PRIMARY RESEARCH PAPER

Inter- and intra-annual apple snail egg mass dynamics in a large southeastern US reservoir

Nicholas Marzolf · Stephen Golladay · Paul McCormick · Alan Covich · Susan Wilde

Abstract The introduction and spread of non-native species represents a significant threat to freshwaters. Non-native *Pomacea* are a recent and detrimental gastropod invader, altering habitats, biodiversity, and ecological function. Despite large size, adult *Pomacea* spp. may be cryptic but their egg masses, which are species specific in color and size, appear useful in determining presence and spatial distribution within invaded areas. We used a combination of annual (2013–2016) and monthly (April 2016–March 2017) shoreline transect surveys to determine the distribution of *Pomacea* spp. egg masses, along with habitat and water quality data, in Lake Seminole, GA, USA. Surveys identified invasive *P. maculata* and native *P. paludosa*, and provided evidence for rapid dispersal of *P. maculata*. Egg masses of both species occupied a wide range of emergent surfaces across the lake. Physicochemical measures suggest elevated specific conductivity corresponds with *Pomacea* presence. Temperature correlated with monthly variation of egg mass; however, egg masses were observed at water temperatures of 11.3 °C, below reported limits. *Pomacea maculata* dispersal throughout Lake Seminole is rapid, and shoreline classification and physicochemical conditions are influencing the on-going dispersal. Continued expansion of this invasive

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herbivore could have ecosystem-level consequences in Lake Seminole and other invaded waters across the southeast US.

Keywords *Pomacea* · Invasive species · Reservoir · Ecosystem function · Invasion wave

Introduction

Non-native species introductions represent a substantial threat to all ecosystems, but have been particularly common in freshwaters (Pimentel et al., 2005; Simberloff, 2014). Mollusks and crustaceans account for a large number of freshwater macroinvertebrate introductions, and aquatic mollusk invaders often colonize most successfully in lentic habitats (e.g., lakes, reservoirs) (Karatayev et al., 2009, 2017). Following colonization, non-native mollusks alter habitats (Burks et al., 2010), biogeochemical cycling and ecosystem function (Carlsson et al., 2004; Atkinson et al., 2010; Patrick et al., 2016), biodiversity and threatened species populations (Darby et al., 2007; Cattau et al., 2016), and food web structure (Valentine-Darby et al., 2015; Dorn & Hafsadi, 2016).

Apple snails in the genus *Pomacea* (family: Ampullariidae) are among the most successful invasive aquatic species in many subtropical and tropical freshwaters, with introductions spanning North America, Hawaii, the Caribbean, and Asia (Rawlings et al., 2007; Hayes et al., 2012, 2015). In the southeastern US, the greatest diversity of non-native *Pomacea* occur in Florida, although non-native populations presently range from Texas to North Carolina (Benson, 2017; Burks et al., 2017). The most prominent of invasive *Pomacea* in this range is *P. maculata* (Perry, 1810), native to the Pantanal wetland in South America (Heckman, 1998) and introduced in the US ca. 1980, likely from the aquarium trade and its current distribution reflects natural and anthropogenic dispersal from Florida (Benson, 2017; Joshi et al., 2017). Range expansion and population growth of invasive *P. maculata* negatively influence native *P. paludosa* (Say, 1829) populations in the Florida Everglades (Conner et al., 2008; Posch et al., 2013). Increasing invasive *P. maculata* replacement of native *P. paludosa* in the Everglades ecosystem decreases foraging success of the threatened Snail Kite (*Rostrhamus*

sociabilis Vieillot), thereby influencing regional water-level management through balancing water demand with maintaining high snail densities for snail kite foraging (Darby et al., 2007; Cattau et al., 2014, 2016).

Quantifying population characteristics of *Pomacea* spp. has proven challenging (Darby et al., 1999). Despite their large size (adult *P. maculata* shell length > 40 mm), adult snail shells are camouflaged by growth of algae, detritus, and other epibiota, and can be difficult to locate and identify underwater. Hatchling, juveniles, and sub-adults are small (shell length < 40 mm) (Youens & Burks, 2008) and often dispersed in habitats difficult to sample (e.g., aquatic vegetation beds, lake sediment) (Glasheen et al., 2017). Snails respond to disturbance by detaching from substrates, withdrawing within their shell and sinking in the water column, which further impedes observation (Joshi & Sebastian, 2006). Although identifying species using shell morphology among non-native *Pomacea* is challenging, determining species distributions and rates of establishment across non-native ranges is crucial for determining the extent of and preventing future dispersal. An alternative approach to assessing *Pomacea* spp. distribution uses their calcareous egg masses, which are deposited above the water on emergent surfaces and useful in determining species presence (Rawlings et al., 2007).

Pomacea spp. egg masses are definitive indicators of both species presence and population reproduction (Hayes et al., 2012). Egg masses are species specific and therefore useful for determining presence/absence, particularly of non-native species (Perez et al., 2017). Quantifying egg mass abundance over time can be used in determining relative abundance of *Pomacea* species over large areas (see Darby et al., 1999). *Pomacea* spp. egg masses are deposited on emergent surfaces, including vegetation (Burks et al., 2010; Perez et al., 2017), man-made structures (Hayes et al., 2012), and boats (pers. obs.). Native *P. paludosa* deposit white egg masses with approximately 30 individual eggs (3–6 mm diameter) in each mass (Turner, 1996). In contrast, invasive *P. maculata* produce pink egg masses with eggs ∼1 mm in diameter with > 800 individual eggs per mass (Kyle et al., 2013), with number of eggs/mass 10–100× more abundant than *P. paludosa* egg masses [up to 4800 eggs per egg mass (Barnes et al., 2008)].

Field surveys for *Pomacea* spp. egg masses determined seasonal reproduction and presence of *P. paludosa*. In the Florida Everglades, *P. paludosa* produced egg masses from March through October (Hanning, 1979) and in northern Florida, Bernatis & Warren (2014) observed *P. maculata* egg masses from March to November. The *P. maculata* native range is more hydrologically dynamic and warmer than introduced areas in the southeast US (Hayes et al., 2008; Yoshida et al., 2014; Matsukura et al., 2016), raising questions on *P. maculata* persistence and adaptation across non-native ranges. Byers et al. (2013) used minimum temperatures to model *P. maculata* establishment, which suggests available habitat through much of the southeastern US, though field studies of activity and fecundity are needed to assess their model predictions across the modeled range. While egg masses are useful in determining presence, correlating egg mass abundance to population size has yet to be determined across the introduced and potentially available range (Darby et al., 1999, 2008). Egg masses, particularly of non-native *Pomacea*, are essential for indicating dispersal of these highly invasive gastropods, and are used by resource managers to initiate management responses and egg mass abundance of non-native mollusks, which is related with fecundity, is a primary predictor of detrimental economic and ecological impact (Keller et al., 2007).

This study was conducted to gain foundational information on native and invasive apple snails in Lake Seminole. First, we examined the spatial distributions of *Pomacea* spp. in Lake Seminole over a four-year period. Second, we examined whether water chemistry or shoreline habitat affect *Pomacea* spp. presence/absence or egg mass abundance? Third, we quantified seasonal variation in egg mass abundance over a 1-year period and examined temperature effects on egg mass abundance for *Pomacea* spp.? Given this background, we use our results from Lake Seminole as a case study to discuss how changes in apple snail populations may alter ecosystem function in Lake Seminole and other aquatic habitats across the southeastern US.

Materials and methods

Site description: Lake Seminole and SLWMA ponds

Lake Seminole is a 15,216 ha impoundment in the Apalachicola-Chattahoochee-Flint (ACF) watershed, located in southwestern Georgia (Fig. 1). The lake has a mean depth of 3 m and maximum depth of 10.7 m. The main surface water inflows include the Flint River, the Chattahoochee River, and Spring Creek, which collectively drain 46,151 km^2 (Shivers et al., 2016). As a result of impoundment, adjacent drainage basins and channels were inundated, and are considered part of the larger Lake Seminole. These inundated areas include fish pond drain (FPD) and cypress pond (CP), both located between Spring Creek and the Chattahoochee River, oriented north–south and east–west, respectively (Fig. 1). Additionally, small ponds within the Silver Lake Wildlife Management Area (SLWMA), located between the Flint River and Spring Creek arms of the lake, are included in this study. These ponds lack surface hydrological connection to the lake and were geographically isolated wetlands prior to Lake Seminole impoundment. The rise of the aquifer potentiometric surface in the region after impoundment resulted in the formation of perennial small lakes (Torak et al., 2005).

Survey method

We identified egg masses, following Rawlings et al. (2007), using the differences in egg mass color and individual egg size to distinguish *P. maculata* and *P. paludosa* egg masses. Egg masses were identified and counted across Lake Seminole through repeated shoreline surveys during each July of 2013–2016. In 2013, fixed survey locations ($n = 97$) were established across the main body of Lake Seminole, and following the 2013 results, subsequent years' surveys included additional locations across smaller drainages and nearby ponds in SLWMA ($n = 167, 141, 129$ for 2014, 2015, and 2016, respectively). Two observers counted egg masses along a transect parallel to the shoreline for 5 min on a boat at idle speed. Total egg mass counts for each species along the transect were averaged for the two observers and recorded. Individual counts were not recorded, and over the course of the surveys, there were few instances where counts
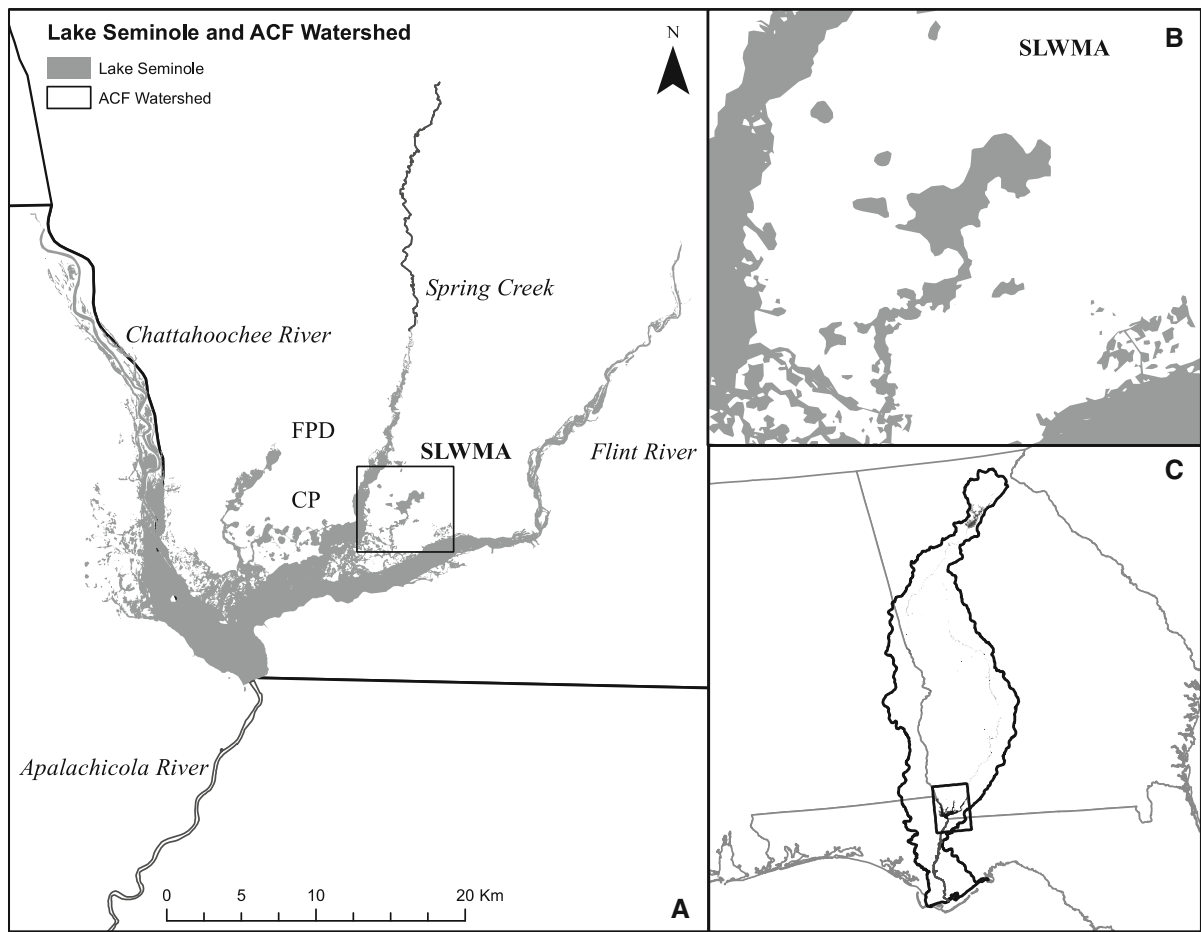
Fig. 1 Lake Seminole (**A**) within the Apalachicola-Chattahoochee-Flint (ACF) watershed (**C**). Main surface water inflows are the Flint River, Chattahoochee River, and Spring Creek; smaller drainages are Fish Pond Drain (FPD) and Cypress Pond (CP), and ponds within the Silver Lake Wildlife Management Area (SLWMA) (inset **B**)

were notably different to the observers. In rare cases of notable differences in observer counts, the transect was re-surveyed. Transect distance varied for each transect, though across all transects, the mean distance surveyed was 281.3 m ($\pm$ 96.5 SD) (Supplementary Table 1). The large variation in survey distance is explained by several factors, including egg mass abundance, vegetation density, water depth, and submerged stumps and snags, which influenced the distance traveled over the 5-min survey time (e.g., shallow water, more abundant egg masses, more submerged stumps, and thick vegetation decreased survey distance).

We classified dominant shoreline habitat at each location into one of five classes: beach, emergent vegetation, artificial (i.e., human structures), rock, and tree. Emergent vegetation habitats were composed of sawgrass (*Cladium* spp.), cattail (*Typha* spp.), softstem bulrush (*Scirpus validus* Vahl), water primrose (*Ludwigia* spp.), horsetail (*Equisetum* spp.), or a mixed community of these plants. Artificial habitats were predominately human structures, such as boat docks or seawalls within the survey transect. The tree classification included downed snags in the lake or trees adjacent to the shoreline or in the lake, predominantly the roots and knees of bald cypress (*Taxodium distichum* L.). In 2014, we used a Hydrolab Quanta (Hydrolab Corp., Austin, TX, USA) at each survey location to measure temperature (°C), pH, and specific conductivity (mS/cm) at the water surface. We anticipated that egg mass presence (i.e., adult presence) would be found at areas of elevated pH and

specific conductivity, given the spatial correlations with solutes essential for snail growth (calcium, carbonates) (Rugel et al., 2016).

To determine within-year egg mass production within a 12-month period, we surveyed *Pomacea* spp. egg masses and surface water temperatures monthly from April 2016 to March 2017 using the survey method described above. Whole-lake surveys were impractical to perform each month. Therefore, we selected a subset of locations from the annual survey locations based on 2015 annual survey. Locations were selected where three adjacent survey transects contained one of the following species designations: only *P. maculata* egg masses observed; only *P. paludosa* egg masses observed; and both species egg masses observed. We selected a one-month interval to allow for egg masses deposited the prior month to develop and hatch and to allow for females to deposit new egg masses (Hanning, 1979; Turner, 1996; Koch et al., 2009; Cowie and Hayes, 2012). All spatial data were collected using a Nomad 800B data logger (Trimble, Sunnyvale, CA, USA) with a Crescent A-100 GPS antenna (Hemisphere, Scottsdale, AZ, USA) using ArcPad v10.2. Analysis and maps were created using ArcMap v10.2 (ESRI, Redlands, CA, USA).

Statistical analyses

We analyzed annual surveys by calculating yearly percent locations occupied for each species, total number of egg masses, and mean egg masses per survey location and species. Within each year, we used t tests ($\alpha = 0.05$) to determine if either species' mean egg mass abundance was greater. For monthly surveys, we calculated total number and mean number of egg masses per species for each month surveyed. Monthly water temperatures from 2013 to 2016 were averaged across Lake Seminole (Golladay, unpub. data). We used linear regression to compare mean monthly temperature and total monthly number of egg masses observed. Physical chemistry was assessed for the 2014 annual survey using scatterplots and Pearson correlation coefficients to determine relationships between temperature, pH, and specific conductivity.

We analyzed relative use of shoreline using generalized linear models (glm) with a Poisson distribution, given our egg mass abundance data are interpreted as counts and failed Shapiro–Wilk test for normality

($P < 0.01$). Models were created for each species separately to determine within-species utilization of shoreline class specified above, with fixed effects of survey year, shoreline class, and an interaction term. Tukey's honest significant differences test identified shoreline classes across all years that exhibited greater number of egg masses. We created glm in the 'stats' package in R (R Development Core Team, 2016).
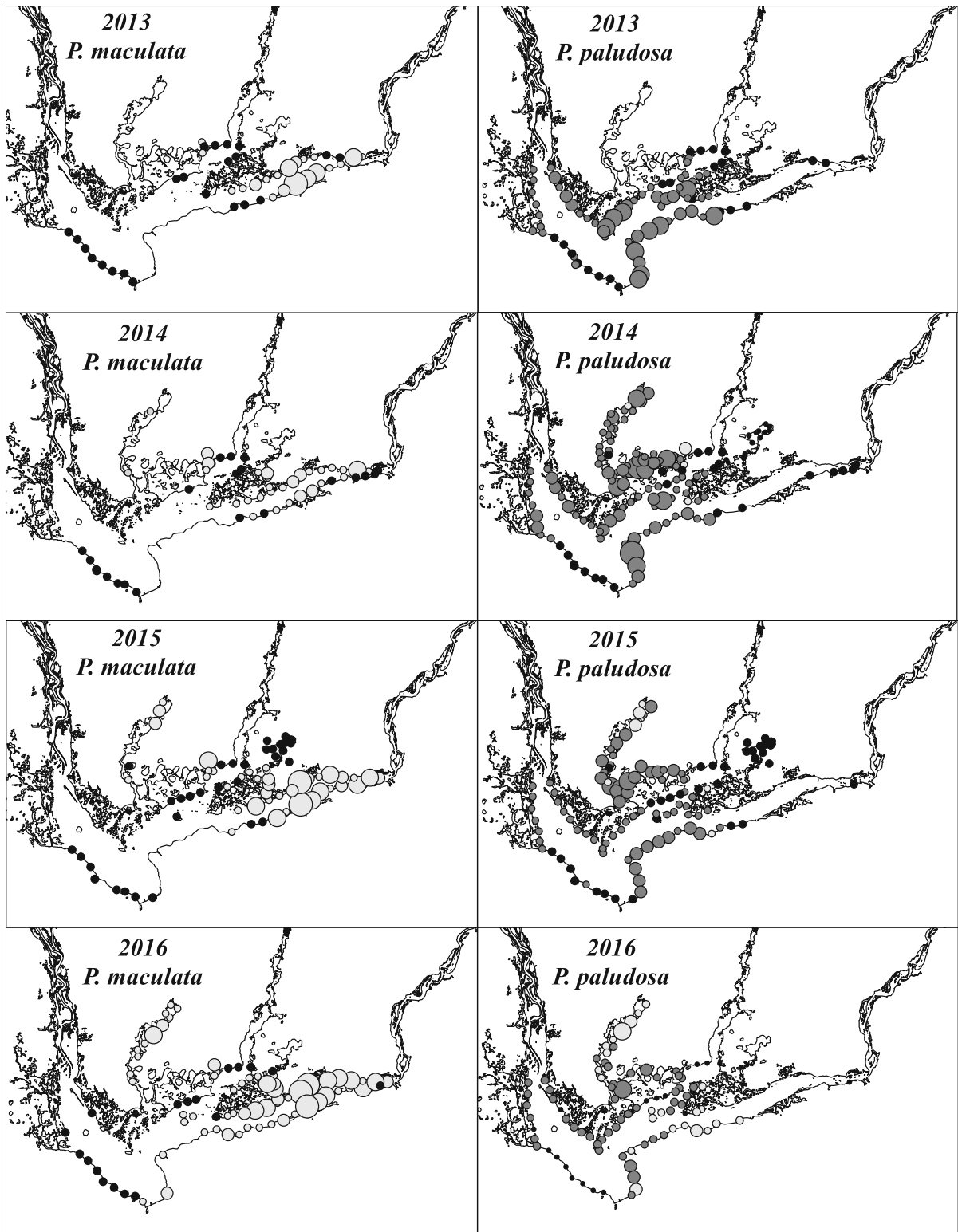
Results

Annual surveys

We observed *P. paludosa* egg masses across all arms of the lake and connecting channels in all survey years (Fig. 2A). In contrast, *P. maculata* egg masses were generally observed in the Flint River arm of the lake, near locations where this species had been previously reported (USACE, 2013). However, *P. maculata* egg masses were also observed in a cove on Spring Creek in 2013, and in subsequent years, they were detected in areas adjacent to previous years' locations (Fig. 2B). In 2014, *P. maculata* egg masses were observed in connecting channels between the Flint River arm, near areas of greatest *P. maculata* abundance, and in Spring Creek. In the following year, *P. maculata* egg masses were observed on the eastern shoreline of Spring Creek. By 2016, we observed *P. maculata* egg masses in the three major surface water inflows, including the Chattahoochee River, where egg masses had not been detected in previous years' surveys. In 2014 and 2015 survey years, no egg masses of either species were observed in the SLWMA ponds.

Pomacea maculata were observed at 22% of locations in 2013 and at 47% of locations by 2016, whereas *P. paludosa* observations ranged between 54 and 63% of sites in all years (Fig. 3A). Mean *P. maculata* egg mass abundance increased from 2013 (15.7 ± 12.5 SE) to 2016 (30.3 ± 9.3) per transect. Mean *P. paludosa* egg mass abundance, however, declined from 2013 (28.0 ± 6.6) to 2016 (9.0 ± 2.5) per transect (Fig. 3B). In 2014, mean *P. maculata* egg masses per transect (4.7 ± 3.0) were significantly less than *P. paludosa* (22.8 ± 4.2) (t test, $P < 0.01$), but greater, though not significant ($P > 0.05$), in 2015. In 2016, *P. maculata* (30.3 ± 9.3) egg mass abundance was significantly greater than mean *P. paludosa* egg mass abundance (9.0 ± 2.5) (t test, $P < 0.01$).

A

B

◀ **Fig. 2** Results of annual surveys 2013–2016. Each species observed is mapped for each of the survey year, *P. maculata* represented by light gray circles, *P. paludosa* by dark gray circles, and no egg masses represented by a black circle. Circle size is proportional to the number of egg masses observed, with the smallest circles ranging from 1 to 46 egg masses, moderately small ranging from 47 to 104 egg masses, moderately large ranging from 105 to 244 egg masses, and largest circles indicating 245–462 egg masses observed for each transect. Column **A** identifies locations where *P. maculata* or no egg masses were observed and column **B** where *P. paludosa* or no egg masses were observed, in each year from 2013–2016, as labeled in each pane

Shoreline and environmental habitat

Physical chemistry indicates moderate correlations between temperature, pH, and specific conductivity. Specific conductivity and pH exhibited greatest correlation ($r = 0.367$), followed by pH and temperature (0.308), and temperature and conductivity (0.175). pH and specific conductivity exhibited strong spatial variability (Fig. 4). Specific conductivity in the SLWMA ponds (0.019 µS/cm ± 0.001 SD) was 9× lower than the mean conductivity in Lake Seminole sites (0.171 ± 0.035) and the nearby connected
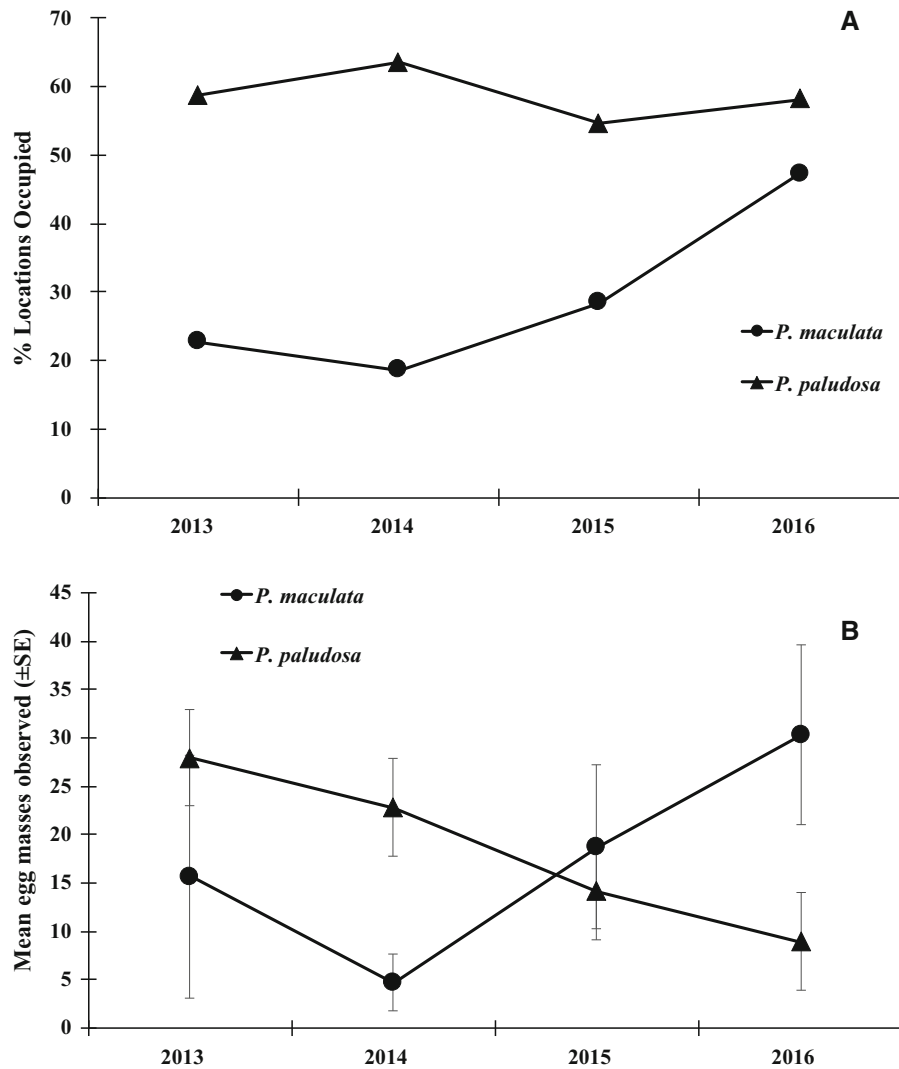

Fig. 3 A Percent of locations occupied for *P. maculata* (circles) and *P. paludosa* (triangles) observed during annual egg mass surveys in Lake Seminole, 2013–2016. **B** Mean egg masses (± SE) per transect for *P. maculata* (circles) and *P. paludosa* (triangles) observed during annual egg mass surveys in Lake Seminole, 2013–2016. Significantly different groups are indicated by non-overlapping error bars ($\alpha = 0.05$)

Fig. 4 Scatterplots of 2014 water chemistry data, showing **A** pH and **B** specific conductivity against temperature across all sites surveyed across Lake Seminole as indicated by different shapes for each pH and specific conductivity
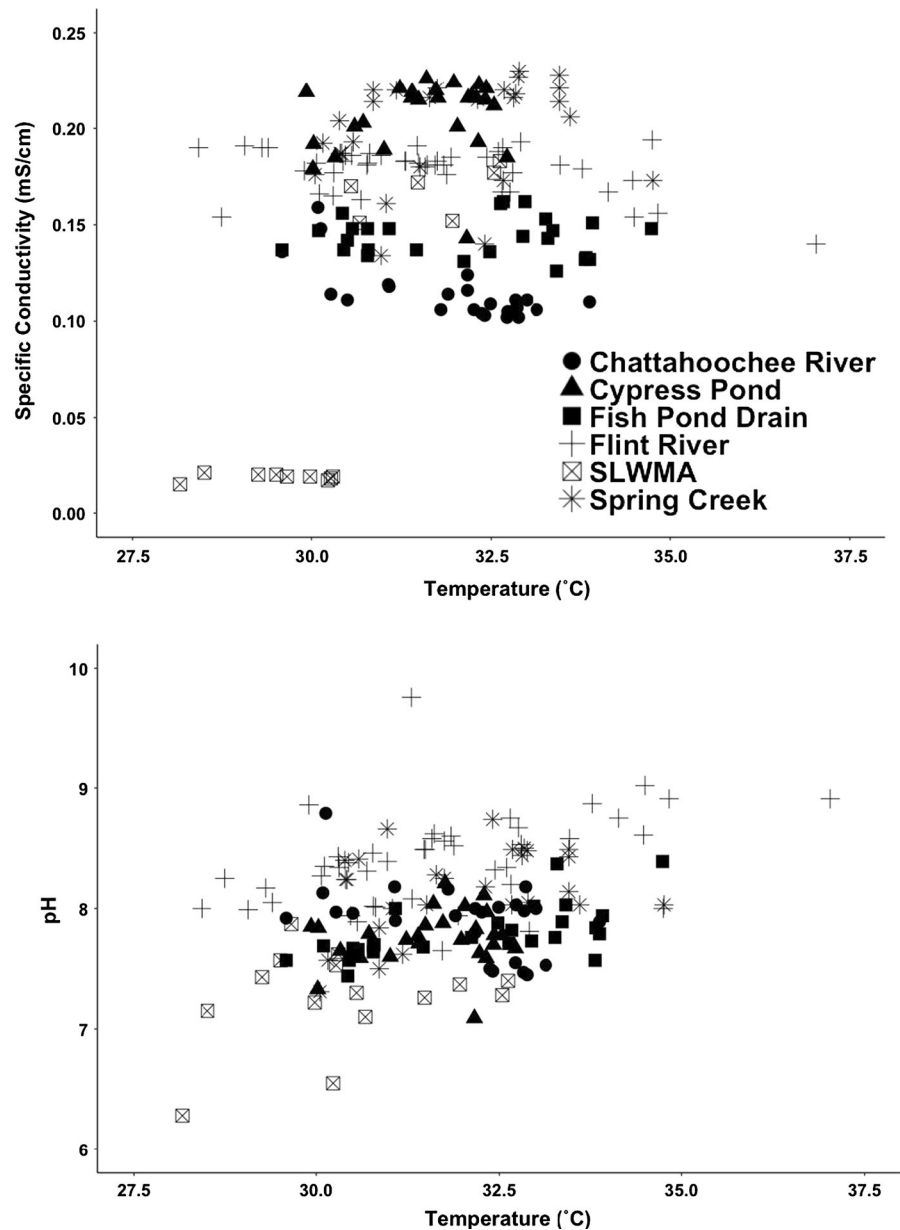
SLWMA channels (0.168 ± 0.011). Mean pH values in the SLWMA ponds were 7.25 (± 0.52), whereas the lowest pH measured in the lake were in the Cypress Pond area (7.76 ± 0.23), though values were as higher (8.40 ± 0.39) in the Flint River. Temperatures ranged from 28.2 to 37.0 °C across all sites, and showed slight spatial variation. Mean temperatures in Lake Seminole were 31.9 °C, whereas in SLWMA, mean temperature was 30.4 °C. Within each site, we measured temperatures across the range of all temperatures, with the

exception of the SLWMA ponds, which ranged from 28.2 to 32.6 °C.

Over the four survey years, transects dominated by emergent vegetation were most common across the lake (71% all shoreline), followed by tree (14%) and man-made sites (12%). Only 8 sites were classified as beach and rock shoreline habitats, and accounted for a very small number (203 total) of egg masses observed, and we removed these site classifications from subsequent statistical analyses. For *P. maculata*, 7441 egg

masses (83%) were observed on emergent vegetation, 1347 (15%) on artificial surfaces, and 183 (2%) on trees across all years. Mean egg masses per transect were similar on artificial surfaces (20.4) and emergent vegetation (19.8) and lower at tree sites (2.5) (Table 1). Mean *P. maculata* egg mass abundance was significantly greater on artificial surfaces in 2013 and 2016 and on emergent vegetation in 2015 (GLM, $P < 0.01$ for each). We counted 9565 total *P. paludosa* egg masses, with 60% on emergent vegetation ($n = 5696$), 21% on man-made surfaces (2017), and 17% on trees (1650). Mean *P. paludosa* egg masses per transect were greatest on man-made surfaces (30.6), followed by trees (23.0), and emergent vegetation (15.1). Mean egg mass abundance was significantly greater on trees in 2013, artificial surfaces in 2014, and 2015 (GLM, $P < 0.01$ for each).

Monthly surveys

Egg mass abundance exhibited strong seasonal variation. We observed 5335 egg masses from April 2016 to May 2017, with 5243 *P. maculata* (98%) and 92 *P. paludosa* (2%). The greatest number of total egg masses (sum of both species) was in June ($n = 956$) and the fewest in February ($n = 14$). *Pomacea maculata* egg masses were observed during each month surveyed, whereas *P. paludosa* egg masses were observed from May through September, with a few noted in November (Fig. 5). Greatest number of *P. maculata* egg masses were observed in June (948), whereas *P. paludosa* were greatest in July (32). Mean surface waters were warmest in August (30.8 °C) and coolest in February (11.3 °C), and total egg masses observed were positively correlated with monthly surface water temperature ($P < 0.001$, $r = 0.89$) (Fig. 5, inset).

Discussion

We present evidence for rapid expansion of *P. maculata* in Lake Seminole, GA, which was first observed in 2003. From the reported introduction site in 2003 (USACE, 2013), we document dispersal of *P. maculata* both upstream and downstream in the Flint River arm and into the other arms of the reservoir, along with apparent increasing *P. maculata* egg mass abundance. Both *P. maculata* and *P. paludosa* use the most available emergent surfaces to deposit egg

masses. We document the seasonal cycle of *Pomacea* spp. egg mass production, showing monthly variation and suggesting a seasonal temperature effect on *P. maculata*. The invasion of *P. maculata* in Lake Seminole requires long-term monitoring as well as further research into potential consequences on food webs and biogeochemical cycling given our observations of dispersal and population growth. Also, abiotic and biotic factors that will potentially limit future dispersal in the southeastern US, at present, are poorly understood. Recent works document the importance of diverse aquatic habitats across the landscape for *P. maculata* expansion in both Texas (Perez et al., 2017) and Florida (Pierre et al., 2017), and physicochemistry in the on-going invasion of gastropods (*Potamopyrgus antipodarum* Gray, 1843) in northern California (Vazquez et al., 2016).

In Lake Seminole, *P. maculata* egg masses were first observed in 2003 by the US Army Corps of Engineers (USACE) in a cove near a popular boat launch and lodge on the Flint River arm (USACE, 2013). Surveys in 2010 corroborated the presence of *P. maculata* in the cove, as well as documenting egg masses along the southern shoreline of the Flint River arm (USACE, 2013). In the period from the first observation (2003) to follow-up surveys (2010), *P. maculata* dispersed both upstream and downstream in the Flint River arm of the lake. Our 2013 survey confirmed *P. maculata* egg masses in the vicinity of the reported introduction, as well as on the northern shoreline of the Flint River (Fig. 2, 2013). Collectively, these observations suggest that rapid, multidirectional dispersal occurred in the Flint River between 2010 and 2013, as well as a satellite introduction of unknown origin in Spring Creek.

In subsequent surveys (2014–2016), locations with *P. maculata* egg masses increased (Fig. 3A), representing expansion into areas adjacent to where we had not documented egg masses in previous years (Fig. 2). This dispersal is consistent with the invasion wave hypothesis, which examines patterns and rates by which non-native species disperse and provides applications for managing non-native species (Caswell et al., 2003). In Lake Seminole, the *P. maculata* invasion wave appears to be expanding from the presumed 2003 introduction location on the Flint River, and exhibiting multidirectional movement throughout the lake. The satellite introduction of *P. maculata* on the western shoreline of Spring Creek

Table 1 Egg mass deposition on shoreline classes in Lake Seminole for both *P. maculata* and *P. paludosa*

Species	Shoreline class	2013				2014				2015				2016			
		# sites	Total egg masses	Mean ± SE	HSD group	# sites	Total egg masses	Mean ± SE	HSD group	# sites	Total egg masses	Mean ± SE	HSD group	# sites	Total egg masses	Mean ± SE	HSD group
P. maculata	Artificial	9	409	45.4 ± 42.9	a	26	83	3.2 ± 2.9	f	16	369	23.1 ± 22.2	f	15	486	32.4 ± 21.4	b
	Beach	1	0	0	f	2	0	0	f	2	0	0	f	2	0	0	f
	Emergent vegetation	71	1109	15.6 ± 5.8	de	115	685	6.0 ± 1.7	f	100	2193	21.9 ± 5.1	d	91	3454	38 ± 8.1	c
	Rock	3	0	0	f	3	0	0	f	3	0	0	f	3	1	0.3 ± 0.3	f
	Tree	13	8	1.0 ± 0.6	f	21	24	1.1 ± 1.1	f	20	81	4.1 ± 3.6	f	18	70	3.9 ± 3.0	ef
P. paludosa	Artificial	9	243	27.0 ± 12.2	e	26	869	33.4 ± 7.4	a	16	659	41.2 ± 9.6	ab	15	246	16.4 ± 4.6	e
	Beach	1	5	5 ± 0	e	2	0	0	e	2	0	0	e	2	1	0.5 ± 0.4	e
	Emergent vegetation	71	1796	25.3 ± 5.5	cd	115	2446	21.3 ± 4.1	bc	100	884	8.8 ± 1.8	e	91	570	570 ± 2.1	e
	Rock	3	167	55.7 ± 45.5	e	3	3	1.0 ± 0.8	e	3	0	0	e	3	26	8.7 ± 7.1	e
	Tree	13	502	38.6 ± 17.0	a	21	495	23.6 ± 10.7	a	20	442	22.1 ± 6.5	de	18	211	11.7 ± 4.6	e

Data represent the count of each shoreline class encountered each year, total egg masses for each species at the specific shoreline, the mean number of egg masses observed per transect at each shoreline class in each year, mean ± SE at each shoreline, and Tukey's honest significant differences (HSD) grouping from GLM models. HSD groups are made separately for each species
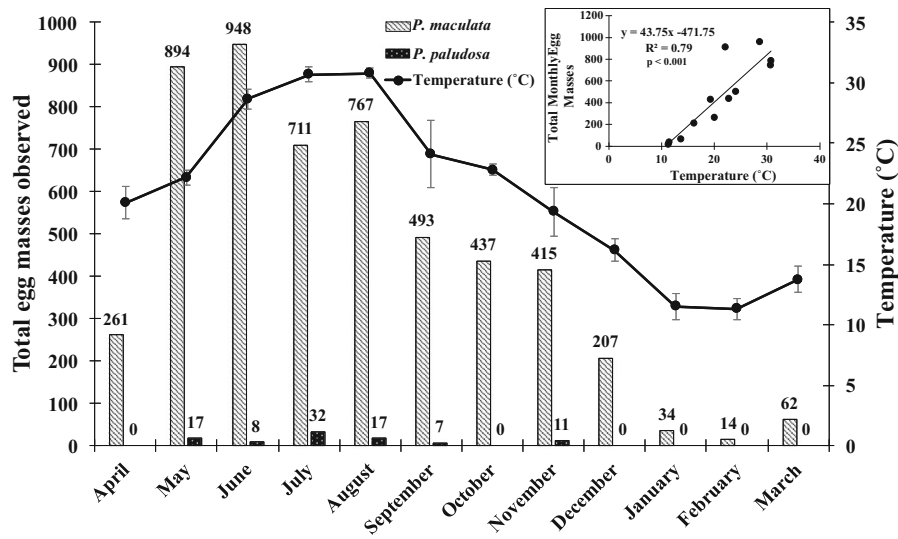
Fig. 5 Total egg masses observed by each *P. maculata* and *P. paludosa* in Lake Seminole from April 2016–March 2017, with total counts presented above each bar. Mean monthly temperature is overlain ± SE. In the inset, total monthly egg masses were regressed against mean monthly temperature, with associated statistical results presented

provides similar evidence for an invasion wave in the Spring Creek arm, following the pattern of new *P. maculata* egg mass adjacent to previous years' species locations. In Texas, egg masses were observed in new habitats, and in subsequent surveys, adults were identified, which supports outlines the use of egg masses as indicators of invader presence and sequential surveys to understand rates and progress trends using life history traits during an on-going invasion (Perez et al., 2017).

The *P. maculata* invasion wave has several possible propagation mechanisms. The first relates to the natural movement, reproduction, and life history of *P. maculata*. Reproductive output in *P. maculata* is remarkable, particularly in habitats outside their native range. The number of eggs in each egg mass can be significantly greater than in their non-native range (Kyle et al., 2013), with hatching success rates of > 50%, producing > 2000 hatchlings per egg mass (Barnes et al., 2008). Similarly, once established, *P. maculata* populations expand through rapid growth rates of juveniles and recruitment as adults (Kyle et al., 2009). This ability to rapidly produce egg mass and mature individuals explains the success of *P. maculata* in introduced water bodies. In contrast to *P. paludosa*, the native species, produce fewer eggs, but larger, hatchling snails (Turner, 1996). Previous studies have

examined the interaction of these congeners, and similar to our results, *P. maculata* generally displaces the native *P. paludosa*, likely a result of its greater fecundity and rate of resource acquisition (Posch et al., 2013). Our results suggest a shift in apple snail species dominance following the introduction of *P. maculata*, likely a result of *P. paludosa* being displaced by the more abundant and efficient foraging *P. maculata* (Monette et al., 2016) and the lack of predators at the adult stage for the larger *P. maculata* (Darby et al., 2007).

A second possible propagation mechanism for the invasion wave relates to the hydrology of Lake Seminole. The lake is a shallow run-of-the-river reservoir with a relatively constant volume, though it can be subject to rapid water-level changes during transient flood pulses. This is particularly true in the Flint River arm, where there is little flow regulation compared to the Chattahoochee River inflow (Waters et al., 2014). During January 2016, the Flint River experienced a large flood pulse, which transported debris with egg masses or floating vegetation mats downstream to areas where *P. maculata* was previously absent. We have observed adult snails and egg masses on floating vegetation mats or snags moving with wind-driven and hydrologic currents during the course of surveys and other outings on Lake Seminole

(pers. obs.). Adult *Pomacea* activity at the water surface has been documented in *Pomacea* spp., associated with lung respiration and foraging (Saveanu and Martín, 2015). We suspect that the spring 2016 flow pulses displaced *P. maculata* adults and egg masses, contributing to the downstream increase in *P. maculata* egg mass locations during the 2016 annual survey (Figs. 2 and 3A) in the lower Flint River and Chattahoochee River arms of the lake. This is consistent with other reports of the dispersal of non-native species in reservoirs (Johnson et al., 2008).

In the face of continued *P. maculata* dispersal, physical chemistry correlations reveal potential limiting characteristics within the lower ACF basin. Although the SLWMA ponds lie near the front of the invasion wave, neither adults nor egg masses have been observed. Our results indicate strong positive correlation between pH and specific conductivity and relationship varies spatially from the SLWMA ponds to the main body of Lake Seminole (Fig. 4B). In the lower Flint River basin, groundwater from the Upper Floridan aquifer, a carbonate-rich system, is known to influence surface waters by increasing pH and specific conductance (Allums et al., 2012; Rugel et al., 2016). In the lower Flint, specific conductivity is also strongly correlated with calcium concentration, which is essential for shell growth in gastropods (Brodersen and Madsen, 2003; Glass and Darby, 2009; Spyra and Strzelec, 2014). The absence of *Pomacea* spp. in the SLWMA ponds, whether due to a lack of hydrologic connection to Lake Seminole or water chemistry limitation, is presently unknown. Evidence from Florida suggests that pH is a strong driver of *P. maculata* presence and survival, though the values from Lake Seminole are greater than wetlands in Central Florida (Pierre et al., 2017). However, evidence suggests that calcium concentrations may not be a deterrent to the survival and growth of juveniles in SLWMA (Glass and Darby, 2009). Additionally, SLWMA ponds receive recreational boat and angler traffic, and we document *P. maculata* egg masses on boats in Lake Seminole. Boat traffic may act as a future introduction vector between Lake Seminole and SLWMA. Boats and anglers were important non-native species vectors in the Great Lake region, particularly from large water bodies (like Lake Seminole) to smaller water bodies (like SLWMA ponds) and warranted consideration in management and conservation efforts (Drake and Mandrak, 2014).

Each species used three of the five dominant shoreline classes for egg mass deposition. Emergent vegetation was the most available shoreline class across Lake Seminole, and used by both *P. maculata* and *P. paludosa*. Much of the lake remains undeveloped, emergent vegetation was present along much of the shoreline, as well as around the many islands found throughout the lake. Burks et al. (2010) present evidence that *P. maculata* prefer non-native emergent macrophytes compared to native species, though additional studies of the emergent communities in Lake Seminole are needed to determine oviposition preferences (Perez et al., 2017). Invasive water hyacinth (*Eichhornia crassipes* Solms-Laubach), a floating macrophyte, is present throughout much of the lake and egg masses were frequently deposited on its leaves. Water hyacinth forms floating mats that abut the emergent vegetation shoreline, but the mats can be displaced during high flow events, as described above, acting as vectors of species dispersal (Villamagna and Murphy, 2010) and possible evidence for an invasional meltdown given the abundance and influence of non-native species (Simberloff and Von Holle, 1999; Braga et al. 2017). Water hyacinth co-exists with *P. maculata* in their native range and egg masses are common on floating leaves, suggesting that in Lake Seminole, *P. maculata* may select hyacinth to deposit egg masses based on evolutionary familiarity (Marçal & Callil 2008). Although limited in extent, artificial shoreline, particularly seawalls, hosted large numbers of egg masses for both species, though the total number of egg masses was fewer than emergent vegetation due to its greater coverage of emergent vegetation across Lake Seminole. Man-made conduits and construction were important in the dispersal and growth of *P. maculata* in Central Florida as well, providing evidence that past and future dispersal of this and other species may be aided by human alterations (Johnson et al., 2008; Pierre et al., 2017). Cypress tree surfaces occurred at a large number of locations, although overall counts were fewer than both emergent vegetation and man-made areas. Water-level change, according to flood or drought conditions, can alter the accessibility of emergent surfaces may change with water level (Darby et al., 2002, 2008). Potentially confounding these results is the detectability of egg masses at each of the shoreline classes. Egg masses on seawalls are much easier to detect and count, whereas in an emergent vegetation stand, egg

masses may be out of view of the observers. This suggests that our results underestimate the total number of egg masses in Lake Seminole, particularly as we surveyed a fraction of the total lake shoreline. However, our extensive and relatively rapid survey methodology allows us to explore larger scale spatial patterns of apple snail distribution given the logistical constraints.

Egg mass abundance, particularly in *P. maculata*, showed strong seasonal variation, likely as a function of water temperature (Fig. 5, inset). Low temperatures (< 15 °C) are potentially harmful to *P. maculata* (Yoshida et al., 2014; Matsukura et al., 2016). At lake temperatures below 15 °C (January–March), we expected no egg mass production from either species. However, egg masses were observed during all months surveyed, including at temperatures < 15 °C. Current climate models for the region project warmer winters, reducing the days in which Lake Seminole water temperatures are < 15 °C (Hopkinson et al., 2013). Previously, water bodies across southern Georgia were thought to be near the northern modeled limit for non-native *P. maculata* based on minimum water temperature (Byers et al., 2013). Yet, our observations during 2016, as well as *P. maculata* documented farther north in the basin show not only persistence but potentially even continued reproduction during winter months. Continued presence at temperatures lower than the expected range for *P. maculata* suggests acclimatization and adaptation, which was similarly documented during a *P. maculata* invasion in Japan (Yoshida et al., 2014; Matsukura et al., 2016). Mean annual minimum temperature departure from the long-term winter mean in both 2015 and 2016 trended toward warmer conditions, and was associated with greater *P. maculata* egg mass abundance during the subsequent summers' survey. In contrast, we noted a reduced number of egg masses in July 2014 following winter where the mean temperature across Lake Seminole was 3.9 °C cooler than in the winter of 2012–2013. Our observed seasonal egg mass production generally followed expectations, being greatest in during the summer (June) and abundance remaining high from May through August, as has been documented throughout North America (e.g., Barnes et al., 2008), though peak production can vary in other invaded regions (Burlakova et al., 2010). Our results suggest that summer egg mass surveys are a good indicator of peak egg mass production and

would be appropriate for assessment and management purposes. This is true for *P. paludosa*, where peak egg mass abundance was observed in July. *Pomacea paludosa* egg mass production has been reported from March to October (Hanning, 1979). In Lake Seminole, we documented egg masses beginning in May and persisting through September. There may have been an effect of site selection in our monthly surveys compared to the frequency we observe *P. paludosa* during annual surveys. In the *P. paludosa*-only monthly survey locations, we unexpectedly began observing *P. maculata*, which may have represented the beginning of shifting dominance, thus reducing *P. paludosa* observation (Posch et al., 2013). However, this represents a site-specific transition in species dominance and further supports our hypothesis of the eventual whole-lake dominance by *P. maculata*.

We believe that the on-going invasion of *P. maculata* needs to be considered in future studies in Lake Seminole, and other freshwater habitats in the southeastern US that represent potential habitat. Conditions across Lake Seminole suggest continued *P. maculata* dispersal and population growth. Potential limitations include (1) spatial variation in pH, specific conductivity, and calcium in adjacent water bodies (Pierre et al., 2017), and (2) increasingly infrequent climate patterns that reduce water temperatures < 15 °C for extended periods. However, *P. maculata* populations in Lake Seminole have persisted during colder than normal winters (e.g., 2014) and produced egg masses during warmer winters (e.g., 2016). Climate projections predict fewer cold winters and warming temperatures, potentially allowing *P. maculata* reproduction throughout the year. Year-round egg mass production and dispersal of *P. maculata* from 2013 to 2016 suggest rapid population expansion. The role of shell-crushing predators (e.g., fishes, alligators, turtles, and crayfish) may eventually limit the abundance of *P. maculata*, particularly smaller hatchling and juvenile snails (Valentine-Darby et al., 2015; Dorn and Hafsadi, 2016). Further, limpkins (*Aramus guarauna* L.) have been recently observed in Lake Seminole, and as important predators of apple snails, their presence in the Flint River arm of the lake is likely tied to the abundance of *P. maculata* in that same lake area (pers. obs.). However, estimating predation rates of *P. maculata* remain challenging due to difficulties in detecting juveniles and adults in the field.

The Lake Seminole ecosystem function is strongly influenced by invasive species (Waters et al., 2014; Patrick et al., 2016), which is consistent with other studies of successful species introductions in reservoir habitats (Johnson et al., 2008; Karatayev et al., 2009, 2017) and may serve as a case study of the invasional meltdown hypothesis on ecosystem function (Braga et al., 2017). The role of submerged aquatic vegetation (SAV), such as non-native *Hydrilla verticillata* (L.f.), in nutrient transformations and cycling in Lake Seminole and the ACF basin has been well documented (Waters et al., 2014; Shivers et al., 2016). Rapid expansion and population growth of the herbivorous *P. maculata* may reduce SAV coverage (Monette et al., 2016) and thus limit nutrient sequestering in SAV biomass, increasing potential for lake eutrophication (Sharfstein and Steinman, 2001; Boland et al., 2008; Baker et al., 2010). A substantial loss of SAV coverage due to *P. maculata* grazing in Lake Seminole potentially reduces some the functionality of the lake within the larger ACF basin, where achieving adequate water quantity and maintaining water quality has been a source of discord between Georgia and Florida for the last two decades (Frick et al., 1996; Eubanks & Morgan, 2001). Reductions in SAV coverage and indirect effects of *P. maculata* grazing on water quality in Lake Seminole could induce ecosystem-level changes with unanticipated consequences. Future studies will examine these interactions and determine the direct top-down food web and reproductive effects of *P. maculata* and macrophytes (e.g., *Hydrilla, E. crassipes*) and indirect effects on water quality. Our results represent fundamental information regarding the invasion and reduction of *Pomacea* spp. in a specific system and therefore, specific to this system. However, the trends of water chemistry, seasonal egg mass production, and displacement of native species serve as a case study for potential concerns in other areas at risk for invasion.

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