 1999; Estoy et al. 2002b) regarding the role of food

and density limitations on spawning. This suggests that direct hand removal of snails and eggs is still necessary to comprehensively control an invasion whenever indirect management of food does not reduce snail reproduction.

Facilitative interactions between invasive exotic species and positive feedback loops between species and their environments are not uncommon (Simberloff and Von Holle 1999, Ricciardi 2001). *Hydrilla* threatens native biota, ecosystem function and freshwater recreation (Bates and Smith 1994; Langeland 1996). It often doubles its mass in just one to two weeks (Steward 1991; Sutton et al. 1992) and was observed in Florida at a density of 820 g/m² dry weight (Van et al. 1978; Bowes et al. 1979) which would easily sustain a *P. canaliculata* population (based on adult snails eating 10g wet weight per day, unpublished data). To complete the positive feedback loop, snail defecations increase nutrient availability (Carlsson et al. 2004) creating a fertilized substrate where *Hydrilla* more efficiently outcompetes native species (Haller and Sutton 1975; Steward 1984; Van et al. 1999). The snails' preference for native plants (Lach, et al., 2000; Cowie, 2001; Carlsson et al. 2004; Burlakova et al. 2008) supports domination by *Hydrilla*. Though *P. canaliculata* was been suggested as a biocontrol for aquatic weeds (see Cowie, 2001 for review), it should not due to these feedback loops with invasive macrophytes.

In mollusks, intensity of intraspecific competition varies between species, environments and even microclines (Peterson and Andre 1980; Baur and Baur 1990). In my study, intraspecific competition had no effect, and interspecific competition influenced reproduction but not growth of the two freshwater mollusks. While *post hoc* tests did not detect significant differences between treatment levels, for both species the difference between exposure to maximum interspecific competition and exposure to none of the other species was greater than

the contrast between any other treatment level. Intraspecific density alone did not negatively affect either growth or fecundity.

Competition between *P. paludosa* and *P. canaliculata* has never been studied. Mean eggs laid per female declined for each species with increasing congener densities, but differently. While mean percentage reduction in reproduction was similar, snails in bins with 2 *P. paludosa* had a greater proportion of spawning (compared to snails in the conspecific only bins) than *P. canaliculata* where 6 *P. canaliculata* had a greater proportion of spawning than 6 *P. paludosa*. (Figure 10). Lotka-Volterra competition models predicted that *P. paludosa* would exclude *P. canaliculata* due to the latter's lower carrying capacity and voracious appetite (Estebenet and Martin 2002). These results alone, however, do not necessarily indicate clear exclusion. Lotka-Volterra modeling assumes nearly complete niche overlap, but this is rarely the case in natural systems and researchers must consider factors in populations not accounted for by the model (Wilbur 1972, Dorschner et al. 1987). Foods other than *Hydrilla* such as macroalgae and detritus are available for *P. paludosa* in Florida (Sharfstein and Steinman 2000; Shuford 2005) whereas *P. canaliculata* likely cannot survive on them (Burlakova et al. 2008). Conversely, *P. paludosa* cannot consume *Hydrilla* as quickly as *P. canaliculata*. Choices in egg-laying substrate in natural areas and energy allocations to clutch/egg sizes also differ. Clutches of *P. canaliculata* have many (200-500), but small (1 mm) bright pink to pink-orange eggs, while those of *P. paludosa* have few (20-30), but larger (2-3 mm) soft pink to white eggs. Faster growth rates and larger energy allocation to clutch size in *P. canaliculata* may contribute to the large appetite and smaller carrying capacity. While calcium availability for shell building was not limited in my study, snails may compete for this resource in calcium-poor water.

Given the extent of *P. canaliculata*'s spread in Florida, it is unlikely that competition with *P. paludosa* is restricting the invasion. The influence of *P. paludosa* may only reduce and not exclude *P. canaliculata* because strict niche competition may be lacking (Slatkin 1980). Moreover, my study provided a stable habitat for the snails, which contributes to success of a k-selected species (*P. paludosa*) in Lotka-Volterra modeling. In natural systems, factors that provide disturbance (i.e., predators, fluctuating hydrology, variable food sources, human disturbance, nutrient-laden Florida waterbodies) would promote success of r-selected species (*P. canaliculata*) (Caswell 1982). Lack of predation promoting *P. canaliculata* supports the enemy release hypothesis (Colautt et al. 2004) and may indicate that the apple snail kite is not predating on *P. canaliculata*. I observed that the shell and operculum are thicker and stronger in *P. canaliculata* than *P. paludosa* possibly increasing difficulty in predation by the kite. Moreover, the larger shells of *P. canaliculata* may not match the beak curvature of the kite, reducing ability of the bird to sever the columellar muscle (Voos and Van Dijk 1973). While these effects of interspecies competition would need to be confirmed by multi-generational studies considering other aspects affecting carrying capacity, it may be useful to stock ponds with *P. paludosa* to reduce spawning by *P. canaliculata*.

Because competition was a significant factor independent of food, other factors influencing interspecific competition need investigation. When the ratio of the snails was 6:2 where both species had the opportunity to spawn, the species that had two individuals did not spawn until the last month of the experiment, if at all. I do not feel that this indicates a competition for egg-laying substrate; clutches laid represented a very low proportion of the available substrate. Rather, I suggest *Pomacea* lack strong species recognition ability as

observed in other species (Ryan and Wagner 1987; McLennan and Ryan 1997; Hankison and Morris 2003). These two *Pomacea* species may attempt mating but are unable to hybridize, wasting effort. Based on probability alone, the species that had 6 snails per tank had a greater chance of mating with a snail of the same species, resulting in greater spawning frequency. Testing species recognition in these two congeners will further evaluate possible *P. paludosa* exclusion.

To extrapolate my results to natural Florida habitats and to further evaluate the long-term effects of *P. canaliculata* invasion, studies that take place in larger water bodies and span longer periods are needed to capture the effect of factors that were not assessed by my 3 mo. study. Experiment 3 was conducted April through June, peak times for *P. paludosa* spawning activity (Darby et al. 2008). Longer studies may detect different effects on *P. paludosa* by *P. canaliculata* as the peak breeding seasons may vary (Albrecht et al. 1999) and because negative environmental changes by *P. canaliculata* that take multiple seasons to occur (eutrophication, biotic shifts to invasive macrophytes) may create an environment inhospitable for *P. paludosa*. *Pomacea canaliculata* can rapidly increase its population over a few generations resulting in *P. canaliculata*:*P. paludosa* ratios beyond what I tested. Such a larger ratio has greater potential for serious negative effects on *P. paludosa*. While *P. canaliculata* has greater fecundity than *P. paludosa*, this alone does not necessarily indicate a large competitive advantage because hatchling survival differs due to food type and seasonality (Lacanilao 1990). Moreover, the two species may have different overwintering abilities that were not captured by the time range of my study. *Pomacea canaliculata* can develop cold-hardiness for short periods (Wada and Matsukura 2007) but cannot survive extended freezing (Ito 2002; Matsukura et al. 2009). The

limited northern range of *P. paludosa* and its reduced activity under cold temperatures (Stevens et al. 2002) suggest that it probably is less cold tolerant than *P. canaliculata*.

This is the first study evaluating the interaction between *P. canaliculata* and *P. paludosa*. The invasion of *P. canaliculata* threatens the quality of Florida lakes, native submersed plants, *P. paludosa* and thus, the endangered Everglades snail kite. Studies regarding snail preference by the kite need to be completed to discern its ability to eat and thrive on *P. canaliculata*. It is necessary to provide wildlife managers with expectations for invasion events and an understanding of the effect on *P. paludosa*. While further studies are necessary for a thorough understanding of *P. canaliculata*, its life-cycle knowledge of food preferences, interactions with *P. paludosa*, responses to intrapopulation density and the lack of factors that effect hatching success and hatchling survival will aid wildlife managers and other decision makers in controlling the invasion of *P. canaliculata*.

APPENDIX A: FEEDING RATE DATA

Table A1. From individual trials. Data estimating consumption of *Hydrilla* by *Pomacea canaliculata* and *P. paludosa*. Mean amounts consumed were 0.499 (± 0.0269 SE) g *Hydrilla* / g snail /day and 0.354 (± 0.160 SE) g *Hydrilla* / g snail /day, respectively.. All masses are wet masses.

	Amount consumed (g/2 days)	mean snail mass (g)	g consumed per g snail per day
<i>P. canaliculata</i>			
	7.35	6.58	0.56
	8.94	6.58	0.68
	9.03	7.23	0.62
	8.98	10.38	0.43
	7.37	8.06	0.46
	13.10	14.08	0.47
	8.32	9.29	0.45
	7.95	8.46	0.47
	9.85	10.52	0.47
	6.98	9.37	0.37
	8.11	7.86	0.52
<i>P. paludosa</i>			
	7.33	13.46	0.27
	8.68	14.66	0.30
	5.81	5.74	0.51
	5.99	9.89	0.30
	5.47	7.05	0.39
	4.33	5.54	0.39
	5.38	8.69	0.31
	4.90	6.77	0.37

APPENDIX B: EXPERIMENT 1 STATISTICS.

Table B1. Statistical results of Experiment 1; Factors affecting the hatching success and survival of hatchling *Pomacea canaliculata*, raw data. t represents the t-value, p represents the p-value, % power of test is the relative strength of the test, and Sample size needed represents the n needed to capture an effect of treatment.

Factor	t	p	% power of test	Sample size needed
Hatching success				
<i>Spirulina</i> only	0.663	0.544	9	52
<i>Hydrilla</i> only	0.569	0.600	8	70
No food	0.769	0.485	10	39
Winter photoperiod	0.525	0.627	7	81
Summer photoperiod	0.928	0.406	13	28
Sediment	0.105	0.921	3	1968
Survival				
<i>Spirulina</i> only	0.681	0.442	6	114
<i>Hydrilla</i> only	0.598	0.975	3	19402
No food	0.806	0.262	4	319
Winter photoperiod	0.372	1.000	14	24

Summer photoperiod	0.213	1.480	24	12
Sediment	0.326	1.184	16	20

Table B2. Statistical results of Experiment 1; Factors affecting the hatching success and survival of hatchling *Pomacea canaliculata*, residuals from linear regressions. t represents the t-value, p represents the p-value, % power of test is the relative strength of the test, and Sample size needed represents the n needed to capture an effect of treatment.

Factor	t	p	% power of test	Sample size needed
Hatching success				
<i>Spirulina</i> only	0.569	0.609	7	59
<i>Hydrilla</i> only	-1.735	0.225	23	8
No food	0.769	0.485	10	39
Summer photoperiod	-0.888	0.440	12	26
Sediment	0.105	0.921	3	1953
Survival				
<i>Spirulina</i> only	0.032	0.977	3	18489
<i>Hydrilla</i> only	-0.107	0.924	3	1266
No food	-0.261	0.807	4	322
Summer photoperiod	1.280	0.290	12	14
Sediment	1.129	0.322	17	20

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