**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 developmental rates 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 developmental rates 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 developmental rates populations could withstand lower survival. Increased reproduction associated with better hydrologic conditions shifted the isocline so that populations could withstand slower developmental rates 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. Developmental rates 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 developmental rates showed populations are declining, but wet season survival and developmental rates showed populations were either at replacement or increasing. Combined survival and developmental rates 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 in terms of population limitation is an important goal in community ecology. Theoretical and lab investigations indicate that dynamic interaction strength between predator and prey is a function of variable environmental conditions (Ma et al., 2021; Meehan et al., 2022; Pepi et al., 2018). Both temperature (Davidson et al., 2021; Nunes et al., 2021) and resource variation (Brown et al., 2019; Davidson & Dorn, 2018; Jeyasingh & Weider, 2005) have been shown to influence 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 (i.e., prey survival, 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 developmental rates 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 has helped developed these theoretical predictions, these predictions have been largely 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 growth rate, cohort 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 recourse to field work that includes net community-level consumption of prey species.

Assessing how seasons influence survival and developmental rates could help elucidate how the net change in long-term interaction strength will strengthen or weaken under a changing environment and natural predation regimes. Seasons represent distinct changes in environmental conditions that can create natural experiments for understanding how long-term predator-prey interaction strength responds to the changing environment. 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 densities (Preston et al., 2019). Prey respond to seasonal changes in environmental conditions through changes in developmental rates, and/or changes in density. But in natural settings prey face a suite of predators that all 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 multiple predator 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 developmental time on the interaction strength for the entire suite of predators. 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 have historically been 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 developmental rates 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 developmental rates have been assessed by size-structured models created for particular places or times (Chockley et al., 2008; Chockley & St. Mary, 2003; McMurray et al., 2010). Combining stage-structured models and isoclines will help identify interactive effects of survival and developmental rates 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 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 the 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 developmental rates and survival that prohibit population growth.  We measured season-dependent survival and developmental rates in experimental and reference 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.

# 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 both 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 differentiate 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 wetland 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 tightly 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 both 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 experience a seasonal die off after reproduction that limits their life span to ~1.5 years (Hanning, 1979). Throughout their life span the Florida Apple Snail experiences substantial size-structure within the population because they increase by up to four orders of magnitude in mass. 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; O’Hare, 2010). 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). Lack of pre-drainage records and post-drainage sampling (prior to 1995) has made it impossible to confirm system wide declines of the populations from pre-drainage to post drainage conditions. Populations in the ridge-slough landscape in the central portion of the ecosystem declined to levels considered too low for substantial Kite nesting between 2002-2003 (Cattau et al., 2016; Gutierre et al., 2019), and for the past 20 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, apple snails are prey to a different set of predators with observed predation events in laboratory experiments from crayfish (*Procambarus* spp: Dorn & Hafsadi, 2016; 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) are known gastropod predators and may be important predators of juvenile sizes but have not been investigated (Kesler & Munns, 1989). Collectively, the effect of juvenile-stage predators on population growth may be substantial (Davidson & Dorn, 2018), but it 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 deeper water levels are generally unfavorable for Florida Apple Snail reproduction (Barrus et al., 2023), we refer the deeper unconstrained hydrologic treatment as “poor reproduction” and the shallower constrained hydrologic as the “good reproduction” treatment. 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 there has been long-term monitoring of fish and invertebrate populations, and they were historically near locations of Snail Kite nesting (Cattau et al., 2016). The WCA sites serve as reference sites of sloughs in the ridge slough landscape (Figure 1B).

## Zero-Population Growth Isocline

We used a published stage-structured model called EVERSNAIL (Darby et al., 2015) (hereafter referred to as ‘the population model’) to identify juvenile survival and developmental rate parameters that are expected to produce growing populations of apple snails. The population model was created to project population size across the extent of the Everglades and includes local scale sub-models that parameterize life history (i.e., survival, developmental rates, and reproduction). The model projects age- and size- structure on a daily time step. Survival during hydrological droughts and depth-dependent reproduction tie the model to hydrologic variation (Darby et al., 2015). Depth and temperature data used in the population model from the Everglades was provided from the Everglades Depth Estimation Network (EDEN; Jones, 2015) and South Florida Water Management Districts online database (DBHydro; www.sfwmd.gov/science-data/dbhydro), respectively. The population model was built with the best available understanding of the Florida Apple Snail life history and includes life history responses to hydrologic variation.

We wanted to use the model to examine individual juvenile stage parameters and at a local scale, so we re-coded the population model for research in R version 4.0.3 using the parameter details found in the supplement (Darby et al., 2015). While most of the parameters were left as described by the original model (Table S1.1), two parameters were altered. First, the number of egg masses produced per female was changed by standardizing reproductive effort across the life span of a female snail. A maximum number of egg masses that a female can produce was discussed in a large unpublished review of apple snail ecology (Pomacea Project, 2013); to standardize reproductive output, the population model’s current parameter (Mass Size) was multiplied by the maximum number of egg masses a female can lay and then divided by the life span of the female (500 days in the model). Second, we removed the carrying capacity from the model to examine what parameter values allow the population to increase.

Four parameters were used to model developmental rates and juvenile survival. Developmental rates were determined by the parameter kgrowth and assumes size- dependence. The initial parameter estimate for kgrowth in the population model was 0.05. There were three parameters (Surv1, Surv2 and Surv3) that determined juvenile survival during wet condition and were based on size classes (Surv1 = 3-6 mm, Surv2= 6-10 mm, Surv3 = 10-16 mm SL). A fourth rate was used for large juvenile and adult snails (Surv4 > 16 mm SL). Under the parameters in the population model, survival through the juvenile stage (3-16 mm SL) was constantly high (98.7% · day-1). Survival slightly increased after snails reached 16 mm SL (99.0% · day-1) and remained constant until the snails reached 500 days when survival declined to 0 reflecting adult senescence (Hanning, 1979). Alternate survival parameters were included in the population model for conditions of hydrological drought (dry sediment surfaces in the dry season), but the drought parameters were not important for our simulations.

To determine growth and survival parameters that controlled population growth, we calculated population growth through combinatorial re-assessments with different values under two different hydrologic regimes. We chose the wet condition parameters for survival to make the simulations most representative of the sloughs in the ridge-slough landscape. Before we started simulations aimed at varying developmental rate and survival parameters under different hydrologic regimes, we obtained an initial population size with a stable size structure. We ran the model using the model’s original developmental rate and survival parameters for ten years of repeated depth and temperature data (January 1st to December 31st, 2020). The hydrologic data was taken from DBHYDRO’s depth transponder in LILA’s wetland M2, and the air temperature data was taken from the transponder nearest to LILA in West Palm Beach, FL (transponder coordinates: 26.6548⁰N, 80.0669⁰W). We tested differences between three starting hatchling numbers (100, 1000, and 10000 hatchlings), but starting numbers did not influence population growth.

Following this 10-year simulation to establish a stable size structure, we introduced two different hydrologic regimes repeated for 5 years that varied in depth-dependent egg-laying conditions. First, we used the poor reproduction hydrologic conditions from LILA that was deeper in the wet season of 2020 (Figure 2A). Next, (2) we used the good reproduction conditions (Figure 2A). The model runs with poor and good reproduction hydrographs were both conducted using natural temperature regimes taken from West Palm Beach, FL (Appendix 1).

Under each hydrological regime, simulations were conducted under different combinations of the parameters kgrowth, Surv1, and Surv2. kgrowth values were allowed to vary from 0.01 to 0.09 using increments of 0.005 and the two small juvenile survival parameters for wet conditions were decreased by 5%, 10% 15%, 20%, 30% and 40% of the starting values (0.987 day-1). Simulations were run under all combinations of the variations in the three parameters (nsimulations = 833 per hydrologic regime). The population size on every simulated February 1st was taken to calculate an annual population growth rate (e.g., λi = Ni/Ni+1; where i = year). February 1st ­was used because it corresponded to the day when the population model initiates the reproductive season. The geometric mean of the annual population growth rates over 5 years was taken to obtain a λavg. The intrinsic rate of increase (r) was then calculated by taking the natural logarithm of λavg. When r = 0 a population is at replacement, when r < 0 a population is declining, and when r > 0 a population is increasing.

The results of the simulations were used to identify combinations of development rates and survival of juveniles that determined thresholds (r = 0) for population growth given the two hydrologic regimes. Although the simulations were conducted with individualized parameters for the two size classes, we reduced dimensionality to aid in interpretation by multiplying the two juvenile survival probabilities which we named cumulative juvenile survival (i.e., survival < 10 mm SL = CJS; Figure 1A). At each level of kgrowth, the intrinsic rate of increase (r) was regressed (Ordinary Least Squared-OLS) as a function of CJS, then the regression equation was used to solve for the CJS for which r = 0. The combinations of individual growth (kgrowth) and juvenile survival (CJS) were plotted as zero population-growth isoclines (Figure 2B).

## Survival Rates

Calculating size-dependent survival for small animals like freshwater invertebrates is challenging. Traditional techniques (e.g. mark-recapture, individual tracking) are especially 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). Size-dependent survival for juvenile snails was measured by tethering snails of varying sizes in the wetland overnight. Tethering is an experimental method to measure survival and can to inflate true mortality estimates of highly mobile prey by limiting antipredator behaviors (Baker & Waltham, 2020). Yet tethering offers the only feasible method for determining juvenile apple snail survival. In addition, tethering less mobile prey (e.g. snails) that have limited antipredator escape behaviors is expected to give informative information on survival and predation. Futher, tethering across field gradients is expected to reliably estimate encounter rates with relatively more mobile predators (Rochette & Dill, 2000; Ruehl & Trexler, 2015).

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 the reference sites each season to relate to the zero-population growth isocline. We tested for 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 our reference sites (WCA02 & WCA03) we only tethered juvenile snails (3-10 mm SL). Each tethering experiment was conducted by placing snail 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). Care was taken to include 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 the reference sites. 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 ran the tethering experiment in LILA for three days, but we only ran the tethering experiment for two days in the reference sites. We checked snail status by lightly 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” 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 surviving snails while snail 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 class. 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. Although we only ran the tethering experiment for two days in the reference sites, we increased replication so that we had similar numbers of daily observations (~30) per size increment. 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 (the length of the longest tethering experiment). No snails escaped or died on tethers in the cages during 72 hours in the wetland.

We analyzed the LILA tethering experiment that tethered the full-size range of snails using logistic regression to test for size and season dependence of daily juvenile 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 (3 way or greater) were excluded. The resulting models were compared using AICc scores, the structure of all models with ΔAICc < 4 were examined, and the most supported model (lowest AICc) 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 simply calculated survival and 95% confidence intervals of snails < 10 mm SL (i.e., CJS) in LILA and in the reference sites.

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 Appendix 3 for details).

## 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 to identify the most likely predators removing snails from tethers. Previous studies have identified that crayfish use their mandibles to crush or peel the snail shell to remove the soma (Davidson & Dorn, 2018; Dorn & Hafsadi, 2016). 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). Thus, 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 a vertebrate (e.g., Fish or Salamander or Limpkin; Figure 4A), and “dead” as a caused by something abiotic. It may have been possible for crayfish or giant water bugs to break the glue and remove snails from tethers, but the lab observations suggested this is unlikely. Other snail predators that penetrate the operculum, like leeches, are exceedingly rare at LILA based on sampling data. These artifact data were analyzed using combinations of contingency and simple χ2 tests to test for difference in proportion between seasons (see Appendix 3 for details).

In LILA, a direct measure of composition of predator communities 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). In both seasons, 1-m2 throw traps were deployed at 14 randomly selected locations in the slough habitats. Each season sampling occurred when slough habitats were flooded but ridge habitats were shallow (< 10 cm) so for each season large predatory fishes were equally concentrated in the sloughs. Throw traps were cleared under the protocol described by Dorn et al., (2005). Captured animals were euthanized in MS-222 (Tricaine-S, Western Chemical Inc.), fixed (after 30-120 min) in 10% buffered formalin, then cleaned and stored in a 70% ethanol solution. In the lab using calipers, invertebrate predators (i.e., crayfish and giant water bugs) were selected and measured to carapace length and total length, respectively. Juvenile crayfish with carapace lengths < 14 mm were excluded from analyses because they are not predators of juvenile apple snails (Davidson & Dorn, 2017). Trap nets (i.e., fyke and hoop nets) were placed in the deep sloughs of wetlands for three consecutive nights each season. Trapping in each wetland consisted of four fyke nets (0.7 x 1 m opening, 3 mm mesh, 2 throats) and five mini hoop nets (0.6 m diam. opening, 1 cm mesh, 2 throats; Sommer, 2021) and captures across all gear types were combined to calculate a nightly catch index. Molluscivorous fishes larger than 5 cm were identified, measured (standard length) and released while Greater Sirens were counted and released. The data were analyzed using combinations of contingency and simple χ2 tests to test for differences in proportion of predators across seasons (see Appendix 3 for details).

## Developmental Rates

We measured the developmental rate parameter (kgrowth) in LILA and in the reference sites to relate to the zero-population growth isocline. Prior to kgrowth calculation, we measured developmental rates using *in situ* cages and a regression that predicted developmental rates using total phosphorus levels of composite samples of floating calcareous mats of algae, aquatic macrophytes, and other microbes (locally called periphyton mats; Barrus et al., 2023). For all *in situ* growth 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 hatching snails (Barrus et al., 2023; Drumheller et al., 2022; Shuford et al., 2005). 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. In LILA as part of a larger effort to test if the non-native apple snail *Pomaccea maculata* inhibited growth of rates of juvenile Florida Apple Snails, 26 cages in the dry season and 14 cages in the wet season were placed in the sloughs of wetlands M2 & M4 for four weeks (Drumheller et al., 2022). Treatments testing for the effect of low exposure to adult non-native apple snails did not influence developmental rates in this study (see Appendix 2 for details). Despite of this, we only measured kgrowth in control treatments (i.e., no non-native apple snail exposure). Growth rates were only measured in control treatments (i.e., no non-native apple snail exposure). As part of this experiment, we deployed a HOBO temperature logger to measure water temperatures throughout the experiment. At the reference sites in the dry season, we only placed 3 cages in the wetlands because this effort did not include treatments for inhibitory effects of non-native apples snails. For the wet season, we obtained periphyton total phosphorus levels to obtain developmental rates of the Florida Apple Snail (Barrus et al., 2023). We were only able to obtain wet season growth rates for the site WCA03 through the regression because low dry season water depths made the site inaccessible for the *in situ* cage experiment.

The population model used the following equation to model develomenta rates 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 (i.e., duration of experiment in days), we could then calculate kgrowth for each snail by rearranging the equation.

To test for differences in seasonal developmental rates, we compared dry and wet season kgrowth using a two-sample t-test. Using kgrowth allows us to compare our season-dependent developmental rates to the zero-population growth isocline.

# Results

Zero-population growth isoclines created with the stage-structured population model formulations produced descending isoclines consistent with an interaction between developmental rates 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 zero-growth conditions slightly more resilient to lower survival (e.g., withstanding 3.1% lower survival at developmental rates of kgrowth = 0.07) and/or lower juvenile growth (e.g., withstanding by 7.7% lower developmental rates at CJS of 0.80). The interaction (i.e., the gap between good and poor reproductive isoclines) appears to strengthen at higher growth rates and lower survival (Figure 2).

## Empirical Measures of Survival and Individual Growth

Overall, there were 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 left an empty shell, 19 snails died on tethers, and 12 snails had been crushed/peeled and removed. 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 exclosure cages without predators was high (cumulative mean = 0.997, se = 0.001, n = 49 days), and daily survival was not size-dependent (overlapping 95% confidence intervals across size classes). In addition, daily survival from exclosure cages in the dry season was slightly lower (mean = 0.994, se = 0.002, n = 27 days) than the wet season (mean = 0.999, se = 0.001, n = 22 days), but the differences were not significant (overlapping 95% confidence intervals; Figure S3.1). In addition, one of the growth cages was colonize by a single giant water bug and all snails had been eaten by the end of the experiment.

In our reference sites (WCA02 & WCA03), we had a total of 276 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).

Snail survival was both size and season dependent and the size-dependency 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 rates. 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 significantly 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).

The mortality artifacts from LILA (i.e., shell conditions) indicated that primary types of mortality for apple snails < 10 mm SL did not differ across seasons (Figure 4; Table S3.1). There were more than 4.0 times as many predation events in the dry season than the wet season (Figure 4A; Table S3.1), but differences between seasons was associated with reduced abundances of invertebrates and Greater Sirens (Figure 4; Table S3.1). These patterns appear to be consistent with our reference sites although there was considerably fewer vertebrate (i.e., missing) predation events than in LILA.

Size-specific growth rates in the wet season (month) were greater than those in the dry season (month, Figure 5). Water temperatures were also warmer in the wet season than in the dry season (Figure 5). Seasonal growth measurements in the WCA wetlands showed qualitatively similar patterns with higher growth in the wet season and lower growth rates in the dry season.

## Seasonal Population-Level Effects

There was considerable variation in the measured survival and growth parameters across sites, seasons, and with or without natural predator regimes (Figure 6). High survival without natural predator assemblages predicted a growing population regardless of the season (Figure 6). With natural predator regimes, the dry season had lower survival and lower growth rates which resulted in decreasing populations regardless of site (Figure 6). In contrast, the wet season had higher survival rates and lower growth rates which resulted in replacement (LILA and WCA03) or growing populations (WCA02; Figure 6). The WCA had larger growth rates than those in LILA (Figure 6). Although, wet season survival and growth rates were higher than in the dry season, the combined effects weighted by seasonal differences in reproduction resulted in declining populations, except for WCA02 which overlapped the isocline from good hydrologic conditions for reproduction (Figure 6).

# Discussion

We used a stage structured population model to produce zero- population growth isoclines illustrating the interactive effects of developmental rates and survival for natural populations of a freshwater gastropod with size-dependent mortality. 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 mortality of the snail, uncovered a seasonal-dependency relationship, and identified predators responsible. The seasonal measurements then allowed us to compare existing rates to the theoretical isocline and conclude that populations are static or declining when parameters are averaged, but that mortality and growth 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.

The juvenile survival results in LILA were relatively consistent with season-dependent survival in the Everglades (WCA) wetlands. The higher wet season survival of snails < 10 mm SL (> 90%; Figure 1) across sites was particularly interesting because it suggests that the wet season was generally more favorable for recruitment. The difference in survival of apple snails < 10 mm SL between seasons was at least partly explained by variation in predator abundances. The artifacts of the mortality events e was able to directly attribute two invertebrate predator sources of mortality to tethering remains (i.e., crayfish to crushed shells, *­*giant water bugs to emptied shells; Figure 2). Crushed shells varied little between seasons compared to emptied shells which suggests that giant water bugs are more responsible for seasonal changes in survival of snails < 10 mm SL than crayfish (Figure 2). The importance of giant water bugs as a predator of the Florida Apple Snail was further supported by the observations that no snails survived when a single *B. lutarium* colonized one of the exclosure cages in LILA. In contrast to the crushed and emptied categories, we relied on indirect assessments to identify predators causing removals. To help explain the results of missing snails we compared diets of fish (i.e., Mayan Cichlids) to diets of Greater Sirens, Greater Sirens ate more gastropods (including direct observations of apple snails in samples) than Mayan Cichlids (no direct observations of apple snails in samples) and ate more gastropods within sizes of small juvenile apple snails (i.e., 3-12 mm SL gastropods in samples) than Mayan Cichlids (i.e., <2mm-5mm SL gastropods: see Appendix 3; Figure S3.2). More gastropods and broader size structure of gastropods in diets of Greater Sirens, suggest that they are energetically stronger predators of the Florida Apple Snail than Mayan Cichlids. Because of the differences in predation strength, the decline in missing snails across season appears to be caused by changes in Greater Sirens abundances (Figure 2). Although seasonal survival has been observed in a wide variety of floral and faunal taxa (Falvo et al., 2019; Jacquemyn et al., 2010; Reusch et al., 2019), the majority of seasonal studies explain differing survival rates through abiotic stress (Hoxmeier & Dieterman, 2013; Reusch et al., 2019; Schroder, 2012) (i.e., winter, flooding) and our results indicate that variation in predator abundance is another mechanism producing seasonal survival which is often ignored (Bauwens & Claus, 2019; Carlson et al., 2008).

## Population Growth

The stark contrast between population growth status in and out of the presence of natural predator assemblages indicates that populations of the Florida Apple Snail are predator limited, but seasonal variation in developmental rates and survival mediated long-term interaction strength. As predicted by current theory of environmental influences of short term interaction strength (Meehan et al., 2022; Pepi et al., 2018), developmental rates of the Florida Apple Snail increased in the warmer wet season. However, current theory on environmental influence short-term interaction strength (prey survival) has focused on changes in individual predator consumption due to changes in metabolism (Meehan et al., 2022; Pepi et al., 2018). We cannot tease metabolic changes from the decreases in seasonal abundance of the predators. Instead, the strength of our study is that we measure net community wide consumption of the Florida Apple Snail, which seems to indicate that consumption at the population and community scale is largely influenced by abundance. Our results indicated that with the increases in development and increases in survival in the wet season, populations state could shift from decreasing to replacement/increasing in the wet season. Therefore, to make accurate predictions about the long-term impacts of natural communities or populations of predators, changes in predator abundance must be considered. Indeed, in a tightly controlled experiment on the effects of increases in temperature on lady beetle and aphid interactions, lady beetle population growth was similar to control levels after constant increases of 3ºC, but decreased close to replacement (λ = 1.08) at constant temperature increases of 5ºC (Ma et al., 2021). Thus, lady beetle population abundance would increase at smaller temperature increases and population level consumption would be compounded by increases in metabolic related consumption at the individual level (Ma et al., 2021). But at higher temperature increases population abundance would remain constant and population level consumption would be attributed only to increases in metabolic related consumption at the individual level (Ma et al., 2021). Further work on assigning population and community level consumption in natural settings to changes in metabolism and changes in abundance would augment theoretical predictions of how the strength of predator-prey interactions change in response to variation in environmental 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 can range anywhere between 30-1000 µg·g-1 with typical TP concentration between 110-400 in the ridge-slough landscape (Gaiser et al., 2011), and growth rates of juvenile apple snails depend on TP in the periphyton (Hansen et al. 2022, Barrus et al 2023). Previous experimental manipulations of phosphorus showed that higher TP increased growth and juvenile apple snail survival in the presence of size-limited crayfish predators (Davidson & Dorn, 2018). Our results build on this this by indicating that TP can mediate the net communitylevel effects of predators on population growth predicted in the field. Periphyton total phosphorus conditions during the wet season in in our study sites averaged 104.6 µg·g-1, 121.9 µg·g-1, and 410.8 µg·g-1 in LILA, WCA03, and WCA02, respectively. As predicted by these total phosphorus levels, wet season developmental rates were lowest in LILA, intermediate in WCA03 and highest in WCA02. Differences in growth were similarly lower in LILA than in WCA02 in the dry season (Figure 4C). The only parameters predicting an increasing snail population were from the wet season in WCA02 (Figure 4C), and WCA02 was the only location where the combined seasonal developmental and survival rates predicted a population at replacement (i.e., the isocline depicting good hydrologic conditions for reproduction just barely overlapped the parameter confidence limits; Figure 4C). From an ecological standpoint the parameters measures in the field across the sites indicated that growth and mortality 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. If growth rates of the Florida Apple Snail continue to increase even in habitats in the Everglades within upper ranges of periphyton total phosphorus, then populations could grow withstand low survival. These results in the Everglades also are consistent with laboratory work from *Daphnia* populations where fewer *Daphnia* were eaten by *Chaoborus* under higher phosphorus conditions. But these results may be the first that attribute this to population level consequence to the prey. Interestingly, generally fewer studies have looked at the effect of increased productivity on the outcome of predator-prey interactions compared to temperature.

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 the population growth did not shift from replacement (λ=1) to increasing (λ >1; 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 growth rates would need to increase in the spring (dry season). We offer three 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 vertebrates (e.g., Greater Siren) and/or macroinvertebrates (crayfish and giant water bugs) in LILA and WCA 3A seem to be more responsible for patterns of mortality 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) would fundamentally alter juvenile mortality rates. The relation between the predators and hydro-patterns could use more work, but measurements of juvenile mortality and growth 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 growth rates of the Florida Apple Snail (moving to the right in Fig. 6). Indeed, recent work has shown that increasing water flow velocity, which is an historical feature of the Everglades (“river of grass”) increases developmental rates 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 developmental rates 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 field with a few people in it

Description automatically generated with medium confidence

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

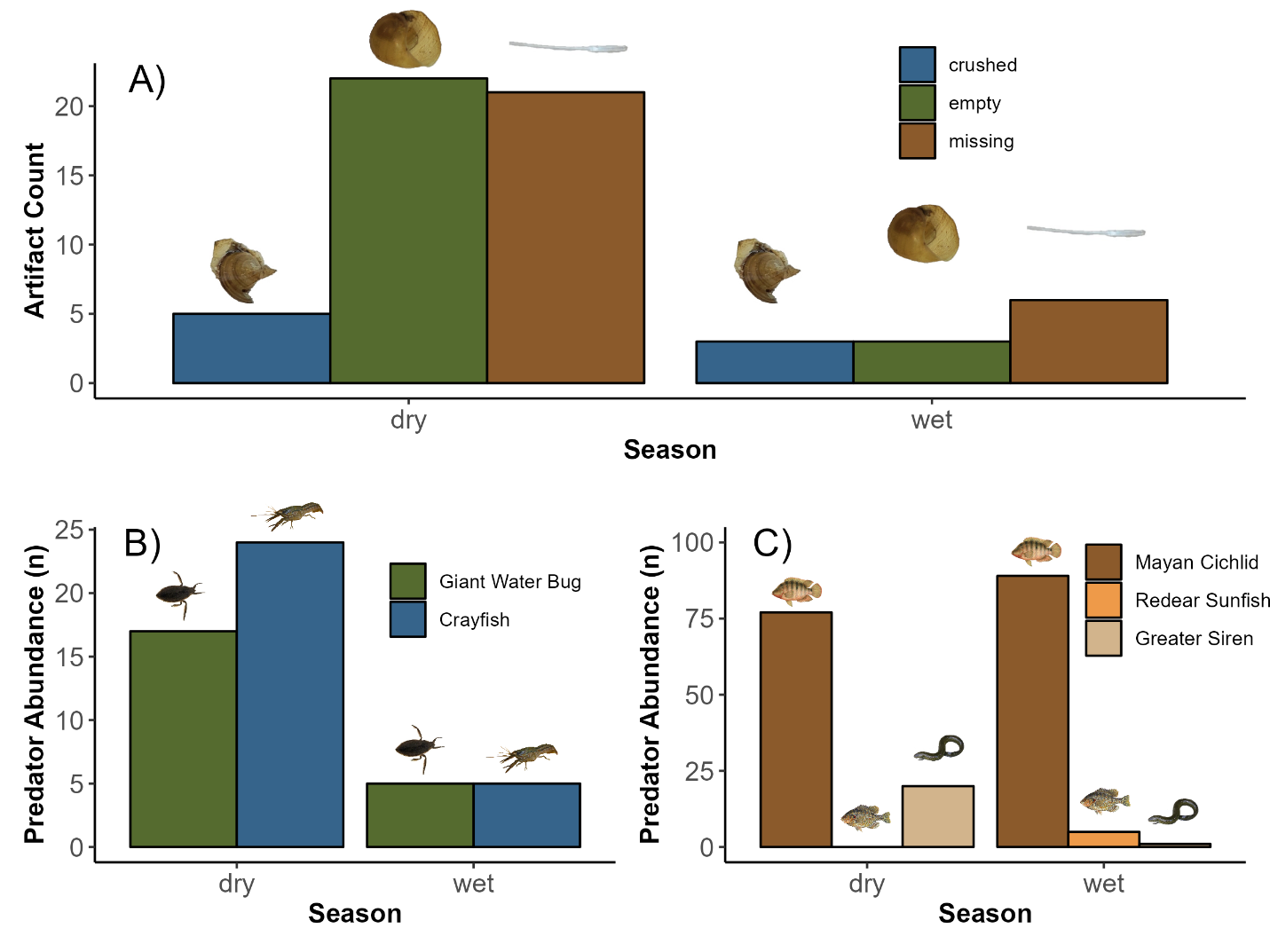


Figure 4: A) Counts of artifacts of biotic factors causing mortality of snails (< 10 mm SL) in the two seasons, and seasonal abundances of B) invertebrate predators of snails from throw-trap samples, and C) vertebrate predators of snails from standard sets of trap nets. Sampling effort was equal in each season.

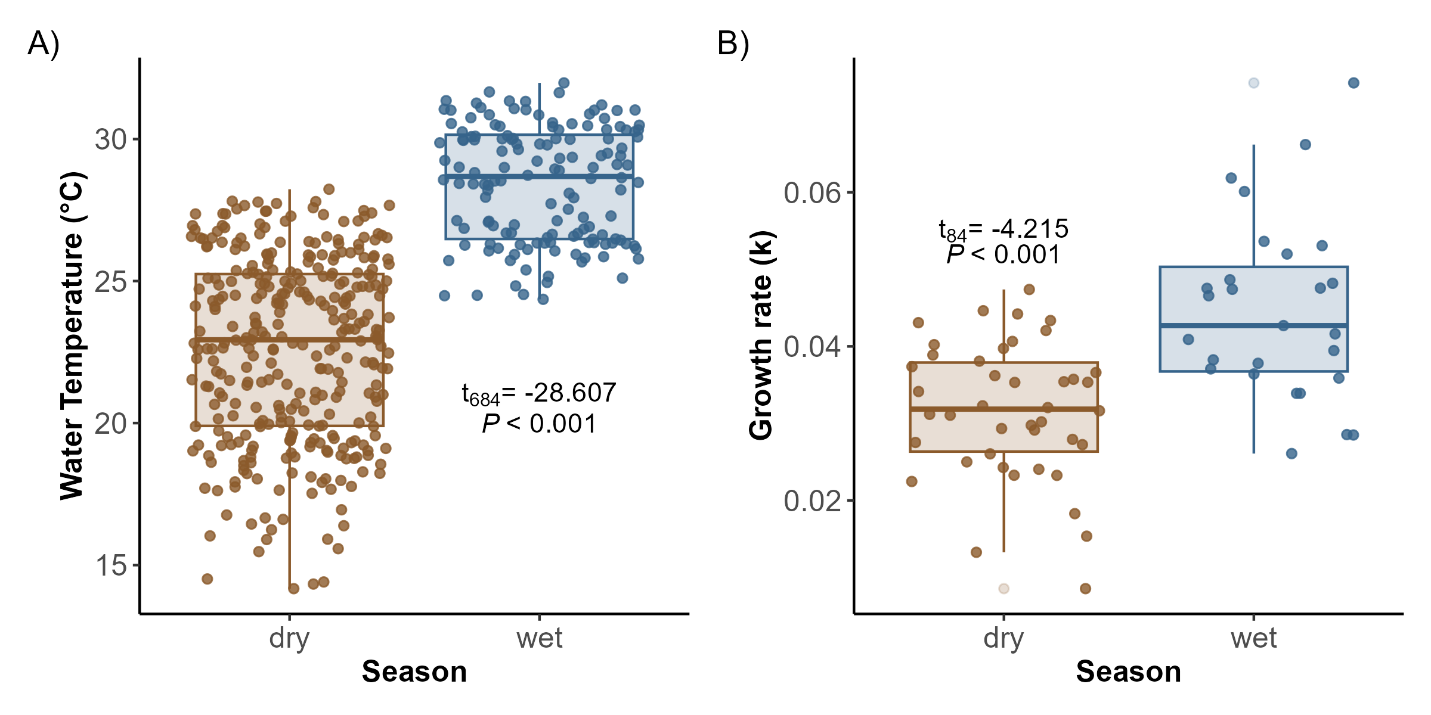


Figure 5: Seasonal A) daily water temperatures and B) Florida apple snail juvenile growth in the LILA wetlands of the Everglades. Each point in panel B represents an individual snail.

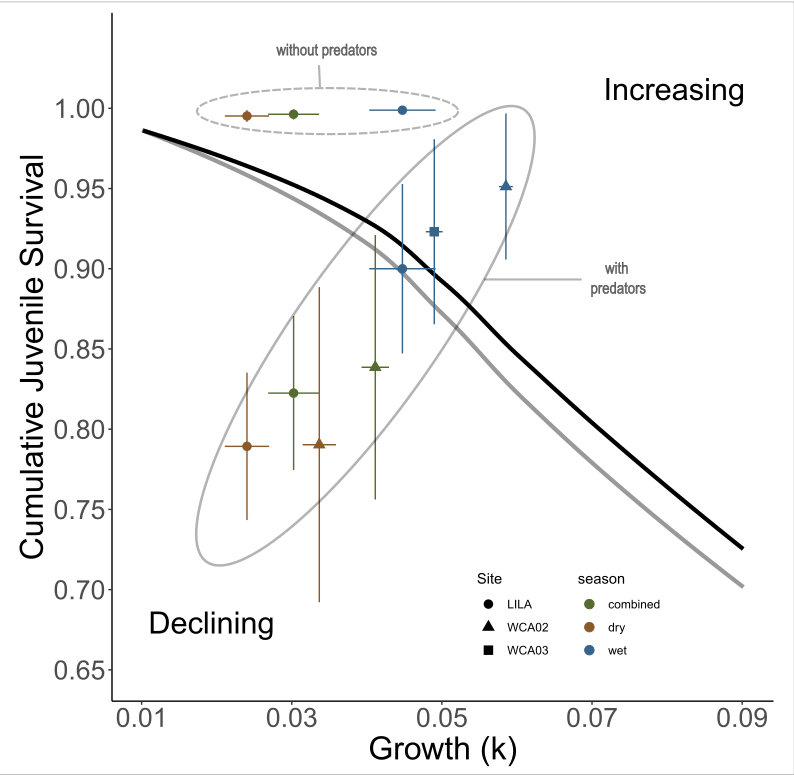


Figure 6: Isoclines illustrating the bivariate effects of juvenile snail individual growth and survival that produce zero net annual population growth for a size-structured model of a freshwater gastropod (*Pomacea paludosa*) under different hydrologic regimes in a wetland. The black isocline and gray isoclines represent two hydrologic scenarios producing better and worse reproductive conditions in the model. Mean cumulative juvenile survival (snails < 10mm SL) and somatic growth rates (k) quantified from wetlands (Loxahatchee Impoundment Landscape Assessment wetlands plus Water Conservation Area 3A sites 2 and 3) are plotted on each panel with seasonal and combined parameters. Site 3 parameters could not be measured in the dry season because the site was too dry in April. The combined parameters were calculated by a weighted average reflecting greater juvenile snail production in the dry season.