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**Growth as a defense: revisiting growth mediated survival in size-structured prey populations**

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# Open Research Statement

Data associated with the manuscript will be archived in the Zenodo public repository should the manuscript be accepted. R scripts for analyses are archived in a Git Hub repository.

# **Key words**

Apple Snail, *Belostoma*, consumptive effects, Everglades, size-dependent survival, temperature, interaction strength, Snail Kite ontogeny

# Abstract (350 words):

Individual size and growth rates are key determinants of performance with population-level consequences. For species that grow to achieve a size refuge from predators, the interaction between juvenile survival rates and growth is widely acknowledged to affect population dynamics, but the interaction has rarely been illustrated theoretically or quantified under natural conditions. We used a published age-structured population model of an annual freshwater snail species with diminishing populations to construct a zero-population growth for theoretical combinations of juvenile daily growth and survival. The resulting isocline produced the expected result that faster juvenile growth would offset greater juvenile mortality (i.e., lower survival). We then measured juvenile survival and growth rates in multiple wetlands with naturally varying predator assemblages and seasonal environmental variation (e.g., temperature, water levels). Seasonal rates and averaged parameters were interpreted relative to the isocline from the model. Daily juvenile survival rates were lower, and more clearly size-dependent, in the cooler dry season than in the warmer wet (rainy) season. Greater abundances of generalist insect and vertebrate predators in the dry season seemed to be responsible for the greater mortality (lower survival). Juvenile growth was faster in the warmer wet season. A model using only parameter combinations of growth and survival in the cooler dry season would predict declining populations, while parameters from the warmer wet season predicted populations at replacement (λ = 1) or increasing. When parameters were combined with weighted averaging to cover a full reproductive season, populations were projected to decline in both wetlands. The averaged predictions were robust to water depth parameters affecting reproductive rates (births), but with better water depth conditions one population was close to replacement. The use of the null clines identified important temporal variation in juvenile parameters; while one season provided better conditions for population statis, or even increases, the other season, with slower growth and higher abundance of generalist predators overlapped with a greater proportion of the annual reproduction. Our work illustrates the growth-mediated predator impacts for strongly size-structured populations with stage- or size-specific predators and we hypothesize that this could be a general finding. Regardless, the use of population growth isoclines from age-structured population models can provide a general framework for making demographically meaningful interpretations about field-measured rates for such species. We encourage population ecologists to consider such an approach for species of management interest, including those that are in steady decline.

# Introduction

Population dynamics for many species with stage or age structure are widely recognized to be influenced by stage or size-specific growth and mortality factors (e.g., predation; Werner and Gilliam 1984, De Roos et al. 2003, Craig et al. 2006). Juvenile growth affects the time a prey animal spends in a vulnerable size class so that greater growth can be a type of defense against stage specific predation; the strength of an interaction is the consequence of environmental mediation (Craig et al. 2006, Davidson and Dorn 2018, Davidson et al. 2021, Ma et al. 2021, Nunes et al. 2021, Meehan et al. 2022). Historical emphases focused on theoretical treatments of density-dependent growth rates, competition, habitat switching, size-structure, and juvenile bottlenecks (e.g., fish: Werner and Gilliam 1984, De Roos et al. 2003). In real systems, spatial and temporal environmental factors influence juvenile growth through temperature and resource supply (Jeyasingh and Weider 2005, Davidson and Dorn 2018, Pepi et al. 2018, Davidson et al. 2021). Temperature, disturbances, migrations, and population dynamics can seasonally affect predation rates and predator assemblages in time and space (McPeek and Peckarsky 1998, McCoy et al. 2011, Soomdat et al. 2014). Taken together, spatial and temporal variation in either growth or mortality may provide windows of opportunity for population growth. Studies of species interactions are often conducted experimentally at the level of interaction strength or total prey mortality (see Jeyasingh and Weider 2005, McCoy et al. 2011, Davidson and Dorn 2018, Pepi et al. 2018, Davidson et al. 2021, Ma et al. 2021) but both ecologists and conservation biologists need to know how the factors relate to population growth (λ) in natural conditions. Furthermore, while size-dependent mortality is well known (Craig et al. 2006, McCoy et al. 2011, Schmera et al. 2015, Brannelly et al. 2019) and population-level consequences of the interaction between juvenile growth and mortality are logical, they have only been generally mentioned (De Roos et al. 2003), theoretical predictions are lacking. Of the two studies that have explored theoretical predictions for growth-mediated effects of on prey survival from predation in size-structured populations, Rice et al. (1993) looked at how variation in mean growth rates and variation growth rates within a population influenced the numbers and proportions of surviving while Pepi et al. (2023) focused on changes in equilibrium densities of predator and prey due to mismatches in thermal responses to increases in temperature while holding prey reproduction rate constant. Thus, despite the increase in interest of predicting the outcome predator-prey interactions in size-structured population in response to changing environmental conditions (Pepi et al. 2018, 2023, Davidson et al. 2021), the population-level consequences (per-capita changes) of increasing growth rates in size-structured prey population due to environmental factors has little theoretical underpinning particularly when adding reproduction.

Size-indexed models combine growth (i.e., developmental) rates and survival to make projections and identify sensitive stages/ages (Chockley et al. 2008), but could also be used to identify combinations of parameters making population growth negative, zero, or positive. Zero-population growth isoclines historically were used to predict how two interacting species can persist with variable abundances of interacting species, population parameters, resources, and environmental variation (MacArthur and Levins 1964, Vance 1985) but zero-growth isoclines can also be calculated from stage- or size- structured population models to identify parameter combinations producing zero population growth. To our knowledge this has not been done, but isoclines from stage-structured models present tools that could project the combinatorial effects of size-dependent survival and growth on population growth while controlling for reproductive conditions. Field-measured parameters could then be compared to the isocline and predict natural spatio-temporal variation in recruitment or population growth.

In this paper, we used a previously parameterized age-structured model for a freshwater gastropod of conservation concern, the Florida Apple Snail (*Pomacea paludosa;* FAS) and identified theoretical combinations of juvenile-stage parameters predicting population stasis, growth, or decline. We illustrate the predictions from the model with zero population growth isoclines. The qualitative predictions of the model should be generalizable to any species with stage-specific losses and high mortality to predators in juvenile ages or stages (plants, fish, invertebrates).We then quantified size- and season-dependent survival and growth in the field to 1) test for size-dependent survival and 2) quantify the net effects that growth and survival have on population growth during the annual reproduction/recruitment period (spring vs early summer). Using the model the measured values in the field thus become interpretable from a population dynamic perspective.

# Materials and methods

## System and study species

The Florida Everglades is a shallow, expansive (~915,000 ha), subtropical, oligotrophic wetland covering much of southern Florida (Richardson 2010; Figure 1). Rainfall is seasonal with approximately 80% of rain falling from June-November (Gaiser et al. 2012). which produces intra-annual water depth fluctuations of ≥ 60 cm. The degree of water level recession and depth in the dry season is a function of rainfall and water management decisions. Historically, water flowed in a single shallow sheet from Lake Okeechobee at slow velocity across the spatial extent of the Everglades (i.e., sheet flow; Sklar et al. 2005), but flow was reduced or eliminated after compartmentalization and drainage. Drainage of the Everglades altered the hydrologic conditions by increasing water depths in some areas but decreasing depths in others. Within the Everglades, the ridge-slough landscape originally covered 55% of the Everglades (McVoy et al. 2011), but now covers ~44% (Richardson 2010). In the ridge-slough landscape, ridges and sloughs differ slightly by elevation (~10-15 cm) which produces habitat/vegetation patterning. The lowest elevation slough habitats dry to sediment surfaces every 3-10 years and are dominated by floating vegetation like water lilies (*Nymphaea odorata*) or emergent spike-rushes (*Eleocharis* spp.). Sloughs are interspersed with higher elevation ridges dominated by sawgrass (*Cladium jamaicense*) that dry most years (Zweig and Kitchens 2008). Ongoing hydro-restoration of the Everglades ecosystem aims to restore hydro-patterns to improve conditions for wildlife and natural communities.

The FAS is the largest native gastropod in freshwaters of North America, inhabits shallow lakes and wetlands, and currently occurs at low adult densities (<<1/m2) in southern Florida (Gutierre et al. 2019). Snails grow from 3-4 mm shell length (SL) at hatching to > 40 mm SL as large adults and do not live beyond 1.5 years (Hanning 1979). Most reproduction (~70%) occurs during cooler spring seasons when water levels are declining, and some reproduction occurs (~30%) during warmer early summer when water levels are rising (Hanning 1979, Barrus et al. 2023). At adult sizes (> 25 mm SL) FAS are a critical resource for the endangered Snail Kite (*Rostrhamus sociabilis*; Cattau et al. 2014), so improving the conditions for FAS populations is imperative. As small juveniles (< 10 mm SL) FAS are prey for crayfish (*Procambarus* spp, sunfish non-native cichlids, large killifishes (*Fundulus seminolis*), greater siren (*Siren lacertina*), and turtles (e.g., *Kinosternon bauri*; Valentine-Darby et al. 2015, Davidson and Dorn 2017). Another known gastropod predator, giant water bugs (Belostomatidae), may also depredate juvenile FAS but has not been investigated (Kesler and Munns, 1989). Juvenile FAS outgrow most common fish and invertebrate predators once they grow to shell lengths of ~10-11 mm (Valentine-Darby et al. 2015, Davidson and Dorn 2017, Supplemental).

## Zero-Population Growth Isocline

We used a published age-structured population model (Darby et al. 2015) to create zero-population growth isoclines from theoretical combinations of two parameters, juvenile growth and survival (FAS < 10 mm SL) holding all other variables stable (more details in Supplemental). The model was coded in R using the original parameters although a few parameters were changed to reflect recent changes in understanding of FAS life history (Table S1, Darby et al. 2015). Isoclines were constructed from combinatorial simulations of the parameters for FAS survival < 10 mm SL and juvenile growth under two reproductive conditions which were represented by different hydrologic conditions (“Good Reproduction” or “Poor Reproduction” below; Figure 2). Each simulation had one combination of the parameters for which population growth rate (r) measured after a stable size distribution was achieved. The combinations for which population growth was constant (r = 0) were identified and plotted as an isocline.

The isoclines graphically represent theoretical combinations of the two parameters that stop growth of the population (λ = 1). Under the assumption of invariant growth and survival rates the isoclines are boundary conditions between a growing or a declining population. Because the juvenile FAS densities are so low and yet can survive and grow at high densities in predator exclusion cages (Barrus et al. 2023) we considered traditional density dependence in the parameters to be irrelevant to our model evaluations which were simply trying to identify parameters that would produce an increasing or decreasing population year over year.

Once the isocline was built, we could then measure survival and growth parameters in the field and plot the results on the isocline state space. Using in situ experimental techniques (detailed further below and in Appendix S2) we calculated survival and growth parameters as well as their 95% confidence intervals. We then plotted on the isocline state space the combination of survival and growth for each season and location. The nature of the model made it impossible to change growth rates seasonally, thus the predictions from isocline plot assume that these season-dependent and growth dependent parameters are experienced throughout the year. The season-dependent predictions then are an estimate of snail recruitment assuming the rates measured each season. To combine the seasonal parameters for any one population, we calculated weighted averages of the seasonal parameters to combine the estimates into a single growth and survival estimate for the year. Because ~70% of reproduction (hatchling production) occurs in the dry season and ~30% occurs in the wet season (Darby et al. 2015, Barrus et al. 2023) the dry season parameters were weighted proportionately more heavily.

## Survival and Growth in the field

Our measures of survival and growth were made in two locations within the Everglades ecosystem. The Loxahatchee Impoundment Landscape Assessment (LILA) wetlands and two sites in the western portion of Water Conservation Area 3A (WCA3A; Figure 1) in Florida, USA. LILA consists of four 8 ha impounded wetlands with ridge and slough elevation features and hydro-patterns that mimic the wetlands of the Everglades (Figure 1B). Both wetlands have seasonally varying water levels but the water levels in LILA are under partial control by pumps and culverts to perform landscape-scale hydrologic experiments (see Supplemental). We worked in two wetlands impoundments that had hydrologic conditions deemed good for FAS reproduction (Barrus et al. 2023). We also measured parameters at two sites near the western boundary of WCA3A near Big Cypress National Park (Figure 1; Sites 2 and 3 in Ruetz et al. 2005) . The sites were chosen because they were near locations of higher FAS densities in the recent past; sites that also supported Snail Kite nesting (Cattau et al. 2016).

To measure survival, we used tethering because traditional mark-recapture and cohort tracking techniques are extremely difficult for the small, hard-to-sample juvenile FAS. We tethered snails by attaching monofilament to the apex of the shell using super glue, then attaching the other end of the monofilament to the PVC poles within the wetland (Appendix S2). Tethered snails were placed on transects in the wetlands ~2 m apart and checked daily. Surviving snails were moved to increase independence between nights while depredated snails were replaced. Although in LILA we tethered snails of all sizes to test for size-dependent, here we focus on the survival of snails < 10 mm SL because this related to the isocline and was what varied the most seasonally (Appendix S2). We only tethered snails < 10 mm SL in the WCA3A. Further details of the tethering experiment can be found in Appendix S2. Here we also focus on relating survival to the isocline, but we observed tethering artefacts of different predators that allowed us to identify common predators (discussed further in Appendix S2).

We measured growth either using *in-situ* 1-m2 mesh cages or with a regression that predicted wet season snail growth using total phosphorus (TP) concentrations in metaphytic mats (R2m = .846; Barrus et al., 2023). The metaphytic (periphyton) in the Everglades are composites of floating calcareous mats of algae, cyanobacteria, other microbes, and algal detritus (Gaiser et al. 2011). For all cages, algae was allowed to accumulate in the cages two weeks prior to the experiment, and two liters of metaphyton was placed inside the cages as a food source (Drumheller et al. 2022, Barrus et al. 2023). Juvenile snails were individually marked and placed in cages to grow for 4-5 weeks. We placed 8 cages in LILA during both seasons and 3 cages in WCA3A site 2 in the dry season. To estimate wet season growth WCA3A site, we measured the TP of metaphytic mats to predict FAS growth of using regressions from (Barrus et al. 2023). We were only able to obtain dry season growth rates for site 2 in WCA3A because low dry season water depths made use of cage experiments impossible. Using the growth results we then calculated the growth parameter kgrwoth to relate the results to the isocline. Kgrowth is a measure of size dependent growth rates that can be calculated from knowing the initial size, the final size and the maximum size. The maximum size was assumed to be 50 mm SL. Details on calculating the growth parameter (kgrowth) are further found in Appendix S2.

# Result

Zero-population growth isoclines created from the age-structured population model produced isoclines consistent with the expected interaction between growth and survival (Figure 2). Populations with faster-growing juveniles could withstand higher rates of mortality (lower survival) and populations with slower-growing juveniles needed lower mortality (higher survival) to persist. Better wetland hydrologic conditions for reproduction made the population more resilient to lower survival (e.g., withstanding 3.1% lower survival at growth of kgrowth = 0.07) and/or lower juvenile growth (e.g., withstanding by 7.7% lower growth at CJS of 0.80; Appendix S1 Figure S2). The effect of better reproduction (i.e., the gap between good and poor reproductive isoclines) strengthened with higher growth and lower survival (Appendix S1 Figure S2).

## Empirical Survival and Growth related to the Isocline

There was variation in the measured survival and growth parameters across sites and seasons (Figure 3). Here, we present data from LILA and WCA3A site 2 which had growth rates measured from both seasons, butl measured parameters from WCA3A site 3 and survival measured from the cages (i.e., predators excluded) were plotted in a full figure in Appendix S1 Figure S3. Growth was higher in the wet season than the dry season (Figure 3, Appendix 3 Figure S2). The dry season had lower survival and slower growth and when applied to the model would predict poor recruitment regardless of wetland site (Figure 3). In contrast, the wet season had higher survival rates and higher growth resulting in replacement (LILA) or even favorable recruitment (WCA3A site 2; Figure 3). Snails in WCA3A site 2 had faster growth than those in LILA (Figure 3). The combined effects, weighted by seasonal differences in egg laying, resulted in annual mortality and growth parameters that predicted declining population for LILA, and confidence intervals that slightly overlapped the zero-growth isocline created with good hydrologic egg-laying conditions for WCA3A site 2 (Figure 3).

# Discussion

We used a stage structured population model to produce zero- population growth isoclines illustrating the interactive effects of growth and survival for natural populations of a freshwater gastropod with size-dependent survival. The approach is potentially applicable to any size-structured predator-prey interaction. The model provided vital rate target regions that might produce growing or declining FAS populations, but FAS populations were so sparse that it was impossible to verify population-level predictions. Seasonal measurements allowed us to compare existing rates to the theoretical isocline and conclude that populations are static or declining when parameters are averaged over the reproductive season, but that survival and growth parameters are particularly poor in the dry season (across both wetlands). The results produce novel hypotheses about environmental variation and predator control that might limit the FAS in the Everglades.

*Survival and growth*

Calculating size-dependent survival for small animals like freshwater invertebrates is challenging. Traditional techniques (e.g. mark-recapture, individual tracking) are problematic because juvenile FAS are difficult to capture, cannot be individually and reliably tracked, and are typically found at exceedingly low densities in the Everglades (including LILA wetlands; Gutierre et al. 2019, Drumheller et al. 2022). Tethering is an experimental method to measure survival and could potentially inflate mortality estimates of prey but the concern is greatest for highly mobile prey for which tethers limit antipredator behaviors (Baker and Waltham 2020). Tethering offered the only feasible method for determining juvenile FAS survival. In addition, tethering less mobile prey (e.g. snails) with limited antipredator escape behaviors should produce informative survival estimates. Further, tethering across field gradients reliably estimates encounter rates with relatively more mobile predators (Rochette and Dill 2000, Ruehl and Trexler 2013).

Florida apple snail growth would increase in the warmer wet season (Figure 5, Figure S2). Increases in prey growth associated with the warmer wet season is consistent with many experimental manipulations of temperature in predator-prey studies including dragonfly-mosquito interactions (Davidson et al. 2021) and predatory ant-caterpillar interactions (Pepi et al. 2018). Further, increases in temperature are generally thought to increase growth of ectothermic animals except for extreme thermal maxima (Kingsolver and Woods 2016).

We found that prey survival was highest in the wet season (Figure 3) Despite apparent increases in per-capita foraging rates of crayfish and salamanders (Appendix S2 Figure S3), declines in abundance of predators overwhelmed theoretical predictions of higher predation rates due to increases in temperature. The declines in abundance of predatory crayfish and bugs are explained by phenology (van der Heiden and Dorn 2017, Pintar et al. 2021) while declines in abundance of greater sirens are probably best explained by seasonal movement patterns. Greater sirens emigrate out of the wetlands into the deeper adjacent habitats to escape the low water depths (< 10 cm) at the end of the dry season, and remained in the deeper water throughout the duration of our study in the wet season (Howell 2023). Typically studies that explore the effects of environmental conditions on predator-prey interaction have controlled predator abundance experimentally, or statistically (Jeyasingh and Weider 2005, Davidson and Dorn 2018, Pepi et al. 2018, Davidson et al. 2021, Ma et al. 2021). But controlling predator abundance and size structure complicates scaling up predictions based on experiments to natural systems, because declines in predator abundances may counteract increases in per-capita foraging rates.

## Long-term Interaction Strength (Population Growth)

The model we used (Darby et al. 2015) had no good empirical measures for juvenile growth so our findings provide more realistic estimates for the Everglades. The dry season parameters were worse than the wet season for recruitment which seems counterintuitive because most egg-laying occurs during the dry season (spring) before the water reaches its annual minimum depth (Barrus et al. 2023). This result suggests that improving dry season conditions for survival and growth of juvenile FAS may have a larger benefit for FAS populations than improving wet season conditions. Furthermore, the different hydrologic scenarios, affecting reproductive conditions, had relatively small effects on the isocline relative to the natural spatial and seasonal variation in the two juvenile parameters.

In addition to seasonal variation in predation regimes, spatial variation in productivity (i.e., TP) may also mediate predator limitation. The Everglades is phosphorus limited and periphyton total phosphorus ranges between 30-1000 µg·g-1 with typical TP concentration between 110-400 µg·g-1 in the ridge-slough landscape (Gaiser et al. 2011).Growth of juvenile FAS depend on TP in the periphyton (Hansen et al. 2022, Barrus et al. 2023), and previous experimental manipulations of phosphorus showed that higher TP increased growth and juvenile apple snail survival in the presence of gape-limited crayfish (Davidson and Dorn 2018). Our results build on this finding by indicating that TP can mediate the net community level effects of predators on recruitment in the field. Periphyton total phosphorus levels were highest at WCA3A site 2 (Table S3), it was the only site to have wet season growth and survival that predicted favorable recruitment, and when combined with dry season parameters WCA3A site 2 predicted slowly declining or static populations. From an ecological standpoint the parameters measured in the field across the sites indicated that growth and survival rates did not vary in counteracting fashion and that addresses an important point about spatial covariance of the two factors. In times and places with greater growth, we did not necessarily have higher mortality counterbalancing the benefit.

Within the Everglades the current paradigm for encouraging population growth of the FAS is to make hydrologic conditions more favorable for reproduction (Darby et al. 2015), but our results indicate that with the current levels of predation and individual growth, improving hydrologic conditions for reproduction at typical TP conditions in the Everglades can only maintain the already small populations of the FAS. This conclusion was strengthened when we set water level and temperature conditions constant to optimize reproductive conditions and population growth did not shift from replacement to increasing (Figure S5). For hydrologic variation to turn FAS population growth positive, either the predation rates would need to be decreased from current levels or growth would need to increase in the spring (dry season). We offer hypotheses about the current and historical conditions for population of FAS in the Everglades. First, the predation rates in the Everglades might currently be higher than historical levels as a function of non-native fishes or hydrologic conditions that somehow encourage juvenile predators (e.g., invertebrates) in the sloughs. Some non-native fishes introduced to the Everglades have been mildly molluscivorous like mayan cichlids and african jewelfish that have invaded the Everglades and could have increased predation, but our observations suggest that native predators (e.g., crayfish, giant water bugs, greater sirens) in LILA seem to be more responsible for survival patterns than non-native species (e.g, mayan cichlids). One option might be to study controls on giant water bug predation to identify hydrologic conditions reducing their abundances in the dry season. But the observed predator community includes native species existing across a wide range of the hydroperiod gradient so it remains unclear how hydrologic variation (i.e., floods or droughts) could fundamentally shift juvenile survival. The relation between the predators and hydro-patterns may require more work, but measurements of juvenile survival and growth could also be repeated in time and space to measure variation in vital rates, especially survival, during windows of time that may produce good survival (e.g., depths of 10-15 cm). If net community-level predation has not changed from historical levels, then current hydrologic conditions could also be unfavorable for growth of the FAS (i.e., shifted to the left in Figure 5). Indeed, recent work has shown that increasing water flow velocity, increases growth of non-native *Pomacea* apple snails through changes to microbial food quality (Hansen et al. 2022). Therefore, an Everglades restored with more discharge might possibly improve growth of the juvenile FAS.

*Survival and growth Isocline*

Despite the intuitive reasoning that growth and survival interact, and many studies include this concept in building theory (e.g. temperature altering predator-prey interactions), we believe the isocline approach is the first to illustrate the theoretical predictions of prey survival and juvenile growth on population growth in a specific case. We showed a negative slope between juvenile survival and growth confirming the logical conclusion and empirically demonstrate result that higher growth can allow populations to withstand lower survival. This result, although shown in a specific case, we expect to hold for any species with size or stage dependent survival. Interestingly, the isocline also seems to indicate that altering reproduction can change the slope of the isocline suggesting that populations disproportionately benefit from increased reproductive rates when conditions for growth are better than when they are worse (i.e., populations can withstand a relatively greater reduction in survival at higher growth rates than lower growth rates). The result that populations disproportionately benefit from increased reproduction at higher growth needs to be further corroborated with future theoretical work but demonstrates at least one reason why exploring this theoretical backing of this well-known concept will be fruitful. Additionally, as we demonstrate here this understanding can aid conservation and management to offer new hypotheses about what limits populations and that could lead to new management regimes for replenishing populations that have declined.

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# Author Contributions

All authors contributed something to the design. The tethering and growth rate design and experiments were established by NJD, NTB and MIC. Data collection was performed by NTB and NJD. Analyses and statistical models were conducted by NTB in consultation with NJD. The paper was written by NTB with edits and comments from all the co-authors. All authors have read and approved the final manuscript.

# Conflict of Interests

We declare no financial interests that could create conflicts for this work.

# References

Baker, R., and N. Waltham. 2020. Tethering mobile aquatic organisms to measure predation: A renewed call for caution. Journal of Experimental Marine Biology and Ecology 523:151270.

Barrus, N. T., D. Drumheller, M. I. Cook, and N. J. Dorn. 2023. Life history responses of two co-occurring congeneric Apple Snails (Pomacea maculata and P. paludosa) to variation in water depth and metaphyton total phosphorus. Hydrobiologia 850:841–860.

Brannelly, L. A., M. E. B. Ohmer, V. Saenz, and C. L. Richards‐Zawacki. 2019. Effects of hydroperiod on growth, development, survival and immune defences in a temperate amphibian. Functional Ecology 33:1952–1961.

Cattau, C. E., P. C. Darby, R. J. Fletcher, and W. M. Kitchens. 2014. Reproductive responses of the endangered snail kite to variations in prey density: Effects of Prey Density on Kite Reproduction. The Journal of Wildlife Management 78:620–631.

Cattau, C. E., R. J. Fletcher, B. E. Reichert, and W. M. Kitchens. 2016. Counteracting effects of a non‐native prey on the demography of a native predator culminate in positive population growth. Ecological Applications 26:1952–1968.

Chockley, B., C. St. Mary, and C. Osenberg. 2008. Population sinks in the Upper Florida Keys: the importance of demographic variation in population dynamics of the marine shrimp Stenopus hispidus. Marine Ecology Progress Series 360:135–145.

Craig, J. K., B. J. Burke, L. B. Crowder, and J. A. Rice. 2006. Prey growth and size-dependent predation in juvenile estuarine fishes: experimental and model analyses. Ecology 87:2366–2377.

Darby, P. C., D. L. DeAngelis, S. S. Romañach, K. Suir, and J. Bridevaux. 2015. Modeling apple snail population dynamics on the Everglades landscape. Landscape Ecology 30:1497–1510.

Davidson, A. T., and N. J. Dorn. 2017. Life history traits determine the differential vulnerability of native and invasive apple snails (Pomacea spp.) to a shared juvenile-stage predator. Aquatic Ecology 51:331–341.

Davidson, A. T., and N. J. Dorn. 2018. System productivity alters predator sorting of a size-structured mixed prey community. Oecologia 186:1101–1111.

Davidson, A. T., E. A. Hamman, M. W. McCoy, and J. R. Vonesh. 2021. Asymmetrical effects of temperature on stage‐structured predator–prey interactions. Functional Ecology 35:1041–1054.

De Roos, A. M., L. Persson, and E. McCauley. 2003. The influence of size‐dependent life‐history traits on the structure and dynamics of populations and communities. Ecology Letters 6:473–487.

Drumheller, D. K., M. I. Cook, and N. J. Dorn. 2022. The role of direct chemical inhibition in the displacement of a native herbivore by an invasive congener. Biological Invasions 24:1739–1753.

Gaiser, E. E., P. V. McCormick, S. E. Hagerthey, and A. D. Gottlieb. 2011. Landscape Patterns of Periphyton in the Florida Everglades. Critical Reviews in Environmental Science and Technology 41:92–120.

Gaiser, E. E., J. C. Trexler, and P. R. Wetzel. 2012. The Florida Everglades. Pages 231–252 Wetland Habitats of North America. University of California Press, Los Angeles California.

Gutierre, Darby, Valentine-Darby, Mellow, Therrien, and Watford. 2019. Contrasting Patterns of Pomacea maculata Establishment and Dispersal in an Everglades Wetland Unit and a Central Florida Lake. Diversity 11:183.

Hanning, G. W. 1979. Aspects of Reproduction in Pomacea paludosa (Mesogastropoda: Pilidae). Florida State University, Tallahassee FL.

Hansen, C., S. Newman, C. J. Saunders, E. K. Tate-Boldt, and N. J. Dorn. 2022. Flow-mediated growth of an aquatic herbivore. Hydrobiologia 849:3161–3173.

van der Heiden, C. A., and N. J. Dorn. 2017. Benefits of adjacent habitat patches to the distribution of a crayfish population in a hydro-dynamic wetland landscape. Aquatic Ecology 51:219–233.

Howell, H. J. 2023, August. The Ecology, Conservation, and Management of the Everglades’ Herpetofaunal Community. Dissertation, University of Miami, Coral Gables, FL.

Jeyasingh, P. D., and L. J. Weider. 2005. Phosphorus availability mediates plasticity in life-history traits and predator-prey interactions in *Daphnia*: Phosphorus alters life-history and predation. Ecology Letters 8:1021–1028.

Kesler, D. H., and W. R. Munns,. 1989. Predation by Belostoma flumineum (Hemiptera): An Important Cause of Mortality in Freshwater Snails. Journal of the North American Benthological Society 8:342–350.

Kingsolver, J. G., and H. A. Woods. 2016. Beyond Thermal Performance Curves: Modeling Time-Dependent Effects of Thermal Stress on Ectotherm Growth Rates. The American Naturalist 187:283–294.

Ma, G., C. Bai, V. H. W. Rudolf, and C. Ma. 2021. Night warming alters mean warming effects on predator–prey interactions by modifying predator demographics and interaction strengths. Functional Ecology 35:2094–2107.

MacArthur, R., and R. Levins. 1964. Competition, habitat selections, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences 51:1207–1210.

McCoy, M. W., B. M. Bolker, K. M. Warkentin, and J. R. Vonesh. 2011. Predicting Predation through Prey Ontogeny Using Size-Dependent Functional Response Models. The American Naturalist 177:17.

McPeek, M. A., and B. L. Peckarsky. 1998. Life histories and the strengths of species interactions: combining mortality growth and fecundity. Ecology 79:867–879.

McVoy, C. W., W. P. Said, J. Obeyseker, J. A. VanArman, and T. W. Dreschel. 2011. Landscapes and Hydrology of the Predrainage Everglades. University Press of Florida.

Meehan, M. L., K. F. Turnbull, B. J. Sinclair, and Z. Lindo. 2022. Predators minimize energy costs, rather than maximize energy gains under warming: Evidence from a microcosm feeding experiment. Functional Ecology 36:2279–2288.

Nunes, L. T., D. R. Barneche, N. S. Lastrucci, A. A. Fraga, J. A. C. C. Nunes, C. E. L. Ferreira, and S. R. Floeter. 2021. Predicting the effects of body size, temperature and diet on animal feeding rates. Functional Ecology 35:2229–2240.

Pepi, A., P. Grof-Tisza, M. Holyoak, and R. Karban. 2018. As temperature increases, predator attack rate is more important to survival than a smaller window of prey vulnerability. Ecology 99:1584–1590.

Pepi, A., T. Hayes, and K. Lyberger. 2023. Thermal asymmetries influence effects of warming on stage and size-dependent predator–prey interactions. Theoretical Ecology 16:105–115.

Pintar, M. R., J. L. Kline, and J. C. Trexler. 2021. The Aquatic Heteroptera (Hemiptera) of Marshes in the Florida Everglades. Florida Entomologist 104.

Rice, J. A., T. J. Miller, K. A. Rose, L. B. Crowder, E. A. Marschall, A. S. Trebitz, and D. L. DeAngelis. 1993. Growth Rate Variation and Larval Survival: Inferences from an Individual-Based Size-Dependent Predation Model. Canadian Journal of Fisheries and Aquatic Sciences 50:133–142.

Richardson, C. J. 2010. The Everglades: North America’s subtropical wetland. Wetlands Ecology and Management 18:517–542.

Rochette, R., and L. M. Dill. 2000. Mortality, behavior and the effects of predators on the intertidal distribution of littorinid gastropods. Journal of Experimental Marine Biology and Ecology 253:165–191.

Ruehl, C. B., and J. C. Trexler. 2013. A suite of prey traits determine predator and nutrient enrichment effects in a tri‐trophic food chain. Ecosphere 4.

Ruetz, C. R., J. C. Trexler, F. Jordan, W. F. Loftus, and S. A. Perry. 2005. Population dynamics of wetland fishes: spatio‐temporal patterns synchronized by hydrological disturbance? Journal of Animal Ecology 74:322–332.

Schmera, D., A. Baur, and B. Baur. 2015. Size-dependent shell growth and survival in natural populations of the rock-dwelling land snail *Chondrina* *clienta*. Canadian Journal of Zoology 93:403–410.

Sklar, F. H., M. J. Chimney, S. Newman, P. McCormick, D. Gawlik, S. Miao, C. McVoy, W. Said, J. Newman, C. Coronado, G. Crozier, M. Korvela, and K. Rutchey. 2005. The ecological–societal underpinnings of Everglades restoration. Frontiers in Ecology and the Environment 3:161–169.

Soomdat, N. N., J. N. Griffin, M. McCoy, M. J. S. Hensel, S. Buhler, Z. Chejanovski, and B. R. Silliman. 2014. Independent and combined effects of multiple predators across ontogeny of a dominant grazer. Oikos 123:1081–1090.

Valentine-Darby, P. L., S. E. Kell, and P. C. Darby. 2015. Predation on Florida apple snails (Pomacea paludosa) by native and non-native aquatic fauna, and predator-prey size relationships. Florida Scientist 78:47–56.

Vance, R. R. 1985. The Stable Coexistence of Two Competitors for One Resource. The American Naturalist 126:72–86.

Werner, E. E., and J. F. Gilliam. 1984. The Ontogenetic Niche and Species Interactions in Size-Structured Populations. Annual Review of Ecology and Systematics 15:393–425.

Zweig, C. L., and W. M. Kitchens. 2008. Effects of landscape gradients on wetland vegetation communities: Information for large-scale restoration. Wetlands 28:1086–1096.

# Figure Captions

Figure 1 A) Map and images of B) LILA impoundment #2 and C) Site 2 in Water Conservation Area 3A. Photo credits to B) Mark I. Cook and C) Nathan T. Barrus.

Figure 2 The zero-population growth isocline illustrating the joint impact of juvenile growth rates and juvenile mortality. Survival was measured for FAS <10 mm SL and juvenile growth rates were quantified with size dependency (Kgrowth).

Figure 3 Isoclines illustrating the bivariate effects of juvenile growth and survival that produce zero net annual population growth for a size-structured model of a freshwater gastropod (*Pomacea paludosa*) under different hydrologic regimes that affect reproduction. The black isocline and gray isoclines represent two hydrologic scenarios producing better (Grey) and worse (Black) reproductive conditions. Mean cumulative juvenile survival (snails < 10mm SL) and growth (kgrowth) quantified in LILA and WCA3A are plotted on each panel with seasonal and combined parameters. The combined parameters (open symbols) were calculated by a weighted average reflecting greater juvenile snail production in the dry season.