



# Life history responses of two co-occurring congeneric Apple Snails (*Pomacea maculata* and *P. paludosa*) to variation in water depth and metaphyton total phosphorus

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**Abstract** Hydrological and trophic gradients influence primary consumer populations in aquatic ecosystems, but their impacts remain unresolved for some species. We quantified the effects of water depth variation on reproduction and the effects of metaphyton (food) total phosphorus (TP) on juvenile growth and survival of two species of apple snails. The two species (native *Pomacea paludosa* and non-native *P. maculata*) are the exclusive prey of the federally endangered Snail Kite (*Rostrhamus sociabilis*) in Florida, USA. Using observations of reproduction

in an ecotone habitat across four wetlands over three years, we statistically modeled seasonal reproductive dynamics. We found that *P. paludosa* reproduction peaked at depths of 30 cm during periods of cool temperatures (20°C; Feb–Apr), and *P. maculata* reproduction peaked at deeper depths (52 cm) and longer photoperiods (Jun–Jul). From in situ cage experiments in the same wetlands, we found that juvenile growth of both species increased with TP (129–403  $\mu\text{g g}^{-1}$ ), but non-native *P. maculata* responded more strongly than native *P. paludosa*. Survival of both species was high (> 97%) across all TP levels. In combination, the results were consistent with anecdotal distributional patterns across hydrologic and nutrient gradients and suggest a wider range of tolerance for the non-native *P. maculata*.

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## Introduction

Spatial and temporal hydrologic and nutrient gradients influence populations of primary consumers in aquatic ecosystems (Carmignani & Roy, 2017; Conde-Porcuna et al., 2002; Elser et al., 2001). Populations of primary consumers have been shown to be regulated by water discharge (Lane et al., 2021; Conde-Porcuna et al., 2002), drought (Dorn & Cook, 2015), and flooding (Grosholz & Gallo, 2006).

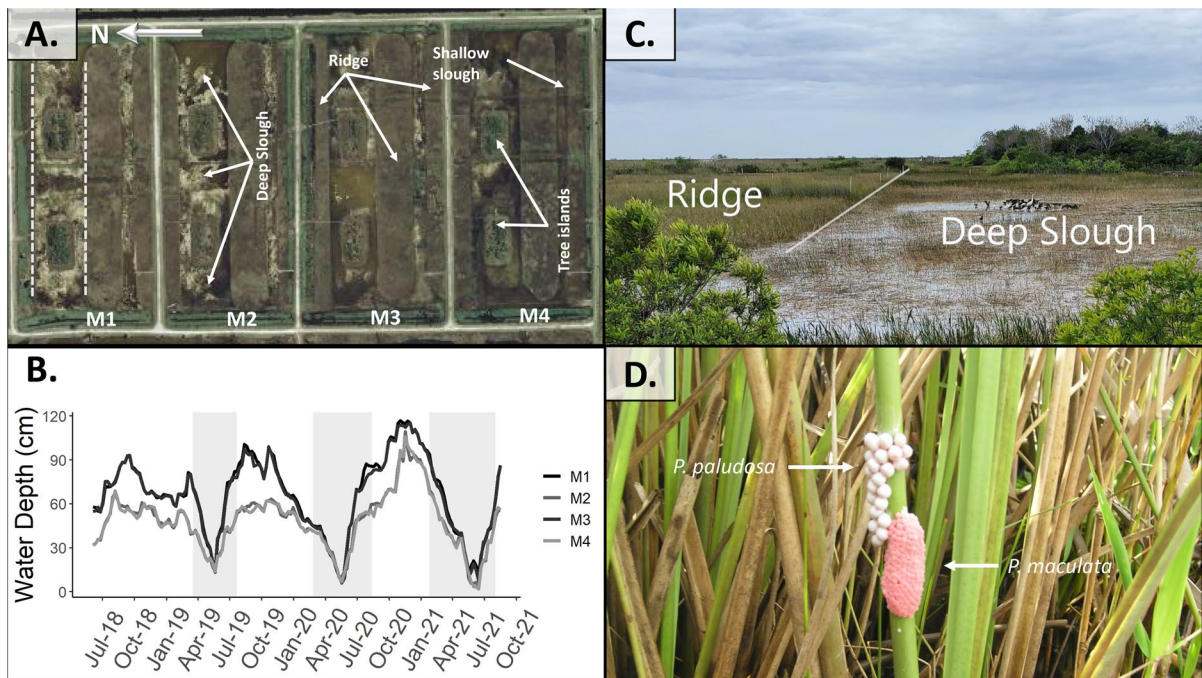
Additionally, availability of nutrients influences populations of primary consumers in lotic (Elser et al., 2005) and lentic habitats (Elser et al., 2001). Yet primary consumers differ in their sensitivity to these gradients (Schulz & Sterner, 1999; Conde-Porcuna et al., 2002) including taxa within the same genus (Seiden-dorf et al., 2010). Species-specific responses to these gradients complicate the prediction of changes in populations to stressors (e.g., climate change, hydro-logic alterations, invasions) and ecosystem management or restoration.

Hydrologic and nutrient gradients can regulate recruitment from juvenile to adult stages (Jeyasingh & Weider, 2005; Lane et al., 2021) which is a key demographic rate that determines population size of many primary consumers (Kellogg & Dorn, 2012; Lane et al., 2021; Strayer & Malcom, 2012), including freshwater molluscs in shallow-aquatic systems (Lane et al., 2021). For example, population growth rates of two species of *Epioblasma* freshwater mussels in Tennessee streams were uncorrelated with water discharge when analyzing adults alone, but when juveniles (i.e., recruits) were included in the analysis a negative correlation with water discharge was revealed (Lane et al., 2021). Recruitment of freshwater molluscs from juvenile to adults is controlled by reproductive rates (i.e., juveniles entering the recruitment period) as well as juvenile growth and survival (i.e., recruits that survive and grow to adulthood). Reproduction, juvenile survival, and juvenile growth have individually been shown to be influenced by hydrologic and nutrient gradients (Jeyasingh & Weider, 2005). Detailed quantitative understanding of how vital rates are regulated by hydrologic and nutrient variation will aid the construction of species-specific population models for predicting population responses to stressors or hydro-management. Nevertheless, the specific effects of hydrologic variation on vital rates are poorly resolved for many macroinvertebrates, including species of special concern and invasive species (Batzler, 2013).

Shallow aquatic systems (i.e., wetlands, canals, and lake littoral zones) in southern Florida exhibit substantial spatial and temporal water depth and nutrient gradients that can influence populations of primary consumers. Water depths are relatively deep and nutrient concentrations are relatively high in the canals and lakes of southern and central Florida. The wetlands of the Central Everglades are shallower

and typically more oligotrophic (James et al., 2009; Gaiser et al., 2011). Phosphorus concentrations in metaphyton and microbial mats reflect nutrient gradients in Everglades waterways (locally called "periphyton"; Gaiser et al., 2011) that range from 40 to 500  $\mu\text{g g}^{-1}$  but reach up to 1000  $\mu\text{g g}^{-1}$  near canals and agricultural fields. Water levels vary seasonally with rainfall producing intra-annual water depth fluctuations of  $\geq 60$  cm with  $\sim 75\%$  of rain falling between June and October (Gaiser et al., 2012). Slight elevational differences create spatially variable hydroperiods with characteristic deep slough, shallow slough (or wet prairie), and ridge habitat (Zweig & Kitchens, 2008). Prior to the end of the nineteenth century, water levels in the Everglades were deeper (McVoy et al., 2011), and water flowed slowly (e.g., 2–3 cm/s) south in a wide shallow "river" for approximately 140 km from Lake Okeechobee to the Gulf of Mexico (i.e., sheet flow; Sklar et al., 2005) in the Everglades (called the "pre-drainage" Everglades). Starting at the end of the nineteenth century, compartmentalization and drainage of the Everglades altered the hydrologic conditions which ceased sheet flow, increased water depths in some areas, and decreased depths in other areas. Ongoing hydro-restoration of the Everglades ecosystem aims to recover historical hydro-patterns to improve production of prey (i.e., trophic support) for historical Everglades predators. The effects of water depth, water quality, and water level variation are key hydrologic variables affecting production of small aquatic animals including gastropods (Trexler et al., 2005; King & Richardson, 2007).

In southern Florida, there are two resident and widely established apple snail species of the genus *Pomacea* (Rawlings et al., 2007): native *Pomacea paludosa* (Say, 1829) and non-native *Pomacea maculata* Perry, 1810. Apple snails of the genus *Pomacea* (Family: Ampullaridae) are large, globose gastropods, with both lungs and gills, making them adaptable to low dissolved oxygen environments (Hayes et al., 2015). *Pomacea* lay conspicuous calcareous egg clutches  $\sim 20$  cm above the water on plants and other emergent structure (i.e., debris; Fig. 1; Hayes et al., 2015). *Pomacea* increase in mass by up to four orders of magnitude from juvenile to adults (taking 1.5–3 months; Hanning, 1979; Drumheller et al., 2022). *Pomacea paludosa* are dioecious and lay light-pink to white egg clutches (20–60 eggs; Fig. 1; Rawlings et al., 2007) with peak reproduction typically



**Fig. 1** **A** Map of the four experimental wetlands in the Loxahatchee Impound Landscape Assessment (LILA). The three major habitat features are identified in different wetlands, but all wetlands contained all habitat types. The dashed lines (M1) illustrate the position of the ridge-deep slough ecotone where the egg clutch surveys were conducted in all wetlands. **B** A

hydrograph depicting the depths of each experimental wetland. Depths are reported as cm above the deep slough soil surface, and gray shaded rectangles indicate the periods when surveys were conducted. **C** Picture of the abrupt ecotone in M2; the white line indicates the location of our transects. **D** Picture of *P. paludosa* and *P. maculata* egg clutches

occurring from Feb to May (Hanning, 1979; Darby et al., 2008). Juvenile *P. paludosa* hatch at 3–4 mm shell length (hereafter, SL), live for 1–1.5 years, and grow to 30–45 mm SL (Hanning, 1979). *Pomacea maculata* are native to floodplains of southern Brazil and Argentina, but have invaded southeast Asia, Japan, Europe, and parts of North America (Hayes et al., 2015). *Pomacea maculata* were first recorded in Florida wetlands in 2001 and have since established populations throughout Florida (Rawlings et al., 2007; Byers et al., 2013). Adult *P. maculata* produce larger clutches of smaller pink eggs (300–3500; Kyle et al., 2013, Fig. 1) and grow much larger (up to 80 mm SL) than *P. paludosa*. While *P. paludosa* and *P. maculata* both eat metaphyton and macrophytes, *P. maculata* are voracious macrophyte herbivores (Morrison & Hay, 2011).

Understanding apple snail recruitment is considered important for conservation because *P. paludosa* and *P. maculata* are readily consumed by the federally endangered Florida Snail Kite

[*Rostrhamus sociabilis* (Vieillot, 1817); ~7–8 snails per day Sykes, 1987; Cattau et al., 2014], and Snail Kite breeding is limited by apple snail densities (Cattau et al., 2014). Snail Kite populations in the Everglades declined prior to the invasion of *P. maculata* (i.e., indirect indication of *P. paludosa* densities, Darby et al., 2006; Cattau et al., 2014, 2016) which also suggest that *P. paludosa* populations declined in the Everglades around 2001–2003. After the invasion of *P. maculata* in 2004, Snail Kite population have increased particularly in regions outside of the central Everglades where *P. maculata* have established (Cattau et al., 2014, 2016). However, since the early 2000s, typical densities of both species remain too low ( $<0.4 \text{ m}^{-2}$ ) to support Snail Kite reproduction in the central Everglades (Gutierrez et al., 2019). The factors limiting population densities of *P. paludosa* and *P. maculata* are unclear in southern Florida. A size-structured population model was recently created to project effects of management and restoration scenarios

on *P. paludosa* population sizes in the Everglades (Darby et al., 2015). Juvenile snail growth and adult reproduction were both important for this model (Darby et al., 2015).

Depth-mediated reproduction has been one suggestion for the limited population success of *P. paludosa* (Darby et al., 2008), and current population projection models for native apple snails include depth-dependent egg laying dynamics for *P. paludosa* (Darby et al., 2015) with peak reproduction occurring when water depths reach 50 cm. The hypothesized mechanism is that living in deeper water is physiologically costly to adult snails leading to lower reproduction (i.e., females require more energy to surface and breath in deeper water; Darby et al., 2015) such that relatively shallow conditions are necessary for supporting higher populations of *P. paludosa* through physiological limitations to reproduction. The depth-dependent reproduction pattern was based on a few observations and requires additional quantification (Darby et al., 2015) in part because depth and seasons are generally confounded in the subtropical wetlands of Florida with distinct rainy seasons. Furthermore, the relationship of *P. maculata* reproduction with water depth has not been examined, and they are common in deeper habitats including lake littoral zones and canal margins (Gutierre et al., 2019).

Juvenile growth and survival could also be limiting apple snail populations. Experimental studies have shown that juvenile apple snail growth rates vary with temperature and pH (Yoshida et al., 2014; Pierre et al., 2017), salinity (Qin et al., 2020), calcium (Glass & Darby, 2009), and copper exposure (Rogevich et al., 2009). Ruehl & Trexler, (2011) hypothesized that gastropods in the Everglades, including apple snails, should be growth- and nutrient-limited in the naturally oligotrophic Everglades. Wetlands in Florida are generally phosphorus limited, and phosphorus availability in soils is spatially variable (Osborn et al., 2014) with a gradient reflected in the metaphyton resources for snails (Gaiser et al., 2005). Two recent studies have documented increased juvenile *Pomacea* growth with increases in phosphorus availability (Hansen et al., 2022; Davidson & Dorn, 2018). One study showed that *P. maculata* growth responded stronger to a categorical influence of lower and higher phosphorus levels in a controlled experiment than *P. paludosa* (i.e., mesocosms; Davidson & Dorn, 2018). Understanding the strength of the response of either

species across a larger phosphorus gradient in a more natural system requires further evaluation.

In this study, we used observational data to quantify the effects of water level on adult snail reproduction and experimental data to quantify the effects of metaphyton phosphorus concentration on juvenile growth and survival. We used three years of repeated observations of egg cluster dynamics (egg laying) of *Pomacea* species in large (8 ha) replicated wetlands to determine the effects of water depth on reproduction. We also measured survival and growth of juvenile snails across a modest range of natural phosphorus variation ( $129\text{--}403\text{ }\mu\text{g g}^{-1}$ ) from field cages embedded in the same wetlands. Water levels in sloughs varied seasonally and across wetlands from 10 to 85 cm. Because recent observations in Florida suggest that *P. maculata* are more closely associated with deeper water and higher nutrient concentrations around canals (Dorn & Hafsadi, 2016; Davidson & Dorn, 2018), we hypothesized that *P. maculata* reproduction would be less restricted by deeper water than *P. paludosa* and that *P. maculata* juveniles would benefit more from higher metaphyton TP than *P. paludosa* (Davidson & Dorn, 2018).

## Methods

### Study system

Our fieldwork was conducted at the Arthur R. Marshall Loxahatchee Wildlife Refuge in Boynton Beach, FL ( $26.4993^{\circ}\text{N}$ ,  $80.2123^{\circ}\text{W}$ ) in the Loxahatchee Impoundment Landscape Assessment (hereafter LILA). LILA consists of four 8-ha landscape scale experimental wetlands (referred to as M1, M2, M3, and M4) that mimic the Everglades ridge and slough landscape (Fig. 1A). In LILA, ridges are 40–45 cm higher in elevation than deep sloughs but only 25–30 cm higher than the shallow sloughs. The water conditions at LILA are oligotrophic and hard with typical total phosphorus (TP) levels between 1.96 and  $13.25\text{ }\mu\text{g L}^{-1}$  and typical  $\text{Ca}^{2+}$  concentrations between 36.98 and  $592.87\text{ mg L}^{-1}$  (Table S1). Water depths fluctuate with rainfall with the deepest water occurring near the end of the wet season (Oct–Nov) and shallowest water occurring near the end of the dry season (May–June; Fig. 1B). Seasonal depth patterns can be constrained using gated culverts, and the



culverts were used to manipulate the hydro-patterns as part of a larger study of wet season water depths. During our study, wetlands (M1, M3) were managed for an unconstrained hydro-pattern with deeper wet season depths than the other wetlands which were managed for a constrained hydro-pattern (M2, M4; Fig. 1B). All wetlands reached the same low depth point at the same time in May (Fig. 1B). The deep slough habitat always maintained some surface water during this study. This hydro-pattern experiment produced variation in seasonal water depths. At the time of the study, three of the wetlands supported co-occurring populations of *P. maculata* and *P. paludosa* and one only had *P. maculata* (Drumheller et al., 2022).

### Egg Clutch Surveys

*Pomacea paludosa* and *P. maculata* egg clutches were surveyed 26 times in each wetland from 2019 to 2021 ( $N_{\text{surveys}} = 26 \text{ wetland}^{-1}$ ;  $N_{\text{surveys}} = 104$  total; Table S4). Each year we increased the number of surveys that we conducted to make sure we included data from the initiation of the reproductive season which resulted in the survey period beginning progressively earlier (Mar, Feb, Jan) but ending at similar times (late July, early Aug; Fig. 1B, Table S4). To standardize the time between surveys, surveys were conducted every three weeks during the survey period. We chose the three week interval because reproductive female *P. paludosa* lay  $\leq 1$  egg clutch per week and egg clutches typically hatch within 16–22 days (Hanning, 1979), therefore the three weeks between surveys would avoid recounting egg clutches. To confirm that we did not recount egg clutches, vegetation with egg clutches were marked on consecutive surveys in Feb–March of 2021 (the cooler months). All marked clutches hatched prior to the subsequent survey. Each survey was conducted by counting unhatched egg clutches within 2 m of either side of two transects (transect length  $658.5 \pm 7.3$  m; total surveyed area:  $2634.0 \pm 29.3 \text{ m}^2$ ; average  $\pm$  SD). Unhatched egg clutches were easily distinguished from hatched egg clutches because hatched egg clutches retain shell fragments on the emergent vegetation. Transects were located at the abrupt ecotone boundary of the ridge and deep slough habitats ( $N_{\text{transects}} = 2 \text{ wetland}^{-1}$  or 8 total; Fig. 1A&C) and were either walked or kayaked depending on water depths. At the boundary, water

depth changed by  $\sim 40$  cm and the vegetation switched from spikerushes (*Eleocharis* spp.) and lilies (*Nymphaea* sp.) in the sloughs to grasses (*Panicum* sp.), sawgrass (*Cladium jamaicense* C. B. Clarke) and *Sagittaria lancifolia* L. in the ridges (Fig. 1C). The ridges in the Everglades and LILA experimental wetlands have similar elevational relations to the sloughs, but in the Everglades they are more thoroughly dominated by dense sawgrass. We chose this ecotone because it is considered high-quality habitat for *Pomacea* reproduction (Wight et al., 2017). The *Sagittaria lancifolia* and *Cladium jamaicense* stems were the most common substrates for egg clutches of both species.

Although we did not independently determine the detection probability of egg clutches on transects, we believe we captured most of the reproduction because the egg clutches are highly conspicuous (Fig. 1D), and we re-identified all the marks (red duct tape) from surveys in Feb–March of 2021. In addition, the surveys were standardized (i.e., same distance and walked at similar speeds), such that the detection probability likely varied little between surveys on the same transect. Except in cases of occasional thick patches of sawgrass, we could easily see through vegetation to observe the conspicuous egg clutches. To account for occasional thick patches of sawgrass on the transects, we stopped and looked thoroughly for egg clutches in the patches of sawgrass. Finally, during the surveys with lower water levels ( $< 40$ – $45$  cm, dry ridges) all clusters were laid abruptly at the slough side of the ecotone.

Egg clutch counts in a wetland (i.e., sum of both transects for each date) were used as the response for modeling. Counts were statistically modeled using environmental variables and estimates of adult snail densities (Table 1; Table S2; Table S3). Hydrologic and air temperature data were obtained from the South Florida Water Management District's environmental database DBHYDRO ([www.sfwmd.gov/science-data/dbhydro](http://www.sfwmd.gov/science-data/dbhydro)) which has air and depth transponders throughout southern Florida that record data every 15 min. Each wetland in LILA has a depth transponder but not an air transponder. Depth data were taken from individual wetlands, but air temperature data was taken from the transponder in West Palm Beach (transponder coordinates:  $26.6548^\circ\text{N}$ ,  $80.0669^\circ\text{W}$ ). Air temperature was used as a surrogate because water temperature transponders were not

**Table 1** List of variables used in modeling *Pomacea paludosa* and *P. maculata* reproduction (egg laying on the ecotone), their descriptions, and the brief rationale for including them

Name	Description	Rationale
Depth	Average depth (cm) from the previous week in the deep slough	Low water depths are associated with reductions in <i>Pomacea</i> activity or even aestivation
Depth <sup>2</sup>	Quadratic Depth Effect	<i>Pomacea</i> may exhibit a unimodal reproductive response such that intermediate depths are favored (always added with Depth)
SD Depth	SD deviation in depth (cm) from previous week	Larger weekly variation indicates larger swings in water depth this may increase the likelihood of egg submersion
$\Delta$ Depth	Change in depth (cm) from three weeks prior	Like SD depth, but indicates directionality—negative decreasing depths and positive increasing depths
Season	Categorical season wet or dry based on yearly maxima and minima depths	Season is a composite variable encompassing water level recession or ascension, temperature, and Photoperiod differences
Temp	Average Air Temperature (°C) from previous week	Air temperature has been correlated with <i>Pomacea</i> reproduction
Photoperiod	Photoperiod (hours)	Photoperiod has been suggested as trigger for seasonal reproduction of <i>Pomacea</i>
Adult Density	Adult Density (Snails $\text{m}^{-2}$ ) from throw trap measurements	A measure of adult population size which should influence the observed number of egg clutches

included in LILA. After obtaining the data, average deep slough depth (hereafter Depth), standard deviation in deep slough depth (hereafter SD Depth), and average temperature (hereafter Temp) were calculated for the week prior to each survey. Because there were 3 weeks between each survey, we calculated 3-week net recessions (negative values) or ascension rates (positive values) to test how depth changes affect egg clutch production (hereafter  $\Delta$  Depth). We included season categorically by finding the yearly maximum and minimum deep slough depths in each wetland. We defined the “dry season” as the period when depths were falling (from max to min), and we defined the “wet season” as the period when depths were rising (from min to max; hereafter Season). Photoperiod was calculated with the “daylength” function in the geosphere package in R v4.0.5 using LILA’s latitude (Hijmans et al., 2019; R Core Team, 2019).

In addition to the environmental variables, the egg counts should be a function of the density of breeding *Pomacea*. The snail densities were quantified seven times from 2018 to 2021 using 1-m<sup>2</sup> throw traps (four wet seasons: 2018–2021 & three dry seasons: 2019–2021). Each season, fourteen traps were randomly deployed across the shallow and deep slough habitats. All animals were cleared from throw traps

using the protocol described in Dorn et al., (2005) and Jordan et al., (1997). Although clearing efficiency has not been measured for apple snails specifically using these methods, we expect that clearing efficiency is high for apple snails because (1) all throw traps were cleared with a combination of bar seines sweeps and dip net sweeps, (2) seine and sweeps were repeated if any animal (including apple snails) was found, and (3) clearing efficiency of other animals (i.e., crayfish and fish) was > 80%. In addition, similar clearing efficiencies (~80%) have been reported for apple snails sampled in throw traps in similar habitats using dip nets alone (Darby et al., 1999). We calculated densities across the “water year” by using the previous calendar year’s wet season and current year’s dry season (e.g., wet season 2018 and dry season 2019 for the water year 2019) as an estimate of the reproducing population (hereafter Adult Density). In two wetland-year combinations (M1-2019, M1-2020), we did not detect any adult *P. paludosa* in our throw traps (Table S2), but reproductive adults were still present because egg clutches were present in low numbers (Table S4). We substituted these zeros with 0.01 snails  $\cdot$  m<sup>-2</sup> which was below our detection limit (low limit = 1 snail/28 traps; 0.035 snails  $\cdot$  m<sup>-2</sup>).

To model reproductive dynamics for each species, we used mixed effect generalized linear models

(GLMM) assuming a negative binomial distribution (i.e., negative binomial regression). GLMMs use maximum likelihood estimation to find statistically meaningful relationships between the response and predictor variables (variables can include fixed and random effects). We chose to use a negative binomial distribution because there was overdispersion (i.e.,  $sd > mean$ ) in the response variable for both species (i.e., egg clutch counts), and this assumption was further corroborated by comparing the AICc scores between models assuming a negative binomial distribution and models assuming a poisson distribution (Bolker et al., 2009; Stoklosa et al., 2022). All negative binomial models had lower AICc values than the poisson models. The fixed effects included in the model selection were Depth, SD Depth,  $\Delta$  Depth, Season, Temp, Adult Density, and Photoperiod (Table 1). We also included a quadratic effect of Depth (hereafter Depth<sup>2</sup>) along with Depth to test for a unimodal reproductive response. Wetland identity (hereafter Wetland) was included as a random effect to account for any unmeasured differences in reproductive habitat quality. Prior to model construction, all fixed effects were z-transformed to standardize the units to the standard deviations from the mean. Pearson's correlation tests were conducted for each combination of fixed effects. Temp, Photoperiod,  $\Delta$  Depth, and Season were highly correlated ( $|r| > 0.5$ ) with each other and described different environmental facets of the changing seasons. We did not include these variables in the same model partly to avoid multicollinearity, but also to test which aspects of season might better explain seasonal reproductive patterns of the two species. We examined models that included combinations of fixed effects and two-way interactions but excluded higher order interactions. The resulting 35 models (Table S5) were compared using AICc scores, the structure of all models with  $\Delta AICc < 4$  were examined. The most supported model (lowest AICc) was selected for variable interpretation and further evaluation, but we noted that the hydrologic variables included in the other supported models were the same and had almost identical interpretations. We also performed a post hoc Principal Component Analysis (PCA) on Temp, Photoperiod, and  $\Delta$  Depth to see if including a single PC axis would improve our ability to model reproductive dynamics. The models including the PC axis performed similarly to the categorical "Season" variable

and were always greater than 2 AICc units away from the best model.

The models were fitted using the lmer4 package using the "lmer.nb" function (Bates et al., 2015). Pseudo  $R^2$ s were obtained for the best model using the delta method in the "r.squaredGMM" function in the MuMIn package which reports the Pseudo  $R^2$  for fixed effects (hereafter,  $R^2_m$ ) and the Pseudo  $R^2$  for the entire model (hereafter,  $R^2_c$ ; Barton, 2020). Predicted values and 95% prediction intervals were obtained using leave-one-out cross validation and the "predict" function. 95% prediction intervals were calculated via 100-simulation bootstrapping using the "bootMer" function in the lmer4 package (Bates et al., 2015). We used Randomized Quantile Residuals (RQR) to assess the assumption of negative binomial regression through residual plots (e.g., Q-Q plots; Feng et al., 2020). RQRs are the proportion of predicted values above the actual value after obtaining a distribution of predicted values for an observation through bootstrapping. All analyses were conducted in R v4.0.5 (R Core Team, 2019).

To determine if the ecotone transects captured most of the reproduction when other higher elevation habitats were flooded, thirteen additional surveys of *P. paludosa* egg clutches were performed in other higher elevation habitats (ridge and shallower slough) when the deep sloughs were relatively deep ( $> 50$  cm; Table 4) and adjacent habitats were flooded. Six surveys were performed in the dry season and seven surveys were performed in the wet season (Table 4). Transects were walked along the ridge-shallow slough boundary in July 2019 and in March 2021, and most of the central ridge ( $\sim 1.8$  ha) was systematically searched with 2–4 observers in August 2020 and in February 2021 (Fig. 1). To make equivalent contrasts, we calculated densities of egg clutches for the ridge, shallow slough, and deep slough. We compared the densities on the ecotone (where we modeled reproduction) to the densities found in other locations.

#### *Juvenile growth and survival from in situ cages*

Using caged enclosures, we performed in situ juvenile growth experiments in July of 2019 and 2020. Two weeks prior to the experiment, 1-m<sup>2</sup> cages with 1-mm mesh a closed bottom and an open top were placed in the sloughs to accumulate algae on surfaces. We added 1000 mL of metaphyton mat (i.e., mostly a

complex of detached metaphyton, *Chara* sp., with a little *Utricularia* spp.) into each cage. The metaphyton was collected from the surrounding sloughs and examined to remove snail predators (i.e., crayfish or hemipterans) and other snails. *Pomacea* egg clutches were collected, still attached to stems, from ditches around LILA and brought back to the greenhouse in the Florida Atlantic University campus in Davie, FL where they were hatched and reared. Egg clutches were hatched in containers filled with approximately 5 cm of water with established algal growth. Juvenile *P. paludosa* used in experiments were 1–20 days old. *Pomacea maculata* hatched at smaller sizes and were reared for longer (20–40 d old) to become size-matched with juvenile *P. paludosa*. There were no differences in initial SL between *P. paludosa* and *P. maculata* across treatment cages (t-tests of group means;  $P > 0.45$ ).

The original purpose of the experiments was to test for competition between *P. maculata* and *P. paludosa* (Drumheller et al., 2022), but the cages also had substantial variation in metaphyton nutrient levels, both within and between years (Table 2). Some of the variation was produced by the setup methods (Drumheller et al., 2022) and some appeared to be caused by avian use of the top edges of the cages (i.e., egrets perching and defecating; personal observations). In this study, we reanalyzed the data to take advantage of the uncontrolled variation to test for effects of metaphyton TP on juvenile growth. In 2019, twelve cages were stocked at high densities (6 cages: 16 *P. paludosa*; 6 cages: 8 *P. paludosa* and 8 *P. maculata*), and six cages were stocked at a lower density (8 juvenile *P. paludosa*). There were no significant differences in growth of juvenile *P. paludosa* at different densities of conspecifics (16 snails cage<sup>-1</sup> vs 8 snails cage<sup>-1</sup>; Drumheller et al., 2022). In 2020, twenty cages were stocked at similar low densities (10 cages: 8 *P. paludosa*; 10 cages: 4 *P. maculata* and 4 *P. paludosa*). We chose these densities based on estimates of densities of snails just after hatching.

For our analysis, *P. paludosa* growth was only reported for cages with conspecific treatments (22 cages), but there were no conspecific treatments for *P. maculata*, so we used heterospecific cages for *P. maculata*. We assumed that *P. paludosa* had negligible effects on *P. maculata* growth because: 1) a laboratory experiment at very high densities ( $> 30 \text{ m}^{-2}$ ) found no evidence for effects of *P. paludosa* on *P.*

**Table 2** Environmental conditions in 1 m<sup>2</sup> mesh cages where juvenile apple snails were reared at the Loxahatchee Impoundment Landscape Assessment (LILA; wetland M2) in 2019 and 2020

Start date	Species	Temperature (°C)		Depth (cm)		TP (µg/g)		Initial size (mm)	
		Mean	Range	Mean	Range	Mean	Range	Mean	(SE)
July, 2019	<i>P. paludosa</i>	31.1	(29.1–32.4)	38	(34–43)	287	(238–403)	3.56	(0.17)
	<i>P. maculata</i>	31.1	(29.1–32.4)	38	(34–43)	297	(253–344)	3.61	(0.09)
July, 2020	<i>P. paludosa</i>	30.3	(22.2–33.3)	45	(40–50)	159	(129–184)	4.40	(0.10)
	<i>P. maculata</i>	30.3	(22.2–33.3)	45	(40–50)	162	(129–190)	4.60	(0.10)



*maculata* (Posch et al., 2013), and 2) *P. paludosa* density had no effect on conspecific growth (Drumheller et al., 2022) which suggests that *P. paludosa* are poor competitors at our experimental densities and field conditions. Furthermore, antagonistic interactions point toward *P. maculata* affecting *P. paludosa*, but the mechanism appears to be through chemical inhibition rather than competition (Drumheller et al., 2022; Conner et al., 2008).

Metaphyton TP, snail growth rates, and snail survival were measured for each cage. Dried metaphyton from each cage was finely ground then sent to the CACHE-NACF facility in the Freshwater Resources Division at Florida International University (Miami, FL) to quantify TP. The metaphyton TP in the experiment were within ranges of metaphyton TP in the Everglades (Gaiser et al., 2011) making the experimental conditions comparable to nutrient variation within the Everglades. Snails grew from a uniform starting shell length for five weeks (Table 2). At the end of the five weeks, we measured final shell lengths. To make our results comparable to other measures of growth used in other studies, we also calculated masses from length–weight regressions (*P. paludosa*:  $R^2=0.98$ ; *P. maculata*:  $R^2=0.97$ ; Davidson & Dorn, 2017; Drumheller et al., 2022). We used the following equations to calculate daily growth rates (mass and length separately) using proportional increases (i.e., standardized growth rate, hereafter SGR) and absolute changes in size (mm or mg):

$$SGR = \frac{\ln(S_f) - \ln(S_i)}{t} \quad (1)$$

$$Absolute\ Growth = \frac{S_f - S_i}{t} \quad (2)$$

where  $S_f$  is the final size (length or mass) of the snails in a cage,  $S_i$  is the initial size (length or mass) of the snails, and  $t$  is length of the experiment (35 days). We averaged growth in each cage and treated cages as independent observations for this analysis. Survival was measured in each cage as the proportion of snails alive at the end of the experiment.

We used a linear mixed effect model to compare juvenile *P. paludosa* and *P. maculata* growth responses to TP variation. These models were fitted using the fixed effects of TP and species, and the interaction between them. A significant interaction

indicated a different response to TP variation. We used experiment year as a random effect to isolate the effect of TP. Our analysis was performed using the “lmer” function in lme4 package (Bates et al., 2015), and linear model assumptions were assessed by visually inspecting the plots of residuals.

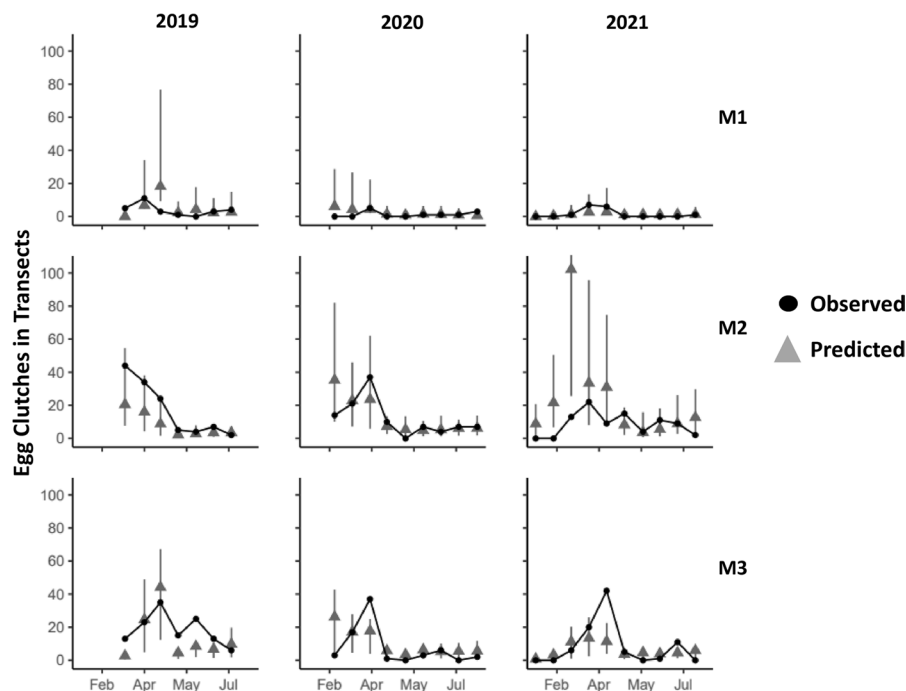
## Results

### Egg clutch survey

Egg clutch counts ranged from 0 to 145 through this study, and egg clutch counts of *P. maculata* were typically higher than those of *P. paludosa* (Fig. 2; Fig. 3; Table S4). *P. paludosa* was only found in three of the four wetlands and some wetlands had consistently higher counts of clutches each year. The majority of *P. paludosa* reproduction occurred between February and April (Fig. 2), and *P. maculata* reproduction typically increased in June–Aug (Fig. 3).

The top three models (cumulative weight=0.95) explaining variation in *P. paludosa* egg clutches all included a unimodal effect of Depth (Depth + Depth<sup>2</sup>), Adult Density, one of the three seasonal parameters (i.e., Season, Photoperiod, or Temp), and an interaction between the unimodal effect of Depth and the seasonal parameter (Table 3). The most supported model included Temperature as the seasonal parameter (Table 3). For the top model, the fixed effects (Adult Density, Depth, Depth<sup>2</sup>, and Temp) explained 60% of the variation in egg clutches, ( $R^2_m=0.60$ ), and the full model, including wetland as a random effect, explained 68% of the variation in egg clutches ( $R^2_c=0.68$ ; Fig. 2; Fig. S1). Holding Temp and Depth constant (averages), a one standard deviation increase in Adult Density (0.03 snails m<sup>-2</sup>) increased predicted egg clutches by 63.8%. Holding Adult Density constant (average), maximum predicted counts occurred at the temperature of 19.7 °C and at depths of 30 cm. Over half (~57.2%) of predicted egg clutches occurred at relatively cooler temperatures (20–23 °C; typically in Feb–Apr) and intermediate depths (16–52 cm; Fig. 4A) in the slough. The interaction indicated that as slough water depth increased with relatively cool temperatures (20 °C; typically in Feb–Apr), the predicted clutches increased until deep slough water depths reached 30 cm and then decreased with further increases in water depth

**Fig. 2** Plots depicting observed egg clutch counts across all years in each wetland for *P. paludosa*. In addition, predicted egg clutch with 95% prediction intervals obtained by leave one out cross validation have been plotted



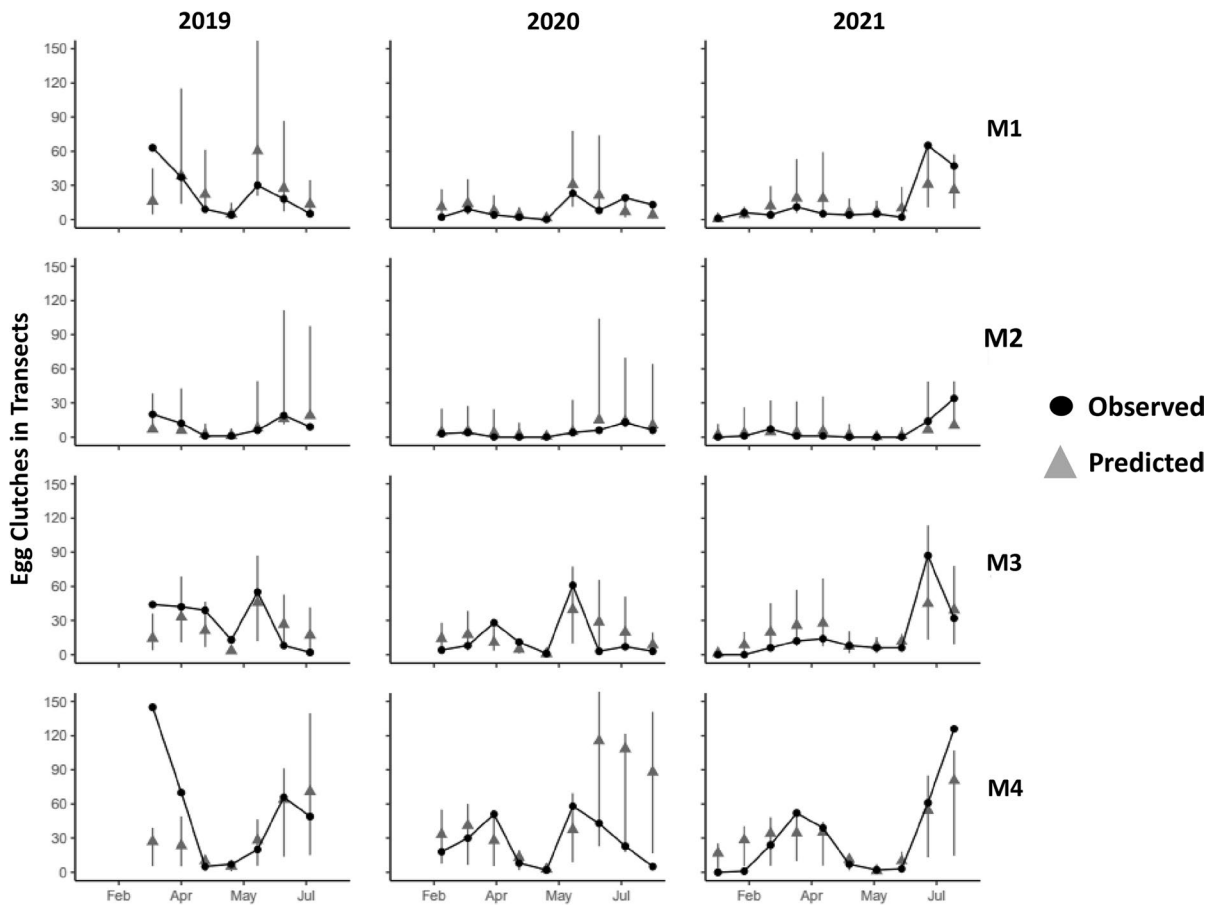
(Fig. 4A; Fig. S1). But as water depth increased with warmer temperatures (29 °C; typically in Jun-Aug), the predicted, albeit low, clutch counts increased until depths reached 69 cm (Fig. 4A).

Our additional surveys in other habitats revealed only three instances where *P. paludosa* reproduction was found in habitats beyond the deep slough ecotone (Table 4). Only one instance (Aug 2020 M3) of *P. paludosa* reproduction had a greater egg clutch density in the adjacent ridge habitat than on the ecotone transects.

The two best models (cumulative weight=0.84) explaining the variation in *P. maculata* egg clutches included a unimodal depth effect (Depth + Depth<sup>2</sup>), Adult Density and Photoperiod (Table 3). The most supported model had no interactions, but the second-best model had an interaction between the unimodal effect of Depth and Photoperiod (Table 3). For the most supported model, analysis of Randomized Quantile Residuals (RQR) identified the observation found in wetland M4 during March 2019 as an outlier (Fig. 3). Because we had no reason to think this was a sampling error or ecologically aberrant, we left it in the model. The fixed effects (Adult Density, Photoperiod, Depth,

and Depth<sup>2</sup>) explained 48% of the variation in egg clutches ( $R^2_m = 0.48$ ), and the full model, including Wetland as a random effect, explained 62% of the variation in egg clutches ( $R^2_c = 0.62$ ; Fig. 3). Holding Adult Density and Photoperiod constant at their averages, predicted clutches increased with Depth until 52 cm and then decreased (Fig. 4B). Over half (~55.8%) of the predicted clutches occurred from 41 to 67 cm water depths (Fig. 4B), and at these depths ridges were just flooded. Holding Depth and Photoperiod constant (averages), a standard deviation increase in Adult Density (0.08 snails m<sup>-2</sup>) produced a 27.9% increase in predicted egg clutches. Holding Depth and Adult Density constant (averages), a standard deviation increase in Photoperiod (0.87 h) yielded a 50.7% increase in predicted egg clutches.

Our additional surveys in other habitats revealed that there were more *P. maculata* egg clutches found in other habitats than in deep slough ecotone during the dry season (Table 4) but were mixed in the wet season (Table 4). Regardless of season there was substantial reproduction observed in other shallower habitats when the water exceeded 50 cm in the deep slough (Table 4).



**Fig. 3** Plots depicting observed egg clutch counts across all years in each wetland for *P. maculata*. In addition, predicted egg clutches with 95% prediction intervals obtained from leave one out cross validation have been plotted

#### Juvenile growth and survival from in situ cages

Greater concentrations of TP in the metaphyton produced higher growth rates of *P. paludosa* and *P. maculata* in field cages but had no effect on survival (Fig. 5). Survival in cages was high; 97.3% of *P. paludosa* survived ( $n_{P. paludosa} = 252$ ;  $n_{cages} = 32$ ; SD: 6.7%; Cage Range: 75–100%), and 100% of *P. maculata* survived the 5 weeks ( $n_{P. maculata} = 88$ ;  $n_{cages} = 16$ ). The four measures of juvenile growth gave qualitatively similar results (Fig. S2), so we report only those for mass SGR (Fig. 5). The fixed effects (TP, Species, TP x Species) explained 36.9% ( $R^2c = 0.369$ ) of the variation in mass SGR, and full model (random effect of year) explained 84.6% ( $R^2m = 0.846$ ) of the variation in mass SGR. The interaction (TP x Species) contributed to explaining the variation in mass

SGR ( $t = -4.601$ ;  $P < 0.001$ ). *Pomacea maculata* responded more strongly to the TP variation than *P. paludosa*. At low TP, *P. paludosa* and *P. maculata* had similar growth rates, but at high TP *P. maculata* had higher growth rates than *P. paludosa* (Fig. 5). In addition, a one standard deviation increase in metaphyton TP ( $187.9 \mu\text{g g}^{-1}$ ) increased mass SGR of *P. maculata* by  $5.34\% \text{ day}^{-1}$ , but only increased mass SGR of *P. paludosa* by  $1.11\% \text{ day}^{-1}$ .

#### Discussion

Though both *Pomacea* species found in southern Florida showed unimodal reproductive responses to water depth, the optimal water depths and seasonality differed. Caged juveniles of both species survived

**Table 3** Model selection table for the top 9 mixed-effect negative binomial regressions for egg clutch dynamics of *P. paludosa* and *P. maculata* in the LILA wetlands over 3 years

Model	AICc	$\Delta$ AICc	w
<i>Pomacea paludosa</i>			
Temp + Adult Density + Depth + Depth <sup>2</sup> + Depth*Temp + Depth <sup>2</sup> *Temp	448.52	0.00	0.63
Season + Depth + Depth <sup>2</sup> + Adult Density + Depth*Season + Depth <sup>2</sup> *Season	450.61	2.10	0.22
Photoperiod + Adult Density + Depth + Depth <sup>2</sup> + Depth*Photoperiod + Depth <sup>2</sup> *Photoperiod	452.15	3.64	0.10
Temp + Depth + Temp*Depth + Depth <sup>2</sup> + Temp* Depth <sup>2</sup>	455.18	6.66	0.02
Depth + Depth <sup>2</sup> + Season + Season*Depth + Season* Depth <sup>2</sup>	455.22	6.71	0.02
Photoperiod + Depth + Depth <sup>2</sup> + Depth*Photoperiod + Depth <sup>2</sup> *Photoperiod	459.49	10.97	<0.01
Season + Depth + Depth <sup>2</sup> + Adult Density	460.80	12.28	<0.01
Temp + Depth + Temp*Depth	461.38	12.87	<0.01
Adult Density + Season	462.12	13.60	<0.01
<i>Pomacea maculata</i>			
Photoperiod + Adult Density + Depth + Depth <sup>2</sup>	749.27	0.00	0.52
Photoperiod + Adult Density + Depth + Depth <sup>2</sup> + Depth*Photoperiod + Depth <sup>2</sup> *Photoperiod	750.24	0.96	0.32
Season + Depth + Depth <sup>2</sup> + Adult Density	753.76	4.49	0.05
Photoperiod + Depth + Depth <sup>2</sup> + Depth*Photoperiod + Depth <sup>2</sup> *Photoperiod	753.78	4.51	0.05
Season + Depth + Depth <sup>2</sup>	756.47	7.20	0.01
Temp + Adult Density + Depth + Depth <sup>2</sup>	756.87	7.60	0.01
Season + Depth + Depth <sup>2</sup> + Adult Density + Depth*Season + Depth <sup>2</sup> *Season	756.94	7.66	0.01
Depth + Depth <sup>2</sup> + Adult Density	759.02	9.75	<0.01
Temp + Depth + Depth <sup>2</sup>	759.65	10.37	<0.01

Adult Density was an estimate of the annual abundance of adults in each wetland from independent throw trap sampling

well in the wetlands regardless of TP levels, but the improvement in juvenile growth with high TP was much greater for *P. maculata*. The different reproductive and juvenile growth response to depth and TP, respectively, appear to be consistent with each species' distributions in southern Florida. In addition, quantifying these life history responses should improve projections of future abundances and distributions with changes in water management or hydro-restoration. High juvenile survivorship in cages raises additional questions about the recruitment and population limitation of *Pomacea* in wetlands like the Everglades.

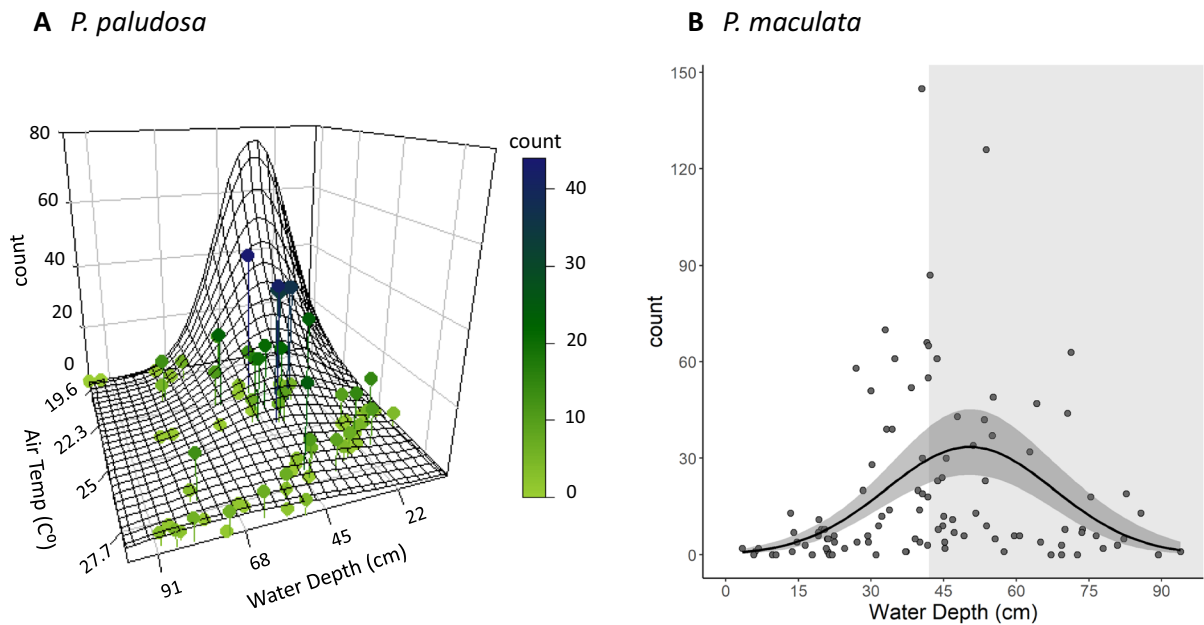
#### Environmental influences on reproduction

*Pomacea paludosa* reproduction typically peaked in the dry season with receding depths (February–April; Fig. 2), while *P. maculata* reproduction typically peaked after the onset of the wet season (June–August; Fig. 3). *Pomacea maculata* reproduction exhibited relatively less seasonality, consistent

with their longer lifespan (Hayes et al., 2015). Both models did a satisfactory job of describing seasonal reproductive dynamics for both species with substantial variation in reproduction being explained by our models (Pseudo  $R^2 > 0.62$ ).

Previous studies suggested that *P. paludosa* reproduction responded unimodally to water depth (Darby et al., 2008, 2015), and our results provide the first empirical model supporting this hypothesis while accounting for other environmental variables (Fig. 4A; Fig. S1). The unimodal reproductive responses indicated that deep water and shallow water were unfavorable for reproduction at the ecotone, with intermediate depths (16–52 cm) being optimal for reproduction. When water depths drop below 10 cm, *P. paludosa* stop moving to prepare for periods of hydrologic drought by burrowing into sediment and retracting into their shells (i.e., aestivation; Darby et al., 2002; Darby et al., 2008; Glasheen et al., 2017). Preparing to aestivate is likely driving the decline in *P. paludosa* reproduction on the ecotone at low depths because although *P. paludosa* have been





**Fig. 4** **A** A regression plane illustrating the interaction between weekly average water depth (Depth) and weekly average temperatures (Temp) for the most parsimonious model in predicting egg clutch counts of *P. paludosa*. To make data points more visible, they were colored along a gradient based on the value (i.e., count) as shown by the scale bar. The additional predictor variable (adult density) was held constant at its mean. **B** Scatter plot of *P. maculata* egg clutch counts and water depth. A line of best fit illustrates the nonlinear effect

of Depth for the most supported model and the shaded envelope is the model prediction standard error. The light gray side of the figure indicates depths when the adjacent ridge habitat was flooded. The additional predictor variables (Photoperiod and Adult Density) were held constant at their mean. For both models the predictor variables were z-transformed which standardizes the variable in terms of standard deviations away from the mean. In these plots, we back-transformed the variables to make them easier to interpret

shown to move to deeper water when water depths reach 10–20 cm, they stop moving at depths < 10 cm and rarely are able to escape drying (Darby et al., 2002). The life-history of *P. paludosa* show seasonality in populations with proportions of immature and reproductively inactive adults highest in Sep-Feb, the proportion of reproductively active adults highest in Feb-May, and the proportion of post reproductive adults highest in Jun-Aug (Hanning, 1979; Darby et al., 2008). The seasonality in populations potentially confounds the interpretation of declines in reproduction during deeper water because there would be relatively few reproductive adults during seasonal periods of deep water (Sep-Feb). We took advantage of the different hydrologic treatments in LILA which broke this association because we had multiple observations of reproduction at different depths during the same time. In addition, the interaction between depth and temperature in the model accounted for seasonal population structure changes

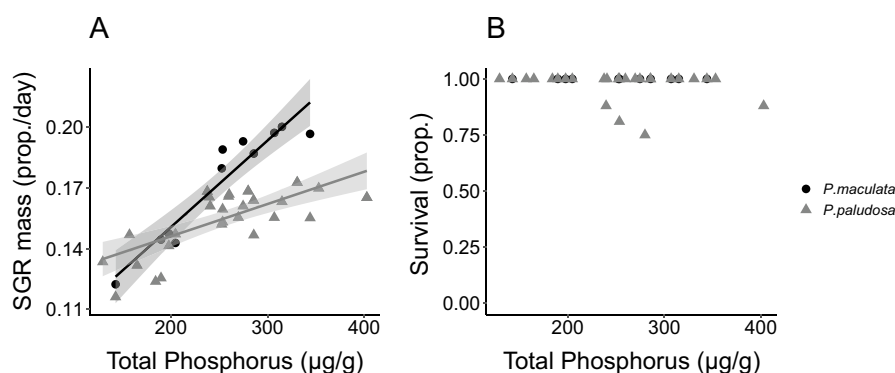
because during cool conditions (i.e., when reproductively active adults are common; typically in Feb-Apr) reproduction still declined with deeper water (Fig. 4A). After accounting for seasonality in life-history, the decline in reproduction during deeper water could not be explained by *P. paludosa* using other habitats for reproduction because our observations on the ecotone captured most of the reproduction when adjacent habitats were flooded (Table 4). Therefore, the decline in reproduction with deeper water is likely reflecting a genuine cessation of reproduction and not a confounded result of the seasonal populations of *P. paludosa* or movement into other habitats. Further experimentation could aid in teasing apart the association between seasonal population dynamics and seasonal depths. The cause of reduced reproduction in deeper water is less clear. Apple snails need to respire at the water surface, so we speculate that snails may be forced to move vertically under deep water conditions which may lower encounter rates with mates.

**Table 4** Observations comparing *Pomacea* egg clutch densities at the ridge-deep slough boundary (transects used in modeling) and egg clutch densities in other habitats when depths > 50 cm in the deep slough

Species	Season	Date	Wetland	Depth(cm)		Ecotone		Other	
				Deep Slough	Other	%	clutches/ha	%	clutches/ha
<i>P. paludosa</i>	Dry	2/15/2021	M1	76.5	33.8	–	0.0	–	0.0
<i>P. paludosa</i>	Dry	2/15/2021	M3	72.6	29.9	–	0.0	–	0.0
<i>P. paludosa</i>	Dry	2/15/2021	M2	55.8	13.1	–	0.0	–	0.0
<i>P. paludosa</i>	Dry	3/8/2021	M1	65.0	49.6	100.0	2.0	0.0	0.0
<i>P. paludosa</i>	Dry	3/8/2021	M3	60.7	45.3	57.5	11.0	42.5	8.0
<i>P. paludosa</i>	Wet	7/1/2019	M1	75.3	59.9	100.0	6.0	0.0	0.0
<i>P. paludosa</i>	Wet	7/1/2019	M3	73.6	58.2	100.0	25.0	0.0	0.0
<i>P. paludosa</i>	Wet	8/13/2020	M1	85.5	42.8	100.0	6.0	0.0	0.0
<i>P. paludosa</i>	Wet	8/13/2020	M3	81.1	38.4	40.6	4.0	59.4	6.0
<i>P. paludosa</i>	Wet	8/13/2020	M1	85.5	42.8	64.3	6.0	35.7	3.0
<i>P. paludosa</i>	Wet	8/13/2020	M2	59.7	17.0	100.0	27.0	0.0	0.0
<i>P. maculata</i>	Dry	2/15/2021	M1	76.5	33.8	37.9	11.0	62.1	19.0
<i>P. maculata</i>	Dry	2/15/2021	M3	72.6	29.9	–	0.0	–	0.0
<i>P. maculata</i>	Dry	2/15/2021	M2	55.8	13.1	100.0	4.0	0.0	0.0
<i>P. maculata</i>	Dry	2/15/2021	M4	55.8	13.1	16.8	4.0	83.2	19.0
<i>P. maculata</i>	Dry	3/8/2021	M1	65.0	49.6	9.4	8.0	90.6	74.0
<i>P. maculata</i>	Dry	3/8/2021	M3	60.7	45.3	25.3	11.0	74.7	34.0
<i>P. maculata</i>	Wet	7/1/2019	M1	75.3	59.9	23.0	34.0	77.0	115.0
<i>P. maculata</i>	Wet	7/1/2019	M3	73.6	58.2	12.2	15.0	87.8	109.0
<i>P. maculata</i>	Wet	8/13/2020	M1	85.5	42.8	71.3	25.0	28.7	10.0
<i>P. maculata</i>	Wet	8/13/2020	M3	81.1	38.4	67.2	6.0	32.8	3.0
<i>P. maculata</i>	Wet	8/13/2020	M1	85.5	42.8	51.7	25.0	48.3	23.0
<i>P. maculata</i>	Wet	8/13/2020	M2	59.7	17.0	65.4	23.0	34.6	12.0
<i>P. maculata</i>	Wet	8/13/2020	M4	51.5	8.8	89.7	19.0	10.3	2.0

Note, *P. paludosa* only have 11 observations because the surveys in wetland M4 were not included because *P. paludosa* have been extirpated from that wetland

**Fig. 5** Growth rate (SGR; proportional mass change per day: **A** and proportional survival **B** of *Pomacea paludosa* and *P. maculata* caged in wetlands measured along a metaphyton TP gradient. The best fit lines and standard error (shaded area) are included for significant relationships



Alternatively, vertical movement may be physiologically costly and lower reproductive output. Further work will be required to determine the mechanisms

responsible for the decline in reproduction during deeper water for *P. paludosa*.

*Pomacea maculata* exhibited a similar unimodal reproductive response with notably deeper optimal depths at the ecotone (Fig. 4B). Because reproduction was minimal at depths of 10–15 cm, we suspect that, like *P. paludosa*, *P. maculata* prepare for hydrologic drought around these depths. Future studies documenting *P. maculata* movement in response to drying may further aid in interpreting the predicted decline of reproduction at shallow depths. *Pomacea maculata* live longer than *P. paludosa*, so reproducing adults are abundant in Jun–Aug. Interpreting the decline in *P. maculata* reproduction during deeper water was complicated by our observations that *P. maculata* reproduced in alternate immediately adjacent “up-gradient” habitats when the water was deeper (Table 4). Peak reproduction by *P. maculata* on the ecotone occurred when the deep sloughs were 52 cm (Fig. 4B), and at these depths the adjacent ridges have recently flooded (depths ~ 10 cm). Thus, *P. maculata* moving to adjacent habitats may be one explanation for the decline in reproduction on the ecotone when water depths rose beyond 52 cm. For *P. maculata* the decline in reproduction with depths > 52 cm could not be interpreted as a simple cessation of reproductive activity. Deeper optimal depths and substantial reproduction in other habitats beyond the ecotone suggest that reproduction of *P. maculata* is less restricted than *P. paludosa* by deep water.

Differences in seasonal depth fluctuations in the native ranges of the species may explain the differences in ideal depths for reproduction. *Pomacea maculata* is native to the river and lake flood plains of South America (Hayes et al., 2015) where they experience greater magnitudes of seasonal depth changes (e.g., Tahuayo River, Peru: ~ 6 m; Bodmer, 1990) than are typical in Florida wetlands (0.5–1.5 m; McVoy et al., 2011). In Florida, the typical habitats of the two species broadly reflect the differences in reproductive depths because *P. maculata* are common and abundant on the margins of deeper lakes and canals (Cattau et al., 2016; Marzolf et al., 2018).

Current restoration efforts aim to increase water depths and hydroperiods in most parts of the central and southern Everglades but reduce them in others. In the pre-drainage Everglades, the long-term average water depths were ~ 90 cm in sloughs at the end of the wet season (Oct–Nov) and ~ 30 cm at the end

of the dry season (May; McVoy et al., 2011). Assuming McVoy et al., (2011) is correct about the depth conditions in sloughs of the historical Everglades, then populations of apple snails would seem to have experienced poor reproductive conditions; the long-term average depths suggest *P. paludosa* reproduction would have been typically limited during the cool months (ideal temperatures) of the dry season because of deep water (> 50 cm) in the sloughs. This apparent paradox then leads to an important question: did *P. paludosa* only reproduce well in the sloughs of the Everglades during years of lower rainfall when early drying produced ideal depths for reproduction (30–40 cm) that coincided with ideal temperatures (i.e., cooler months: Feb–Apr)? We cannot answer this question fully in our paper, but unless snails shift their egg laying toward the summer (hotter temperatures), it is possible that raising water depths in the sloughs of the central Everglades to depths > 50 cm in February to April would likely lead to populations smaller than they currently are. If central Everglades sloughs were not historically favorable to *P. paludosa* then we surmise they may have been historically more successful in prairie-like wetlands on the margins of the ecosystem (see Karunaratne et al., 2006). We hasten to add that we do not know whether egg-laying conditions limit the native snails in the current Everglades, in LILA, or in any emergent wetlands, and determining the limiting factor will require comprehensive work on various vital rates and stage structured models (e.g., Darby et al., 2015). Addressing such questions will be important for future management and restoration scenarios that may determine where, in the reduced spatial extent of the Everglades, *P. paludosa* can persist. Experimental whole wetland systems like LILA may allow for depth and temperature variations to further parameterize population models and help test such questions.

Other important covariates for modeling reproduction of *Pomacea* included Air Temperature, Photoperiod and Adult Density. Experimental evidence suggested that photoperiod was unimportant for seasonal increases in *Pomacea canaliculata* (Lamarck, 1822) reproduction (Albrecht et al., 1999) which led a review to conclude that photoperiod was unimportant for seasonal reproduction of the entire genus (Hayes et al., 2015). In our study we found mixed support for this conclusion, we did find air temperature (as a proxy to water temperature) was included in the top

model for *P. paludosa* (Table 2), but photoperiod was included in the third best model ( $\Delta\text{AICc}=3.64$ ) of *P. paludosa* reproduction, and photoperiod was in the best models for *P. maculata* reproduction (Table 2). The general role of photoperiod for *Pomacea* reproduction is further complicated by a study in the freshwater springs of Silver Springs Florida where water temperatures were relatively constant throughout the year (varying from 22 to 23°C; Odum, 1957). *Pomacea paludosa* continued to reproduce seasonally in these thermally constant springs indicating that photoperiod could be important for the seasonality of *P. paludosa* reproduction (Odum, 1957). Water temperatures and Photoperiod are often highly correlated, so further experimentation with species other than *P. canaliculata* would be necessary to ascertain whether water temperature or Photoperiod generally explain the seasonal reproduction of *Pomacea*.

#### Resources and juvenile growth and survival

This analysis is the first that we know of to measure juvenile growth in situ for *P. paludosa* and *P. maculata* in field settings, and it was performed with variation in metaphyton TP (129–403  $\mu\text{g g}^{-1}$ ). Because we re-analyzed data that was previously focused on testing for competitive effects of the non-native *P. maculata* on the native *P. paludosa*, we were forced to analyze the response of *P. maculata* to TP in the presence of *P. paludosa* which may present some limitations for the quantitative conclusions about field growth rates of *P. maculata*. In particular, we assumed that *P. maculata* growth was unaffected by the presence of juvenile *P. paludosa* (see explanation in methods; Posch et al., 2013; Drumheller et al., 2022). Even if our assumption was incorrect and there were negative effects of *P. paludosa* on juvenile *P. maculata* growth, it would make our growth estimates for that species low. While the quantitative conclusions about the response are conservative, the qualitative results would remain unchanged.

Our results indicated that at metaphyton TP levels  $< 200 \mu\text{g g}^{-1}$  there was no difference in juvenile growth rates between species, but because juvenile *P. maculata* growth responded stronger to increased TP there was a large difference in juvenile growth rates at metaphyton TP levels  $> 300 \mu\text{g g}^{-1}$  (Fig. 5). Juvenile *P. paludosa* hatch at larger sizes and with thicker shells and allocate more energy to shell growth than

*P. maculata* (Davidson & Dorn, 2017) which suggests that there may be a tradeoff between shell growth and soma that could explain why juvenile *P. maculata* respond more strongly to TP. The different responses to metaphyton TP suggest that population growth or compositional dominance in a location could be TP-dependent. The Everglades has similar natural ranges in metaphyton TP to LILA (40–500  $\mu\text{g g}^{-1}$ ) but can reach up to 1000  $\mu\text{g g}^{-1}$  in locations near canals and agricultural fields (Gaiser et al., 2011). Recent observations on the prevalence of *P. maculata* egg clutches were negatively correlated with distance from the canal edges in the Everglades (Dorn & Hafsadi, 2016; Dorn, personal observation) suggesting that populations benefit from high TP halos near canals (Rehage & Trexler, 2006). The different responses to the TP variation may explain why *P. maculata* reach densities that can regularly support kite nesting in nutrient rich habitats like marginal wetlands of Lake Okeechobee, and the Kissimmee Chain-of-Lakes region (Cattau et al., 2016) where TP levels in the water column are higher (0.5 mg/l–2 mg/l and 0.06 mg/l–0.16 mg/l, respectively; James et al., 2009; SFWMD, 2015) than the Everglades (0.001–0.06 mg/l; Gaiser et al., 2011).

Future restoration in the Everglades aims to restore flow by connecting wetlands with culverts (SFWMD, 2018), but flow can increase TP levels in metaphyton by resuspending phosphorus from the sediment (Hansen et al., 2022). The flow and TP in the source water (e.g., canal vs. wetland) can also affect the P content of metaphyton in the recipient wetlands (Gaiser et al., 2005). Stormwater Treatment Areas (STA) that remove TP from the water column and canal back filling will mitigate these changes (Pietro & Ivanoff, 2015). Thus, the effects of restoration on metaphyton TP may vary spatially, and these data can be used to help produce predictive spatially explicit models of *Pomacea* habitat suitability in response to hydro-restoration.

Survival rates of juvenile *P. paludosa* and *P. maculata* in field cages were unrelated to the TP gradient (Fig. 5). Previous work on gastropods (including *Pomacea*) in the Everglades hypothesized that standing stocks are limited by TP availability (Ruehl & Trexler, 2011). Our results support this hypothesis although for *Pomacea* they suggest that mechanistically TP availability may mediate size-structured predator–prey interactions rather than through starvation or development failure.



Specifically, increases in metaphyton TP should increase growth rates and allow *Pomacea* to reach a size refuge more quickly. This is further supported by mesocosm experiments under oligotrophic conditions where crayfish [*Procambarus fallax* (Hagen, 1870)] predators have been shown to sort *P. maculata* and *P. paludosa* communities in favor of *P. paludosa* because *P. maculata* hatch at smaller sizes of higher vulnerability. Predator sorting (biotic resistance to the non-native) was dampened by increased TP availability because the rapid increase in growth rates of juvenile *P. maculata* allowed them to quickly reach a size refuge (Davidson & Dorn, 2018). The high survival (100%) of *P. maculata* size in our study may be a result of their age (i.e., reach a less vulnerable age), but again these results indicate that juvenile *P. paludosa* and *P. maculata* of similar sizes (~4 mm SL at the start of the experiment) are not starving in the oligotrophic condition of the Everglades. The identity and effects of different juvenile-stage predators remains to be examined in the field, but several species of vertebrates and invertebrates feed on snails the sizes of juvenile apple snails (Valentine-Darby et al., 2015).

## Conclusion

The differences in *Pomacea* reproduction and juvenile growth response to environmental variables were consistent with their general distributions in southern Florida. We observed that variable wetland water depth and phosphorus availability in resources differentially favored reproduction and growth of the two species of *Pomacea* and these reproductive observations were strengthened by use of large replicated experimental wetlands. The apparent disconnect between the ideal shallow depths for the reproduction of native *Pomacea paludosa* in the cooler parts of the year and historical projections of water depths in the Everglades will require further investigation. Because water depth gradients and nutrient gradients are widespread in shallow freshwater systems (Carmignani & Roy, 2017), understanding the ways water depth and nutrients influence aquatic macroinvertebrate populations may help predict regional distributions of native and invasive species, identify important habitats for conservation and optimize hydrological management and restoration scenarios.

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**Data availability** Data are available from the corresponding author upon reasonable request.

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