# Abstract:

1. 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.
2. 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).
3. 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..

1. 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.
2. 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.
3. 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.
4. Our work illustrates the growth-mediated predator impacts for strongly size-structured populations with stage- or size-specific predators and we hyothesize 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.

# **Key words:**

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

# Introduction

Predicting the strength of size-dependent predator-prey interactions (i.e., prey survival, prey recruitment, prey population growth) is an important goal in community ecology (Cuthbert et al., 2020). Theoretical and lab investigations indicate that prey survival between one predator and prey is a function of variable environmental conditions (Ma et al., 2021; Meehan et al., 2022; Pepi et al., 2018). Temperature (Davidson et al., 2021; Nunes et al., 2021) and resource variation (Brown et al., 2019; Davidson & Dorn, 2018; Jeyasingh & Weider, 2005) influence prey survival. In size- or stage- structured predator-prey interactions, the changing environment (e.g., variable temperature) can affect foraging rates of predators (Davidson et al., 2021; Nunes et al., 2021; Pepi et al., 2018), and can also affect growth rates of prey which alters the time prey remain vulnerable to the predator (Davidson & Dorn, 2018; McCoy et al., 2011; McPeek & Peckarsky, 1998). Therefore, prey survival depends on the direction and degree of asymmetry between the response of predator foraging rates and the response of prey growth to varying environmental conditions (Davidson et al., 2021; Pepi et al., 2018). Several studies have developed related models and tests of the model predictions in controlled experimental settings with single-predator-single prey systems focused prey survival (Davidson et al., 2021; Nunes et al., 2021; Pepi et al., 2018). Few have translated these size- and environmental condition-dependent predation to unmanipulated field settings, and few scale up prey survival from natural predator assemblages (i.e., through consumption) to population-level effects (prey recruitment and population growth; Osenberg & Mittelbach, 1996).

Scaling up predictions of prey survival from changing environmental conditions in the lab to population-level predictions in natural settings is challenging for several reasons. First, environmental conditions vary across space and time, and growth and survival interact to determine population growth, so it will be necessary to measure parameters across relevant spatial and temporal conditions to make meaningful predictions. Second, natural settings have multiple predators that respond differently to variation in environmental conditions, and these responses may include simultaneous changes in per-capita foraging rates and abundance. Thus, to understand the relative contributions of a predator from the impact of natural and varying predator assemblages which are perennially important matters for ecological understanding of recruitment variation and biotic resistance (Dorn & Cook, 2015; Roland & Embree, 1995; Twardochleb et al., 2012), there needs to be a way to assign losses of prey to a specific predator. Finally, population growth is influenced by survival and reproduction, so to understand how growth and survival interact in size- or stage-structured populations, reproduction responses to environmental conditions need to be controlled to isolate the combinatorial impacts of survival and growth.

Seasons represent distinct temporal changes in environmental conditions and resources and predator communities that will change prey survival and recruitment. Lab experiments that control predator abundance across temperature treatments indicate that per capita consumption rates increase with warmer conditions (Davidson et al. 2021). In natural settings during short time frames when the influence of prey growth is minimal (e.g., daily) and assuming predator communities do not vary, we could predict that daily prey survival should decrease across all sizes in warmer- seasons. But predator communities likely vary seasonally (since they are not controlled in natural settings), so variation in predator abundances could overwhelm the temperature dependent processes (i.e., consumption and growth) that governed prey survival in controlled settings. Further, changes in predator composition may additionally alter the shape of the size-dependent predator-prey relationship (Soomdat et al., 2014). However, predicting how survival and growth interact to determine recruitment across seasons is complicated because it depends on the combined variation in seasonally varying predator communities, prey growth rates, and predator consumption rates, plus the reproductive context of the prey. Thus, quantifying the net consumption rate of a community of predators on a focal prey of different sizes *in situ* can be accomplished for different places and times, but a model would be required to project survival and growth to the population level.

Population dynamics for many species with stage 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 consequence of environmental mediation (Craig et al. 2006, Davidson and Dorn 2018, Davidson et al. 2021, Nunes et al.). Historical emphases focused on theoretical treatments of density-dependent growth rates, competition, habitat switching, size-structure, and juvenile bottlenecks (e.g., fish: De Roos et al. 2003; Werner and Gilliam 1984). In real systems both spatial and temporal environmental factors influence juvenile growth through temperature and resource supply (cite). Temperature, disturbances, migrations, and population dynamics can seasonally affect predation rates and predator assemblages in time and space (citations). Taken together, spatial and temporal variation in either factor may provide windows of opportunity for population growth. Studies of species interactions are often conducted in the lab at the level of interaction strength or total prey mortality (see McCoy et al. ) but both ecologists and conservation biologists need to know how the factors relate to population growth (λ) in the field. Furthermore, while size-dependent mortality is well known (cite) and the population-level consequences of the interaction between juvenile growth and mortality are logical, they have only been generally mentioned (De Roos et al. 2006); the theoretical prediction for growth-mediated effects of predation in size-structured populations has not been illustrated for any general or particular case.

Age or size-structured population 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 & 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. The nature of the predation study also allowed us to identify putative predators likely responsible for the seasonal and spatial variation in survival.

# 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 & Kitchens, 2008). Ongoing hydro-restoration of the Everglades ecosystem aims to restore hydro-patterns to improve conditions for wildlife and natural communities (National Academies of Sciences, Engineering and Medicine 2021).

The FAS is the largest native gastropod in freshwaters of North America (Pennak 1953), 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 (Barrus et al., 2023; Hanning, 1979).

At adult sizes (> 22 mm SL)are As small juveniles (< 15 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 have not been investigated (Kesler & 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).

agetheoretical ionsjuvenile 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 for two reproductive conditions which were represented by different “Good Reproduction” or “Poor Reproduction” below;

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.

*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 better for FAS reproduction (Barrus et al., 2023). In the isocline model evaluations we created an additional isocline after adjusting the seasonal depth values to reflect the poorer reproductive condition (faster water level rise in the summer; Darby et al. 2015) to report the effects on the interpretation of isocline and the parameters (see supplement). 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).

*Replication Statement*

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| --- | --- | --- |
| **Scale of inference** | **Scale at which the factor of interest is applied** | **Number of replicates at the appropriate scale** |
| Population | Population | 3-4 |

## Survival Rates

We conducted tethering experiments to measure survival of snails < 10 mm SL in LILA and in WCA3A each season to relate to the zero-population growth isocline. The experiments in the LILA wetlands also allowed us to test for size-dependent survival more broadly.We tested size- and season-dependent survival in two wetlands in LILA by tethering lab-reared juvenile snails from hatchling to adult sizes (3-30 mm SL) each season and measuring 24 h survival. In WCA3A, we only tethered juvenile snails (3-10 mm SL). Each tethering experiment was conducted by attaching snails to PVC poles with monofilament line on transects within the sloughs (Figure 3). The transects attempted to capture potential spatial variation in survival and were arranged “near” or “far” from the ridge edge (~5m and 15-20m, respectively). Across transects, tethered snails were placed apart to increase spatial representation and independence (Figure 3). We included 5-10 replicates of 3-mm size increments (i.e., 3-6mm, 6-9mm, 9-12mm,12-15mm, 15-18mm, 18-21mm, and >21mm SL) on each transect in LILA and 10-15 replicates of each 3-mm size increment (i.e., 3-6mm, 6-9 mm, >9 mm) in WCA3A. Snails were tethered by gluing 20 cm of either 2.4 lb (FAS ≤6mm SL) or 4 lb (FAS ≤6mm SL) monofilament line to the shell apex. Poles were placed ≥2 m apart and additional methodological details and the spatial considerations can be found in the supplement..

Tethering experiments were run for two-three days and snail status was checked daily. We checked snail status by prodding the operculum to incite movement, and we scored the status by five categories: (1) “missing” if the snail was removed from the tether, (2) “crushed/peeled” if the tether had shell fragments remaining on the tether, (3) “empty” if the soma from the shell had been removed, (4) “dead” if snails did not respond when prodded and (5) “alive” if snails responded when prodded. Using the snail status measures, snails that were “alive” were counted as survivals, while snails that were deemed “missing”, “crushed”, “dead”, or “empty” were counted as mortalities. Surviving snails were placed back onto PVC poles and mortalities were replaced with tethered snails of the same size. To generalize measured survival to a larger area than the initial locations, tethers were moved two meters in a randomly chosen cardinal direction to increase independence between nights. The fate of each snail-day combination was considered an independent measure of daily survival. We ran the tethering experiments to achieve ~ 30 observations of mortality per size class. To ensure that snails could not escape tethers, tethered snails within each size class were caged in LILA for 72 hours to exclude predators. No snails escaped or died on tethers during 72 hours in the cages.

We analyzed the tethering dataset from LILA that tethered the full-size range of snails using logistic regression to test for size and season dependence of daily survival. We modeled survival using length (SL mm), transect (“near” or “far”), wetland (“M2” or “M4”), and season (“wet” or “dry”) as covariates. We created a list of logistic models that included all possible combinations of these covariates and their two-way interactions (Table S2). Higher order interactions were excluded. The resulting models were compared using AIC scores, the structure of models with ΔAIC < 4 were examined, and the most supported model (lowest AIC) was selected for interpretation and evaluation (Anderson, 2008). Logistic regression was fitted using the “glm” function in R v4.0.3 (R Core Team, 2019).

## Relative composition of predation from tethering remains and abundances

For the full tethering experiment in LILA, we determine the relative strength of predation by each juvenile predator between seasons by exploring three different aspects of predation. 1) We looked at the differences in the counts of the three artefacts related to predators (crushed/peeled, empty, missing) across seasons. Crayfish use their mandibles to crush or peel the snail shell to remove the soma (Davidson & Dorn, 2018). In contrast, giant water bugs pierce the snail operculum then suck out and remove snail soma without damaging the shell (Kesler & Munns, 1989). We confirmed the artefactual differences by placing tethered snails in aquarium in the presence of predators.

2) We looked at seasonal changes in abundance of the three predators (i.e., giant water bugs, crayfish, and greater sirens) that were most likely responsible for the artefacts. Predator abundance data was taken from small and large animals sampling in the dry and wet season of 2021 using throw traps and trap nets (i.e., fyke and hoop nets) under a protocol similar to Dorn & Cook, (2015) (see Sommer, 2021 and SI). 3) We divided the counts of the artefacts by the seasonal abundance of the different predators to estimate per-capita predation rates.

## Prey Growth

We measured the growth parameter (kgrowth) in LILA and in the reference sites to relate to the zero-population growth isocline. Prior to kgrowth calculation, we measured growth either using *in-situ* 1-m2 mesh cages or with a regression that predicted snail growth using total phosphorus (TP) concentrations in metaphytic mats (R2 =, ). The metaphytic (periphyton) in the Everglades are composites of floating calcareous mats of algae, cyanobacteria, other microbes, and algal detritus; Gaiser et al. ). 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 (methods in Barrus et al., 2023; Drumheller et al., 2022). 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.

The age-structured population model (Darby et al. 2015) used the following equation to model growth of FAS.

where time is the duration of growth, and Sizeinitial is the initial length of the snail, Sizemax is the maximum length that an adult can reach (assumed to be 50 mm SL). Because we knew the Sizeintial, sizemax and time, we could then calculate kgrowth for each snail by rearranging the equation.

*Relating Empirical Measures to Isocline*

We calculated survival and 95% confidence intervals for tethered snails < 10 mm SL at all sites and seasons. We also calculated survival and 95% confidence in *in situ* cages that excluded predators in LILA (Figure S4). We also calculated mean and 95% confidence intervals of kgrowth from the snails grown in cages. 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 (Barrus et al., 2023; Darby et al., 2015) the dry season parameters were weighted proportionately more heavily.

# Results

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 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). The effect of better reproduction (i.e., the gap between good and poor reproductive isoclines) strengthened with higher growth and lower survival (Figure 2).

## Survival and Growth in the Field

Overall, we observed a total of 759 independent observations of survival across two wetlands and two tethering seasons in LILA. After 24 hours, 654 snails survived, 43 snails were missing, 31 snails were empty, 19 snails died on tethers, and 12 snails were crushed/peeled. Daily survival across all sizes was 0.862. The daily cumulative survival for smaller juvenile snail size classes (< 10 mm) was slightly lower (0.821) than survival across all sizes (0.862). Daily survival in predator exclosure cages was almost 100% (cumulative mean = 0.997, se = 0.001, n = 49 days) and did not differ between seasons (overlapping 95% confidence intervals; Figure S4). One of the cages was eliminated from the analysis because it was colonized by a single giant water bug and only empty shells were left by the end of the experiment.

In WCA3A, we observed a total of 276 independent observations of survival across the sites and seasons. After 24 hours, 240 snails survived, 21 snails were left empty, 3 snails had been crushed/peeled, 3 snails died on tethers, and 2 were missing. Only small snails were tethered, and daily survival for these small sizes was higher (0.892) than those in LILA (0.821).

The size-dependency of FAS survival changed with seasons. The top four models (cumulative weight = 0.95) for predicting daily survival probability included SL, Season, and the interaction between Length and Season (Table S2). The top model did not include any additional variables, but the next three best models (ΔAIC ≤ 2.74) included combinations of spatial factors. The parameter values for the spatial factors appeared to provide little additional predictive capacity (parameter *p-values* ≥ 0.276) to survival, so we restricted interpretation to the size and season parameters (Figure 3). During the dry season, FAS daily survival probability increased with size (z = 2.667: *p* = 0.008; Figure 3), but in the wet season, daily survival probability was size independent (z = -0.902: *p* = 0.367; Figure 3). Small juvenile snails (< 10 mm SL) survived better in the wet season than the dry season (Figure 3).

*Predator identity*

Tethers retained crushed/peeled shells when consumed by crayfish and empty shells when consumed by giant water bugs (supplemental). We interpreted lost snails as vertebrate predation. We examined the stomach and fecal contents of greater sirens and mayan cichlids collected from trap-net monitoring to determine which vertebrate predators was likely to have removed snails from the tethers (Table S4; Figure S3). The size range of snails found in mayan cichlids (snails < 3 mm SL) was typically smaller than hatchling FAS (3 mm SL) whereas the size range of snails found in the diets of greater sirens overlapped the sizes of juvenile FAS (3-10 mm SL; Figure S3). And juvenile FAS were found in the diets of greater sirens but not mayan cichlids (Figure S3). No redear sunfish were caught in the trap nets during this study. From the laboratory, dietary, and capture observations, we interpreted a “crushed/peeled” shell as mortality caused by crayfish (Figure 4A), “empty” shell as mortality caused by giant water bugs (Figure 4A), a “missing” shell as caused by greater sirens (Figure 4A), and “dead” as a caused by something abiotic.

The mortality artefacts of juvenile snails from LILA wetlands (i.e., shell conditions) indicated that there were more than 60% more juvenile predation events in the dry season than the wet season (Figure 4A). Giant water bugs, crayfish, and greater sirens were 45, 66, and 77 percent less abundant in the wet season sampling than the dry season, respectively (Figure 4). Except for giant water bugs, per-capita predation (artefacts/abundance) increased in the warmer wet season. Although predator abundance and per-capita predation rates were not explored in WCA3A, the seasonal change in artefact counts in WCA3A were consistent with those found in LILA, except vertebrate predation (missing artefacts) was essentially absent.

## Seasonal Population-Level Effects

There was variation in the measured survival and growth parameters across sites and seasons (Figure 5). Growth was higher in the wet season than the dry season (Figure 5, Figure S2). High juvenile survival from cages without natural predator assemblages in LILA predicted a favorable recruitment regardless of season (Figure 5). With natural predator regimes, the dry season had lower survival and slower growth and when applied to the model would predict poor recruitment regardless of wetland site (Figure 5). In contrast, the wet season had higher survival rates and higher growt resulting in replacement (LILA and WCA3A site 3) or even favorable recruitment (WCA3A site 2; Figure 5). Snails in WCA3A had faster growth than those in LILA (Figure 5). The combined effects, weighted by seasonal differences in egg laying, resulted in annual mortality and growth parameters that predicted declining populations, except for WCA3A site 2 which had confidence intervals that slightly overlapped the zero-growth isocline created with good hydrologic egg-laying conditions (Figure 5).

# 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. Independently measured parameters in field settings confirmed the size-dependent survival of the snail, uncovered a seasonal-dependency relationship, and identified responsible predators. The 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.

*Seasonal FAS 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; Drumheller et al., 2022; Gutierre et al., 2019). 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 & 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 & Dill, 2000; Ruehl & Trexler, 2015).

Our results supported our prediction that 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 & Woods, 2016). Increased FAS growth rates had little opportunity to mediate survival because survival was measured daily, thus survival likely reflects predator related process (per-capita foraging, predator abundances).

We found that predator abundances dominated the processes governing prey survival because prey survival was highest in the wet season, despite apparent increases in per-capita foraging rates of crayfish and salamanders consistent with temperature dependent expectations for the wet season. The declines in abundance of predatory crayfish and bugs are explained by phenology (Pintar et al., 2021; van der Heiden & Dorn, 2017) 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). Crayfish and greater sirens increased per-capita foraging rates in the warmer wet season which is consistent with current experimental evidence testing short-term interaction strength (i.e., prey survival) under warmer temperatures (Davidson et al., 2021; Pepi et al., 2018). And increases in temperature have been shown to increase per-capita foraging in Atlantic Reef fishes (Nunes et al., 2021). Typically studies that explore the effects of environmental conditions on predator-prey interaction have controlled predator abundance experimentally, or statistically (Davidson et al., 2021; Davidson & Dorn, 2018; Jeyasingh & Weider, 2005; Ma et al., 2021; Pepi et al., 2018). 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 (Figure 4). Future work will be necessary to integrate current theoretical predictions under the context of varying predator abundances.

## Long-term Interaction Strength (Population Growth)

Studies examining effects of environmental variation on predator-prey interactions have typically focused on prey-survival (Davidson et al., 2021; Davidson & Dorn, 2018; Jeyasingh & Weider, 2005; Pepi et al., 2018). Tethering snails shortened the length by which we observed survival (i.e., only daily), but coupled with the population model demonstrated that seasonal variation in growth and survival mediated recruitment. 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 (Barrus et al., 2023; Hansen et al., 2022), 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 & 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.

# Conclusions

Studies of functional responses and environmental variation have developed complex predictions for the strength of short-term interaction strengths (Davidson et al., 2021; Nunes et al., 2021; Pepi et al., 2018) and have conducted elegant studies in the lab to test the predictions. Our study was an attempt to empirically bring together multiple sources of variation (i.e., predator assemblages, seasonal growth conditions) in the field to predict the net impact of size-mediated predation on recruitment and population growth using a population model. The effects of warmer seasonal conditions partly increased per capita predation rates (Davidson et al., 2021; Nunes et al., 2021; Pepi et al., 2018), but were counteracted by decreased abundances of predators and faster growth of the prey, effectively reducing size-dependent predation and net predator impacts. Nevertheless, the higher reproduction of prey in the spring when growth was slow weighted the average parameters to predict strong predator limitation over the year. We encourage other researchers working on predator limitation, either of pests or species of conservation/management interest, to consider using size-structured models and field parameter estimates (see also Chockley et al. 2008) to scale-up their predator-prey work and study the net effects of predators on prey population growth.

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# Figures and Tables

**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** A) The hydrologic treatments used in the modeling of the isocline.. B) The zero-population growth isoclines illustrating the joint impact of juvenile growth rates and juvenile mortality. For the FAS juvenile snails are < 10 mm SL and survival is cumulative while juvenile growth rates were quantified with size dependency (Kgrowth). The two isoclines represent two reproductive (birth rate) conditions associated with water depth variation. The FAS breeding season is represented by the blue shaded area.

**FIGURE 3** Field picture showing the transects of tethers in LILA wetlands used to estimate daily survival (photo credit: Brandon Güell). Daily survival probabilities estimated from logistic regression from tethering data. Shaded areas indicate standard error.

**FIGURE 4** A) Counts of artefacts of biotic factors causing mortality of snails (< 10 mm SL) in the two seasons in the LILA wetlands, and B) seasonal abundance of predators of juvenile snails from throw-trap samples (crayfish and giant water bug), and from standard sets of trap nets (greater siren). Sampling effort was equal in each season. C) Per-capita predation rate from the different predators in the two seasons.

**FIGURE 5** 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 were calculated by a weighted average reflecting greater juvenile snail production in the dry season.