

RESOURCE USE, COMPETITION, GRAZING BEHAVIOR, AND ECOSYSTEM
INVASION IMPACTS OF *POMACEA MACULATA*

by

Dean J. Monette

A Dissertation Submitted to the Faculty of
The Charles E. Schmidt College of Science
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This dissertation was prepared under the direction of the candidate's dissertation advisor, Dr. Scott H. Markwith, Department of Geosciences, and has been approved by the members of his supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

SUPERVISORY COMMITTEE:



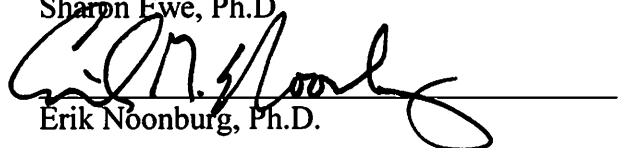
Scott H. Markwith, Ph.D.
Dissertation Advisor




Leonard Berry, Ph.D.



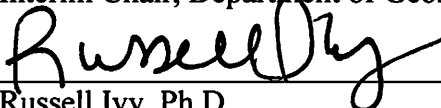
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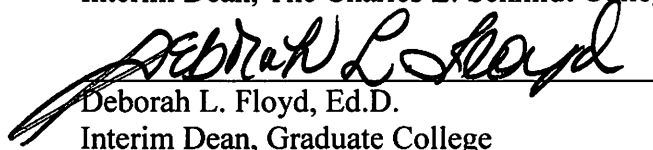
Erik Noonburg, Ph.D.



Charles Roberts, Ph.D.
Interim Chair, Department of Geosciences



Russell Ivy, Ph.D.
Interim Dean, The Charles E. Schmidt College of Science



Deborah L. Floyd, Ed.D.
Interim Dean, Graduate College

Date

11/13/2014

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ABSTRACT

Author: Dean J. Monette
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Dissertation Advisor: Dr. Scott H. Markwith
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Invasion of exotic species is a global threat to native species, biological diversity, and ecological restoration projects. *Pomacea maculata* is a macrophyte herbivore often misidentified with one of the world's most invasive and destructive exotic snail, *Pomacea canaliculata*, but has a broader geographical distribution and climate tolerance, and greater egg production. This research examines whether the exotic *P. maculata* and native *Pomacea paludosa* occupy identical vegetation communities, mechanisms of interference competition, grazing impact differences on *Vallisneria americana* and to develop an exploratory agent based model. This model uses historical and present data to project how differences between species in life history and grazing patterns can potentially impact South Florida ecosystems. This model examined how *P. maculata* invasion of South Florida could affect two of the Central Everglades Planning Project's main environmental restoration goals: function of key vegetative communities and conservation of endangered or threatened species.

DEDICATION

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1. INTRODUCTION

Public agencies throughout the world recognize the harmful effects of biological invasions (Lockwood 2007). Over 50,000 exotic species have entered in the United States resulting in over \$120 billion dollars in environmental damages or losses (Pimentel, et al. 2005). In Florida, over 900 exotic species are established in native ecosystems (Frank and McCoy 1995, Frank, McCoy et al. 1997, Simberloff and Schmitz 1997). In 2013, the South Florida Water Management District spent over \$19 million dollars to control, eradicate, and research exotic species (SFWMD 2014).

Invasion of exotic species can undermine the desired results of restoration projects (D'Antonio and Meyerson 2002). Invasive exotic species can modify food webs, alter habitats, displace native species, reduce diversity, and impair ecosystem function (Rodda and Fritts 1997, Simberloff and Schmitz 1997, DiTomaso 2000, Pimentel, Zuniga et al. 2005). Restoration projects often require altering stable but human influenced ecosystem drivers to achieve restoration goals. Any changes to the current ecosystem driver will cause a disturbance to the existing ecosystem that may allow opportunities for exotic invasion. Restoration processes alone do not cause exotic expansion since exotics need to be present in order to invade (Lockwood 2007). The issue is how to manage exotics that may be present during restoration. In the U.S., Federal and State agencies develop restoration projects that should include plans to address exotic species to mitigate ecosystem impacts including trophic level disruptions.

Trophic level disruptions can significantly alter existing high valued vegetation communities for restoration (e.g. tapegrass, *Vallisneria americana*), and habitats critical for endangered species (e.g. snail kites, *Rostrhamus sociabilis plumbeus*) (USACE 1999). The exotic Island Apple Snail (*Pomacea maculata*) is invading habitat in the Greater Everglades and possibly competing with the native Florida Apple Snail (*Pomacea paludosa*), leaving the snail kite possibly in danger of extinction as well as impacting desirable target submerged aquatic vegetation (Perona, Camporeale et al. 2009). Snail kites feed on the native apple snail, making them an essential component for survival (Bennetts, Darby et al. 2006). Apple snails utilize tapegrass as habitat and as a food resource. The interactions between hydrology and the success of important flora and fauna such as tapegrass, apple snails and snail kites are tied to their ability to survive during the environmental changes wrought by disturbance and restoration.

Until recently, most of the research has focused on the snail kites and *P. paludosa* interactions (Frakes, Bargar et al. 2008, Cattau, Martin et al. 2010). While snail research has continued, an emphasis on understanding important life history (Corrao, Darby et al. 2006, Boland, Meerhoff et al. 2008) vegetation communities (Darby, Valentine-Darby et al. 2003, Darby, Valentine-Darby et al. 2004, Bennetts, Darby et al. 2006, Darby, Bennetts et al. 2008), and food preferences (Boland, Meerhoff et al. 2008, Baker, Zimmanck et al. 2010) of *P. paludosa* has emerged. Although this is important foundational research, currently, there is no scientific data on the possible mechanism of competition between *P. paludosa* and *P. maculata*. Research focusing on the competition mechanisms would increase our predictive capabilities concerning the potential negative consequences of species interactions. Studies are needed that identify

where interactions occur and provide valuable information about the potential frequencies of these interactions. Niche overlap studies can help us determine if *P. paludosa* is out-competed by *P. maculata* for resources, habitat structure is altered (Morrison and Hay 2010) and whether snail kite fitness and survival is affected (Cattau, Martin et al. 2010).

The goal of this project was to develop an agent based spatial-temporal model that uses historical and present data to project how differences between species life history and grazing patterns can potentially impact aquatic ecosystems. Determining the abiotic and biotic factors or factor influencing animal distributions over a temporal scale is critical for a broader understanding of invasion emergent behavior and predictive capabilities. This model examined how *P. maculata* invasion of South Florida could impact two of the Central Everglades Planning Project's main environmental restoration goals: function of key vegetative communities and conservation of endangered or threatened species. In order to examine the impact of *P. maculata*, lab and field experiments and computer modeling were conducted that address the following research objectives and their corresponding specific research questions:

1. To determine if *P. maculata* impacts SAV communities that are desirable to restoration
 - a. Is there differences between *P. maculata* and *P. paludosa* consumption behavior that can influence above ground biomass and plant community structure for *V. americana*?
2. To examine the mechanism of competition occurring between *P. maculata* and *P. paludosa*

- b. What best describes the species interaction between *P. maculata* and *P. paludosa*; neutralism, amensalism, predation and competition by interference?
- 3. To determine the influence that abiotic and biotic factors have on *P. maculata* distribution.
 - c. Does water depth, water quality, and habitat communities, affect the presence of *P. maculata* and *P. paludosa* occurrence?
- 4. To develop an agent based spatial temporal model of both species in a Stormwater treatment area (STA) based on predation rates, behavioral interactions and reproductive patterns.
 - d. How do differences between *P. maculata* and *P. paludosa* in life history, grazing behavior and juvenile to adult survivability potentially impact *V. americana* communities?

2. RESOURCE COMPETITION BETWEEN *POMACEA MACULATA* AND *POMACEA PALUDOSA* IN LAKE OKEECHOBEE

2.1 Abstract

Invasion of exotic species is a global threat to native species, biological diversity, and ecological restoration projects. *Pomacea maculata* is a macrophyte herbivore often misidentified with one of the world's most invasive and destructive exotic snail, *Pomacea canaliculata*, but has a broader geographical distribution and climate tolerance, and greater egg production. This research examines whether the exotic *P. maculata* and native *Pomacea paludosa* occupy identical vegetation communities. Non-metric multidimensional scaling analysis in 3D showed visually strong separation of vegetation communities based on snail species presence, with few sites exhibiting species overlap. ANOSIM analysis showed a significant difference in vegetation communities between the three groups: native, exotic, and mixed populations. The exotic plant *Hydrilla verticillata* was the greatest contributor to plant community similarities among sites supporting *P. maculata*, whereas *Eleocharis cellulosa*, *Nymphaea odorata*, and *Schoenoplectus americanus* were the greatest contributors to similarities among plant communities supporting *P. paludosa*. Within mixed snail populations, *Paspalidium geminatum*, *Vallisneria americana*, and *Potamogeton illinoensis* were the most important contributors to site similarity. Our research shows niche partitioning may be occurring between *P. maculata* and *P. paludosa*. *P. paludosa* occurrence is more strongly associated with dominant native aquatic vegetation, while *P. maculata* has a tight

relationship with the abundant exotic macrophyte *H. verticillata*, which may act as refugia and dispersal mechanism for invasion. Resource competition may exist in *V. americana* communities and populations of this plant important to Central Everglades Planning Project in South Florida may be severely impacted due to the coupled top down herbivory pressure.

2.2 Introduction

One of the prevailing drivers threatening global diversity and species extinctions is the increasing rate of exotic species invasions (Carlsson, Bronmark et al. 2004, Clavero and García-Berthou 2005). The competitive exclusion principle states that two species cannot inhabit identical ecological space competing for resources without affecting survival (Hardin 1960). In aquatic environments, introductions can occur unnoticed by humans, potentially leading to direct competition with native species (Byers 2000), food web modification, or increase top down grazing pressure on vegetation due to coupled exotic and native grazers. Increased herbivory may negatively affect plant survival, resulting in vegetation community alteration and changes in ecosystem function. The loss of aquatic vegetation can alter water quality parameters in shallow lakes (Carlsson, Bronmark et al. 2004, Burks, Hensley et al. 2011) resulting in changes to ecosystem function (Carpenter, Cole et al. 2001, Carlsson, Bronmark et al. 2004), and potentially impacting the ecosystem's ability to provide sustainable ecosystem services (Costanza, d'Arge et al. 1997).

In Florida *Pomacea maculata*, formerly known as *Pomacea insularum*, was first collected in 2003 but not identified until 2007 and reclassified in 2012 (Rawlings, Hayes et al. 2007, Hayes, Joshi et al. 2008, Baker, Zimmanck et al. 2010, Hayes, Cowie et al.

2012). *P. maculata* is a dioecious freshwater snail that exhibits many of the classic invasive exotic species characteristics with a high fecundity rate (Keller, Drake et al. 2007, Barnes, Fordham et al. 2008, Burks, Hensley et al. 2011), including laying one or more egg mass per week, mean production >2000 individual eggs that hatch in ~1-2 weeks (Barnes, Fordham et al. 2008), lifespan between 3-5 years, and a voracious and flexible macrophytophagous diet, i.e. consuming floating or submerged aquatic vegetation (Baker, Zimmanck et al. 2010). Possessing a ctenidium and an air sac, *P. maculata* has the ability to tolerate fluctuating temperature regimes and locations with low dissolved oxygen by using a siphoning tube to collect oxygen from the air. *P. maculata* may prove to be more destructive than one of the world's most damaging ampullariids, *Pomacea canaliculata*, due to a higher fecundity, wider distribution, and a wider range of temperature tolerance in its native South America (Hayes, Cowie et al. 2012).

The Florida Apple Snail, *Pomacea paludosa*, is a native dioecious herbivore considered a bioindicator of Everglades restoration success (Karunaratne, Darby et al. 2006). While commonly called the Florida Apple Snail, it's a spatially dispersed species that can be found throughout the southeastern United States. Similar to *P. maculata*, *P. paludosa* has a ctenidium and air sac, but only lays approximately 20-30 eggs per mass that hatch in ~2-3 weeks, and its lifespan is approximately 1-1.5 years (Darby, Bennetts et al. 2008, Pomacea Project 2013). *P. paludosa* is important prey for numerous wetland species, including fish, reptiles, and birds such as the endangered Florida Snail Kite, *Rostrhamus sociabilis*. Historically, the Florida Snail Kite, a dietary specialist, exclusively preyed upon *P. paludosa* (Beissinger, Donnay et al. 1994, Bennetts and

Kitchens 1997, Bennetts and Kitchens 2000, Bennetts, Darby et al. 2006, Martin, Nichols et al. 2006, Darby, Fujisaki et al. 2012), but *P. maculata* has become an additional prey resource (Cattau, Martin et al. 2010). Such a prey switch or supplement could have significant implications for the survival and management of the Snail Kite. All three species, *P. maculata*, *P. paludosa*, and *R. sociabilis*, co-occur in Lake Okeechobee, Florida's largest lake and an important source of water for the large human population of South Florida..

The objective of the research presented herein is to examine resource utilization in the context of the vegetation preferences of *P. maculata* and *P. paludosa* in Lake Okeechobee, Florida. Preference is the likelihood that a species chooses a resource over other equally available resources (Manly, Manly et al. 2002). Understanding if these species have similar or different resource preferences will help determine the potential strength of competitive species interactions and herbivory pressure within the food web of the invaded aquatic systems. While the use of similar resources may indicate the potential for negative consequences, such as competitive exclusion or food web modification, differential resource use may indicate that *P. maculata* and *P. paludosa* can coexist without strong competitive species interactions or that competitive pressure may be alleviated through niche partitioning and spreading the pressure among resources (Rosenzweig 1981, Manly, Manly et al. 2002). The following questions are specifically addressed: 1) do *P. paludosa* and *P. maculata* share preferences for similar vegetation resources, and 2) what plant communities are potentially at risk to an increase in grazing pressure? This research will significantly increase our understanding of an exotic invasive gastropod's impact on an important indicator species in the Greater Everglades

ecosystem. Understanding how *P. maculata* can influence top-down pressure on desirable targeted vegetation communities and impact bottom-up resource availability for protected species is crucial for restoration and conservation wherever *P. maculata* invades.

2.3 Methodology

Located in south-central Florida, Lake Okeechobee is approximately 1900 sq. kilometers (Figure 2.1), and second only to Lake Michigan in area within the lower 48 states (Henkel, 2010). Lake Okeechobee is a shallow managed lake system with a littoral zone containing varying submerged, floating and emergent vegetation communities. The system is influenced by strong seasonality, with a wet period usually occurring June through November followed a dry period from December to May, and as a managed system it can be significantly impacted by human demands. Research has shown ecosystem benefits function best when water levels for the system range within 3.4 – 4.6 m, allowing littoral zone locations to gradually recede and flood and for natural vegetation community response (Havens and Gawlik 2005).

Field sampling occurred from late April through June, sampling 22, 31 and 32 sites in 2010, 2011 and 2012, respectively. All sites were located in the northern and western littoral zone and determined by current and historical Snail Kite nesting and foraging behavior, and native and exotic apple snail egg clusters. At each site, to include representative water depths and vegetation, transects were randomly surveyed 5-10 meters apart by two teams moving independently of each other. Exact site locations were not resampled each year, but varied in order to capture the influence of hydrology on snail distribution. Additional sites were added each year as additional Snail Kite

locations were observed, snail populations were identified, and to increase the sampling area throughout the lake.

The sampling teams made a minimum of 20 throws of 1 m² steel throw traps in water depths of 10-60 centimeters. Within the 1 m² trap, vegetation stem counts were recorded per 0.5 m² for dominant and secondary emergent vegetation. Additionally, dominant and secondary submerged aquatic vegetation (SAV) were recorded for percent coverage. Plants were then pulled and the trap checked for snails. Drift nets were used to sweep along the bottom of the inside of the trap to collect all snails present. At a minimum, a total of 20 clean sweeps were performed inside each trap. After drift net sweeps, one person would step inside the trap in an attempt to capture snails partially buried within the soils, or floating in the water column. All hard surfaces were investigated for snail presence. If snails were not found within the first 20 throws, further sampling along the transect was terminated. However, if an exotic or native snail was captured within the first 20 throws, an additional 50 throws for a total of 70 were made. At each site, we recorded dissolved oxygen, water temperature, and water depth. Water depths were recorded at the first and the last throw along the transect at each site.

Snails were captured at a total of 33 sites, but two of the locations only contained unidentifiable decomposing vegetation, thus, 31 sites were included in the analysis. Data were standardized by converting plant and snail species composition data from the traps to presence or absence. Presence/absence values were summed for each species then divided by the number of throws made at each site. Thus, stem density and percent coverage per trap were standardized into percent frequency for species at each site.

Standardized site data was imported into Primer v6 (Clarke 1993, Clarke and Warwick 2001) and transformed using the Bray-Curtis distance based RESEMBLANCE procedure to rank sites. Non-metric multi-dimensional scaling (NMS) was conducted on the ranked data, and the scores represented in 2D joint plots to visually assess the site vegetation community similarities and differences between independent *P. maculata* and *P. paludosa* populations, and mixed snail populations (Clarke 1993, Clarke and Warwick 2001, Blake 2007).

We conducted a one way cross analysis of similarity (ANOSIM) to test for significant difference in plant communities for sites supporting different groups of snail species, i.e. populations exclusively composed of native or exotic species, or mixed populations. ANOSIM is a non-parametric test that uses Monte Carlo simulation to analyze the levels of dissimilarities between groups (Clarke 1993, Clarke and Warwick 2001, Blake 2007, Laura Josens, Alicia Haydee et al. 2009). Pairwise t-tests were performed to examine differences between groups of sites supporting different snail species, e.g. native vs. exotic, native vs. mixed, or exotic vs. mixed.

We applied similarity of percentages (SIMPER) analysis to examine the contribution of each plant species to the observed similarity of plant communities within each group of sites supporting common species (e.g. all sites supporting *P. maculata* exclusively). We also applied SIMPER analysis to examine the contribution of each plant species to the observed dissimilarity of plant communities between sites supporting different snail species (e.g. sites supporting *P. maculata* vs. sites supporting *P. paludosa*).

2.4 Results

Over the three year study a total of 3550 throw traps were thrown, within which a total of 21 emergent and 13 SAV species were identified. A total of 455 individual snails were capture at 33 sites, with 391 being *P. maculata* and 65 *P. paludosa*. Both native and exotic snail inhabited sites had the same plant species richness, 28 species overall and 18 emergent and 10 SAV. The most common plant species were *Hydrilla verticillata*, *Eleocharis cellulosa*, *Schoenoplectus americanus* and *Paspalidium geminatum*.

For the NMS analysis, the three dimensional solution with a stress level of 0.12 was best. A clear grouping of sites inhabited by *P. paludosa* is visible in the NMS ordination space using axis scores (Figure 2.2). In comparison, sites supporting *P. maculata* showed a more dispersed pattern, but *P. paludosa* and *P. maculata* sites were substantially distinct from each other. The two sites with comingling of native and exotic snails were closely grouped in NMS space.

The ANOSIM analysis, with Global R = 0.451, showed significant differences in vegetation composition between sites supporting native only, exotic only, and mixed populations ($P < 0.001$). Pairwise test results between groups showed significant differences between sites inhabited by native and exotic ($P < 0.0001$), native and mixed ($P < 0.033$), and exotic and mixed, ($P < 0.006$).

A one way SIMPER analysis on plant assemblages found within sites inhabited by *P. maculata* had a species similarity of 25.38%, with *Hydrilla verticillata* (67.15 %) contributing the most to community similarity, followed by *Schoenoplectus americanus* (12.11%) (Table 2.1). Sites supporting populations of *P. paludosa* had a plant species similarity of 36.22%. Three species contributed most to *P. paludosa* plant assemblages;

Eleocharis cellulosa (29.62%), *Nymphaea spp* (18.55%), and *S. americanus* (17.63%).

Between groups comparison showed that *E. cellulosa* and *H. verticillata* were the greatest contributors to species dissimilarity between sites supporting only *P. maculata* or *P. paludosa* (Table 2.2). Comparing *P. paludosa* and *P. maculata* to Mixed sites showed *Paspalidium geminatum*, *V. americana* and *Potamogeton illinoensis* were the three dominant contributors to community dissimilarity.

2.5 Discussion

P. paludosa and *P. maculata* predominately occupy different plant species assemblages in Lake Okeechobee. Assemblage variations stemmed primarily from the importance of an exotic SAV, *H. verticillata*, at sites supporting populations of the exotic *P. maculata* and omission of the native *E. cellulosa* and *Utricularia spp.* at those sites, both of which were prevalent at sites supporting the native snail *P. paludosa*. *H. verticillata* was approximately five times more abundant than the next most abundant species at sites inhabited by *P. maculata*, whereas four different native plant species were found in nearly equal proportions at sites inhabited by *P. paludosa*. Sites supporting *P. paludosa* were also more internally similar than sites supporting *P. maculata*, indicating that *P. paludosa* may be sensitive to species assemblage variation. *P. paludosa* preferred mosaic of vegetation is driven by native emergent and submerged aquatic vegetation that is consistent with Lake Okeechobee historical records (Pesnell G.L. 1976).

H. verticillata is commonly found throughout the lake, and is difficult to manage due to its high vegetative reproduction rate via fragmentation (Van and Steward 1990). It is also a fast growing species that can outcompete native SAVs, e.g. *V. americana*, for sunlight and substrate, and may impact entire vegetation communities and alter water

chemistry in high density locations (Van Dijk 1985, Pesacreta 1988). Juveniles of *P. maculata* can be found in high concentrations in dense patches of *H. verticillata* communities, which may act as dispersal mechanisms for *P. maculata* juveniles attached to floating mats and fragments. Floating mats and fragments can also act as refugia from predators and a source for food. As the juveniles mature, they may become a driver for *H. verticillata* expansion as they fragment the host plant and consume its native plant competitors, potentially creating a feedback effect that further reduces biotic resistance of the ecosystem. In essence, these synergistic relationships among exotic species are consistent with the Invasional Meltdown Concept (Simberloff 1999). Consequently, in addition to increased nutrient levels, native apple snail habitat may be declining as a result of *P. maculata* facilitated species competition between *H. verticillata* and the native plant species of their preferred habitat.

The presence or absence of key plant species appears to influence snail species presence, and may provide a means to mitigate exotic impacts and target community assemblages for restoration. Native species, such as *Utricularia spp.*, *E. cellulosa*, and *Nymphaea spp.*, were important at sites supporting the native *P. paludosa* and differentiated those sites from locations where the exotic *P. maculata* was found.

Previous research indicated that *Utricularia spp.* was a valued food source for both *P. paludosa* and *P. maculata*, but the plant was not important in communities supporting mixed snail populations or *P. maculata* exclusively (Morrison and Hay 2010).

Monitoring preferred vegetation like *Utricularia spp* communities especially in locations of high *P. maculata* populations is important to identify how grazing pressures affect vegetation assemblages. Plant communities dominated by *E. cellulosa* are known to

contain large densities of native snails, and are considered ideal conditions for snail kite foraging (Harris, Hoctor et al. 1996, Karunaratne, Darby et al. 2006). Due to low consumption preference and stem rigidity, *E. cellulosa* role may be more structural component for attachment or containment allowing other plants to attach for food, such as filamentous algae, periphyton, or SAV such as *Utricularia spp* (Morrison and Hay 2010).

In contrast to sites where only one snail species was found, native and exotic snails co-occurred in high densities in plant communities containing *V. americana*, a known food source of both species (Baker, Zimmanck et al. 2010). Thus, under certain conditions adult native and exotic apple snail may coexist in the same habitats. Personal laboratory observations seem to indicate that species avoidance by both species of adult snails did not exist (Monette unpublished data). Without the competitive exclusion at the adult stage, herbivore coexistence could have substantial top down effects on primary producers. In addition, (Van, Wheeler et al. 1999) found that displacement of *V. americana* by *H. verticillata* correlated with increasing levels of nitrogen and phosphorus in sediments, and agricultural runoff into the lake has enriched water nutrients. Increased grazing pressure with the addition of an exotic herbivore and competition with an exotic macrophyte could have a cumulative impact on *V. americana* populations. This is particularly a concern for resource managers, as *V. americana* is a desirable target species for the Comprehensive Everglades Planning Project.

By acting as drivers of habitat change, exotic species can have a significant influence on restoration managers' ability to restore ecosystems degraded by human activities (Funk, Cleland et al. 2008). Exotic species can alter ecosystem processes,

increasing stochasticity to the system, and resulting in successional responses (D'Antonio and Meyerson 2002). During these invasion events, an ecosystem's resistance can be reduced, increasing exotic species invasion probabilities for sustained populations, provided a consistent propagule stream exists. Managing these endogenous changes within aquatic system can be complex, given the intrinsic linkages within food webs. Management is especially difficult when established populations of invasive exotic species act as complimentary food resources to newly introduced species, facilitating the establishment of other exotic species, i.e. the Invasion Meltdown Process (Simberloff and Von Holle 1999). Mitigating and managing these potential scenarios, resource managers need to consider the spatial and temporal impact of exotic species and identify potential synergistic effects that interspecies interactions can have on an ecosystem restoration.

2.6 Acknowledgements

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2.7 Tables and Figures

Table 2.1: Percentage similarity by site locations within groups and their respective plant species individual and cumulative contributions. Plant species contributing less than 5% were not listed

Snail Groups	Average Similarity (%)	Plant Species	Species Contribution (%)	Cumulative Contribution (%)
<i>P. maculata</i>	25.38	<i>Hydrilla verticillata</i>	67.15	67.15
		<i>Schoenoplectus americanus</i>	12.11	79.26
<i>P. paludosa</i>	36.22	<i>Eleocharis cellulosa</i>	29.62	29.62
		<i>Nymphaea spp.</i>	18.55	48.17
		<i>Schoenoplectus americanus</i>	17.63	65.8
		<i>Paspalidium geminatum</i>	12.98	78.78
<i>Mixed</i>	77.46	<i>Utricularia spp.</i>	7.26	86.04
		<i>Paspalidium geminatum</i>	33.58	33.58
		<i>Vallisneria americana.</i>	31.34	64.93
		<i>Potamogeton illinoensis</i>	28.36	93.28

Table 2.2. Percentage dissimilarity by snail groupings and species contributions to site locations habitats. Species contributing less than 5% were noted (*)

Groups	Average dissimilarity(%)	Species Contributions (%)							
		<i>Eleocharis cellulosa</i>	<i>Hydrilla verticillata</i>	<i>Nymphaea. spp.</i>	<i>Schoenoplectus americanus</i>	<i>Paspalidium geminatum</i>	<i>Utricularia. spp.</i>	<i>Vallisneria americana</i>	<i>Potamogeton illinoensis</i>
<i>P. maculata & P. paludosa</i>	81.11	14.26	12.07	11.34	9.52	7.95	6.39	*	*
<i>P. maculata & Both</i>	93.08	6.01	12.39	*	5.11	19.27	*	22.16	16.04
<i>P. paludosa & Both</i>	73.1	9.86	*	10.21	8.7	13.25	5.51	18.62	11.43

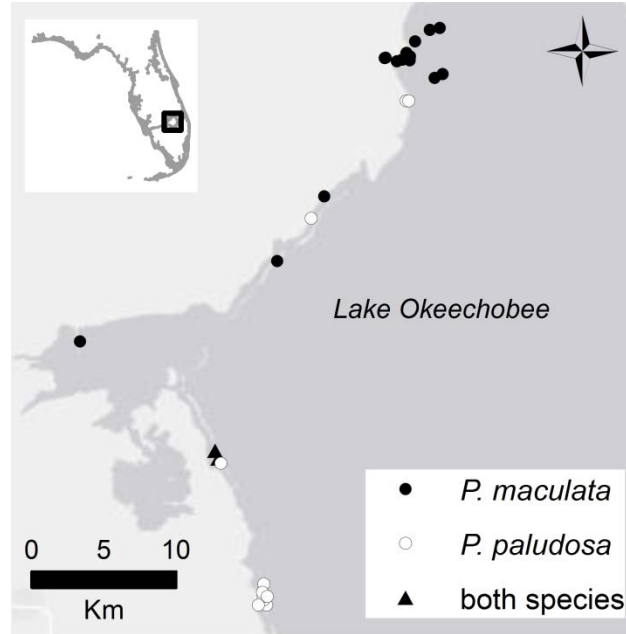


Figure 2.1: Sample locations of *P. paludosa* and *P. maculata* in the littoral zone within the western portion of Lake Okeechobee, south central Florida

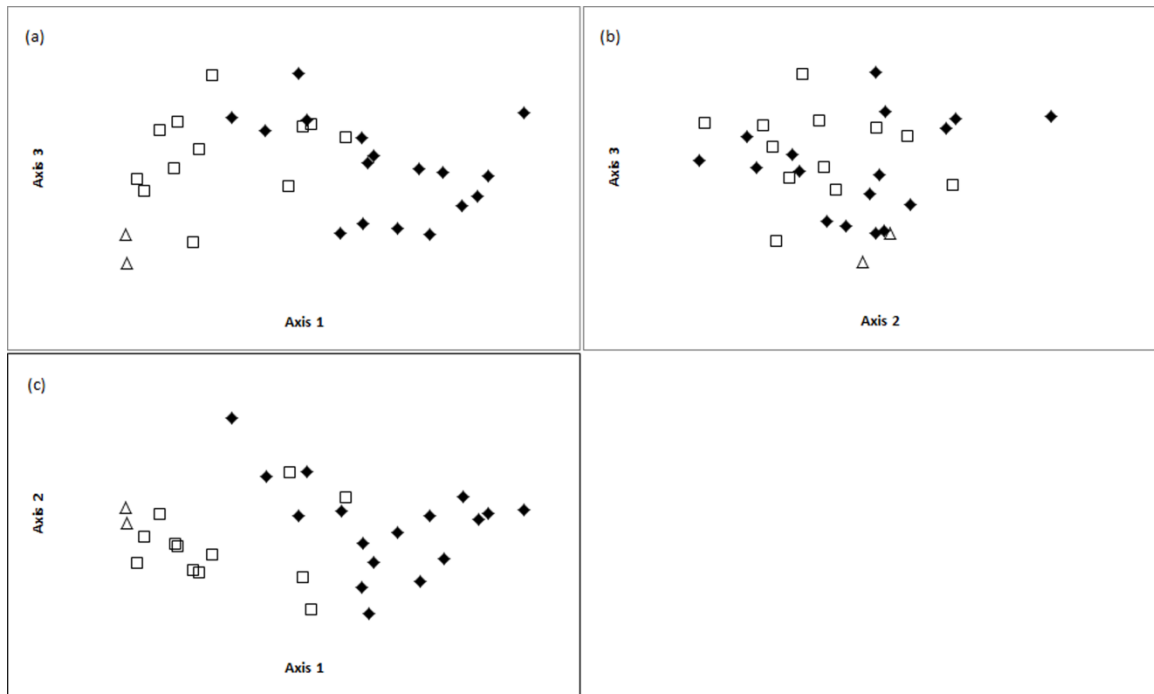


Figure 2.2: Non-metric Multidimensional Scaling (NMS) analysis 2D joint plots based all three axis scores for plant species composition at sites supporting *P. maculata* (solid filled diamond), *P. paludosa* (unfilled square) and mixed populations (unfilled triangle)

3. EFFECTS OF INTERSPECIES COMPETITION ON GROWTH RESPONSE OF *POMACEA MACULATA* AND *POMACEA PALUDOSA*

3.1 Abstract

Biological invasions have been documented to alter species assemblages due to direct competition, shifting competitive balance, and altering habitats. *Pomacea maculata* is an exotic snail that has successfully invaded ecosystems in Florida containing the native snail species *Pomacea paludosa*, but we do not know if the declining populations of *P. paludosa* result from species interactions with *P. maculata*. To test species interactions, we examined four different interaction mechanisms, amensalism, neutralism, direct competition, and native visual intimidation, to investigate their effects on growth relative to controls. No statistically significant differences were found between controls and *P. maculata* and *P. paludosa* growth rates for amensalism ($P=0.396$, $P=0.556$), neutralism ($P=0.163$, $P=0.340$), direct competition ($P=0.144$, $P=0.524$), and native visual intimidation treatments ($P=0.863$). Further analysis on *P. maculata* specimens divided between individuals >20 grams and <20 grams returned no statistically significant results for amensalism ($P=0.204$, $P=0.064$), neutralism ($P=0.071$, $P=0.062$), and direct competition ($P=0.317$, $P=0.192$). Existing research indicated that native and exotic snails have differing growth rates when competing for resources during the juvenile life stage, but species avoidance and interactions at adult life stages may not occur nor meaningfully impact growth rates.

3.2 Introduction

Interspecies competition can influence habitat selection and avoidance behaviors and patterns of niche overlap (Rosenzweig 1987, Young 2004). Competition with exotic species can also lead to an increase in species extinctions (Clavero, Brotons et al. 2009) and contribute to habitat alteration. Predicting the outcome of native and exotic species interactions is a critical piece of information for resource managers and scientists developing mitigation or prevention plans. Such information on exotic herbivores may provide important insight on how interactions between exotic and native species may alter abundances and behaviors that may influence top down pressure on vegetation communities.

Some of the more prominent invaders throughout the world are species from the *Pomacea* genus, including *Pomacea canaliculata*, *Pomacea paludosa* and *Pomacea maculata* (Naylor 1996, Cowie and Thiengo 2003, Cowie and Hayes 2005, Hayes, Cowie et al. 2012). *P. maculata*, Island Apple Snail, is an invasive exotic gastropod invading freshwater aquatic system throughout the southeastern United States. Originally from South America, *P. maculata* is a voracious herbivore with high fecundity rates and a broad geographical range due to wide tolerances to environmental conditions (Hayes, Cowie et al. 2012). Similar to other aquatic invaders, *P. maculata* can be difficult to detect, allowing persistent propagule pressures for continued invasion within connected freshwater systems (Byers 2000). Once established, *P. maculata* can alter submerged vegetation communities and therefore influence ecosystem function.

In contrast, *P. paludosa* is a native gastropod that evolved and interacted with other native freshwater species within the southeastern United States over the course of millennia. An example of these tight relationships is *P. paludosa* and the Everglade snail

kite, *Rostrhamus sociabilis plumbeus*. *P. paludosa* is identified as the sole historical native prey source for the Everglade snail kite (Karunaratne, Darby et al. 2006). The Everglade snail kite is an endangered species of importance to Everglades restoration, and the invasive *P. maculata* is assumed to have a potential negative effect on their survival by displacing the native snail and being predated upon due to the increase in snail drops, increased handling times and reduction in consumption rates (Cattau, Martin et al. 2010). As a result, there are questions concerning *P. maculata*'s competitive relationship with *P. paludosa* and whether these interactions could reshape existing community structure.

Ecological theories suggest competitive effects play an important role in structuring biological communities (Salles, Bredeweg et al. 2002, Krebs 2009). Communities are made up of a set of interactions between species vying for resources in identical space. The motivation to examine interactions between *P. paludosa* and *P. maculata* is driven by concern that *P. paludosa* may be displaced (Pomacea Project 2012). *P. maculata* and *P. paludosa* populations share habitats and lay egg clutches on the same structure (Monette unpublished data), indicating that adult exotic and native apple snails share resources in overlapping geographic regions. While overlapping geographic ranges and the overall decline of native snail populations suggest the possibility of species displacement, it does not prove that niche competition for resources is occurring. In this study, we examine four different interaction mechanisms of interference competition, amensalism, visual intimidation, neutralism, and direct competition, to investigate the effect on growth between adult *P. paludosa* and *P. maculata*.

3.3 Methodology

To examine the effects of interspecies competition we conducted a series of experiments with 4 treatment groups and 1 control group, each lasting 2 months, from October to December 2012 at Florida Atlantic University's Biogeography Lab in Boca Raton, Florida. The indoor tank system consisted of 56 independent ten gallon tanks, each with its own filtration and lighting system. Tank substrate was 3 cm of crushed coral aragonite sand with grain sizes ranging from 2 to 5.5 mm for additional filtration and added calcium (Garr, Lopez et al. 2010). Each of the tanks was lined with opaque paper to minimize direct visual contact with neighboring tanks. Each tank was scraped with an algae brush, siphoned of wastes, and received a twenty percent weekly water change (Conner, Pomory et al. 2008). Tank filters were cleaned weekly to maintain proper filtration. Light cycles were set for a 12 hours light / dark cycle. Tanks were topped off with dechlorinated water to maintain consistent water levels. Weekly readings of pH, nitrate, nitrite and ammonium were recorded. All tanks were established and running for one week prior to snail placements.

To avoid behavioral effects due to captive rearing, wild caught adult snails were used throughout this study. Adult snails varied in size and weight, with initial sizes ranging in weight from 5.3 to 20.6 g for native and 7.6 to 83.0 g for exotic snails. *P. maculata* snails were captured in Lake Okeechobee, Florida, and native *P. paludosa* snails were captured in a quarry outside of Jacksonville, Florida. Captured snails were acclimated in separate tanks for approximately 8 weeks and fed catfish chow (Garr, et al., 2010) in the greenhouse facility to ensure all specimen were healthy. Only adult male snails were used during this study to avoid the confounding factor of egg production that

may influence weight gain and/or loss. Snails were starved 48 hours prior to tank placement.

Nine tanks were manipulated to test each of the following competitive interactions, visual intimidation, amensalism, direct competition and neutralism, while ten tanks were used for experimental controls, for a total of 56 tanks. Direct competition and neutralism were tested by placing a single exotic snail with a single native snail into the same tank with Romaine lettuce. Similar to Conner et al.'s (2008) juvenile competition study between *P. maculata* and *P. paludosa*, Romaine lettuce leaves were washed, weighed to provide approximately 40 g per snail, and replaced every three days (Conner, Pomory et al. 2008). To test for neutralism, two Romaine lettuce leaves, for a total of 80 g, were placed in the tank. Each leaf was attached to clips that were placed at opposite ends of the tanks. Direct competition followed the same experimental design as neutralism, except only one Romaine lettuce leaf was placed in the tank (40 g). To test for amensalism, a screen divider made of a plastic screen mesh and an opaque plastic sheet was used to separate the species, with each side containing Romaine leaves of 40 g. The plastic sheet was scored vertically to allow continuous water flow between separated compartments, but still block visual contact between species. The visual intimidation study used one live *P. paludosa* and one dead empty adult *P. maculata* shell. Both the empty shell and Romaine leaves were placed in the center of the tank. In the control treatments, two 40 g Romaine leaves were placed on opposite sides with each tank containing conspecific snails to maintain snail densities. Snails were scored upon the top of the shell to provide a clear differentiation between individuals.

At the beginning of the competition experiments the weight of each snail was measured. Biweekly measurements followed using a digital scale to the nearest tenth of a gram. We standardized individual snail weights by dividing the new weight of the snail at the end of the study by the original weight multiplied by 100 to give percentage growth. A total of five weighing events occurred throughout this study with the beginning of the study being assigned zero and four being the end (i.e. T0 - T4). Snails were assigned a unique identification by the type of competitive interaction, species name and tank number. During the experiments snails were monitored daily to record snail deaths and to observe basic behavioral avoidance or interaction characteristics that may provide some insight into the results. Dead snails were replaced to maintained comparable snail densities throughout the remainder of the study. Dead snails were not included in the statistical analysis (Morrison and Hay 2011, Posch, Garr et al. 2013) due to difficulties determining cause of death. Replacement snails were added after specimen death to maintain consistent snail densities throughout the study and replacements were weighed prior to tank inclusion but not included in the statistical analysis. Snails were determined dead when pressed upon the operculum and no muscle response occurred for two consecutive days. After the second day, all dead individuals were removed and replaced. Throughout this study, a total of 5 snails died, one in the control, two in the direct competition, and two in the neutralism treatments. The survival rates for the native were 91% and exotic 100%.

Due to varying initial snail size, we performed an analysis of covariance (ANCOVA) with initial snail mass as a covariate on differences in percent growth between each species' treatments and controls (Morrison and Hay 2011). If snail mass

was not significant in the ANCOVA results, we performed an analysis of variance (ANOVA). If ANCOVA or ANOVA assumptions were violated, we performed a nonparametric Mann-Whitney Test except for border line significance of ($P=0.05$) where a Welch and Brown-Forsythe analysis for Robust Tests of Equality of Means was applied.

For native specimen experiments, one way ANOVA was applied to neutralism and amensalism treatments, while the Mann-Whitney Test was used for visual intimidation and direct competition treatments. For exotic specimen experiments, statistical analyses were conducted on all exotics pooled, and divided between snails >20 g and <20 g. The reason for the weight based division for analysis was the clear bimodal distribution of weight classes among exotic specimens (Figure 1). ANCOVA analysis was performed on exotic amensalism for snails >20 g and neutralism <20 g. One way ANOVA was conducted on exotic amensalism >20 g, while a Mann-Whitney analysis was applied to the remaining treatments, neutralism <20 g and both trials for direct competition.

3.4 Results

Specimen of both species grew consistently across all competition experiments (Table 3.1). In general, *P. maculata* exhibited greater weight gains than *P. paludosa* (Figure 3.1 and 3.2). The control treatment exhibited positive growth for both species (Figure 3.3), with *P. maculata* ($n=20$) more than doubling in mean weight, while *P. paludosa* ($n=19$) showed positive mean weight gain over time (Table 1). Snails were found interacting during feeding, and aggressive or avoidance behavior was not observed during this study.

For the direct competition experiments, the Mann-Whitney test showed no significant difference between native snails and their controls ($P=0.524$, $n=8$). Interestingly, native snail specimens grew more rapidly for the first two events (Figure 3B). This did not occur during any of the other treatments. As a result, the difference in mean percent growth between the native and exotic was the smallest of all treatments (Table 1). ANCOVA showed no significant difference between exotic snail direct competition treatment and exotic controls for all exotic snails taken together ($P=0.144$, $n=9$). Mann-Whitney analysis also exhibited no significant difference for exotic snails >20 g and <20 g ($P=0.317$, $n=5$ $mw=61.1\pm2.1g$; $P=0.192$, $n=4$, $mw=13.2\pm1.6g$) respectively.

For the neutralism experiments, the one way ANOVA comparing the native treatments to the controls (Figure 3C) returned no significant differences ($P=0.340$, $n=7$). Due to a Levene test for homogeneity of variances showing border line significance ($P=0.05$), a Welch ($P=0.491$) and Brown-Forsythe ($P=0.491$) analysis for Robust Tests of Equality of Means was conducted to support the ANOVA results of no significant difference. ANCOVA results for percent growth were not significant for pooled exotic snails ($P=0.163$, $n=9$), snails >20 g ($P=0.814$, $n=6$, $mw=65.1\pm5.9g$), and <20 g ($P=0.063$, $n=3$, $mw=11.8\pm2.8g$) between neutralism treatment and controls.

In the amensalism treatments, *P. paludosa* mean growth rate decreased after event 3, while *P. maculata* mean growth rate was positive and consistent throughout the experiment (Figure 3D). The results of the ANOVA indicated no significant differences between treatments and controls for the native ($P=0.556$, $n=9$) and exotics >20 g ($P=0.204$, $n=3$, $mw=69.9\pm1.2g$). ANCOVA for exotics <20 g ($P=0.064$, $n=6$,

mw=11.2±0.6g) and Mann-Whitney test for the pooled exotics showed no statistical significance (P=0.396, n=9).

Mean growth was positive, 130% (SE ±3%), for *P. paludosa* specimens in the visual intimidation experiment (Figure 3E). Although significant differences were not found between treatment and control with the Mann-Whitney Test (P>0.863). This was the only trial in this study without a corresponding treatment for exotics.

3.5 Discussion

This study tested several different competitive mechanisms to examine different possible scenarios concerning how competition occurs in areas of niche overlap (Salles, Bredeweg et al. 2002). Results of these experiments suggest that competition for resources between *P. paludosa* and *P. maculata* may be weak at the adult stage. More importantly for the native species, there were no significant statistical differences in mean weight change for *P. paludosa* between treatments and controls for competition over time, indicating the presence of the exotic snail did not prohibit consumption and growth. Based on the trend of positive weight change for both species, interactions between species seem to generate minimal pressures on weight gain.

Most of the competition or density research to date was conducted with small juvenile snails, and found evidence that competition has an effect on growth (Conner, Pomory et al. 2008, Morrison and Hay 2010, Posch, Garr et al. 2013). Variation in species competition at different life stages is not uncommon. This is may be the case with *P. paludosa* and *P. maculata*. Both snail species shift from algal grazers to macrophyte consumers, opening up new habitats and resources for both adult species and potentially reducing interspecies interactions. *P. maculata* eventually grows to almost

five times the weight and over twice the operculum width and length of native apple snails. This size differential illustrates morphological differences at the adult stage, and suggests varying ability to adapt to diverse food resources. Overlap in food and habitat preference still exist for some vegetation communities between the snail species, but field studies indicate strong correlations to different habitats for adults of the two species (Monette unpublished data). This is consistent with Morrison and Hay's (2011) study that showed differences in food preference for native and exotic plants between snail species. The ability for adult snails to migrate toward differing preferred habitats reduces pressure from snail densities and species interactions; however the opposite may occur in overlapping locations. The lack of observed interspecies avoidance and effects of species interactions in controlled experiments reflects field observations where both native and exotic individuals were found in the same locations and with both species' egg clutches found on the same emergent plant stem (Monette unpublished data).

Previous research has shown that adult exotic snails reduce the growth rate of juvenile native snails (Conner, Pomory et al. 2008, Posch, Garr et al. 2013). This can have a negative impact on the overall reproductive cycle by shortening the reproductive time scale, relationship of egg production to food availability, and egg quality of female egg clutch production (Posch, Garr et al. 2013). While this study did not find significant effects of competition on growth rates for snails <20 g, both amensalism and neutralism studies had P-values approaching the α threshold ($P < 0.05$) of significance, while direct competition did not. One of the reasons for the lack of significance may be a limited sample size of individuals < 20 g or initial snail size. Based on initial operculum size, the snails used in our study appear to be conservatively over four times larger than those used

in Posch, Garr et al. (2013), indicating a heavier more mature exotic snail was examined (Baker, Zimmanck et al. 2010). The difference in weight may indicate a change in consumption behaviors, growth patterns and species interactions. All important factors in understanding the life history, ecological impacts, mitigation and management plans for resource managers.

Interestingly, *P. maculata* percent growth exhibited greater variability across trials when compared to *P. paludosa*. Variable growth in juvenile snails was found in previous studies examining food preference and growth rates, including *P. canaliculata* and *P. maculata* (Boland, Meerhoff et al. 2008, Morrison and Hay 2011). This study shows that *P. paludosa* has a more constrained growth pattern. *P. maculata* has a broader growth pattern, phenotypic plasticity, across different food resources than *P. paludosa* and more similar to *P. canaliculata* (Morrison and Hay 2011). Both *P. maculata* and *P. canaliculata* are known invasive exotics in parts of the world that have caused tremendous economic and ecological impact (Naylor 1996, Takeichi, Hirai et al. 2007, Matsukura, Okuda et al. 2013) and growth variability may be a contributing factor to their population persistence in newly invaded areas.

Growth plasticity is an assumed inherent trait for invasiveness in colonizing plant species and may contribute to species persistence, survival and reproduction (Mal and Lovett-Doust 2005, Molina-Montenegro and Naya 2012). High growth rates and phenotypic plasticity may contribute to flashy population explosions causing cascading effects on aquatic systems. Data found in existing studies have shown plant availability can positively or negatively influence growth and phenotypic plasticity (Sharfstein and Steinman 2001, Morrison and Hay 2011). Generalized global *P. maculata* studies may

not apply to local environments due to differing ecosystem heterogeneity and species assemblages where the species may plastically respond in newly invaded systems. While the research may be region specific, examining local abiotic and biotic factors influencing life history traits, including phenotypic plasticity, may help managers understand why *P. maculata* population explosions occur, how to mitigate herbivory impact and establish integrative pest management protocols.

Mortality rates in the current study were lower than in other competitive pressure studies (Posch, Garr et al. 2013). Because all the specimens were wild caught, we were unable to reliably estimate the age of each individual. These losses could be attributed to the natural age limits of 1-1/2 years of *P. paludosa* (Darby, Valentine-Darby et al. 2003, Darby, Bennetts et al. 2008). Future research may include using snail specimens reared in a managed system to mitigate mortality due to age, different adult densities with declining food resources, and different food resources as weight growth studies have found different plants can influence weight gain (Sharfstein and Steinman 2001, Morrison and Hay 2010).

3.6 Conclusions

This study demonstrates that although native and exotic snails may compete for resources during the juvenile life cycle under specific densities (Conner, Pomory et al. 2008, Posch, Garr et al. 2013), species avoidance and competition may not occur nor meaningfully impact growth rates in conditions of one to one exotic native ratio with unlimited food resources. As a result, increased herbivory could occur causing changes to ecosystem processes in locations where niche overlaps exists. Moreover, studies of the potential impacts from increased herbivory and phenotypic plasticity with local

environments would provide useful insight into how *P. maculata* may impact freshwater systems throughout Florida.

3.7 Acknowledgements

The authors would like to thank the following Florida Atlantic University students for their invaluable lab assistance: Mike Cantaloube, Kelli Grim, Manny McIlroy, Adriana Olavarria, Alexandra Samuel, Andy Vala, and Tony Welch. Without the support from the people above, this project would not be possible.

3.8 Tables and Figures

Table 3.1: Native and exotic snail mean weight change standard errors calculations for overall growth for the following treatments: controls, amensalism, neutralism, direct competition and visual intimidation.

Treatment	<i>P. paludosa</i>	<i>P. maculata</i>	<i>P. maculata</i>	
			<20grams	>20grams
Controls	125% \pm 6%	222% \pm 71%	481% \pm 76%	116% \pm 6%
Direct	137% \pm 11%	158% \pm 23%	229% \pm 28%	107% \pm 1%
Neutralism	127% \pm 10%	190% \pm 39%	335% \pm 53%	118% \pm 5%
Amensalism	115% \pm 8%	177% \pm 24%	215% \pm 22%	102% \pm 2%
Visual	130% \pm 3%			

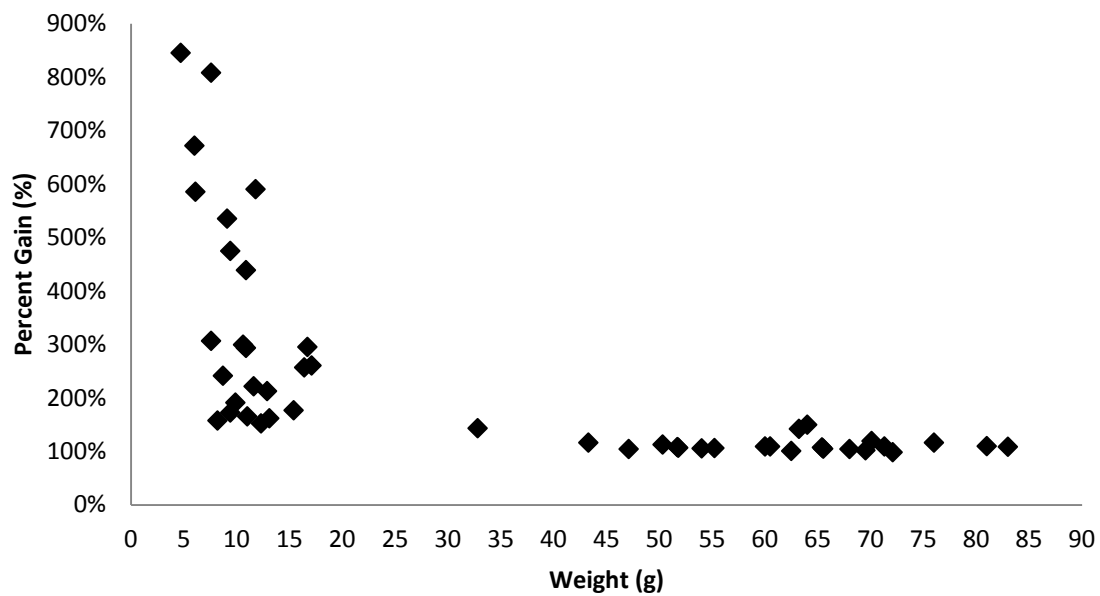


Figure 3.1: *P. maculata* percent weight gain by initial weight.

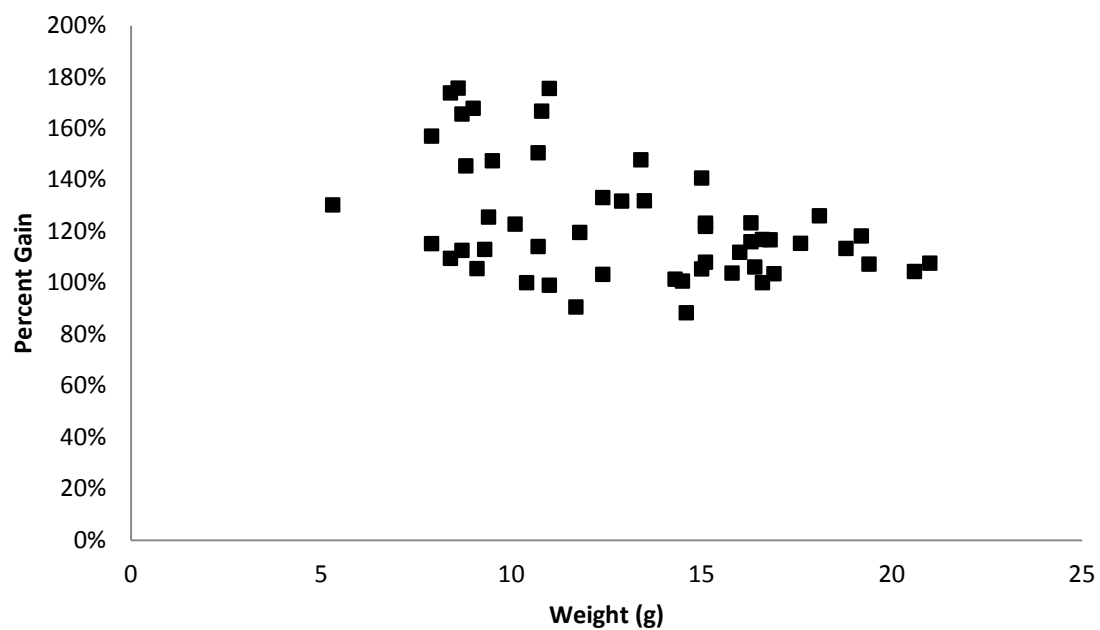
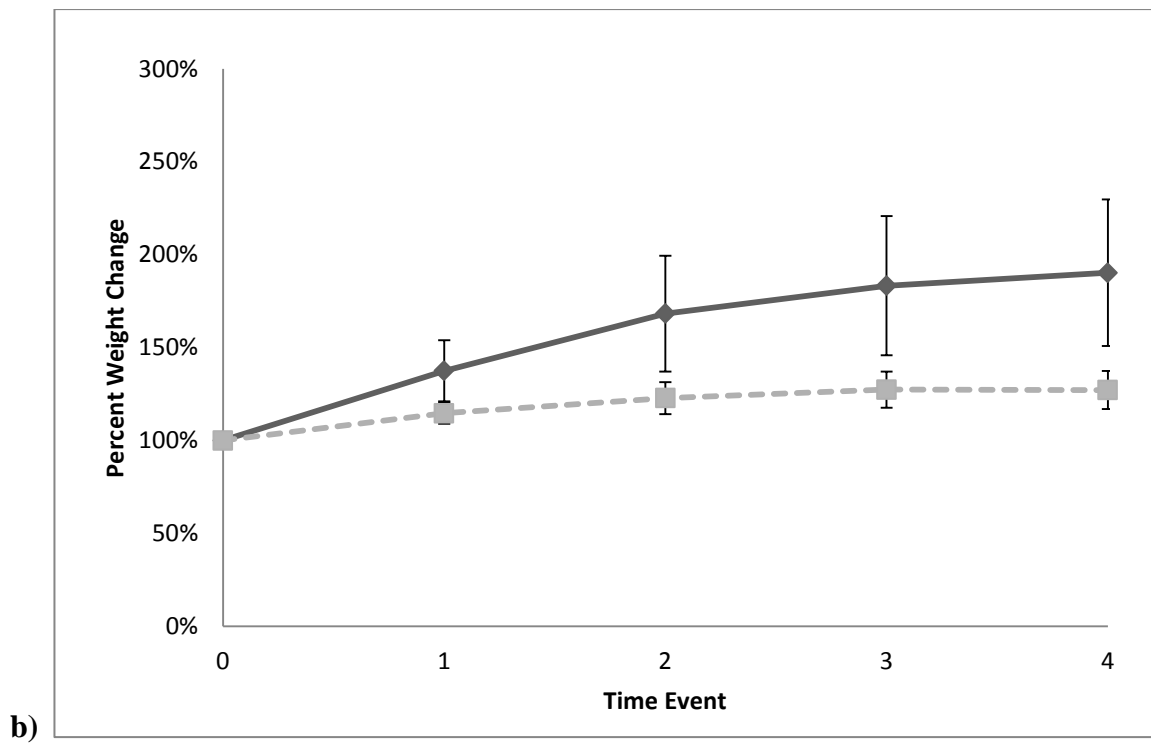
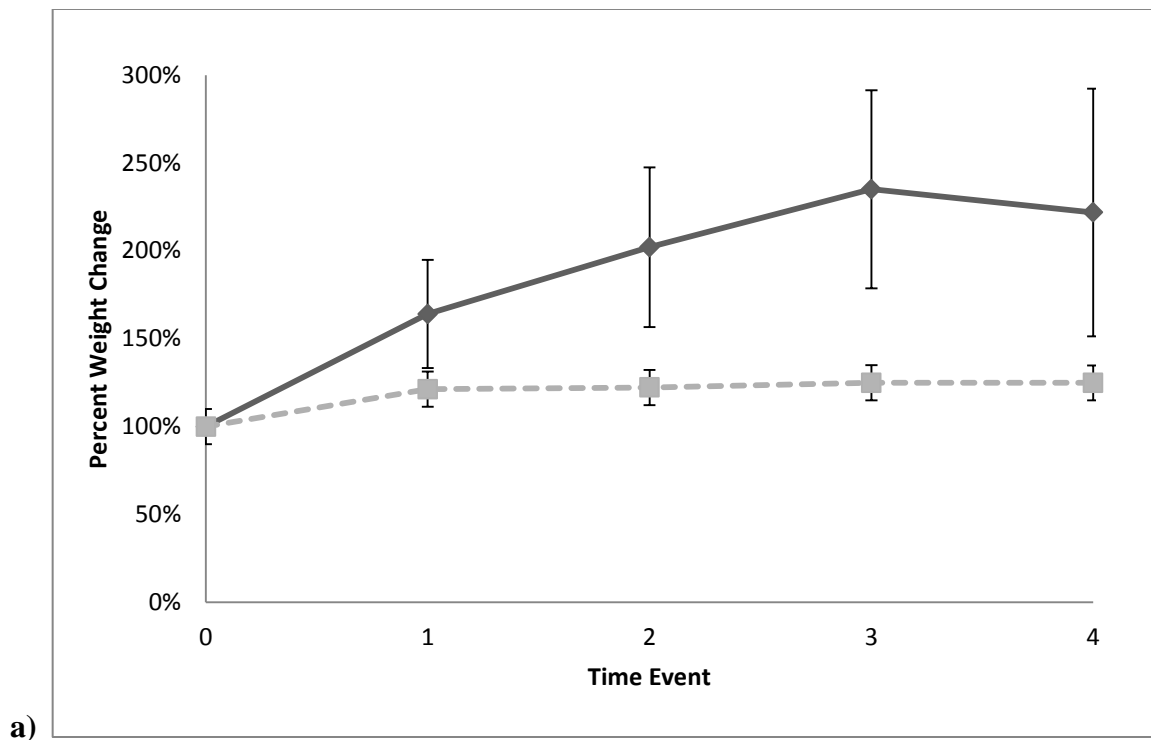
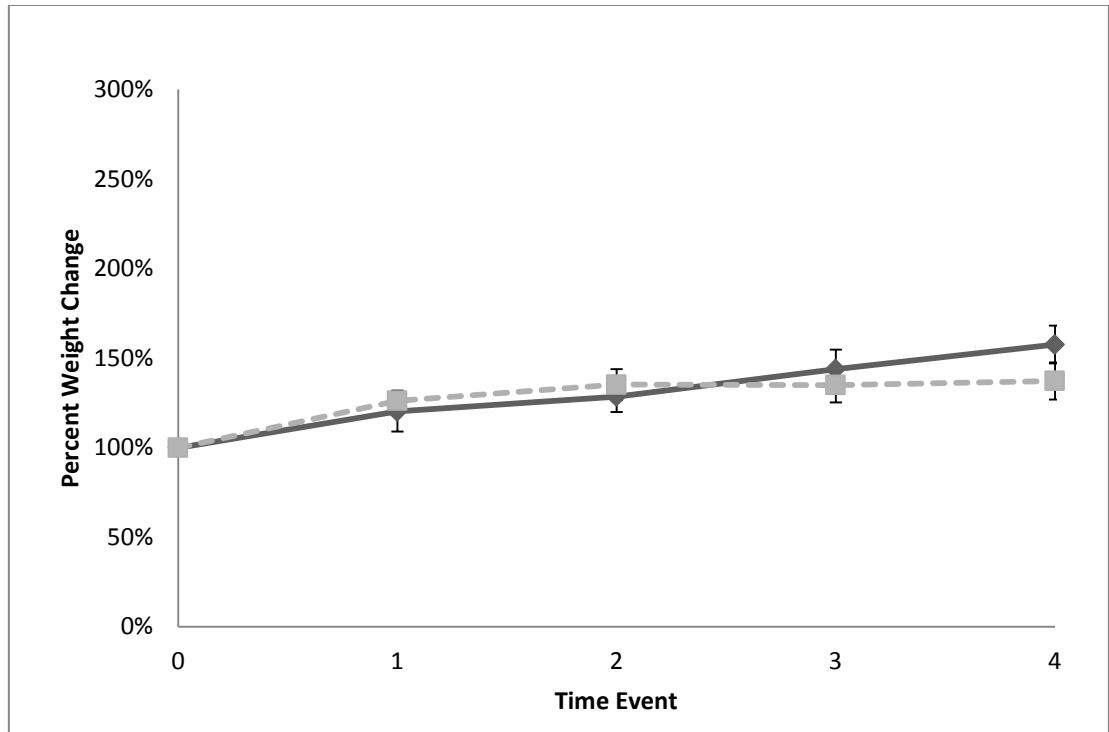


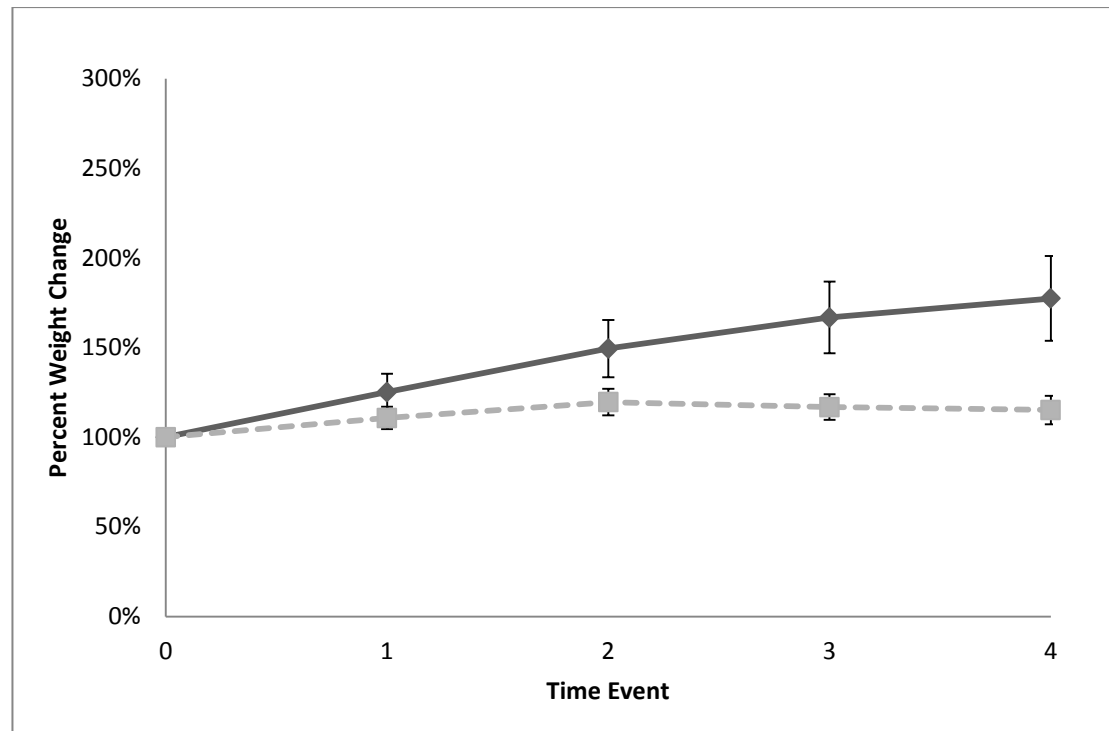
Figure 3.2: *P. paludosa* percent weight gain by initial weight.



c)



d)



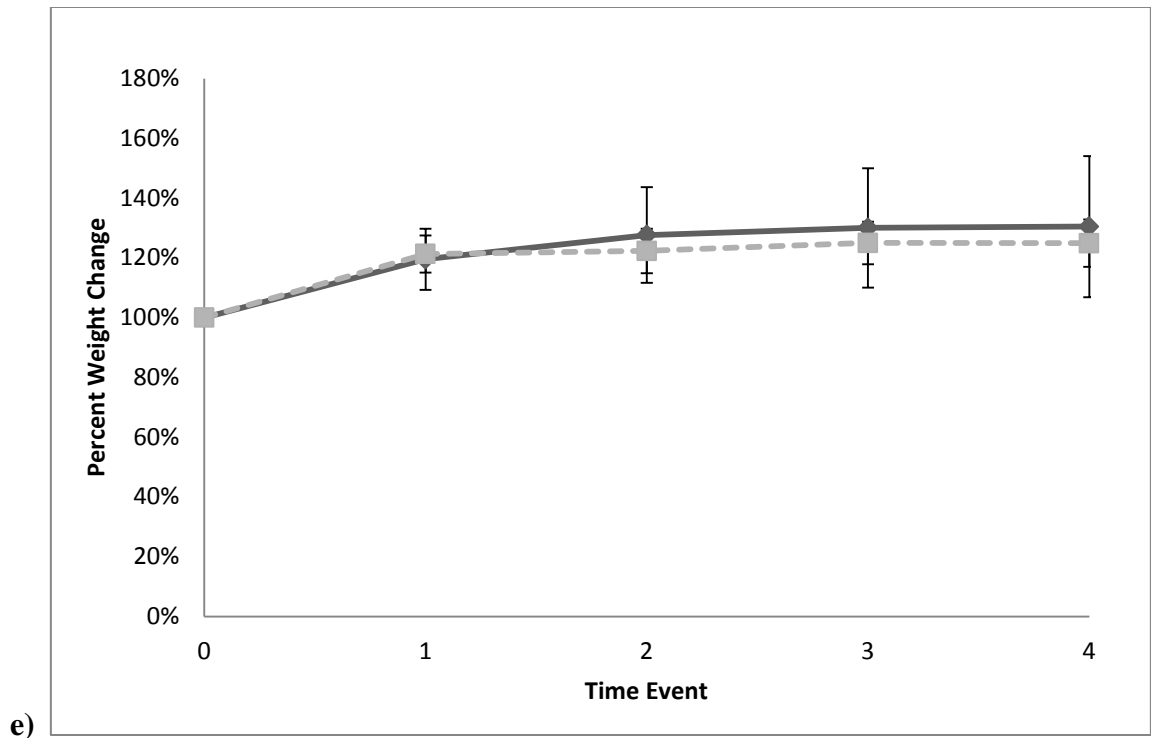


Figure 3.3: Weight change over time for both *P. maculata* and *P. paludosa*, from initial weight through 4 subsequent measurements to the end of each experimental treatment. *P. maculata* is symbolized with solid line with a solid filled diamond marker. *P. paludosa* is a dashed line with a solid filled rectangle except for Figure E where *P. paludosa* controls reflect solid line with solid filled diamond marker. A) Control treatment, B) neutralism treatment, C) direct competition treatment, D) amensalism treatment, E) visual intimidation treatment

4. EXAMING THE EFFECTS OF CONSUMPTION BEHAVIOR OF *POMACEA MACULATA* AND *POMACEA PALUDOSA* ON *VALLISNERIA AMERICANA*

4.1 Abstract

Understanding behavioral characteristic differences between invasive exotic species and native species is an important step in preventing, managing and mitigating environmental impacts. This study examines these differences in grazing pattern rates between *P. paludosa* and *P. maculata* on *V. americana*, a plant of restoration importance, to assess the potential ecological impact. We used one-way ANOVAs to test for statistically significant differences between *P. maculata* and *P. paludosa* for herbivory ($P=0.006$) and total damage rates ($P=0.024$) on *V. americana*. Statistical difference was not found for physical damage ($P=0.18$) between *P. maculata* and *P. paludosa*. Statistical differences was found between controls without snails and *P. maculata* and *P. paludosa* herbivory ($P=0.001$, $P=0.05$), physical ($P=0.007$, $P=0.001$) and total damage ($P=0.001$, $P=0.002$). These results show *P. maculata* consumes and removes more *V. americana* material at a faster rate than native *P. paludosa*. This study demonstrates that *P. maculata* consumption behavior has the potential to alter native *V. americana* communities.

4.2 Introduction

Invasive exotic species can alter food webs, alter habitats, displace native species, reduce diversity, and impair ecosystem function (Rodda and Fritts 1997, Simberloff and Schmitz 1997, DiTomaso 2000, Pimentel, Zuniga et al. 2005). Understanding behavioral

characteristics of invasive exotic species in their new environments and interacting with native species is an important step in preventing, managing and mitigating environmental impacts. Management typically relies on existing scientific literature focusing on one of the three stages of the invasion process; introduction, establishment and spread (Engel, Tollrian et al. 2011). Information gaps related to exotic-native interactions at any of these three stages can be problematic for resource managers searching for successful management techniques.

Pomacea maculata (Island Apple Snail), formerly known as *Pomacea insularum*, is an aquatic freshwater snail native to South America that is invasive in Southeast Asia, Spain, and parts of United States (Hayes, Cowie et al. 2012, EFSA 2014, Yoshida, Matsukura et al. 2014). *P. maculata* were probably introduced in the United States in the 1990s (Rawlings, Hayes et al. 2007, Burlakova, Padilla et al. 2010), and is now established throughout the southeastern United States (Byers, McDowell et al. 2013), including the entire state of Florida. Because the species has clearly entered the established stage of invasion, managers will in order to control this species require an understanding of their population dynamics, behavior and associated ecological impacts. *P. maculata*'s environmental impacts are difficult to estimate, but may include trophic level disruptions that significantly alter existing vegetation communities of value to restoration (e.g. tapegrass, *Vallisneria americana*), littoral and near shore habitats critical for endangered species (e.g. snail kites, *Rostrhamus sociabilis plumbeus*), and migratory water birds and sport fishing (Aumen NG 1995, USACE. 1999, Havens and Steinman 2013).

P. maculata has invaded habitat in the Greater Everglades that supports the only native Pomacea species in Florida, *Pomacea paludosa*. Prior to *P. maculata* invasion, historically snail kites fed nearly exclusively on the native apple snail (Bennetts, Darby et al. 2006), making them an essential component for snail kite survival. This selective prey item behavior exhibited by snail kites now includes the vastly growing populations of *P. maculata* (Cattau, Martin et al. 2010), therefore placing additional emphasis on snail-plant interactions as both apple snails utilize tapegrass as habitat and as a food resource (Monette unpublished data). Understanding this interplay of SAV communities, predator-prey and snail-plant interactions is important for species management. Consequently, studies examining the differences in grazing rates on *V. americana* between *P. paludosa* and *P. maculata* will give us a better understanding of ecological impact of this species.

Studies examining food resource consumption are often designed to capture food preferences and rates of consumption without understanding where the physical damage may occur (Boland, Meerhoff et al. 2008, Baker, Zimmanck et al. 2010, Morrison and Hay 2011). Food presentation normally doesn't include the visual arrangement of the whole plant structure but only small pieces or reconstituted plant fragments to capture food preferences or herbivory rates. The aim of this study is to investigate *P. maculata* and *P. paludosa* consumption behavior when presented the whole plant of *V. americana*, quantifying vegetation impact resulting from grazing. The results of this study provide a better understanding of the grazing behavior of *P. maculata* and *P. paludosa* under similar visual conditions that simulate field environments and differences in grazing impacts on a plant of restoration importance.

4.3 Methodology

To test consumption behavior, in each of 24 ten gallon tanks we placed one *V. americana* plant with five blades. *V. americana* plants were harvested from Lake Okeechobee Florida and acclimated for eight months at Florida Atlantic University Everglades Botanical Greenhouse. Each tank was equipped with its own lighting and Tetra carbon filtration. Lighting was digitally timed for 12 hours day and night cycle. Tanks were filled with dechlorinated water and temperature was recorded at the beginning and end of the study. Tank substrate consisted of crushed coral aragonite sand with grain size approximately 2 to 5.5 mm (Garr, Lopez et al. 2011). Tanks were lined with an opaque sheet of paper to obstruct direct line of sight between adjacent tanks. All tanks were run a week prior to snails being introduced in June 2012. *V. americana* plants were cleaned of any periphyton, detritus and algae prior to being placed within its own self-containing pot filled with potting soil. The top layer consisting of crushed coral aragonite was then laid on top of the soil to maintain surface consistency. The *V. americana* pot was nestled within the substrate so the base of the plant was even with the substrate.

Wild caught adult male snails were used during this study to avoid potential behavioral effects of captive rearing and egg production. All specimens were captured within Florida, with *P. paludosa* snails collected from a quarry outside of Jacksonville and *P. maculata* specimens collected from Lake Okeechobee. Snails varied in size, with *P. paludosa* snails weighing between 14.2 g to 28.9 g and *P. maculata* measured between 55.6 g to 135.3 g. Collected snail were fed catfish chow (Garr, Lopez et al. 2011) for approximately eight weeks during acclimation in the greenhouse staging facility to ensure

snail specimens were healthy. Snails were starved 24 hours prior to being used for the study.

We used an experimental design of three groups, 1) *P. maculata*, 2) *P. paludosa*, and 3) control with no snails, with eight tanks to each group. Each plant blade was uniquely marked by pinholes at the base and blade tip of the plant (Zieman 1974). The length of each blade was recorded and summed for total blade length. Tanks were checked every four hours to remove any floating leaf blades. All removed floating blades were measured, and recorded as physical damage. Physical damage rate was determined per tank by totaling the lengths of floating blades then dividing by time of the study duration in hours. Herbivory rate was calculated per tank by the difference between the pre- and post-study total blade length minus both physical damage (Figure 4.1) and remaining blades, all divided by the sample time in hours. The total damage rate is the difference between pre- and post-study measurements of all blades divided by sample time in hours (Figure 4.1). Due to the variation in grazing behavior, snail and plant size, we stopped each tank when approximately 50% of the plant was removed, snail weights were recorded and the remaining blades were measured. Statistical analysis was conducted using a one-way ANOVA to determine significant differences between trials.

4.4 Results

The overall study lasted 152 hours with both species causing significant total damage to *V. americana*. The mean total blade length for each *V. americana* plant in *P. maculata* and *P. paludosa* trials were 154 cm and 170 cm respectively. The mean growth rates for tanks consisting of only *V. americana* was 0.13 cm/hr. On average, *P. maculata* trials lasted 29 hrs (SE ± 4.49 hrs) with shortest duration 16 hrs and the longest 52 hrs.

The average duration for *P. paludosa* trials was 80 hrs (SE \pm 20.44) with trials as short as 16hrs and lasting as long as 152 hr. Subsequently, *P. maculata* rates of herbivory, physical and total damage rates were 1.8 cm/hr, 2.5cm/hr and 4.2 cm/hr (Figure 4.2). *P. paludosa* rates of herbivory, physical and total damage were 0.2 cm/hr, 1.2 cm/hr and 1.4 cm/hr (Fig 2). The one-way ANOVA resulted in statistical differences between *P. maculata* and *P. paludosa* for herbivory (P=0.006) and total damage rates (P=0.024). Statistical difference was not found for physical damage (P=0.18) between *P. maculata* and *P. paludosa*. The one-way ANOVA showed statistical differences between controls without snails and *P. maculata* herbivory (P=0.001), physical (P=0.007) and total damage (P=0.001). Statistical differences were also found comparing controls without snails and *P. paludosa* herbivory (P=0.05), physical (P=0.001) and total damage (P=0.002).

4.5 Discussion

Pomacea maculata and *P. paludosa* have different grazing behavior patterns resulting in different levels of structural effects on *V. americana*. While both snails exhibited top down grazing pressure on *V. americana* growth rates, *P. maculata* demonstrated significantly greater consumption and total damage rates under controlled conditions. While not statistically significant, *P. maculata* also caused higher rates of physical damage than *P. paludosa*. All of these differences suggest a substantial deviation from the native *P. paludosa* grazing regime in stands of *V. americana*.

The two species showed some similarities in consumption strategies by starting near the base or middle of the plant, but differed in destructive capabilities stemming from herbivory rates and physical damage. *P. paludosa* predominately grazed along the edges of the blades while *P. maculata* chewed completely through the blades, i.e.

severing the majority of the blade completely from its base. This difference in behavior may be a consequence of snail mass and the blade's ability to support the weight of each herbivore species. *P. paludosa* consumption behavior caused less biomass removal leaving more photosynthetic tissues available for photosynthesis and regrowth. In contrast, the substantial loss of photosynthetic material due to *P. maculata* grazing could dramatically reduce the plant's ability to sustain growth over time.

V. americana communities are under pressure from abiotic and biotic factors. These factors range from abiotic factors like increasing nutrients from non-point source pollution and biotic factors of invading exotic species. Studies have shown established *V. americana* communities can resist invading *Hydrilla verticillata* under natural conditions through competitive suppression (Doyle, Grodowitz et al. 2007, Owens, Smarts et al. 2008). However, competitive success between these two species can shift under different conditions. In areas of greater soil nutrients the competitive advantage exhibited by *V. americana* shift towards *H. verticillata*, illustrating the sensitivity of these interactions as they compete for sunlight (Van, Wheeler et al. 1999) and substrate availability. *V. americana* can suppress *H. verticillata* fragments from establishing, but when substrate becomes available *H. verticillata* can establish (Owens, Smarts et al. 2008), increasing the likelihood of species persistence and further expansion. An increase in grazing pressure by *P. maculata* may remove too much *V. americana* biomass and increase substrate and light availability for invading *H. verticillata*. *P. maculata* occurs in both *H. verticillata* and *V. americana* communities (Monette unpublished data), therefore potentially altering the competitive balance in areas of interactions.

The effect of *P. maculata*'s grazing strategy could impact established SAV communities. Biomass removal by cutting plants at the base creates an opening in the canopy near the water surface, increasing sunlight availability and allowing neighboring plant species to utilize the available energy for additional tissue growth (Van, Wheeler et al. 1999). *P. maculata* population growth thus may lead to changes to community structure through exotic snail-plant interactions and altering plant competitive interactions. SAV community composition will favor less palatable plant species with faster growth rates, or species are resistant to this type of grazing. In comparison, native communities have evolved under the less damaging grazing pressure of *P. paludosa*, which may have less influence on the competitive balance among plants. However, species avoidance between *P. maculata* and *P. paludosa* may not occur, allowing both species can potentially occupy a similar habitat niche within a *V. americana* community (Monette unpublished data). This may lead to a scenario where both species' consumption behaviors may be additive, resulting in an increase in total damage, snail-plant interaction pressure and grazing duration.

4.6 Conclusions

This study demonstrates that *P. maculata* consumption behavior has the potential to alter native *V. americana* communities. *P. maculata* consumption behavior and food preference may be influencing vegetation composition in areas of established populations. Follow-up studies should be performed to help understand how *P. maculata* top down grazing pressure may affect other plant species and identify specific snail species densities that may tip the competitive balance between plant species interactions and shape species composition.

4.7 Tables and Figures

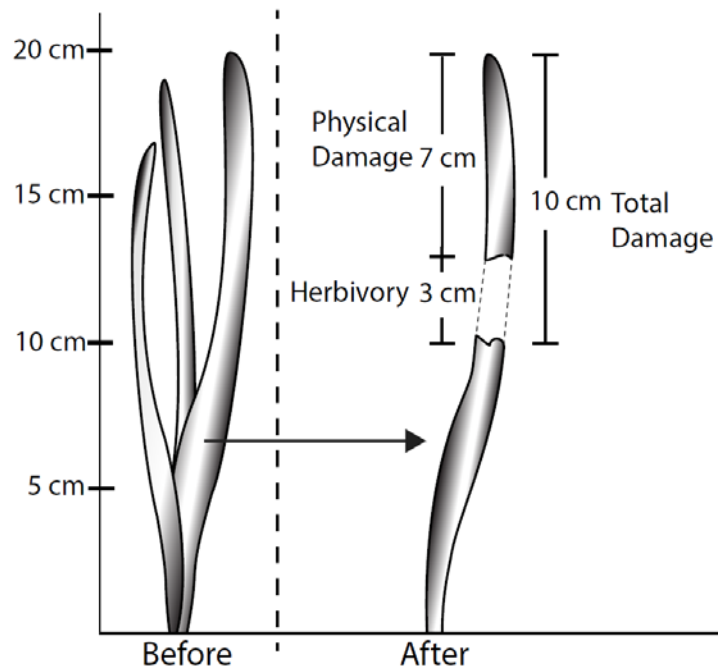
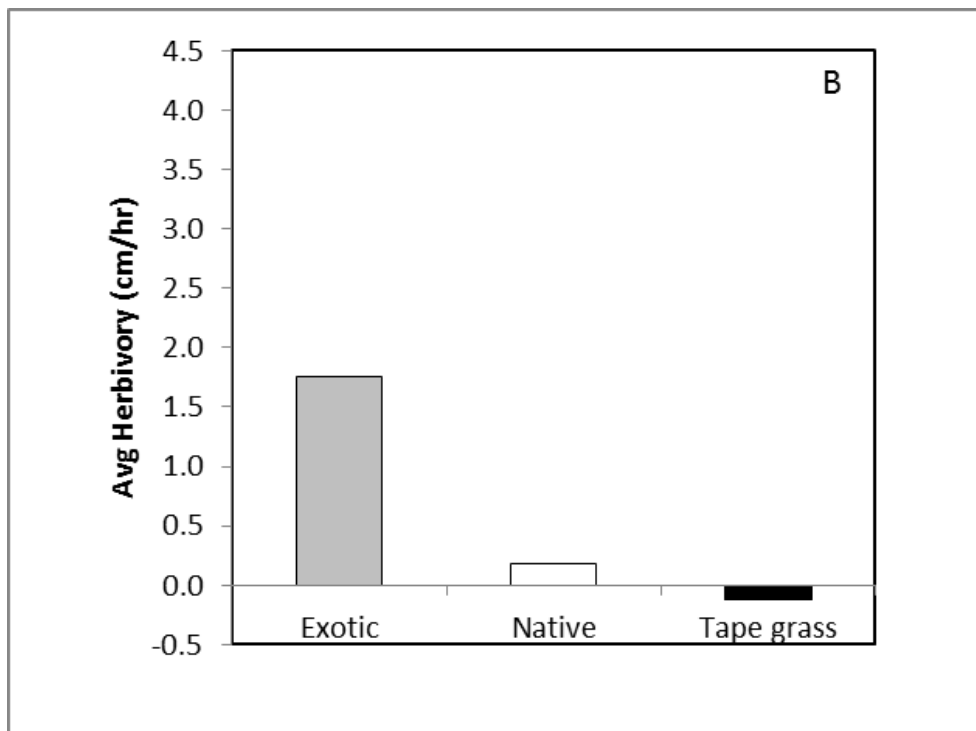
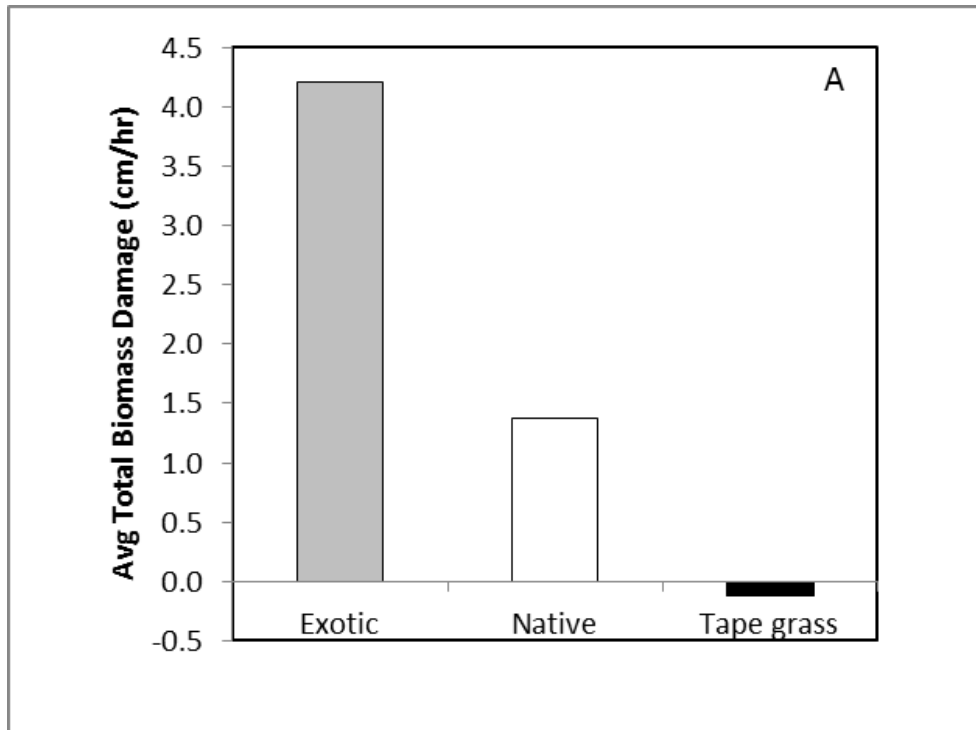


Figure 4.1: Illustrates the differences in how we measured grazing patterns for herbivory, physical damage and total damage.



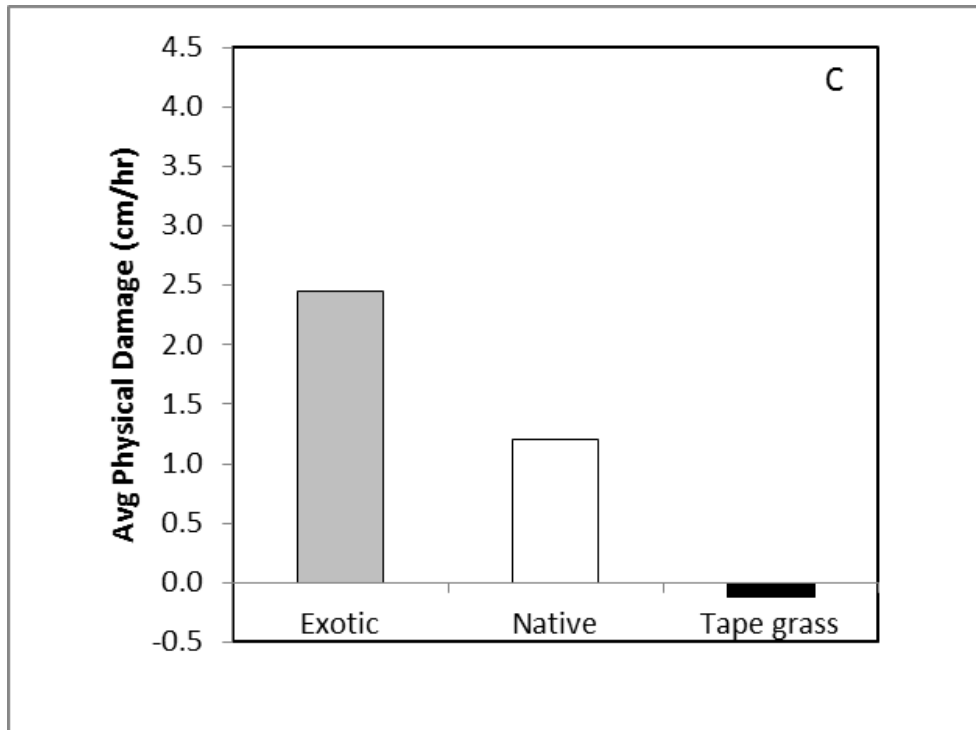


Figure 4.2: Exotic, Native and Tape grass Mean Rate Comparisons (A) Compares exotic and native snails average Total Biomass Damage rates (cm/hr) with Tape grass growth rates (cm/hr). (B) illustrates the average Herbivory Rates (cm/hr) for *P. maculata* and *P. paludosa* with Tape grass growth rates (cm/hr). (C) Examines the exotic and native snails average Physical Damage Rate (cm/hr) with Tape grass growth rates (cm/hr).

5. AN ECOSYSTEM BASED APPROACH FOR EXAMINING EMERGENT BEHAVIORS, POPULATION PATTERNS, AND GRAZING IMPACTS OF AN INVASIVE HERBIVORE IN WETLAND COMMUNITIES

5.1 Abstract

Invasive species spatio-temporal models are becoming an important tool for resource managers in predicting invasion trends and their potential impacts. An ecosystem based approach incorporating abiotic and biotic factor(s) influencing animal distributions over time is critical for model accuracy and predictive capabilities. Understanding how these factors influence population structure and grazing behavior between an invasive exotic *Pomacea maculata* and native *Pomacea paludosa* is important. Spatio-temporal models are designed to incorporate these temporally changing abiotic and biotic parameters, allowing managers to predict and identify key differences between species by examining how they interact with temporally changing environmental parameters. The aim of this paper is to introduce a spatio-temporal agent based model using Nova Software Platform for analyzing *P. maculata* and *P. paludosa* population structure, juvenile survivability and ecosystem impacts on *Vallisneria americana* vegetation communities in a managed wetland. Results of this study showed small changes in *P. maculata* juvenile survival rates can significantly impact *V. americana* communities, and how differences in population age structure, adult life span, grazing and reproductive behaviors can affect the variation in the impact of the exotic and

native snail on the ecosystem. Understanding these factors can help assess and predict *P. maculata* impacts in designed wetlands and naturally occurring systems.

5.2 Introduction

Reductionist approaches to invasion ecology can lead to examining species-based characteristics such as life history traits, exotic-native species interactions, and behavioral characteristics. While these studies provide important foundational information on the species biology, these projects may miss higher level processes and patterns that are affected by the invaders. An ecosystem based approach focuses on examining species interactions with the environment, including resource availability, competition between species, and community diversity (Qiu, Chan et al. 2011). Examining the interactions of species and ecosystem characteristics may provide insight concerning how specific invasive behaviors lead to successful invasions and resulting ecological impacts. An ecosystem approach has been successfully used in modeling exotic species (Liu, Lin et al. 2014) for bio-controls (Watt, Whitehead et al. 2007, Kriticos, Watt et al. 2009, Senior, Krkosek et al. 2013), and agricultural pests (Parry, Evans et al. 2006).

Exotic species can be problematic when restoring degraded ecosystems (Doren, Volin et al. 2009). These species can alter species assemblages and ecosystem functions (Mack, Simberloff et al. 2000, Feroz Khan and Panikkar 2009), and be agents of change during the restoration process (Doren, Volin et al. 2009). Understanding exotic species invasive behavior that alters ecosystem functions can provide insight into their potential ecological impact. Predicting ecological impact from exotic species is difficult because the invasive behavior needs to account for both community and species based characteristics (Qiu, Chan et al. 2011).

One of the world's largest restoration projects is guided by the Central Everglades Planning Project (CEPP), formerly Comprehensive Everglades Restoration Plan. The purpose of the CEPP is to provide a framework to restore, protect and preserve water resources in the southern half of the State of Florida (USACE 1999), with goals to improve the function of vegetation communities and address impacts on wildlife due to changes in hydrology, water quality, and exotic species. Ecological Conceptual Models were developed to provide a planning tool for all the interconnected ecosystems and focus scientific support and understanding to develop ways to achieve these goals (Ogden, Davis et al. 2005, Ogden, Davis et al. 2005). These models provided an important framework for the development of bio-indicators and restoration tools. One of the restoration tools used in achieving those goals is the Stormwater Treatment Areas (STA). STAs are constructed and managed seasonally persistent shallow systems with slow moving currents comprised of emergent and submergent aquatic vegetation, mimicking natural wetland structure (Burlakova, Karatayev et al. 2009). STAs are used to reduce phosphorus levels prior to water entering the Everglades marsh system. These systems also provide habitat for aquatic and terrestrial species, including the endangered Everglade Snail kite *Rostrhamus sociabilis plumbeus*, native Florida Apple snail *Pomacea paludosa*, *Vallisneria americana* (tapegrass) and invasive exotic *Pomacea maculata*.

Pomacea spp are freshwater gastropods. Some species in the genus are significant pests in Asia, altering wetland, impacting littoral zones (Carlsson, Bronmark et al. 2004, Naylor 1996), and in the United States the STAs in South Florida (unpublished data). *P. maculata*, formerly known as *Pomacea insularum*, is a major

invasive exotic pest throughout the world, considered one of the most persistent and destructive ampullariids, causing significant ecological and economic impacts (Hayes, Joshi et al. 2008, Matsukura, Okuda et al. 2013). *P. maculata* is a dioecious freshwater snail with an incredible appetite for macrophytic plants, to the extent that large populations have been reported to completely denude SAV communities in STAs. Similar to *P. canaliculata*, one of the world's top invasive species (Lowe 2000, Morrison and Hay 2011), these herbivores increase the top-down effects on vegetation communities and subsequently altered water quality (Carlsson, Bronmark et al. 2004). *P. maculata*'s consumption behavior is different than the native *P. paludosa*'s behavior in native SAV communities. *P. maculata* is a major threat to STAs, poses significant risk to SAV communities, can alter plant species assemblages and change ecosystem functions throughout the southeastern United States.

Biological invasion models are needed to identify information gaps for targeting research, assessing risk, and providing insight into real world management problems. We developed an agent based spatio-temporal simulation model examining ecosystem interactions of a managed wetland systems with life history traits of *P. maculata* and *P. paludosa* and consumption behavior on *V. americana*. This program was an exploratory ecosystem process approach using empirically based seasonal data. This research will increase our understanding of how differences between *P. maculata* and *P. paludosa* in life history, juvenile survivability rates and grazing characteristics can influence top-down pressure on desirable targeted vegetation communities, potentially impacting areas crucial for protected species, restoration and conservation.

5.3 Methodology

The spatio-temporal ecosystem model used existing literature and on-going research to simulate *P. maculata* and *P. paludosa* population dynamics in an STA supporting *V. americana* and other submerged and emergent vegetation. The model was developed in Nova Software modeling platform (www.novamodeler.com) using Novascript. Novascript is an object oriented programming language derived from Javascript (<http://java.sun.com>). The simulation landscape consisted of a 2500 m² ASCII raster file with 1 m² grid cells. The raster file was created in ArGIS from an aerial photograph taken in 2013 of STA 1 cell 4 south in West Palm Beach, Florida. The raster was imported into Nova Software. Raster data was categorized into emergent and submerged vegetation types. Emergent vegetation was classified as *Typha domengensis* and submergent as *V. americana*. *V. americana* biomass data was randomly assigned across the submerged landscape based on Hauxwell et al. (2007). Plant biomass, growth, and senescence rates were all derived by dividing monthly values taken from (Hauxwell, Frazer et al. 2007) (Table 5.1). Due to grazing impact resistance from snails, *T. domengensis* biomass values were assigned an assumed value with growth rates equal to the grazing rate. Daily biomass values were retained, minus any changes to the individual grid cell from grazing impacts, and carried over to the next day step in the simulation.

Model time series was set to daily time steps for a 60 month period. Each model time step ran a series of calculations in grid cells containing plant seasonal data and specific snail life history (agent). Each time step contained snail agents immigrating and emigrating within the study area. Snail movement was based on resource availability within the landscape and snail gender reproduction interactions. Snail agents were

categorized as either a male, female, pregnant female or juveniles. Each agent followed a set of rules pertaining to a species life cycle consisting of birth, growth, death, grazing impact to vegetation landscape, and pregnant females depositing eggs. An agent within the program contained individualized data pertaining to the number of days alive, sex, grazing rates and date of birth. Daily agent movement, grazing impact, snail life history, and survival factors were recalculated using the appropriate seasonal data. Outer boundaries of the grid cells were open allowing snails to pass through barriers and re-enter on the other opposite side.

When *P. maculata* and *P. paludosa* female snails achieved reproductive maturity, a mating event occurred when female and male agents occupied identical grid space. Egg laying females for both species were tracked and recorded on the grid scale vegetation landscape to maintain geographic location of newly born juvenile snails. *P. maculata* females were capable of laying a single egg clutch containing approximately 2000 eggs every 10-14 days for up to 4 months after the last mating event (Barnes, Fordham et al. 2008, Burela and Martín 2011) with egg hatching every 10-14 days. Similar to *P. maculata*, *P. paludosa* remained egg productive up to 4 months after male female mating with egg mass laying every 3 to 4 days containing 20-60 eggs with egg hatching occurring within 16-22 days. Reproduction for both *P. maculata* and *P. paludosa* occurred only during the months of March – November. Our model assumption included an aestivation period for both species during the months of January, February and December. During aestivation snails burrow into the ground or reduce movement, with grazing and reproduction reaching zero, however daily mortality rates still applied.

The initial population in the model was set at 25 snails, 1.0 snail/m², with sex, age and landscape location randomly selected. *P. maculata* agents lived a maximum of 1825 days, approximately 5 years (Barnes, Fordham et al. 2008) with juvenile to adult maturity set at 180 days (Ostrom 2014). *P. paludosa* agents were alive for 547 days, approximately 1 ½ years and the juvenile to adult maturity was set for 270 days (Pomacea Project 2013). Both *P. maculata* and *P. paludosa* sex determination were set randomly at 1:1 ratio at maturity.

Adult survival rates for both species were determined by an adult predation field experiment in August 2013 (Monette unpublished data). The conceptual design was based on experiments performed by (Kurz 1995, Englund and Krupa 2000). The study design consisted of ten transects of five poles (10 m apart) with each pole tethering a single snail. Transect placement was randomly selected in mixed habitat communities to avoid potential habitat representation biases. Predation rates were calculated using the time recorded for placement and retrieval of the snail over a 21 day period. A total of 25 tethered exotic and native snails using 20 inch fishing line were used in this study with specimen loss or presence recorded every three days. Water depths ranged from 30 to 75 cm. Poles were fully submerged preventing artificial raptor perching that may increase local raptor predation. Missing specimens were considered mortality due to predation. *P. maculata* and *P. paludosa* daily survival rates from the study were calculated as 2.86% and 3.81% respectively. We manipulated juvenile to adult survival rates for comparison on both species to achieve an average population growth rates of one percent over 40 runs. Only juveniles achieving adulthood were born as agents and included in the model.

Species spatial movement distances were determined by independently conducted telemetry studies by these authors and Valentine-Darby, (2011). Both studies used miniature radio-transmitters weighing 1.2-1.6 grams from Advanced Telemetry Systems. Geographic locations were recorded between one to two weeks during the dry season. *P. maculata* movement had a maximum distance of 114m/week with the rate of movement inversely correlated ($R^2=-0.85$) to water depth. Both species showed movement over 14 m per week during the study, but movement declined entering the summer months. During this time, *P. maculata* displayed a gender-based movement difference per week, similar to *P. paludosa* (Valentine-Darby, Darby et al. 2011) with the males traveling a greater distance than females. Gender different movement for both species was reflected in the model as males moving 2 m/day and females 1 m/day with spatial movement halting for both sexes and species during aestivation. Rules of agent movement in the landscape were that all snails should move towards the highest plant biomass values in neighboring grid cell with a 15% chance selection error. Males followed this rule unless a female was located in the neighboring cell. Neighboring females influenced male direction choice with a 15% chance of selection error due to pheromone (Takeichi, Hirai et al. 2007).

Consumption impacts were based upon differences among species in grazing patterns in *V. americana* communities. Grazing rates were determined by the snail consumption behavior study on *V. americana*, 4.2 cm/hr for *P. maculata* and 1.4 cm/hr for *P. paludosa* (Monette, Markwith et al. 2014). Grazing rates per hour for both species were changed into grazing rate per day then multiplied by Hauxwell's (2007) conversion factor (0.0034 g/cm^2) for grazing rate per day per dry weight for *P. maculata*, 0.257

g/day, and *P. paludosa*, 0.0857 g/day. Model time steps incorporated grazing impact values into the affected cell, then applied growth or senescence rates and carried over into the next model step. Overall biomass data was recorded for both species at the end and during model simulation for assessing grazing impact. A descriptive statistical analysis was used on the first day of each month for simulation year 4, except for aestivation periods, across model runs between *P. maculata* and *P. paludosa*.

5.4 Results

A one percent total population growth rate for *P. maculata* showed in year 4 an age structure of adult snails consistently greater in number than juveniles (Figure 5.1). *P. maculata* adult peak population size occurred in November, and August for juveniles. In contrast, *P. paludosa* total population growth rate of one percent during the same time period resulted in more juveniles within the population than adults (Figure 5.2). *P. paludosa* adult population size generally peaked in August and for juveniles during the month of November. Comparatively, over year 4 years the adult population of *P. paludosa* experienced a seasonal drop between August and November, which was expected due to their life history, while the *P. maculata* adult population increased (Figure 5.3). *P. maculata* juveniles were consistently, and at times vastly, less abundant than *P. paludosa*, except during the aestivation period from December through February when both species experienced a precipitous decline in overall abundance (Figure 5.4). *P. maculata* population size (Figure 5.5) was more consistent across each of the 40 individual runs than *P. paludosa* (Figure 5.6), indicating less volatility and more stability in the exotic population.

Under conditions of *P. maculata* population growth rate of 1%, the juvenile to adult survivability rate over the 5 year model run was 5.4 juveniles for an egg clutch containing 2000 eggs (Figure 5.7). By comparison, a negative population growth rate of 1% was the result of 5.2 juveniles surviving to adults for every egg clutch of 2000 eggs.

Based on population age structure and the number of individuals within the population for each species, our results show *P. maculata* average total grazing impacts per day were greater than *P. paludosa* at each measured time period (Table 5.2). The descriptive statistical analysis results showed *P. maculata* had a considerably higher grazing impact than *P. paludosa* for each monthly time step (Table 5.2).

5.5 Discussion

Results of this study show how differences in species life history and snail changes in juvenile survival rates between *P. maculata* and *P. paludosa* can affect population age structure and grazing impacts on *V. americana* communities.

Comparatively, *P. maculata* life history supports a population structure primarily of adults that can live up to five years, while *P. paludosa* population structure has more juveniles within the population due to adults only surviving up to 18 months. The shorter adult life-span leads to a short reproduction period, therefore placing a greater emphasis on juvenile survivability and shorter return interval between each egg clutch laying event. *P. maculata*'s prolonged reproduction period may provide population persistence and a consistent source of juvenile recruitment to newly invaded ecosystems.

This model shows a relationship between distance between individuals, reproduction, and grazing impacts. Snails in close proximity or high densities increase the likelihood of reproduction. Reproduction is a function of these factors increasing the

initial female fertilization allowing earlier egg clutch production and potentially over a longer duration throughout the year. Considering *P. maculata* invasive characteristics and higher grazing impacts, ecosystems containing select vegetation communities, like *V. americana*, could be altered to a system of lower biodiversity. Ecosystems with low biodiversity may have lower ecosystem resistance to biological invasion that may lead to cascading ecosystem effects. Reduced resistance to biological invasion coupled with naturally occurring disturbance events that may reduce predation rates may promote persistent propagule pressure from established *P. maculata* populations that can rapidly spread throughout connecting aquatic systems.

Our results show that *P. maculata*'s grazing pressure is greater than *P. paludosa*'s. The intensification of grazing pressure across the landscape can alter how an ecosystem functions by consuming macrophytic communities, increasing the available phosphorus, and promoting a shift to a planktonic algae steady state system that leads to a feedback of greater turbidity in the water column that perpetuates the state (Carlsson, Bronmark et al. 2004). This shift to an alternative steady state of algal communities could makes returning to the original state difficult (Beisner, Haydon et al. 2008, Nikanorov and Sukhorukov 2008). As it is known, *P. maculata* population structure indicates adult snails living longer within the ecosystem, possibly stunting growth of any new macrophytes due to continued grazing, and further exacerbating ecosystem inertia for a stable algae transformation. This ecosystem stressed process has already occurred in one of the cells in the STA due to high densities of *P. maculata* (unpublished data). This process is dynamic and long term successional processes may return the system to the original state, but snail removal would probably be required.

One objective of this study was to develop a modeling tool that would allow resource managers to identify key components of the *P. maculata* invasion process. Our data shows negative population growth rates occur when 5 or fewer juveniles achieve adulthood. Egg clutch eradication (Bernatis and Warren 2014) and increase in biocontrols could reduce juvenile survival rates resulting in negative population growth rates. Identifying critical population densities in a system will help resource managers reduce potential impacts and develop mitigation strategies. These strategies need to investigate the threshold in *P. maculata* populations when ecological hysteresis and degradation occur. Understanding these factors can help assess and predict snail impacts in naturally occurring and designed wetland systems.

Future research should focus on examining how juvenile survivorship varies in vegetation communities, with size and depth of the water body (Burlakova, Padilla et al. 2010), during aestivation period, and under the influence of native aquatic predators (Yusa, Sugiura et al. 2006). Further research should study how native aquatic plants and abiotic factors such as temperature affect egg production and viability. Understanding how native biological system bio-feedbacks alter *P. maculata* life history patterns including phenotypic plasticity in growth will have a role in how to control population growth and resulting grazing impacts to native plant communities. Resource managers and scientists can use this information to create location specific models.

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5.7 Tables and Figures

Table 5.1: *V. americana* table showing a digital measurement of initial above ground monthly biomass, plant growth and senescent rates (Hauxwell et al. 2007)

Date	Monthly Biomass dry g/m ²	Growth and Senescent Rate (%)
4/1	378	3.5814
5/1	685	0.8122
6/1	482	-0.2962
7/1	477	-0.0109
8/1	581	0.2183
9/1	630	0.0851
10/1	619	-0.0175
11/1	444	-0.2835
12/1	367	-0.1730
1/1	416	0.1346
2/1	120	-0.7108
3/1	82	-0.3147

Table 5.2: Simulated model comparing *P. maculata* and *P. paludosa* total grazing impact of forty individual runs for year four

Year 4		<i>P. maculata</i>	<i>P. maculata</i>	<i>P. paludosa</i>	<i>P. paludosa</i>
Simulation	Simulation	Mean Grazing	Standard	Mean Grazing	Standard
Date	Day	(dry wt/day)	Deviation	(dry wt/day)	Deviation
4/1	1461	0.480	0.313302	0.157	0.128692
5/1	1491	0.525	0.351607	0.173	0.147535
6/1	1522	0.558	0.369527	0.189	0.167276
7/1	1552	0.584	0.390733	0.197	0.180328
8/1	1583	0.601	0.413379	0.203	0.188028
9/1	1614	0.653	0.450630	0.206	0.200355
10/1	1644	0.704	0.492076	0.199	0.202547
11/1	1675	0.739	0.525679	0.192	0.196656
3/1	1795	0.481	0.351378	0.123	0.127280

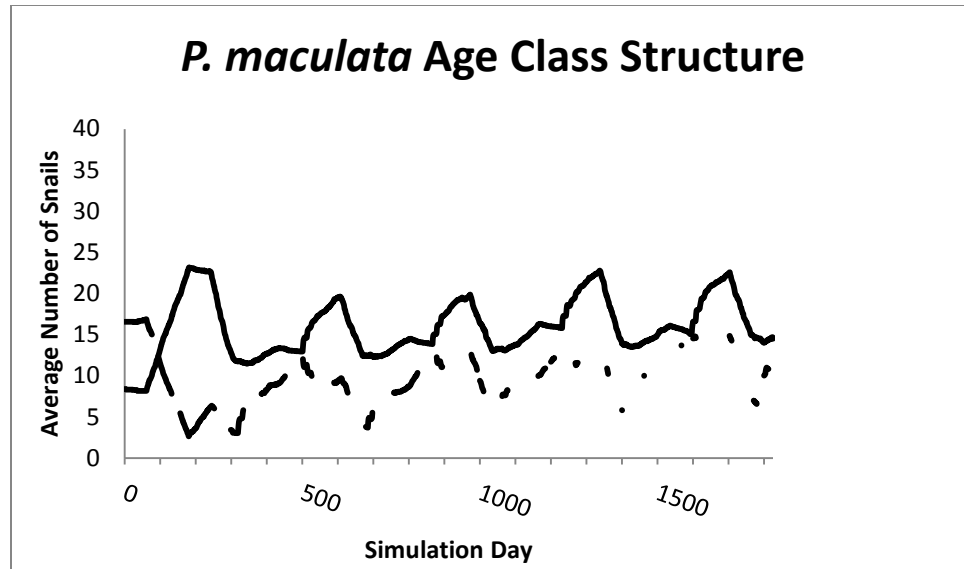


Figure 5.1: Simulated population age structure for *P. maculata* with solids line representing adults and dashes juveniles

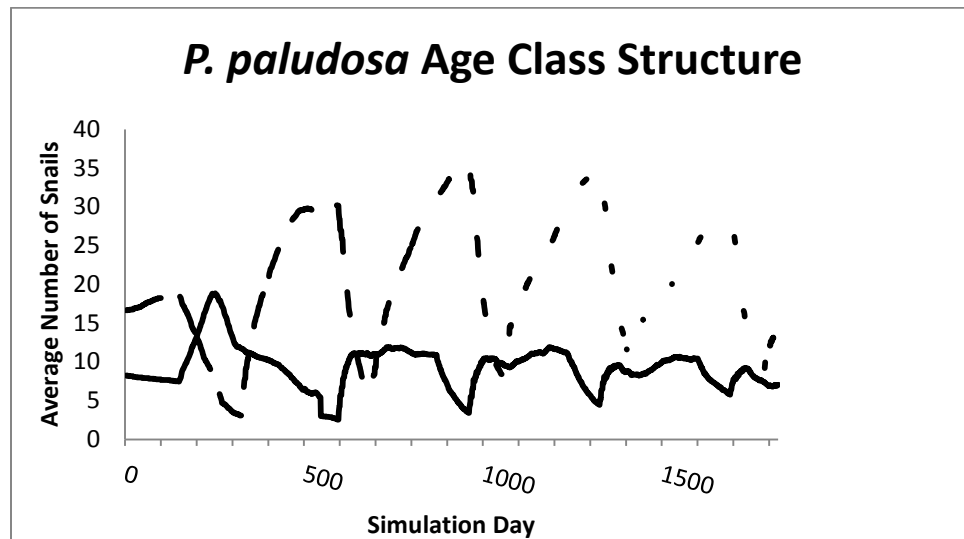


Figure 5.2: *P. paludosa* simulated population age class structure with solid lines representing adults and dashes juveniles

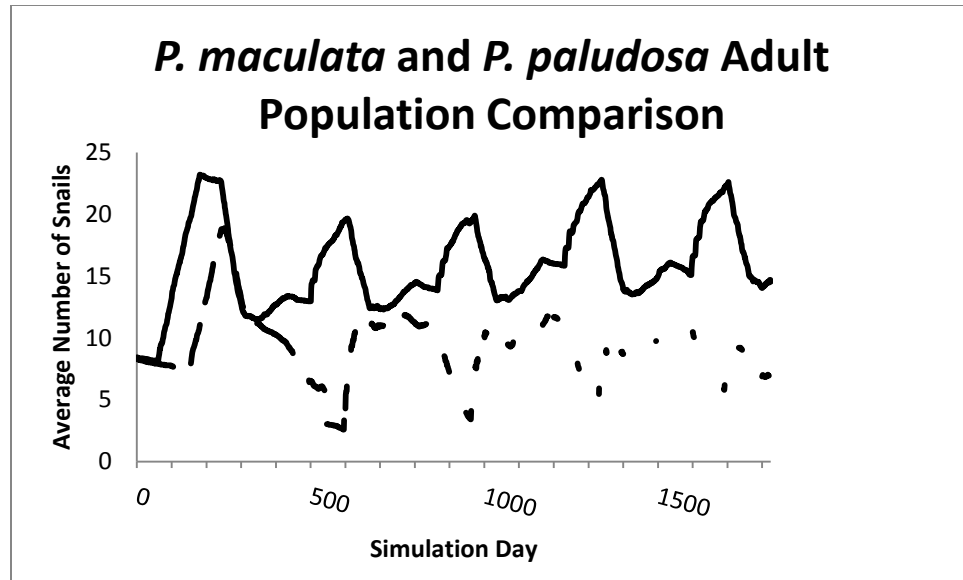


Figure 5.3: Simulated population age class comparison between adult *P. maculata* and *P. paludosa*. In this graph solid lines representing *P. maculata* adults and dashes indicating *P. paludosa* adults

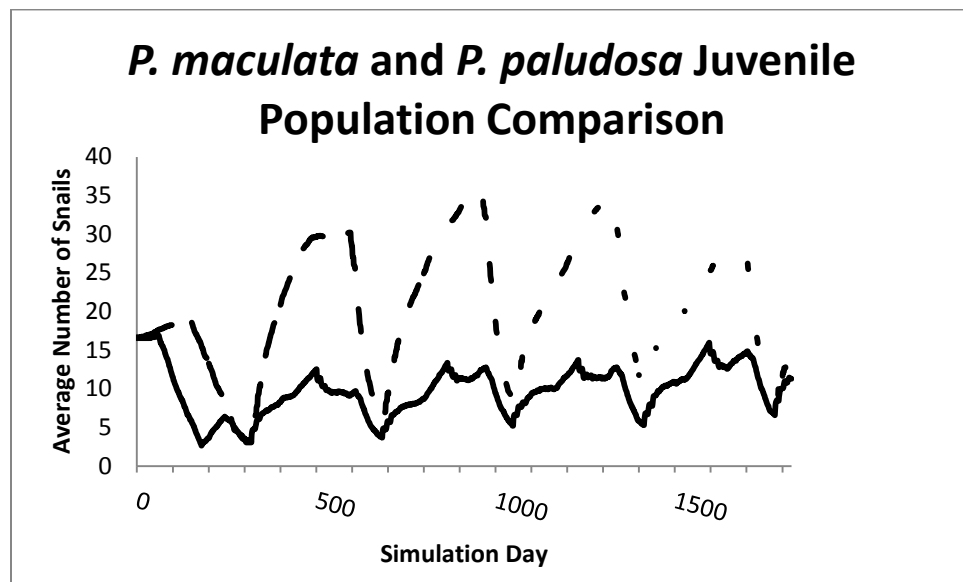


Figure 5.4: Simulated *P. maculata* and *P. paludosa* population comparison age class with solid lines representing exotic juveniles and dashes indicating native juveniles

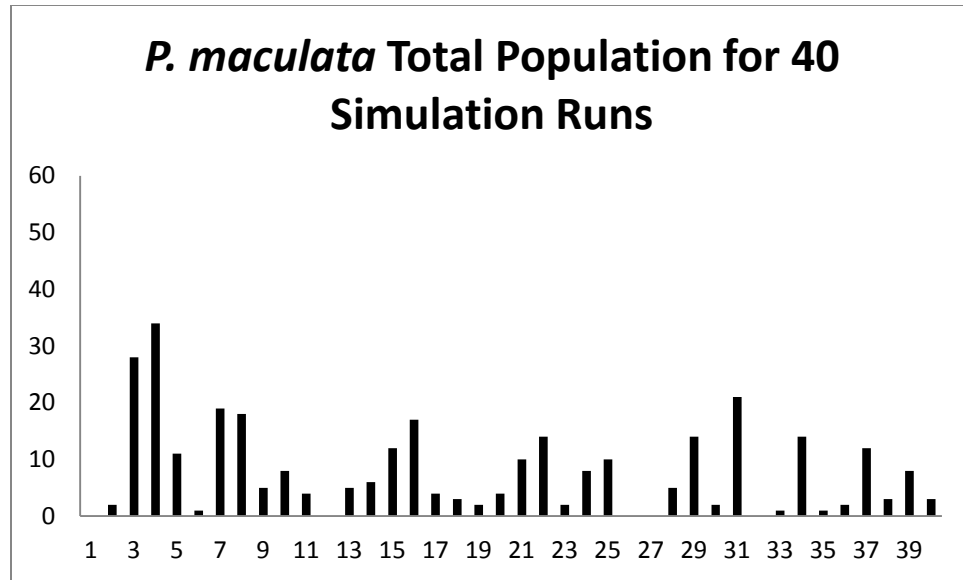


Figure 5.5: Simulated *P. maculata* total population with a growth rate of one percent showing the number of individuals being represented by solid lines for each model run

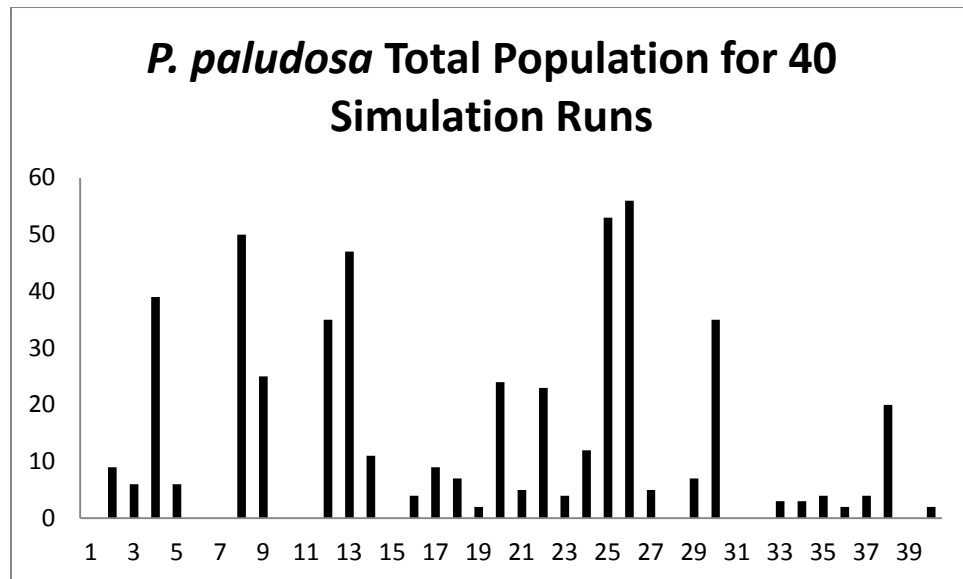


Figure 5.6: *P. paludosa* total population simulated for a growth rate of one percent showing the number of individuals being represented by solid lines for each model run

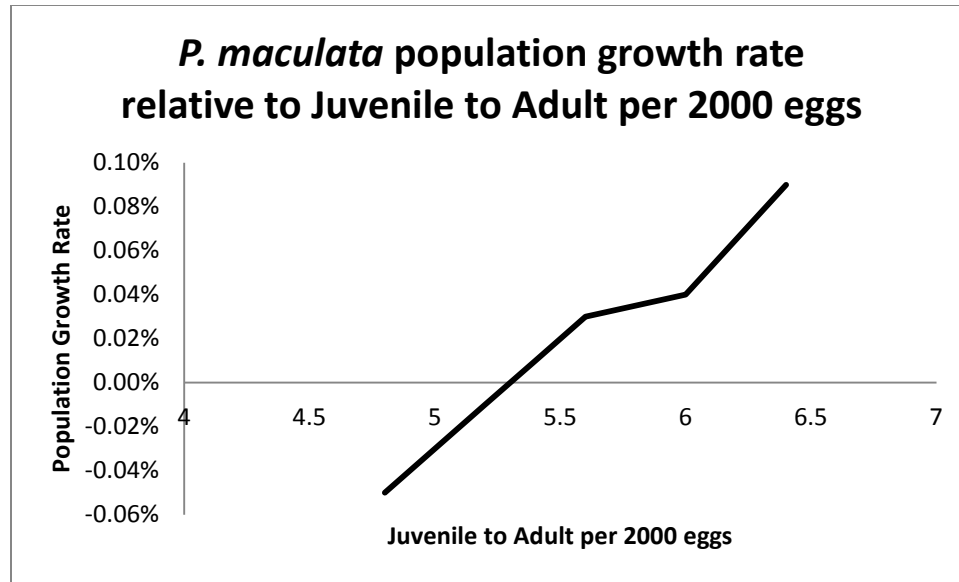


Figure 5.7: *P. maculata* simulated model comparing population growth rates to juvenile to adult survivability for every egg clutch containing 2000 eggs

6. CONCLUSIONS

Research suggests that exotic species infiltrating restoration projects can be an extremely difficult problem to manage. Furthermore, increased transportation by humans increases opportunities for exotic species establishment (Strayer 2010). Decisions made to resolve these complex issues often require scientists to synthesize, analyze and validate results from empirical studies from different temporal spatial scales. Understanding how an exotic benthic gastropod can influence top-down pressure on desirable targeted vegetation communities and impact bottom-up resources to federally protected species is a crucial question for restoration research.

The native Florida Apple Snail, *P. paludosa*, is the only native freshwater apple snail in the United States (Rawlings, Hayes et al. 2007, Morrison and Hay 2010). *P. paludosa*'s limited life span is an important factor shaping its population age structure that has coevolved with other species forming complex food webs throughout southern eastern United States. Due to the unique nature of being an important prey source for snail kites and in aggregating in target restoration habitats, *P. paludosa* has been identified as an indicator species for restoration success in the Florida Everglades (Karunaratne, Darby et al. 2006).

P. maculata is a large macro-invertebrate herbivore from South America with highly invasive characteristics (Rawlings, Hayes et al. 2007, Barnes, Fordham et al. 2008). These characteristics include high fecundity, diverse resource consumption, and the ability to tolerate a wide range of environments (Barnes, Fordham et al. 2008, Boland,

Meerhoff et al. 2008, Burks, Kyle et al. 2010). *P. maculata* is considerably larger than the native *P. paludosa*. The invasion of *P. maculata* could dramatically impact the native food web throughout the landscape (Burlakova, Karatayev et al. 2009) including *P. paludosa* habitat locations. This research shows that adult native and exotic apple snails have overlapping geographic regions in areas of shared resources. In particular, *P. maculata* grazing habits may alter the structure and function of important vegetation communities like *V. americana*. The herbivory impact of *P. maculata* in South Florida STAs could impede the use of important resources by managers for long-term sustainability of the Everglades restoration project (USACE 1999, Morrison and Hay 2010).

This study addressed important questions pertaining to *P. maculata* invasion and how it may impact *P. paludosa* and local ecosystems by using empirical studies and developing an agent based model to better analyze the varying scales of impact, interactions, and spatial/temporal patterns. Results of these studies quantified how key life history differences between *P. paludosa* and the exotic *P. maculata* can affect vegetation changes in South Florida. This data highlighted key differences between species in ecological niches, population age structure, grazing pressure, and lack of competitive effects in adults. This information and other empirical data were synthesized to develop a modeling tool for resource managers as they try to understand *P. maculata* invasion and their impact in South Florida's ecosystems.

This research increased our understanding of an exotic invasive gastropod's, *P. maculata*, impact on an important indicator species in South Florida. The model developed for this project is the first broad scale spatial temporal agent based model on *P.*

maculata invading a freshwater system. This model provided a framework of understanding how differences in top-down grazing pressure relative to coevolved key native species can potentially cause a shift in ecosystem structure and function. This study introduced a natural systems approach to resource managers to get a better understanding of the complex interactions of *P. maculata*, the potential impediment it may cause to restoration goals, and the impact on *V. americana* communities

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