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Contrasting Patterns of *Pomacea maculata* Establishment and Dispersal in an Everglades Wetland Unit and a Central Florida Lake

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Abstract: The spread of non-native species raises concerns about native species displacement, while other negative effects on native species (e.g., habitat degradation) should also be considered. The highly invasive non-native apple snail *Pomacea maculata* has raised such concerns as it has become established in a wide range of aquatic systems worldwide. While monitoring native Florida *P. paludosa* populations in Lake Tohopekaliga (LTOHO) from 2001 to 2009 and in Water Conservation Area 3A (WCA3A, Everglades) from 2006 to 2015, we opportunistically documented the establishment and distribution of *P. maculata*. We estimated snail densities and recorded egg cluster presence in three study sites (12 total plots, LTOHO) and 137 sites (WCA3). On LTOHO, native snails were absent or at very low densities prior to finding *P. maculata*. Few snails of either species were found in high-stem-density vegetation of the littoral zone. *Pomacea maculata* immigration into the littoral zone occurred following managed vegetation removal, and *Hydrilla verticillata* proliferation in LTOHO likely contributed to the spread of *P. maculata*. We found both native and non-native apple snail species in many WCA3A sites following *P. maculata* invasion. We initially found the non-native snail in two sites in southern WCA3A; they were mostly restricted to within three kilometers of initial sites over the next four years. Overall plant community compositions in LTOHO and WCA3A appeared less impacted than expected based on previous reports of *P. maculata* invasions.

Keywords: gastropod; snail; non-native; aquatic; invasive species; *Pomacea maculata*; dispersal

1. Introduction

According to the Nonindigenous Aquatic Species database [1], there are 70–80 introduced mollusk species in North American waters. Many of these non-native mollusks have a high potential of spreading in large freshwater ecosystems [2], as well as in man-made canals, reservoirs, and agricultural ponds [3]. Invasive mollusks can cause the decline of native aquatic organisms, alter nutrient cycling, have direct and indirect effects on the food web, and alter the physical habitat [3–5].

Invasive mollusk species use both active and passive means of dispersal. To invade new habitats, mollusks can have longitudinal (e.g., up or downstream) or lateral (across neighboring distinct environments) dispersal [6]. In addition, mollusks can be carried long distances by biotic vectors [2]. Mollusks from marine, lentic, lotic, and terrestrial environments show different abilities to disperse according to habitat characteristics, age-size dependent life history traits, and the degree of anthropogenic facilitation. For example, most of the highly invasive bivalve species, such as the zebra mussel (*Dreissena polymorpha*), the Asian clam (*Corbicula fluminea*), and the golden mussel (*Limnoperna fortunei*), have almost no capacity for active dispersal. However, these species have a small, free-floating, larval stage (veliger) that is easily dispersed by flowing water, zoochoric methods, or ballast water [3,7–9]. Their success as invaders is attributed to the rapid dispersal in larval form [6,10,11]. The invasive New Zealand mudsnail (*Potamopyrgus antipodarum*) is a small gastropod (typically 4–6 mm—adult) that disperses in ways similar to those just described, as well as by moving upstream [8]. In contrast, invasive terrestrial species, such as the giant African land snail (*Achatina fulica*), are dependent upon crawling for dispersal, moving up to 500 m in six months [12]. The eggs, which are laid on the ground, and early life stages of the giant African land snail, have a limited dispersal capacity. The spread of these terrestrial snails outside of their native range relies on humans, including through intentional introductions (e.g., for food for humans and barnyard fowl, released pets) and unintentional introductions (e.g., through commerce [as hitchhikers], escape from breeding facilities) [13,14].

In recent years, considerable attention has been given to invasive Ampullariidae snails of the genus *Pomacea* (apple snails), with numerous reports of rapid range expansions in locations scattered throughout the world [6,15,16]. Their establishment outside their native range can be attributed largely to anthropogenic facilitation via the aquarium trade, as a food source, or as a biocontrol for other agricultural pests [4,15,17]. In considering dispersal mechanisms, once established in a new area, we view these non-native apple snails as having characteristics of both the aquatic mollusks and terrestrial snails described earlier. Hatching from cleidoic eggs, the relatively large, shelled hatchlings of most *Pomacea* snails (hatchling size measured in mm) [18], likely depend less on water-column dispersal compared to species with larval forms (size measured in µm) [19,20]. Apple snails of all size classes can float freely at the surface [15,21,22] and can disperse in the water column in lotic systems [23], although it is unclear if this contributes significantly to dispersal in general. Adult apple snails also have the capacity to crawl over 50 m per week (see [22]). As has been reported for other, smaller, freshwater snail species, it is possible that small apple snail size classes could be transported by birds, floating vegetation, and boats (including in macrophytes attached to boats) [6,24,25].

Non-native *Pomacea* species have become widespread in aquatic systems in the southeastern United States in ponds, lakes, and wetlands [4,18,26]. Although direct observations of snails in a laboratory setting, or otherwise at small scales, may explain potential mechanisms for dispersal (e.g., rates of crawling) once established in a system, the dispersal patterns in relatively large aquatic systems for an introduced population of non-native *Pomacea* snails have rarely been described in the U.S. One such study was conducted recently in a Georgia reservoir using shoreline surveys of egg clusters to determine the presence of *Pomacea maculata* as it spread throughout the system [26]. *Pomacea maculata*, native to South America, was first found in Florida in the 1980s [4,18,27]. The species is found in some of the same wetlands as Florida's native *P. paludosa*, but in some cases *P. maculata* is observed where the native species is no longer found (P. Darby unpublished). Unlike other non-native Ampullariidae found in Florida in recent decades [18], *P. maculata* has become widespread in several counties from the panhandle to peninsular Florida [18,28,29]. Recently, this non-native snail has provided the primary food source for the endangered snail kite [30]. *Pomacea maculata* can grow larger than *P. paludosa*, often exceeding 80 mm in diameter compared to approximately 30–40 mm for the typical adult native snail [31]. *Pomacea maculata* has a distinctive shell morphology [18], and it produces large, bright-pink egg masses readily distinguished from *P. paludosa* eggs [18,32]. For many years, *P. maculata* was misidentified as *P. canaliculata* because of their morphological and behavioral similarities. However, recent molecular studies led to clarified genetic relationships and taxonomy, and differences between the two species were described [33]. *Pomacea maculata* is now synonymous with *P. insularum* and *P. gigas* [33].

Variation in the habitat structure, hydrologic connectivity, and hydrology (especially dry downs) of different lakes, ponds, canals, and wetlands in Florida may promote or deter the dispersal of *P. maculata*. During our more than two decades of monitoring and researching *P. paludosa* populations throughout Florida, we increasingly encountered the non-native *P. maculata*. As *P. maculata* became established in two wetlands, two for which we have the most data in terms of multiple sites and years, we had the opportunity to describe its establishment and dispersal in these distinct systems. The two wetland units, Lake Tohopekaliga (LTOHO), in central Florida, and Water Conservation Area 3A (WCA3A), in the Everglades, have been important in supporting endangered snail kites at various times in the last 30 years [34]. In our study, we examined the chronological pattern of *P. maculata* dispersal in each system and report on changing distributions from presence/absence and snail density data. We studied the effects of habitat management on *P. maculata* in LTOHO that at the time was undergoing a major littoral zone habitat restoration. In WCA3A, we documented the relative densities of co-existing populations of already existing native and newly arrived (during our study) non-native snails. We recognize our sampling protocol was not designed to document the invasive non-native snail and that our observations were collected opportunistically. However, our data provide some basic information on the establishment of *P. maculata* where we sampled throughout two large wetlands, and we provide estimates of snail densities not readily available from landscape-level field sampling for *P. maculata*.

2. Materials and Methods

2.1. Study Sites

Lake Tohopekaliga (LTOHO) is located in Osceola County in central Florida, U.S. The lake has approximately 60 km of shoreline, with a total area of approximately 9,800 ha [35]. Water flows into LTOHO via the Saint Cloud Canal, or Canal 31, that links East Lake Tohopekaliga to LTOHO. Our study used three sites on LTOHO, each containing four study plots (Figure 1). This was part of a larger study monitoring wildlife responses to lake management activity in these same plots [36]. Site selection was based in part on finding similar assemblages of plants and substrates to avoid confounding factors (e.g., site to site differences in substrate type) and to support the testing of specific hypotheses. The designated sites were Brown's Point (BP), Goblets Cove (GC), and South Steer Beach (SSB) (Figure 1). We demarcated 50-m × 50-m plots within these sites for sampling apple snails. When the study began in 2001, all plots were clearly dominated by pickerelweed (*Pontederia cordata*). Further out from shore we found floating mats of pickerelweed and the invasive hydrilla (*Hydrilla verticillata*). Lily pads (*Nuphar luteum* and *Nymphaea odorata*) and cattail (*Typha sp.*) bordered our study sites in the deepest portion of the littoral zone. A detailed description of plant zonation in these same locations at the time is provided in Welch [37]. During the study, two events affected LTOHO and the sampling areas. First, there was a planned drawdown, completed in the winter of 2004, followed by vegetation management consisting of organic substrate scraping (via bulldozers, down to the sand layer [37]) and herbicide applications [35]. Second, three hurricanes struck LTOHO directly in 2004 (Charlie, 13 August; Frances, 5 September; Jeanne, 26 September), resulting in shoreline disturbances and uprooted vegetation. We sampled BP, GC, and SSB once each fall in 2001-2007. In 2009, we returned to LTOHO to sample, but this time in the context of snail kite foraging sites: (1) just outside of GC (foraging site designated as GCx), (2) in SSB, and (3) to the south of SSB (designated as SSBx).

Water Conservation Area 3A is part of the Everglades and is located on the western side of Miami-Dade and Broward Counties in southern Florida (Figure 1). This wetland unit was historically a major conduit for the sheet flow that characterized Everglades hydrology prior to drainage and water control [38]. The present study was conducted in the 116,000-ha portion of WCA3A bounded to the north by Interstate 75 (I-75) and to the south by State Route 41 and the Tamiami canal (Figure 1). All data from WCA3A for 2006–2015 were obtained in emergent marsh habitats dominated by grasses and sedges, and bordered by sawgrass (*Cladium jamaicense*) (see [39,40]). An east-west peat depth gradient exists in WCA3A, with peat shallowest on the west side and deepest on the east side. There is also a north-south elevation gradient, with slightly higher elevations in the north and flow of water towards the south [41,42]. As a result of impoundment, there is also an artificial north-south water depth gradient, with deeper depths in the south due to pooling [42].

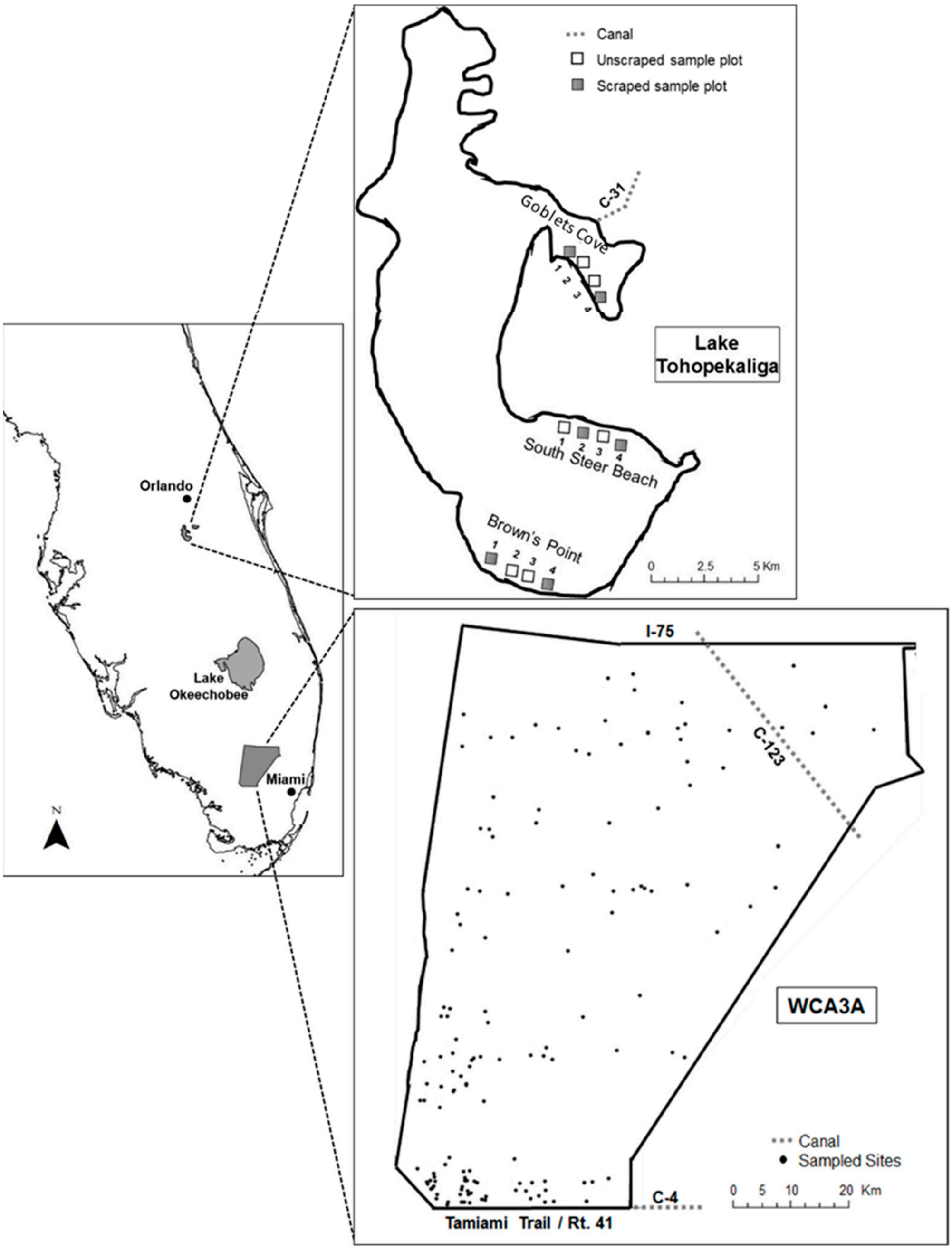

Figure 1. Portion of peninsular Florida showing the locations of Lake Tohopekaliga (LTOHO) and Water Conservation Area 3A (WCA3A). We selected three study sites on LTOHO, with four sampling plots (two scraped, two unscraped) per site. We sampled throw traps or documented apple snail egg clusters in 137 sites in WCA3A over the reporting period.

2.2. Water Depth Data

Although we collected depth data from our throw traps (see below), showing the hydropatterns for the long term required that we access databases available from government agencies. For LTOHO, we obtained stage data (that is, the water level expressed as meters above sea level) from the South Florida Water Management District database called "DBHYDRO" (https://www.sfwmd.gov/science-data/dbhydro). We retrieved LTOHO data from the LTOHO gauge named "LTOHOW" (database key LQ978). The original stage data are in feet above mean sea level (MSL), so we converted them to meters. To assess the potential impacts of fluctuating water levels on snails, we needed estimates of ground level at each sampling location. Ground level estimates were derived by subtracting water depths measured in our throw traps on a given day from the stage reading for the same day. We then subtracted our ground level estimates from daily stage data to obtain a water depth estimate for each site for any day during the period of interest (see [43]). For WCA3A, we accessed the Everglades Depth Estimation Network (EDEN) from the U.S. Geological Survey (USGS) [44]. EDEN provides site-specific water stage data and ground level estimates for the major wetland units of the Everglades (see [44]).

2.3. Estimates of Apple Snail Density

We collected data on apple snail densities from 2001 to 2009 in LTOHO, and from 2006 to 2015 in WCA3A. For both LTOHO and WCA3A studies, our interests focused on native snails. However, we had different objectives for estimating snail densities in the two wetlands. Numbers of sites sampled varied year to year depending on objectives and funding. On LTOHO our objective was to sample pre-established study sites, each with treatment and control plots, to study the effects of habitat management on native apple snails (also see Section 2.1). In WCA3A, the vast majority of throw trap sampling was done in sites that showed some evidence of native snail presence (e.g., apple snail eggs, kites foraging) before we sampled for snails. For WCA3A, this includes studying snail preference for habitat patch type within a site [39,40] or snail densities associated with kite foraging [45,46]. Some of the densities reported here have been published [39,40,45,46], so readers can see those references for details on objectives and sample site selection protocols. We conducted scouting surveys of WCA3A in search of foraging kites, but also relied on kite location data provided by the annual snail kite survey (R. Fletcher, unpublished location data; see [30] describing the survey). Snail and vegetation data were collected using the same protocol in both LTOHO and WCA3A, as described below. For both systems, our data included several years with no record of *P. maculata* (i.e., we have pre-invasive data).

We estimated density from snails counted in 1-m^2 throw traps using dip nets made with 13-mm mesh netting, as described by Darby et al. [47] with some minor modifications adopted more recently [40]. The number of traps sampled at each location (plots within sites on LTOHO, or just sites in WCA3A) depended on the number of snails encountered and coefficients of variation (see [47]), but typically ranged between 25 and 50 traps and sometimes exceeded 100 (depending on differing objectives referred to above). We estimated the capture probability to measure the proportion of snails captured in different habitats, by including one to three marked snails in some throw traps (typically 7–20 traps per site) [48]. We estimated the capture probability per trap as the number of marked snails retrieved during the sampling process divided by the number of marked snails placed in the trap. Mean capture probability for a site and/or plot was based on averaging values obtained from 7–15 traps per site in which we had placed marked snails.

We recorded two observations regarding vegetation found in each throw trap. First, we recorded the genus and species (if distinguishable) of plants we identify as apple snail oviposition substrate; these are emergent species that typically have >3 mm stem diameter and >20 mm of structure above water. In the results, we present these as "oviposition" plants. Second, we recorded the genus and species of plants that remain entirely or primarily underwater (i.e., not oviposition substrate). Technically, many of the latter (e.g., *Bacopa caroliniana*) are not submerged aquatic vegetation; they maintain some structure above water in most conditions. We present the second category of plants as "other." Finally, in each throw trap, we measured water depth using a meter stick.

2.4. Estimates of Egg Presence

We report egg clusters, readily observed because they are deposited above the water line, to document apple snail presence. Documenting eggs is much less labor intensive than sampling snail density using throw traps; therefore, a much larger area can be sampled in the same amount of time compared to throw traps. However, egg clusters are reliable only as an indicator of snail presence/absence—not to quantify snail abundance [47]. *Pomacea maculata* eggs are easily distinguished from those of native apple snails based on egg size, egg number per cluster, and color [18], with *P. maculata* = *P. insularum*.

In LTOHO, we recorded eggs, when present, along fixed 50-m long transects in all plots in sites BP, GC, and SSB from 2003 to 2007. Presence/absence of eggs complements the throw trap data, and this source of information can be important if throw traps yield no snails but a small number of snails may be in the site laying eggs (P. Darby, unpublished). Additionally, from 2005 to 2007, we drove the airboat along the entire LOTHO shoreline for a whole-lake egg survey, recording coordinates with a global positioning system at each location where we observed one or more egg clusters. In WCA3A, we monitored eggs from 2006 to 2015 in randomly selected sites using a quasi-systematic protocol (the wetland being too large to adopt the approach on LTOHO). At each random point (generated using ESRI/ArcGIS™ software, Redlands, CA, USA), we drove the airboat slowly along ~100 m of sawgrass ecotone, and recorded egg cluster presence/absence from the boat. Egg cluster data more than doubled the scale of our WCA3A sampling beyond the labor-intensive throw trap effort alone.

2.5. Data Analyses

We estimated mean snail density per 1-m^2 separately for both *P. paludosa* and *P. maculata* for each of the sites (WCA3A) and plots within sites (LTOHO) by year. We adjusted our estimates to reflect sampling bias associated with varying site characteristics by dividing the estimated mean density by the mean capture probability to obtain an adjusted mean. All graphs and analyses representing throw trap data show the adjusted mean total snail density estimate (snails above 13 mm, the mesh size of our nets) with standard errors.

Our primary reporting here is on the chronology and spatial distribution of the non-native apple snail across the landscape over time, although we also report on how *P. maculata* densities compare to native snail densities in LTOHO and WCA3A. Most WCA3A snail density estimates were from different sites sampled in different years (details in Results), whereas LTOHO density estimates were from the same treatment and control plots sampled over multiple years. Note that we are working on a separate comprehensive analysis of what hydrologic and habitat characteristics explain apple snail density in the Everglades for a future publication, so it will not be covered herein [49]. On LTOHO, sampling included a treatment effect, so we analyzed 2004–2007 density data for treatment (scraped vs. unscraped), year, and interaction effects (data precluded the inclusion of a site effect; see Results for details). LTOHO analyses were restricted to sites and plots where we found at least one snail. We analyzed these effects using the Generalized Linear Models (GENMOD) procedure in SAS [50] with density data fitted to a negative binomial distribution [39,47]. Capture probabilities were incorporated into the analyses by using mean capture probability for a given plot-year as an offset in the GENMOD model [39,50].

3. Results

3.1. P. paludosa Occurrence—LTOHO and WCA3A

We encountered native Florida apple snails in LTOHO in 2001 and 2002, but in few plots and at low densities (Figure 2). By 2003, native apple snails were absent in our study sites, and, anecdotally, we saw no evidence of snails throughout most of the lake (i.e., few or no eggs throughout, and few snail kites foraging). The low densities (or zero, in most plots sampled) of *P. paludosa* in LTOHO occurred before the establishment of the non-native snail in our study sites (Figure 2). Based on stage and water depth data, the low densities of *P. paludosa* in the lake were not related to dry downs or extreme high water events (Figure 2); we found no native snails prior to the 2004 drawdown.

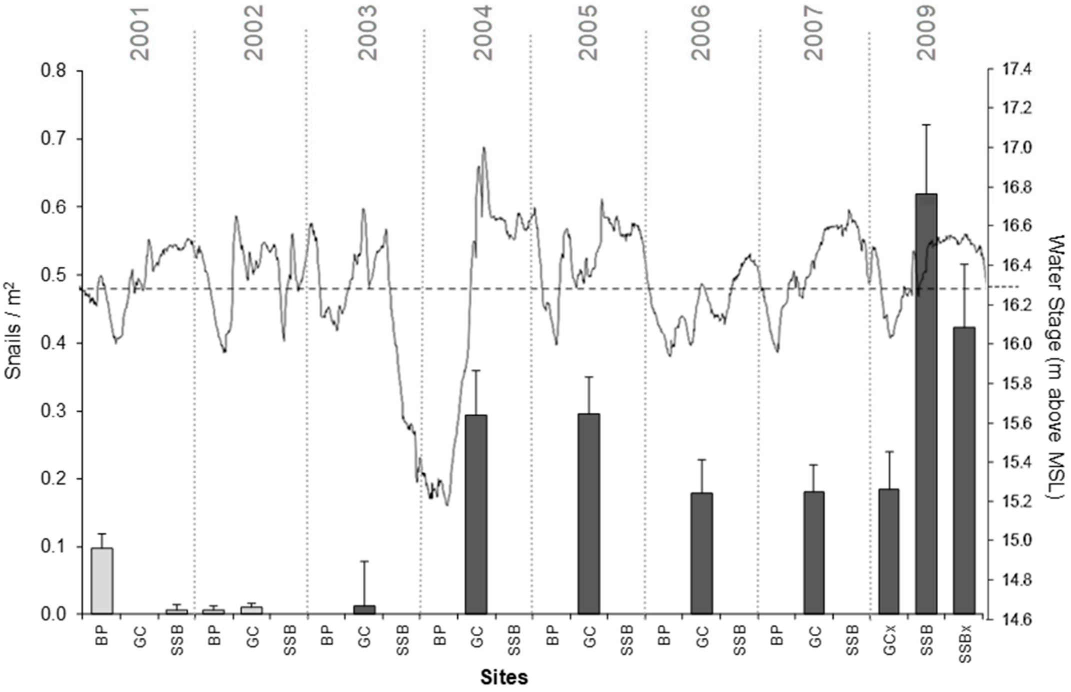

Figure 2. *Pomacea paludosa* (gray bars) and *Pomacea maculata* (black bars) snail densities (per m^2) in LTOHO sites from 2001 to 2009. We did not sample in 2008. Water stage data shown as meters above mean sea level (MSL). Dashed horizontal line represents approximate ground level at the sites. BP = Brown's Point. GC = Goblets Cove. SSB=South Steer Beach. GCx and SSBx = sampling sites in the vicinity of GC or SSB.

In contrast, WCA3A sites supported native apple snails throughout the 2006–2015 sampling period (Figure 3). Throw traps yielded native snails almost exclusively in southern WCA3A (as with non-native, see below). The presence of native snails in the remainder of WCA3A was indicated by egg cluster counts only, so we report no snail densities for the wetland unit other than those found in southern sites (Figure 3). Native snail densities were consistently <0.4 snails/m^2 (and < 0.2 for 28 of 36 estimates) in these southern sites through 2013. By 2014–2015 we documented densities in several sites in this region above 0.4 snails/m^2 and up to 0.9/m^2. This was a relatively wet period for these southern sites, except for a limited dry period in 2011 (additional details provided below).

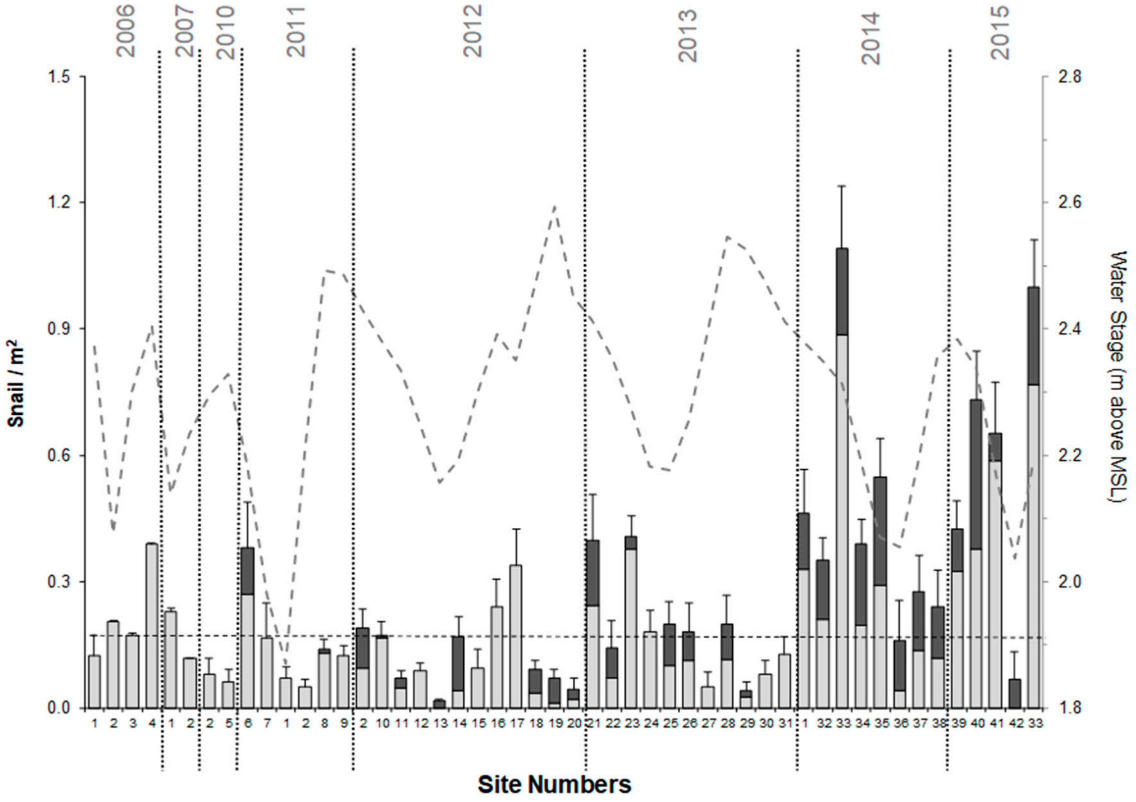

Figure 3. *Pomacea paludosa* (gray bars) and *Pomacea maculata* (black bars) snail densities (per m^2) in southern WCA3A, and its associated lower ground elevations, from 2006 to 2015 (Figures S1–S8). For each year, the number of reported density estimates equals the number of sites sampled except for two sites in 2011 and one site in 2015 in which we found zero snails in throw traps. We did not sample in 2008–2009. Here, we report snail density estimates only from sites where we found snails in traps (42 different sites, some sampled more than once, for a total of 50 density estimates). Sites 1, 2, and 33 were sampled in more than one year. Water stage data shown as meters above mean sea level (MSL). Dashed horizontal line represents approximate ground level at these southern WCA3A sites.

3.2. *Chronology of Establishment of P. maculata in LTOHO*

Eggs and empty shells of the non-native apple snail were found in LTOHO for the first time in the fall of 2001 in Goblets Cove (GC; Figure 4), but not in our GC sampling plots in the littoral zone (Figure 5). *Pomacea maculata* egg clusters were found only on cattail in the outer littoral zone bordering open deep-water. We observed empty shells from snail kite and limpkin predation along the Goblets Cove shoreline near the C-31 canal (outflow into Goblets Cove). In 2002, we found hundreds of non-native egg clusters near the outflow of the canal (Figure 4). From 2001–2003, based on egg cluster sightings, *P. maculata* were restricted to the C-31 outflow of GC. During this period, we did not find *P. maculata* or their eggs in other sampling sites (i.e., SSB, BP) or anywhere else in the lake (e.g., along the littoral zone while travelling to/from sites via airboat). In 2003, we captured two adult-sized *P. maculata* in throw traps in GC in plot 1 (Figures 2 and 5). In a whole-lake airboat survey for egg clusters in 2004, we observed eggs in the north end of GC where the cove opens to the main body of the lake, but nowhere else on the lake. In 2005, we found *P. maculata* eggs for the first time outside of GC, including in the vicinity of, but not in, site SSB (Figure 4). From 2003–2007, throw traps yielded no snails in SSB or BP sites. However, snail kites were foraging on non-native snails in hydrilla in the vicinity of these sites. We first encountered *P. maculata* snails in traps in SSB in 2009 (we did not sample in 2008); snail kites were foraging there and in SSBx, and snail densities in the two places exceeded those just outside Goblets Cove (Site GCx) (Figure 2). We observed snail kites foraging on non-native snails in hydrilla mats throughout LTOHO in 2007 and 2009, and we observed *P. maculata* grazing on hydrilla at the water's surface.

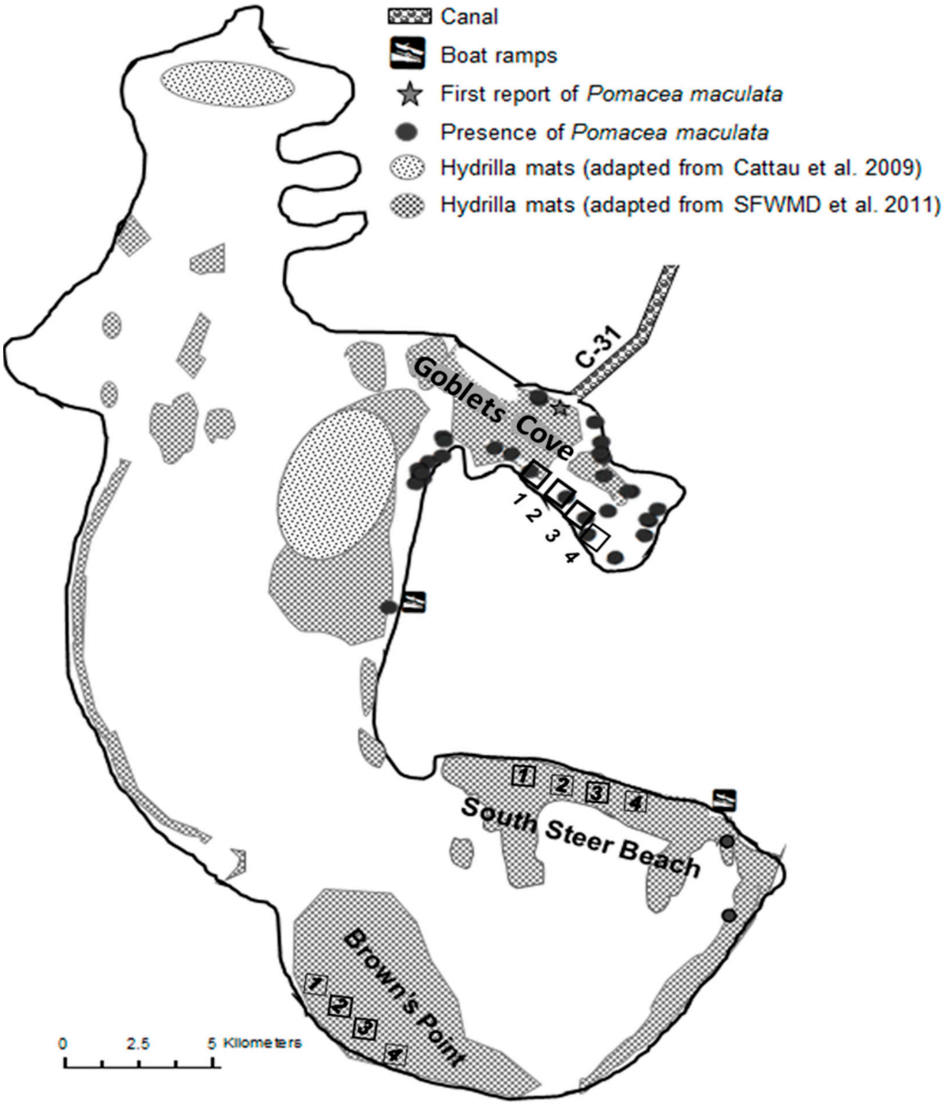

Figure 4. Locations of non-native apple snails in sites we sampled from 2003–2009 on LTOHO. First record, which was outside of sampling sites (2001), shown near the outflow of the C-31 canal. *Pomacea maculata* eggs and snails were subsequently observed outside of Goblets Cove, including throughout hydrilla that covered large portions of the lake. Hydrilla coverage adapted from Cattau et al. [51] was based on descriptions for 2009. Hydrilla coverage adapted from SFWMD et al. [52] was for 2008 for coverage levels of >50%. Our observations on hydrilla coverage were consistent with these cited reports.

Our data from LTOHO suggest that the combined effects of the 2004 drawdown, vegetation management, and hurricanes leading up to our 2004 sampling may have facilitated *P. maculata* dispersal into our GC littoral zone study plots. High-stem-density, monoculture pickerelweed dominated all sites and plots in 2003 with 100% coverage. Following 2004 treatments and hurricanes, pickerelweed coverage dropped to 45% of our traps in GC (Table 1), and *P. maculata* density increased from near zero up to 1.0 snails/m^2 (see Figure 5; recall that snails were found bordering our study plots on the littoral zone edge in 2001–2003). We found statistically significant effects of the year ($X^2 = 8.26$, 3 *df*, $p = 0.041$), treatment ($X^2 = 4.08$, 1 *df*, $p = 0.0433$), and their interaction ($X^2 = 20.25$, 3 *df*, $p = 0.0002$) on *P. maculata* densities from GC (We found no snails in SSB or BP from 2004–2007; we excluded these sites from analyses, precluding the inclusion of a site effect in our models.). Treatment effects were most evident in GC plots 1 and 4 (scraped) compared to GC plots 2 and 3 (control) in 2004 (Figure 5; X^2 =21.6, 1 *df*, *p* = 0.0001); however, over time this initial effect appeared to wane. The 2005 through 2007 samples in GC exhibited no discernible pattern in scraped vs. control plots (Figure 5).

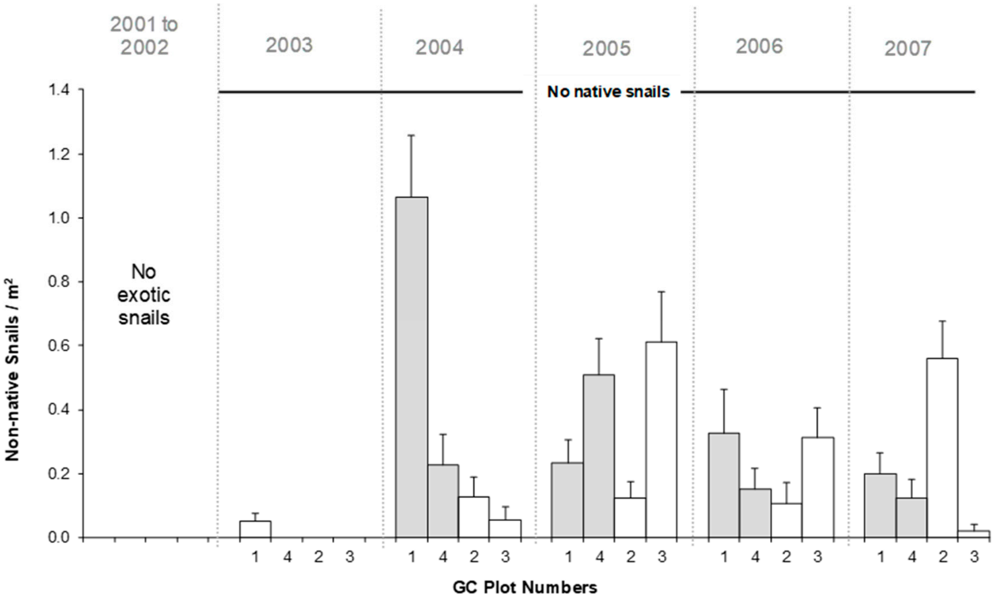

Figure 5. Densities of *P. maculata* in LTOHO in each plot (1–4) in the Goblets Cove (GC) sampling site. Plots 1 and 4 were scraped sites (gray bars) and Plots 2 and 3 (white bars) were control sites. Sites were scraped approximately six months prior to our 2004 sampling.

Table 1. Percentage of 1-m^2 throw traps containing dominant vegetation characterized as 'oviposition' substrate, or 'other' plants (including submergent and some emergent plants) on LTOHO littoral zone sites. Sample sizes to calculate percentages typically ranged from 25–50 traps (see Methods for details). Data shown only for species detected in 5% or more of traps in a site on at least one occasion over the years sampled.

Vegetation Type	Species	% of Traps					
		2001–2003			2004–2007		
		GC*	BP	SSB	GC	BP	SSB
Oviposition	*Pontederia cordata*	100	100	100	45	51	75
Oviposition	*Panicum repens*	–	–	–	44	48	25
Oviposition	*Sagittaria lancifolia*	–	–	–	5	1	–
Oviposition	*Eleocharis cellulosa*	–	–	–	5	–	–
other	*Alternanthera philoxeroides*	80	–	–	44	45	37
other	*Luziola fluitans*	4	–	26	37	34	44
other	*Utricularia purpurea*	8	100	74	1	7	4
other	*Bacopa caroliniana*	8	–	–	6	1	1
other	*Hydrilla verticillata*	–	–	–	1	9	–
other	*Vallisneria americana*	–	–	–	6	–	–
other	Unknown grass	–	–	–	5	4	14

*GC = Goblets Cove; BP = Brown's Point; SSB = South Steer Beach.

3.3. Chronology of Establishment of *P. maculata* in WCA3A

We have no evidence of *P. maculata* in WCA3A prior to 2011 (Figure 3). Note that we did not conduct sampling in 2008 or 2009, and we sampled only two sites in 2010 (Figure 3). We found non-native apple snails in throw traps and via egg clusters in 2011 in two of our sampling sites in southern WCA3A (Figures 3 and 6). From 2011 through 2015, the frequency of finding *P. maculata* in our sampling sites steadily increased from 33% (two of six sites) to 100% in both 2014 and 2015 (Note that sample site location changed from year to year [see Figure 3 and supplemental figures for details] so we are reporting on observations in southern WCA3A, not site specific trends.). *Pomacea maculata* distribution remained concentrated mainly in the southwestern part of WCA3A within four years of our finding them initially. We found native apple snails co-existing with non-natives in the majority of these southern WCA3A sites in 2011–2015. Except for one site approximately 13 km due north of the westernmost C-4 boat ramp, the remainder of our WCA3A sampling points were devoid of evidence of non-native snails (Figure 6).

In WCA3A, the longest period of dry down conditions occurred in 2011 (Figure 3). Portions of central and northern WCA3A with ground elevations >1.90 m above MSL (i.e., north of latitude N 25.85^0) went dry for approximately 40 to 90 days in mid-April through early July (data not shown). The vast majority of sites yielding snails in throw traps were found at elevations <1.90 m of MSL (southern sites), and these sites were dry for fewer than 30 days in 2011 (Figure 3). These southern sites experienced no dry downs for all of the other years reported. Therefore, the majority of the *P. maculata* dispersal during our reporting period was limited to the near constant wet conditions in southern WCA3A.

Our plant composition data for WCA3A sites invaded by *P. maculata* (2011–2015) indicated no substantial changes compared to the pre-invasion period of our study (2006–2010) (Table 2). Compared to sites where only native apple snails were present in 2011–2015, sites with only *P. maculata* had more occurrences of the submerged plants *Chara* sp. and *Potamogeton* sp. in throw traps (Table 2).

Table 2. Percentage of 1-m^2 throw traps containing dominant vegetation characterized as 'oviposition' substrate, or 'other' plants (including submergent and some emergent plants) in WCA3A. Sample sizes to calculate percentages typically ranged from 25–50 traps (see Methods for details). Data shown only for species detected in 5% or more of traps in a site on at least one occasion over the years sampled.

Vegetation Type	**Species**	**% of Traps**		
		2006–2010	**2011–2015 Non-native only Sites**	**2011–2015 Native only Sites**
Oviposition	*Eleocharis cellulosa*	76	74	79
Oviposition	*Panicum hemitomon*	23	5	7
Oviposition	*Paspalidium geminatum*	1	14	14
Oviposition	*Bacopa caroliniana*	38	35	62
other	*Chara* sp.	24	20	5
other	*Potamogeton* sp.	15	15	5
other	*Utricularia purpurea*	18	27	28

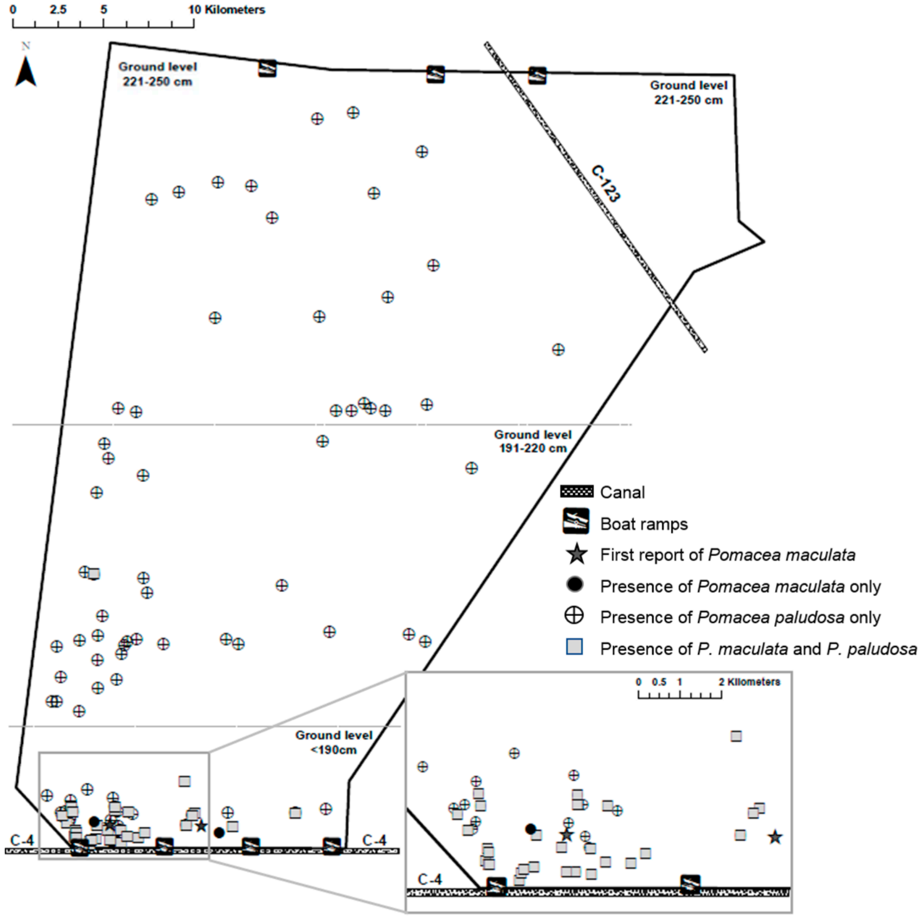

Figure 6. Native and non-native snail distribution in WCA3A from 2006–2015 based on randomly selected egg cluster monitoring sites and throw trap sites. Stars indicate first record of non-native snails in 2011. All other data from sites with *P. maculata* present were collected in 2012–2015. The majority of data from sites with ground level estimates >1.9 m above MSL (north of where most snails were found in traps) were random egg cluster counts.

4. Discussion

4.1. Overview of *P. maculata* Establishment and Dispersal

In both LTOHO and WCA3A we documented an increased presence of *P. maculata* in our sampling sites following their initial detection. Furthermore, in both systems, native snail densities were very low or zero prior to *P. maculata* invasion, suggesting the non-native snail did not out-compete or otherwise suppress the native snail. Hydrologic conditions and/or habitat conditions were apparently not suitable for *P. paludosa* leading up to our 2004 LTOHO sample (more details below). Since 2004, we found only *P. maculata* on LOTHO. In southern WCA3A, we documented increased native snail densities after *P. maculata* was detected, again suggesting that *P. maculata* was not out-competing the native (if so we would have expected native densities to decrease in southern WCA3A). This is not to say that *P. maculata* could not potentially out-compete native snails, but during our study period we saw no such trend. LTOHO snails were widespread and associated with hydrilla that covered a large portion of the lake, and by the third year of our study (2003) only *P. maculata* were found. In contrast, southern WCA3A supported native snails co-existing with non-natives following first detection of the latter in 2011, and non-native occupancy was limited to the nearly constant wet conditions associated with the southern portion of WC3A. The data we report here were largely descriptive, and were collected opportunistically (see Introduction and Methods), but include some observations (e.g., scraping, association with hydrilla, co-existing native and non-native species) that raise questions about dispersal mechanisms and how *P. maculata* might impact wetland flora and fauna in Florida.

4.2. *P. maculata* Dispersal in LTOHO

Evidence suggests that the introduction of *P. maculata* in LTOHO began in the early 2000s at the outflow of C-31 canal. A human-mediated release of snails into the C-31 would be a plausible explanation. All signs of non-native snails were near the C-31 and the outer edge of the littoral zone in deep water near our GC plots. *Pomacea maculata* appeared to respond positively to the 2004 reduction of monoculture pickerelweed and floating mats of vegetation, especially in scraped plots. A similar situation, except with *P. paludosa* and at much lower snail densities, was observed on Lake Kissimmee in 1996, when native snail density increased (up from zero) in scraped plots [53]. These findings are consistent with Karunaratne et al. [39], who found significantly fewer snails in high-stem-density *Eleocharis* habitats compared to those with lower stem densities. Darby et al. [31] reported that all of the non-native snails found in these plots on LTOHO in 2004 were full-sized adults (>70 mm approximate diameter), likely having crawled into the shallow littoral zone following the reduction in plant stem densities.

Expansion of *P. maculata* occurrence outside of GC was associated with hydrilla mats in the deeper portions of LTOHO. From 2005 onward, we directly observed non-native snails in deep-water hydrilla, or we observed snail kites foraging for snails over hydrilla in the middle of the lake. Our observations were consistent with Cattau et al. [54] and Darby et al. [31]; this continued into 2010–2011 [55]. Hydrilla is an aquatic plant that is usually rooted in substrates, but detached fragments can survive free-floating [56]. Floating fragments may be dispersed by boats, trailers, and fishing gear, and fragments and other plant parts may be spread by waterfowl [56,57]. Although we found no published reports to support the idea, it seems that disturbances, such as strong wind and waves from storms (including during a tropical storm or hurricane) would also be a plausible mechanism for the spread of hydrilla within a system. In environments like LTOHO, where there are large areas of open water, hydrilla fragments could be moved around readily by the aforementioned activities and disturbances. Marzolf et al. [26] studying *P. maculata* spreading on a Georgia reservoir, observed adult *P. maculata* and eggs transported on floating vegetation mats (hydrilla was not specified) by the wind and water movement. Observing *P. maculata* directly or via kite foraging throughout much of LTOHO by 2009 was consistent with reports of up to 80% coverage of hydrilla on the lake surface during the course of our study [52,58].

As discussed by Havel et al. [25] and Marzolf et al. [26], another potential vector of snail dispersal is recreational boating activities. Marzolf et al. [26] observed *Pomacea maculata* eggs on boats in the reservoir they studied. A substantial amount of recreational boating occurs on LTOHO, and because the snails and eggs can attach to artificial surfaces such as boat hulls, their dispersal may have been facilitated in this way.

4.3. P. maculata Dispersal in WCA3A

Darby et al. [47] did not report *P. maculata* in WCA3A while sampling from 1995 to 1996 or from 2002 to 2007 [45,46,49]. The first time we documented this species in WCA3A was in 2011. Given where non-native snails were concentrated in WCA3A during our study, it appears to have originated from canals, and specific boat ramps, especially the ramp at the 40-mile bend off State Route 41 bordering southern WCA3A (westernmost boat ramp, see Figure 6). The species' distribution has thus far remained largely restricted to a few kilometers from boat ramps and bordering canals in southern WCA3A. Portions of WCA3A further north dry out more frequently, and we speculate that drying could be a deterrent to expansion of *P. maculata* into the interior of WCA3A. Human and avian-mediated dispersal of *P. maculata* may be possible as noted for other snail species, but this dispersal mode has not been documented to date in the Everglades. We observed frequent airboat traffic out of the 40-mile bend ramp, and large concentrations of wading birds (in the hundreds), especially in low water years like 2011, in the areas where we sampled. These high concentrations of birds where non-native snails are increasingly abundant may increase the likelihood of bird-mediated dispersal of *P. maculata* in the Everglades. Initial encounters of non-native snails in southern WCA3A were in a relatively low water year (2011), but hydrologic conditions in this part of WCA3A were generally favorable (see [43] regarding favorable conditions) for apple snails from 2012 to 2015. Both *P. maculata* [32] and *P. paludosa* [43] tolerate dry down conditions to some degree, but how periodic dry downs affect dispersal into new areas, such as central WCA3A, requires further investigation.

4.4. Implications of P. maculata Range Expansion

The most frequently cited concern over non-native apple snails is their impact on vegetation, both natural and in wetland-based agricultural systems (e.g., [59,60]). Impacts in agricultural systems have been well documented [17,60,61] and will not be reviewed here. Impacts on wetland vegetation were not a focus of our data collection, but at the relatively large scale at which we sampled, we observed little to no impact on the plant communities of LTOHO (a mix of native and non-native plants) or WCA3A (entirely native plants). A number of factors may explain our observed lack of an impact compared to studies showing significant impacts of non-native *Pomacea* on plants. Scale alone may be an issue; available reports of aquatic macrophyte consumption by snails were conducted at small scales. For example, Carlsson et al.'s [59] study of impacts on wetland plants confined *P. canaliculata* to in situ 1-m^2 mesocosms in which macrophytes were nearly eliminated. Other studies on the capacity for *Pomacea* to consume macrophytes were conducted in the laboratory (e.g., [62–64]). Experiments on *Pomacea* impacts also included snail densities significantly higher than those we estimated from our LTOHO and WCA3A samples. We most often found *P. maculata* at <0.4 snails per m^2 (noting that we did not collect snails <13 mm in size). Carlsson et al. [59], for example, observed macrophyte consumption at two, four, or six snails (> 25 mm) per m^2 that were more applicable for his study since *P. maculata* in that small wetland were much higher in number than what we encountered.

Monette et al. [65] sampled on Lake Okeechobee (southern Florida) at a scale similar to our study. However, they did not have baseline data on pre-invasion plant composition in their study sites to show any changes to the habitat associated with *P. maculata* invasion (they sampled 2010–2012). Cattau et al. [30] reported non-native snails on Lake Okeechobee prior to 2010, so they were already present by the time Monette et al. sampled. Monette et al. [65] recorded more detailed plant abundances than we did, for a total of 32 species (emergent, floating, and submerged species). Unlike our WCA3A observations, the majority of their sampling sites contained either *P. maculata* only (19 sites) or *P. paludosa* only (13 sites), with two sites with both species. They found significant differences in plant community structure in native only vs. non-native only sites, with *Eleocharis cellulosa* associated with *P. paludosa* and *Hydrilla verticillata* associated with *P. maculata*. Although we found these two plant species dominant in the two different systems, the associations in Monette et al. were consistent with ours.

Gettys et al. [66] conducted a food choice experiment where *P. maculata* exhibited a preference for *H. verticillata* over other macrophytes. The fact that hydrilla continues to proliferate in LTOHO despite the presence of *P. maculata* may be associated with rapid growth rates for hydrilla [56]. Lack of vegetation impacts in our study could reflect a lack of sufficient time for *P. maculata* at relatively low densities to have had an impact, and the fact that hydrilla coverage on the lake is so extensive. In a smaller system (≈100 ha), Lake Munson in the panhandle of Florida, hydrilla was almost entirely eliminated over a two-year period following initial observations of *P. maculata* in the lake [67]. Lack of vegetation impact from our data may also reflect the dominant plants in our sampling sites not being preferred or not vulnerable to grazing by *P. maculata*. However, non-native apple snails appear to consume most macrophytes available in aquatic systems in Florida [63,64,68], and given particular scenarios (as on Lake Munson) we agree that natural resource managers should be concerned about impacts of *P. maculata* on wetland plant communities. From our data, however, we did not see substantial vegetation impacts of the non-native snail in the conditions and over the time period we sampled. Our data from WCA3A include *P. paludosa*, and we cannot distinguish impacts from native versus non-native snail foraging on vegetation from our data. Controlled experiments on plant communities over a range of apple snail densities similar to what we have recorded for both species is warranted. Experiments on the mechanisms of how hydrilla (and possibly other types of vegetation) may contribute to the spread of apple snails is also warranted.

LTOHO and WCA3A have been critical for snail kite foraging and reproduction at various times in the last 30 years [34]. Previously published data indicate native apple snail densities that constitute a sufficient snail kite forage base and that support successful nesting [45,46,69]. Densities reported here for LTOHO and WCA3A indicate that native snail densities in both LTOHO and WCA3A were insufficient to support these ecological thresholds for snail kites. The relatively low native snail densities that we observed prior to *P. maculata* invasion were consistent with zero or relatively low reported active snail kite nests in LTOHO and WCA3A (see [34]). Following *P. maculata* establishment, snail kite nesting activity increased, especially on LTOHO [34]. In WCA3A, snail kite foraging and nesting locations in southern WCA3A (location data provided by R. Fletcher, University of Florida, unpublished) were consistent with our data on non-native snails.

There were initially some concerns that because of the potential for *P. maculata* to exceed 100 mm in size there would be problems with snail kite foraging success [31,54]. However, these concerns appear to have been associated with the early invasion of large adults into the littoral zone of LTOHO [31]. Since that time, successful snail kite nesting and recruitment in Florida has been associated with the availability of non-native snails throughout the kite's range [30]. Snail kite reliance on *P. maculata* as a primary food source in recent years has raised some additional concerns. Ampullariids serve as intermediate hosts of vertebrate parasites [70], and snail kite deaths in Florida have been linked to these parasites [71]. Links between *P. maculata*-born parasites and snail kites have not been made thus far, but it certainly warrants concern. A specific link has been made between the LTOHO population of *P. maculata* and toxins in bacteria that grow on hydrilla. In a laboratory study where researchers fed toxin-laden apple snails to chickens, the birds developed avian vacuolar myelinopathy (AVM). This is a neurodegenerative disease that impacts behavior and has been shown to eventually kill some wild avian species [72].

Our field data provide no evidence that *P. maculata* displaced or otherwise out-competed native apple snails. Similar to what we stated in our discussion about non-native snail impacts on vegetation, there may be some issues with scale, snail density, or lack of detail that contrast with laboratory studies that have shown negative impacts of non-native snails on *P. paludosa*. Laboratory studies have shown decreased growth rates of juvenile native snails in the presence of non-native snails [73,74]. Monette et al. [65] concluded that any potential competitive effects of *P. maculata* over *P. paludosa* in adult stages were weak (and not statistically significant).

4.5. Summary and Conclusions

Ampullariids in general, and *P. maculata* in Florida in particular, have proven to be highly successful invaders of aquatic systems [70]. Our data demonstrate that a localized initial introduction can result in a system-wide (LTOHO) or otherwise significant expansion of this invader (WCA3A) in just a few years. Although interest has been expressed in controlling the spread of non-native apple snails in Florida, we have to recognize that the scale of the invasion, now throughout Florida in wetlands, lakes, canals, ponds, and rivers [29], will likely preclude eradication. Hand removal of snails and eggs may be effective at a small scale [75], but likely not plausible, and too costly, to be effective in systems the size of LTOHO and WCA3A. Other snail removal methods, such as introducing predators or application of molluscides, would target native as well as non-native snails, and potentially harm other species [75,76]. Considerably more data is needed to support management activities to ameliorate potential impacts of non-native apple snails in Florida's wetlands.

Clearly, it would be of value for future experiments or targeted field studies to document mechanisms of dispersal for *P. maculata*. Active dispersal by crawling has been reported for *Pomacea spp.* [22,23] but not yet at sufficient spatial and temporal scales to explain our observations. The literature also offers some potential contributing mechanisms including distribution by wetland birds [77,78] and plants and boats [15,25,79]. Human mediated causes for spreading apple snails could also include footwear [80]. The degree to which *P. maculata* could potentially out-compete *P. paludosa* is also of interest, but our sampling protocols were not designed to address that issue (WCA3A) or the opportunity did not arise (LTOHO, where native snails were absent by the time non-native snails appeared in our sampling sites).

We are concerned that the success of *P. maculata* and the low densities of *P. paludosa* reflects a larger problem for the wetlands of central and southern Florida. Didham et al. [81] made the case that the scientific community has, in many cases, been quick to blame native species declines on invasive species, while failing to recognize additive or synergistic causes of native species declines associated with habitat degradation. Snail kites had largely abandoned WCA3A and LTOHO prior to the establishment of *P. maculata* [34]. We know from snail kite foraging and nesting data from the 1980s and 1990s that there were sufficient *P. paludosa* densities to support kites in LTOHO and especially WCA3A [34]. Our snail density data reported here show much lower densities, indicating potential issues of habitat quality and hydrology for the native apple snail [34], not competition from *P. maculata*. Further analyses of our long-term data sets from multiple wetlands in central and southern Florida should prove helpful in elucidating the cause *of P. paludosa* decline exclusive of *P. maculata* (e.g., [49]), as will modeling that has been informed by our data [82].

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/11/10/183/s1, Figure S1. Throw trap site locations in southern WCA3A in 2006, Figure S2: Throw trap site locations in southern WCA3A in 2007, Figure S3: Throw trap site locations in southern WCA3A in 2010, Figure S4: Throw trap site locations in southern WCA3A in 2011, Figure S5: Throw trap site locations in southern WCA3A in 2012, Figure S6: Throw trap site locations in southern WCA3A in 2013, Figure S7: Throw trap site locations in southern WCA3A in 2014, Figure S8: Throw trap site locations in southern WCA3A in 2015.

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