**Zero-population growth isocline predicts seasonal variation in environmental conditions and predator abundance limits populations of annual gastropod**

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# Abstract:

1. Predicting the outcome of predator-prey interactions under varying environmental conditions is an important goal in community ecology, but theoretical frameworks have rarely been extended to natural settings.
2. To make predictions about the interactive effects of survival and development on population growth, we develop a zero-population growth isocline from a size-structured population model of a species of conservation concern (Florida Apple Snail; *Pomacea paludosa*) for two hydrologic regimes that affect reproduction. We then measure survival and development in experimental and reference wetlands with natural predator regimes and seasonal environmental variation in order to predict the long-term interaction effects (i.e., population growth) of the predator regimes on the Florida Apple Snail.
3. The isoclines indicated that with increased development populations could withstand lower survival. Increased reproduction associated with better hydrologic conditions shifted the isocline so that populations could withstand slower development and lower survival.
4. Daily survival rates of the Florida Apple Snail were size-dependent in the dry-season and size-independent in the wet-season, with juvenile snails 3-10 mm shell length (SL) being most responsible for the seasonal differences. The difference in seasonal juvenile snail survival was explained by seasonal differences in predator abundance, particularly Giant Water Bugs and Greater Siren.
5. Development were faster in the wet season than the dry season which was consistent with temperature differences between seasons.
6. Consistent between the experimental and reference wetlands, dry season survival and development showed populations are declining, but wet season survival and development showed populations were either at replacement or increasing. Combined survival and development showed populations are declining in the experimental wetlands under both hydrologic scenarios that affect reproduction, but at the reference wetland populations are declining under the poor hydrologic reproductive conditions and at replacement under the good hydrologic reproductive conditions.

# **Key words:**

Predator-prey, size-dependent survival, Temperature, interaction strength, consumer-resource

# Introduction

Predicting the strength of predator-prey interactions is an important goal in community ecology. Theoretical and lab investigations indicate that short-term interaction strength (i.e., prey survival) between 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 short-term interaction strength. In predator-prey interactions, the changing environment (typically through increases in temperature) increases foraging rates of predators which should increase short-term interaction strength (Davidson et al., 2021; Nunes et al., 2021; Pepi et al., 2018). But in size- or stage- structured prey populations, the changing environment can also increases development which should decrease the time spent in vulnerable stages or sizes to gape-limited predators and decrease short-term interaction strength (Davidson & Dorn, 2018; McCoy et al., 2011; McPeek & Peckarsky, 1998). Therefore, the net increase or decrease in short-term interaction strength depends on the direction of the asymmetry in the responses of predator foraging rates or prey development rates to changing environmental conditions (Davidson et al., 2021; Pepi et al., 2018). While previous work developed these theoretical predictions, these predictions were developed in controlled experimental environments, in single-predator-single prey systems, and focused on short-term interaction strength. Few have examined how the changing environment influences long-term predator-prey interaction strength (i.e., prey population limitation) in natural settings under a suite of predators. In natural settings variable environmental conditions include seasonal changes in predator assemblages and temperature-dependent processes (Preston et al., 2019). While the effects of temperature can be simulated for individual predator-prey pairs in the lab, the seasonal effects of predator assemblages cannot be examined without examining net community-level consumption of prey species in the field.

Seasons represent distinct changes in environmental conditions that can create natural experiments for understanding how the net change in long-term interaction strength will strengthen or weaken under a changing environment and natural predation regimes. Predators respond to seasonal changes in environmental conditions by changes in prey consumption rates (Preston et al., 2019), changes in spatial overlap with their prey (Basille et al., 2013), and/or changes in abundance (Preston et al., 2019). Prey respond to seasonal changes in environmental conditions through changes in development, and/or changes in abundance. But in natural settings prey face a suite of predators that may respond differently to the seasonal changes in environmental conditions. In size- or stage-structured populations, this could alter the relative vulnerability of the size or stage. For example, in a study exploring the effects of small and large predators on size-structured prey, the small predator ate prey of a size-range nested within the size-range of the larger predator making the smaller predator functionally redundant (Soomdat et al., 2014). Therefore, if the larger predator emigrated while the smaller predator remained during a season, then the vulnerable size range of the prey would shrink and exacerbate the importance of the prey development on the interaction strength. Thus, for stage-structured populations it is important to understand the size-specific net impact of the entire natural assemblage of predators upon prey across seasonally varying environmental conditions.

Zero-population growth isoclines historically were used to predict how two interacting species can persist with variable parameters and environmental variation (MacArthur & Levins, 1964; Vance, 1985) in theoretical models. Isoclines identify thresholds of interacting parameters that split conditions into two or more qualitative conclusions (MacArthur & Levins, 1964; Vance, 1985). Isoclines developed from stage- or size- structured population models have rarely been done but present a tool that could help understand the interactive effects of survival and development on long-term predator-prey interaction strength. The interactive effects of size- or stage-dependent survival have been demonstrated in simple controlled experimental systems (Davidson & Dorn, 2018; McCoy et al., 2011; Soomdat et al., 2014), but in natural environments the combined effects of survival and development have been assessed by size-structured models created for particular places or times (Chockley et al., 2008; McMurray et al., 2010). Combining stage-structured models and isoclines will help identify interactive effects of survival and development when exploring long-term interaction strength of a single size-structured prey population.

Using an already parameterized stage-structured model for a species of conservation concern, the Florida Apple Snail (*Pomacea paludosa*) we identify theoretical combinations of parameters allowing for population growth and then we quantified new parameters in the field to explore, using isoclines, the net effects of predator-prey interactions under seasonally varying environmental conditions (wet and dry season) and a natural assemblage of predators. The Florida Apple Snail occurs at low densities throughout its natural range (Gutierre et al., 2019) and is a critical resource for the endangered Snail Kite (*Rostrhamus sociabilis*; Cattau et al., 2014), so understanding the conditions that can increase Florida Apple Snails populations is imperative. For two different hydrologic regimes that affect reproduction, we create zero-population growth isoclines by re-coding a published size-structured population model of the Florida Apple Snail (Darby et al., 2015) and exploring the combinations of development and survival that prohibit population growth.  We measured season-dependent survival and development in experimental and natural wetlands to compare to the isoclines. While measuring survival in the field, we identified types/sources of mortality from tethering remains and used independent observations of predator communities and their diets to identify key predators responsible for seasonal survival patterns.  We predict that if predator composition does not change between seasons prey size-dependent survival would decrease across all sizes in the wet season because of increased per-capita predator foraging rates associated with warmer temperatures. But if predator composition does change, then we would expect there to be changes in size-dependent survival between seasons associated with the declines in abundance of the different predators even if per-capita predation rates increase due to warmer temperatures. We predict that prey development should increase in the warmer wet season enabling populations to withstand lower survival. Predicting how prey development and prey survival rates interact to determine the predator assemblage’s effect on population growth and recruitment in the warmer wet season is dependent on the relative strength of the increase in development and the relative strength of the increase or decrease in survival.

# Materials and methods

## Study species and system

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 ceased after compartmentalization and drainage. Compartmentalization and 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 changes the likelihood of seasonal flooding and drying. The likelihood of seasonal flooding and drying differentiates distinct habitat/vegetation patches. The lowest elevation slough habitats dry to sediment surfaces every 3-10 years and are dominated by floating vegetation like 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 Florida Apple Snail is a species of conservation concern that was historically abundant within the Everglades ridge and slough landscape. The federally endangered Florida Snail Kite forages almost exclusively on adult apple snails (Cattau et al., 2010). Because of their reliance on apple snails, Snail Kite demography is linked to adult apple snail densities (Cattau et al., 2014). The Florida Apple Snail is the largest native freshwater snail in North America (Pennak 1953), and it has a lung and a gill characteristic to the Ampullariidae family (Hayes et al., 2009). Florida Apple Snailshatch at 3-4 mm (shell length, SL), mature at lengths of >27.5 mm SL, and senesce after reproduction that limits their life span to ~1.5 years (Hanning, 1979). Throughout their life the Florida Apple Snail grows by up to four orders of magnitude in mass which creates substantial size-structure within the population. The Florida Apple Snailaredioecious and lay light-pink to white conspicuous calcareous egg masses (20-60 eggs/mass) on emergent vegetation 10-20 cm above the water (Hanning, 1979). Reproduction peaks in the spring (dry season; Feb-May), and then declines through the early summer (wet season; June-July; Barrus et al., 2023; Hanning, 1979). Populations in the ridge-slough landscape in the central portion of the ecosystem declined to levels considered too low for substantial Kite nesting since 2007 (Cattau et al., 2016; Gutierre et al., 2019), and for the past 15 years Florida Apple Snail populations have been sparse (densities < 1·m-2­­) (Cattau et al., 2010; Gutierre et al., 2019).

The Florida Apple Snail experiences a wide range of predators besides endangered kites. At adult sizes, The Florida Apple Snail are prey for wildlife like alligators (*Alligator mississippiensis*), limpkins (*Aramus guarauna*), and soft-shell turtles (*Trionyx ferox;* Dalrymple, 1977; Snyder & Snyder, 1971). At sizes < 22 mm SL, laboratory experiments showed that apple snails are prey for crayfish (*Procambarus* spp; (Davidson & Dorn, 2018; Valentine-Darby et al., 2015), Redear Sunfish (*Lepomis microlophus*; Valentine-Darby et al., 2015), Mayan Cichlid (*Mayahero uropthalmus*; Valentine-Darby et al., 2015), African Jewelfish (*Hemicromis bimaculatus*; Valentine-Darby et al., 2015) (*Hemicromis bimaculatus*), Seminole Killifish (*Fundulus seminolis*; Valentine-Darby et al., 2015), Greater Siren (*Siren lacertina*, Valentine-Darby et al., 2015), and Turtles (*Kinosternon bauri* & *Sternotherus odoratus;* Valentine-Darby et al., 2015). Giant water bugs (Belostomatidae) may be predators of juvenile apple snail because they are known gastropod predators but have not been investigated (Kesler & Munns, 1989). Collectively, the effect of juvenile-stage predators on population growth has not been investigated in any natural wetland.

Our work was in the Loxahatchee Impoundment Landscape Assessment (LILA) and two sites in the western portion of water conservation area 3A (WCA3A; Figure 1) in Florida USA. LILA consists of four 8 ha experimental wetlands named M1-M4, that mimic the ridge and slough landscape of the Everglades (Figure 1B). The water levels in LILA are controlled by pumps and culverts that allow for landscape scale hydrologic experiments. Wetlands M1 & M3 were managed for an unconstrained hydrologic treatment while M2 & M4 were managed for a constrained hydrologic treatment. The unconstrained and constrained wetlands hydrologic treatments differ in wet season water depths such that unconstrained wetlands are generally deeper than constrained wetlands although wetlands reach the same low water levels in the dry season. Because shallower water levels are generally favorable for Florida Apple Snail reproduction (Barrus et al., 2023), we refer to the deeper unconstrained hydrologic treatment as “poor reproduction” and the shallower constrained hydrologic as the “good reproduction” treatment. The quality of the hydrologic conditions for reproduction is meant as a relative comparison between the two treatments and does not necessarily represent conditions that are naturally good or poor in the ridge-slough landscape. However, the treatments are realistic conditions experienced within the ridge-slough landscape. In addition to our work in LILA, we did work at two sites (WCA02 & WCA03) near the western boundary of WCA3A near Big Cypress National Park (Figure 1). These sites were chosen because they were near locations of historical Snail Kite nesting (Cattau et al., 2016).

## Zero-Population Growth Isocline

We used a published stage-structured population model (Darby et al., 2015) to create zero-population growth isoclines from combinatorial reassessments of two parameters, juvenile development and cumulative juvenile survival (survival of snails < 10 mm SL, CJS) under different hydrologic conditions important for reproduction (see SI; Figure 2). The isoclines graphically represent population state (i.e., growing, declining, or at replacement) under many juvenile development and survival rates given LILA’s hydrologic treatments (i.e., good and poor reproduction; Figure 2). After measuring CJS and development empirically, we can use the isocline to make predictions about population state each season and at each site.

## Survival Rates

We conducted tethering experiments to 1) test for size-dependent survival, 2) test for differences in survival between seasons, and 3) measure CJS in LILA and in WCA3A each season to relate to the zero-population growth isocline. We tested size- and season-dependent survival in two wetlands in LILA by tethering snails across hatchling to adult sizes (3-30 mm shell length, SL) each season. But to measure CJS in WCA3A, we only tethered juvenile snails (3-10 mm SL). Each tethering experiment was conducted by placing snails into two transects (Figure 3). The transects defined as “near” were within 5 m of the ridge, and the transects defined as “far” were between 15 and 20 m from the ridge. Tethered snails within a transect were placed no closer than two meters 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 (for small sizes) or 4 lb (for large sizes) monofilament line to the apex of the shell then attached to PVC poles pushed into the wetland soils (Figure 3). To obtain snails for tethering, Florida Apple Snail egg masses were collected from canals then hatched, and snails were reared in aquaria or outdoor mesocosms to the desired length.

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 into 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 statuses, 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 another tethered snail of the same size. To generalize measured survival to a larger area than the initial location where snails were set, tethers were moved two meters in a randomly chosen cardinal direction to obtain increased 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 daily observations of mortality per size class. To ensure that snails could not escape tethers, tethered snails within each size class were caged in LILA to exclude predators and observed for 72 hours. No snails escaped or died on tethers in the cages during 72 hours in the wetland.

We analyzed the tethering data 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. 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). To relate empirical survival to the zero-population isocline, we calculated survival and 95% confidence intervals of snails < 10 mm SL (i.e., CJS) at all sites and seasons.

Finally, we measured CJS in *in situ* cages that excluded predators (1-mm mesh). We measured daily survival rates rather than survival probabilities across the duration of the experiment of snails reared in these cages (predator free) to compare to the survival from tethering (natural predator assemblages; see SI).

## Relative composition of predation from tethering remains and abundances

For the full tethering experiment in LILA, we used the conditions of shell remains for deceased snails and measures of predator abundance to identify the most likely predators removing juvenile snails from tethers. 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 artifactual differences by placing tethered snails in aquarium in the presence of predators; tethers retained crushed shells when consumed by crayfish and retained empty shells when consumed by giant water bugs (Barrus, personal observation). The lab observations suggest that it is unlikely that crayfish nor giant water bugs could break the glue and remove snails from tethers. We examined the stomach and fecal contents of Greater Sirens and Mayan Cichlids obtained from the trap net monitoring to determine which vertebrate predators may have removed snails from the tethers (see SI). The size range of snails found in Mayan Cichlids (snails < 3 mm SL) was typically smaller than hatchling apple snails (3 mm SL) whereas the size range of snails found in the diets of Greater Sirens overlapped the sizes of juvenile apple snails (3-10 mm SL; Figure S#). And juvenile apple snails were found in the diets of Greater Sirens but not Mayan Cichlids (Figure S#). From the laboratory and dietary 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.

To determine the relative strength of predation by each juvenile predator between seasons, we explored three different aspects of predation. 1) We looked at the differences in the counts of the three artifacts related to predators (crushed/peeled, empty, missing) across seasons. 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 artifacts. 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 artifacts by the abundance of the different predators to measure per-capita predation rates.

## Development

We measured the development parameter (kgrowth) in LILA and in the reference sites to relate to the zero-population growth isocline. Prior to kgrowth calculation, we measured development using *in situ* cages and a regression that predicted development using total phosphorus levels of periphyton mats (i.e., composite samples of floating calcareous mats of algae, aquatic macrophytes, and other microbes; Barrus et al., 2023). For all *in situ* cages, algae was allowed to accumulate on the surfaces of the cages two weeks prior to the experiment, and two liters of periphyton mat was placed inside the cages as a food source for hatchling snails (Barrus et al., 2023; Drumheller et al., 2022). Periphyton was examined prior to placement to remove other snails and predatory invertebrates. Four juvenile snails were individually marked with differing colors of nail polish and placed in cages to grow for four to five weeks in the wetlands. We placed 8 cages in LILA and 3 cages in WCA3A. For the wet season in the WCA3A, we used total phosphorus of periphyton mat to predict development of the Florida Apple Snail using a regression (Barrus et al., 2023). We were only able to obtain wet season development for the site WCA03 through the regression because low dry season water depths made the site inaccessible for the *in situ* cages.

The population model used the following equation to model development of apple snails.

where time is the duration of development, and Sizeinitial is the initial size of the snail, Sizemax is the maximum size 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.

We calculated mean and 95% confidence intervals of kgrowth to compare our season-dependent development to the zero-population growth isocline.

# Results

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

## Empirical Measures of Survival and Development

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 high (cumulative mean = 0.997, se = 0.001, n = 49 days). Daily survival from predator exclosure cages in the dry season was not different (mean = 0.994, se = 0.002, n = 27 days) than the wet season (mean = 0.999, se = 0.001, n = 22 days; overlapping 95% confidence intervals; Figure S##). In addition, one of the cages was colonized by a single giant water bug and snails were left empty by the end of the experiment.

In WCA3A, we observed a total of 276 independent observations of survival across the two sites and season. 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 snail 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 1). The top model did not include any additional variables, but the next three best models (ΔAICc ≤ 2.744) 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, apple snail daily survival probability increased with size (z = 2.667: *p* = 0.008; Figure 3), but in the wet season, apple snail daily survival probability did not vary with size (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 3B).

Exploring the mortality artifacts of juvenile snails from LILA (i.e., shell conditions) indicated that there were more than 4.0 times as many juvenile predation events in the dry season than the wet season (Figure 4A; Table S3.1). Giant Water Bugs, Crayfish, and Greater Sirens were 3.4 , 4.8, and 24 times less abundant in the wet season than the dry season, respectively (Figure 4; Table S3.1). Except for Giant Water Bugs, per-capita predation increased in the warmer wet season. Although, predator abundance and per-capita predation rates were not explored in the WCAs, the seasonal change in artifact counts in the WCAs were consistent with those found in LILA, except for missing artifacts which were largely absent.

## Seasonal Population-Level Effects

There was variation in the measured survival and development parameters across sites, seasons, and with or without natural predator regimes (Figure 5). Development was generally higher in the warmer wet season than the dry season (Figure 5, Figure S1). High survival without natural predator assemblages predicted a growing population regardless of the season (Figure 5). With natural predator regimes, the dry season had lower survival and lower development which resulted in decreasing populations regardless of site (Figure 5). In contrast, the wet season had higher survival rates and lower development which resulted in replacement (LILA and WCA03) or growing populations (WCA02; Figure 5). WCA3A had larger development than in LILA (Figure 5). The combined effects weighted by seasonal differences in reproduction resulted in declining populations, except for WCA02 which only overlapped the isocline from good hydrologic conditions for reproduction (Figure 5).

# Discussion

We used a stage structured population model to produce zero- population growth isoclines illustrating the interactive effects of development and survival for natural populations of a freshwater gastropod with size-dependent survival. The approach is potentially applicable to any size-structured consumer-resource interaction. For the apple snail it provided vital rate target regions that might produce growing or declining populations. Independently measured parameters in field settings confirmed the size-dependent survival of the snail, uncovered a seasonal-dependency relationship, and identified predators responsible. 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, but that survival and development parameters are particularly poor in the dry season (across both wetlands). The results produce novel hypotheses about environmental variation that might have historically sustained apple snails in the Everglades.

*Seasonal survival and development*

Calculating size-dependent survival for small animals like freshwater invertebrates is challenging. Traditional techniques (e.g. mark-recapture, individual tracking) are problematic because juvenile apple snails are difficult to capture, cannot be individually and reliably tracked, and are typically found at low densities in the Everglades and in LILA (Drumheller et al., 2022; Gutierre et al., 2019). Tethering is an experimental method to measure survival and can inflate mortality estimates of highly mobile prey by limiting antipredator behaviors (Baker & Waltham, 2020). Yet tethering offered the only feasible method for determining juvenile apple snail 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 development would increase in the warmer wet season (Figure 5, Figure S1). Increases in prey development 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 development of ectothermic animals except for extreme thermal maxima (Kingsolver & Woods, 2016).

We predicted that if predator composition was constant between seasons, then changes in prey survival rates would decrease across all sizes because of increased pre-capita foraging rates, but if predator composition changed between season, then prey size-dependent survival would depend on the changes in abundance of the different predators even with increased per-capita predation from warmer temperatures. Our results generally support our second prediction because: 1) we found that predator composition changed in the wet season with ≥ 3.4 fold decline in abundance of juvenile snail predators, 2) juvenile apple snail survival increased in the wet season, and 3) per-capita foraging rates increased in the wet season (except for Giant Water Bugs; Figure 4). The declines in abundance of predatory Crayfish and Giant Water Bugs are explained by phenology (Pintar et al., 2021; van der Heiden & Dorn, 2017) while declines in abundance of Greater Sirens are explained by movement patterns. Greater Sirens emigrated out of the wetlands into the deeper canals to escape the low water depths at the end of the dry season, and Greater Sirens remained in the deeper water during the wet season throughout the duration of our study (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 environmental conditions effects 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 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 is necessary to integrate current theoretical predictions under the context of varying predator abundances.

## Long-term Interaction Strength (Population Growth)

Most studying how environmental variation influences predator-prey interactions have focused on short-term interaction strength (i.e., 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 isocline showed that seasonal variation in development and survival mediated long-term interaction strength (i.e. population growth). Interestingly, the dry season was worse than the wet season for population growth which seems counterintuitive because most reproduction occurs during the dry season. This suggests that improving dry season conditions for survival and growth of juvenile Florida apple snails would have a larger benefit for Florida Apple Snail populations than improving wet season conditions.

In addition to seasonal variation, spatial variation in productivity (i.e., TP) may also mediate predator limitation. Within in the Everglades periphyton total phosphorus ranges between 30-1000 µg·g-1 with typical TP concentration between 110-400 in the ridge-slough landscape (Gaiser et al., 2011).  Development of juvenile apple snails 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 development and juvenile apple snail survival in the presence of gape-limited crayfish (Davidson & Dorn, 2018). Our results build on this by indicating that TP can mediate the net community level effects of predators on population growth in the field. Periphyton total phosphorus levels were highest at WCA02 (Table S#), and WCA02 was the only site to have wet season development and survival that predict an increasing population as well as the only site that had combined parameters that barely overlapped the isocline. From an ecological standpoint the parameters measures 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. Where we found greater growth, we did not necessarily have higher predator activity counterbalancing the benefit.

Within the Everglades the current paradigm for encouraging population growth of the Florida Apple Snail 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 Florida Apple Snail. 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 (Appendix A). For hydrologic variation to turn apple snail population growth positive, either the predation rates would need to be decreased from current levels or development would need to increase in the spring (dry season). We offer hypotheses about the current and historical conditions for population of apple snails 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 partly 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. Also, 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 alter juvenile survival. The relation between the predators and hydro-patterns could use more work, but measurements of juvenile survival and development could also be repeated in time and space to measure variation in vital rates, especially survival, as a function of hydrologic conditions. If net community level predation has not changed from historical levels, then current hydrologic conditions could also be unfavorable for development of the Florida Apple Snail (moving to the right in Figure 5). Indeed, recent work has shown that increasing water flow velocity, which is an historical feature of the Everglades (“river of grass”) increases development of non-native apple snails through changes to microbial food quality (Hansen et al., 2022). Therefore, an Everglades restored with more discharge might possibly improve development of the juvenile Florida apple snails.

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# Figures and Tables

Table 1: AIC model selection table for logistic regression predicting daily survival probability of apple snails (*Pomacea paludosa*) in two LILA wetlands. Daily survival was measured with snails (Length: X-X mm SL) on tethers during the dry and wet seasons on transects located closer and further from habitat edges in sloughs.

|  |  |  |  |
| --- | --- | --- | --- |
| Model description | AICc | ΔAICc | w |
| Length + Season + Length\*Season | 519.870 | 0.000 | 0.398 |
| Length + Season + Wetland + Length\*Season | 520.755 | 0.885 | 0.256 |
| Length + Season + Transect + Length\*Season | 521.482 | 1.612 | 0.178 |
| Length + Season + Wetland + Transect + Length\*Season | 522.387 | 2.517 | 0.113 |
| Length + Season | 527.249 | 7.379 | 0.010 |
| Season + Wetland | 527.993 | 8.123 | 0.007 |
| Transect + Season + Length | 528.705 | 8.835 | 0.005 |
| Length + Wetland + Season + Length\*Wetland | 528.824 | 8.954 | 0.005 |
| Transect + Wetland + Season + Length | 529.119 | 9.248 | 0.004 |
| Season + Wetland + Length + Season\*Wetland | 529.546 | 9.676 | 0.003 |
| Season | 529.576 | 9.706 | 0.003 |
| Wetland | 529.771 | 9.900 | 0.003 |
| Transect + Length + Transect\*Length | 529.844 | 9.973 | 0.003 |
| Length | 529.982 | 10.112 | 0.003 |
| Transect + Season | 530.487 | 10.617 | 0.002 |
| Transect + Wetland + Season | 530.704 | 10.834 | 0.002 |
| Length + Wetland | 531.284 | 11.413 | 0.001 |
| Season + Wetland + Season\*Wetland | 531.438 | 11.567 | 0.001 |
| Transect + Length | 531.829 | 11.959 | 0.001 |
| Transect + Season + Transect\*Season | 531.998 | 12.128 | 0.001 |
| Length + Wetland + Length\*Wetland | 532.028 | 12.158 | 0.001 |
| Transect + Wetland + Length | 533.135 | 13.265 | 0.001 |
| Length + Wetland + Season | 534.472 | 14.601 | 0.000 |
| Transect | 535.316 | 15.446 | 0.000 |
| Transect + Wetland | 535.997 | 16.127 | 0.000 |
| Transect + Wetland + Transect\*Wetland | 537.412 | 17.542 | 0.000 |

A collage of different views of land

Description automatically generated

Figure 1: A) Map and images of B) LILA impoundment #2 and C) WCA02 in Water Conservation Area 3A. Photo credits to B) Mark I. Cook and C) Nathan T. Barrus.

A graph of a graph of a graph of a graph of a graph of a graph of a graph of a graph of a graph of a graph of a graph of a graph of a graph of

Description automatically generated

Figure 2: A) The hydrologic treatments in LILA in 2020, and B) the zero-population growth isoclines developed using the hydrologic treatments for good and poor reproduction.

A diagram of a plant growing

Description automatically generated with medium confidence

Figure 3: Field picture showing the transects of tethers in LILA wetlands used to estimate daily survival (photo credit: Brandon Güell). Daily survival probabilities (A&B) estimated from logistic regression from tethering data. Shaded areas indicate standard error. A) shows daily survival probabilities across all sizes and B) shows the zoomed in daily survival probabilities for snails < 16 mm SL that were the focus of the isocline analysis.

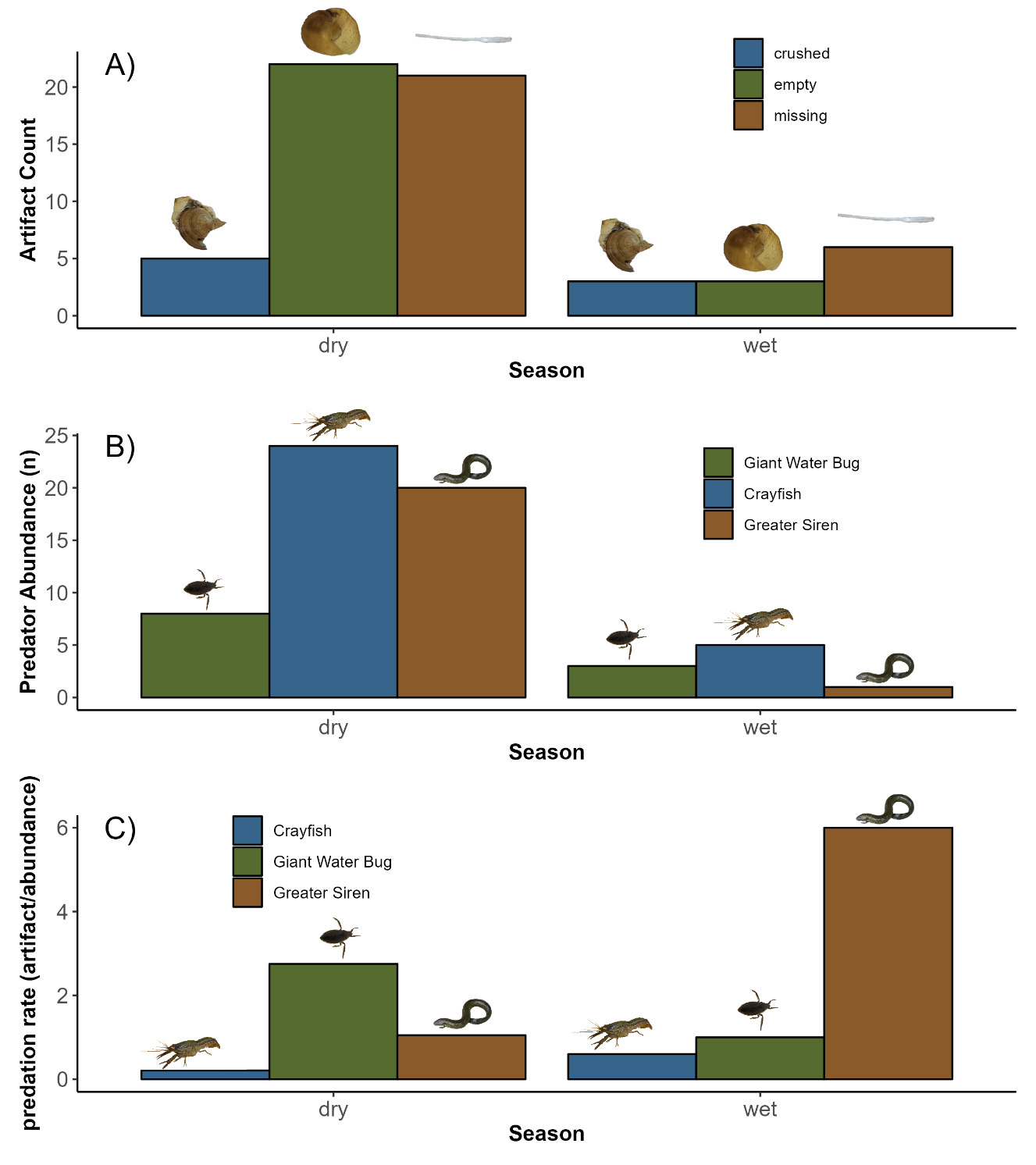


Figure 4: A) Counts of artifacts of biotic factors causing mortality of snails (< 10 mm SL) in the two seasons, and B) seasonal abundance of predators of juvenile snails from throw-trap samples (Crayfish and Giant Water Bug), and from standard sets of trap nets (Greater Siren). Sampling effort was equal in each season. C) Per-capita predation rate from the different predators in the two seasons.

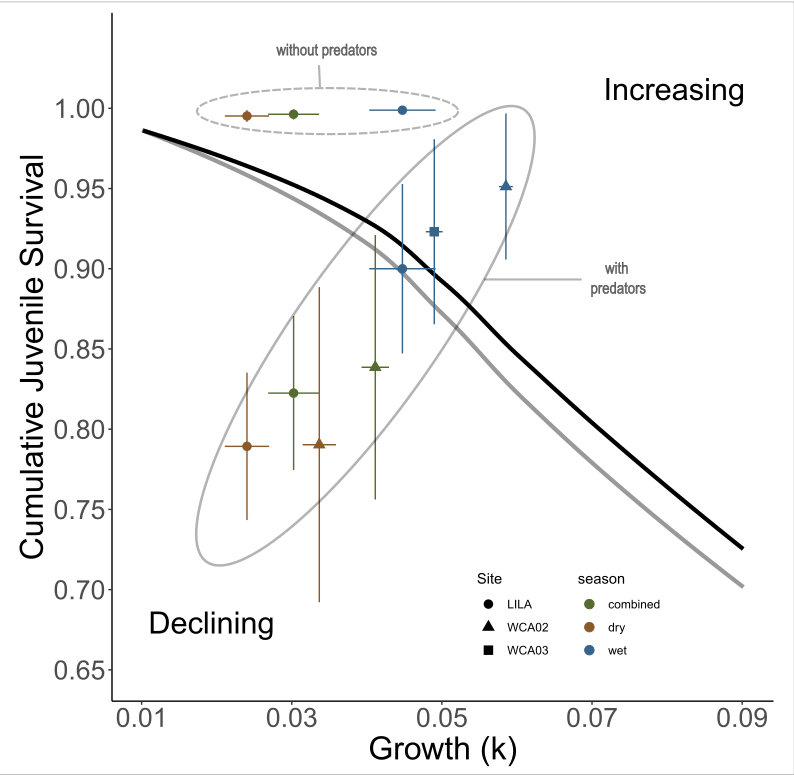


Figure 5: Isoclines illustrating the bivariate effects of juvenile development and survival that produce zero net annual population growth for a size-structured model of a freshwater gastropod (*Pomacea paludosa*) under different hydrologic regimes that affect reproduction. The black isocline and gray isoclines represent two hydrologic scenarios producing better (Grey) and worse (Black) reproductive conditions. Mean cumulative juvenile survival (snails < 10mm SL) and development (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.