Introduction

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

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

Seasons represent distinct temporal changes in environmental conditions and resources and predator communities that will change interaction strengths from a prey population perspective. Quantifying the net consumption rate of a community of predators on a focal prey of different sizes *in situ* can be accomplished for different places and times, but a model would be required to make combinatorial projections. Lab experiments that control predator abundance across temperature treatments indicate that per capita consumption rates increase with warmer conditions. In natural settings we might therefore predict that daily prey survival should decrease across all sizes in warmer- seasons except that prey growth also increases with temperature (see Davidson et al. 2021). In addition, if predator communities vary seasonally (since they are not controlled in natural settings), variation in predator abundances could overwhelm the temperature dependent processes (i.e., consumption and growth) that governed prey survival in controlled settings. Further, changes in predator composition may additionally alter the shape of the size-dependent predator-prey relationship (Soomdat et al., 2014). Predicting the impacts of how survival and growth interact on recruitment or population growth across seasons is complicated because it depends on the combined variation in seasonally varying predator communities, prey growth rates, and predator consumption rates, plus the reproductive context of the prey. To combine the sources of variation will require a size-structured model applied to a natural setting.

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

In this paper, we used a previously parameterized stage-structured model for a freshwater gastropod of conservation concern, the Florida Apple Snail (*Pomacea paludosa;* FAS) and identified theoretical combinations of juvenile-stage parameters predicting population stasis, growth, or decline. The isocline produced the expected relationship between juvenile growth and survival; faster juvenile growth begets greater resistance to mortality. We then quantified size- and season-dependent survival and growth in the field to 1) test predictions of size-dependent survival and 2) quantify the net effects that growth and survival have on population growth during the annual reproduction/recruitment period (spring vs early summer). The nature of the predation study also allowed us to identify predators likely responsible for the limitation and the recruitment periods/seasons of lowest survival.

# Materials and methods

## System and study species

The Florida Everglades is a shallow, expansive (~915,000 ha), subtropical, oligotrophic wetland covering much of southern Florida (Richardson, 2010; Figure 1). Rainfall is seasonal with approximately 80% of rain falling from June-November (Gaiser et al., 2012) which produces intra-annual water depth fluctuations of ≥ 60 cm. The degree of water level recession and depth in the dry season is a function of rainfall and water management decisions. Historically, water flowed in a single shallow sheet from Lake Okeechobee at slow velocity across the spatial extent of the Everglades (i.e., sheet flow; Sklar et al., 2005), but flow was reduced or eliminated after compartmentalization and drainage. Drainage of the Everglades altered the hydrologic conditions by increasing water depths in some areas but decreasing depths in others. Within the Everglades, the ridge-slough landscape originally covered 55% of the Everglades (McVoy et al., 2011), but now covers ~44% (Richardson, 2010). In the ridge-slough landscape, ridges and sloughs differ slightly by elevation (~10-15 cm) which 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 FAS is the largest native gastropod in freshwaters of North America (Pennak 1953), inhabits shallow lakes and wetlands, and typically occurs at low adult densities (<<1/m2) in southern Florida (Gutierre et al., 2019). The FAS is a critical resource for the endangered Snail Kite (*Rostrhamus sociabilis*; Cattau et al., 2014), so improving the conditions for FAS populations is imperative. Snails grow from 3-4 mm shell length (SL) at hatching to > 40 mm SL as large adults and do not live beyond 1.5 years (Hanning, 1979). Most reproduction (~70%) occurs during cooler spring seasons when water levels are declining, and some reproduction occurs (~30%) during warmer early summer when water levels are rising (Barrus et al., 2023; Hanning, 1979).

The FAS experiences a wide range of predators besides endangered kites. At adult sizes, the FAS 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 observations show FAS 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). Another known gastropod predator, giant water bugs (Belostomatidae), may also depredate juvenile FAS but have not been investigated (Kesler & Munns, 1989). The effect of juvenile-stage predators on population growth has not been investigated.

Our work was conducted in the Loxahatchee Impoundment Landscape Assessment (LILA) wetlands and two sites in the western portion of Water Conservation Area 3A (WCA3A; Figure 1) in Florida, USA. LILA consists of four 8 ha experimental wetlands (macrocosms 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 to perform 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 wetlands are generally deeper than constrained wetlands and depths rise faster in the wet season although wetlands reach the same low water levels in the dry season. Shallower water levels are generally favorable for FAS 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” hydrologic treatment. The depth flux in LILA are realistic conditions experienced within the natural Everglades landscape but their net effects on population growth are less clear than their impacts on reproduction. In addition to our work in LILA, we did work at two sites (WCA3A long-term monitoring sites 2 and 3; Ruetz et al. 2005) 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, growth and survival (FAS < 10 mm SL) under different hydrologic conditions important for reproduction (Table S1; Figure 2). The isoclines graphically represent if the population growing, declining, or at replacement under many juvenile growth and survival rates given the two hydrologic treatments in LILA that affect reproduction (Figure 2). The model was coded in R using the original parameters although a few parameters were changed to reflect recent changes in understanding of FAS life history (Table S1, Darby et al. 2015).

*Replication Statement*

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

## Survival Rates

We conducted tethering experiments to 1) test for size-dependent survival, 2) test for differences in survival between seasons, and 3) measure survival of snails < 10 mm SL 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 SL) each season and measuring 24 h survival. In WCA3A, we only tethered juvenile snails (3-10 mm SL). Each tethering experiment was conducted by placing snails on two transects in the sloughs (Figure 3). The transects attempted to capture potential spatial variation in survival and were arranged “near” or “far” from the ridge edge (~5m and 15-20m, respectively). Across transects, tethered snails were placed ≥2 m apart to increase spatial representation and independence (Figure 3). We included 5-10 replicates of 3-mm size increments (i.e., 3-6mm, 6-9mm, 9-12mm,12-15mm, 15-18mm, 18-21mm, and >21mm SL) on each transect in LILA and 10-15 replicates of each 3-mm size increment (i.e., 3-6mm, 6-9 mm, >9 mm) in WCA3A. Snails were tethered by gluing 20 cm of either 2.4 lb (FAS ≤6mm SL) or 4 lb (FAS ≤6mm SL) monofilament line to the shell apex. Tethers were attached to PVC poles pushed into the wetland soils (Figure 3). To obtain snails for tethering, FAS egg masses were collected from adjacent canals hatched, and snails were reared in aquaria or outdoor mesocosms to the desired lengths.

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

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

## Relative composition of predation from tethering remains and abundances

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

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

## Prey Growth

We measured the growth parameter (kgrowth) in LILA and in the reference sites to relate to the zero-population growth isocline. Prior to kgrowth calculation, we measured growth using *in-situ* cages and a regression that predicted growth 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 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. We placed 8 cages in LILA during both seasons and 3 cages in WCA3A site 2 in the dry season. For the wet season growth estimates in the WCA3A, we measured total phosphorus of metaphytic mats to predict FAS growth of using regressions (Barrus et al., 2023). We were only able to obtain dry season growth rates for site 2 in WCA3A because low dry season water depths made use of cage experiments impossible.

The population model used the following equation to model growth of FAS.

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

*Relating Empirical Measures to Isocline*

We related empirical measures of survival and growth to the zero-population isocline. We calculated survival and 95% confidence intervals of snails < 10 mm SL at all sites and seasons from the tethering data. We also calculated survival and 95% confidence in *in situ* cages that excluded predators in LILA (Figure S4). We also calculated mean and 95% confidence intervals of kgrowth from the *in-situ* cages. We then plotted on the isocline state space the combination of survival and growth for each season and location. The nature of the population model made it impossible to change growth rates seasonally, thus the predictions from isocline plot assume that these season-dependent and growth dependent parameters are experienced throughout the year. Essentially, the season-dependent predictions then are an estimate of snail recruitment for each season. For a given season, if above and to the right of the isocline then more snails are recruited into the population than die, and if down and to the left of the isocline then more snails die than are recruited into the population. We also wished to predict if favorable seasons can compensate for poor seasons, so we calculated weighted averages of the seasonal parameters to combine the estimates into a single growth and survival estimate for the year. ~70% of reproduction occurs in the dry season and ~30% occurs in the wet season (Barrus et al., 2023; Darby et al., 2015). An equal weight of dry and wet season parameters underestimates the influence of the dry season and overestimates the influence of the wet season on the number of snails entering the population. Thus, we weighted the combined growth and survival estimates to reflect these differences in reproductive effort.

# Results

Zero-population growth isoclines created from the stage-structured population model produced descending isoclines consistent with an interaction between growth 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 growth of kgrowth = 0.07) and/or lower juvenile growth (e.g., withstanding by 7.7% lower growth at CJS of 0.80). The effect of better reproduction (i.e., the gap between good and poor reproductive isoclines) strengthened with higher growth and lower survival (Figure 2).

## Empirical Measures of Survival and Growth

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 S4). One of the cages was colonized by a single giant water bug and only empty shells were left by the end of the experiment.

In WCA3A, we observed a total of 276 independent observations of survival across the 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 FAS survival changed with seasons. The top four models (cumulative weight = 0.95) for predicting daily survival probability included SL, Season, and the interaction between Length and Season (Table S2). The top model did not include any additional variables, but the next three best models (ΔAIC ≤ 2.74) included combinations of spatial factors. The parameter values for the spatial factors appeared to provide little additional predictive capacity (parameter *p-values* ≥ 0.276) to survival, so we restricted interpretation to the size and season parameters (Figure 3). During the dry season, FAS daily survival probability increased with size (z = 2.667: *p* = 0.008; Figure 3), but in the wet season, daily survival probability was size independent (z = -0.902: *p* = 0.367; Figure 3). Small juvenile snails (< 10 mm SL) survived better in the wet season than the dry season (Figure 3).

*Predator identity*

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

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

## Seasonal Population-Level Effects

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

# Discussion

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

*Seasonal FAS survival and growth*

Calculating size-dependent survival for small animals like freshwater invertebrates is challenging. Traditional techniques (e.g. mark-recapture, individual tracking) are problematic because juvenile FAS are difficult to capture, cannot be individually and reliably tracked, and are typically found at exceedingly low densities in the Everglades (including LILA wetlands; Drumheller et al., 2022; Gutierre et al., 2019). Tethering is an experimental method to measure survival and could potentially inflate mortality estimates of prey but the concern is greatest for highly mobile prey for which tethers limit antipredator behaviors (Baker & Waltham, 2020). Tethering offered the only feasible method for determining juvenile FAS survival. In addition, tethering less mobile prey (e.g. snails) with limited antipredator escape behaviors should produce informative survival estimates. Further, tethering across field gradients reliably estimates encounter rates with relatively more mobile predators (Rochette & Dill, 2000; Ruehl & Trexler, 2015).

Our results supported our prediction that apple snail growth would increase in the warmer wet season (Figure 5, Figure S2). Increases in prey growth associated with the warmer wet season is consistent with many experimental manipulations of temperature in predator-prey studies including dragonfly-mosquito interactions (Davidson et al., 2021) and predatory ant-caterpillar interactions (Pepi et al., 2018). Further, increases in temperature are generally thought to increase growth of ectothermic animals except for extreme thermal maxima (Kingsolver & Woods, 2016). Increased FAS growth rates had little opportunity to mediate survival because survival was measured daily, thus survival likely reflects predator related process (per-capita foraging, predator abundances).

We found that predator abundances dominated the processes governing prey survival because prey survival was highest in the wet season, despite apparent increases in per-capita foraging rates of crayfish and salamanders consistent with temperature dependent expectations for the wet season. The declines in abundance of predatory crayfish and bugs are explained by phenology (Pintar et al., 2021; van der Heiden & Dorn, 2017) while declines in abundance of greater sirens are probably best explained by seasonal movement patterns. Greater sirens emigrate out of the wetlands into the deeper adjacent habitats to escape the low water depths (< 10 cm) at the end of the dry season, and remained in the deeper water throughout the duration of our study in the wet season (Howell, 2023). Crayfish and greater sirens increased per-capita foraging rates in the warmer wet season which is consistent with current experimental evidence testing short-term interaction strength (i.e., prey survival) under warmer temperatures (Davidson et al., 2021; Pepi et al., 2018). And increases in temperature have been shown to increase per-capita foraging in Atlantic Reef fishes (Nunes et al., 2021). Typically studies that explore 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 and size structure complicates scaling up predictions based on experiments to natural systems, because declines in predator abundances may counteract increases in per-capita foraging rates (Figure 4). Future work will be necessary to integrate current theoretical predictions under the context of varying predator abundances.

## Long-term Interaction Strength (Population Growth)

Studies examining effects of environmental variation on predator-prey interactions have typically focused on prey-survival (Davidson et al., 2021; Davidson & Dorn, 2018; Jeyasingh & Weider, 2005; Pepi et al., 2018). Tethering snails shortened the length by which we observed survival (i.e., only daily), but coupled with the population model demonstrated that seasonal variation in growth and survival mediated population growth/ recruitment. The model we used (Darby et al. 2015) had no good empirical measures for juvenile growth so our findings provide more realistic estimates for the Everglades. The dry season parameters were worse than the wet season for population growth which seems counterintuitive because most egg-laying occurs during the dry season (spring) before the water reaches its annual minimum depth (Barrus et al., 2023). This result suggests that improving dry season conditions for survival and growth of juvenile FAS may have a larger benefit for FAS populations than improving wet season conditions. Furthermore, the different hydrologic scenarios, affecting reproductive conditions, had relatively small effects on the isocline (conditions producing growth) relative to the natural spatial and seasonal variation in the two juvenile parameters.

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

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

*Conclusion*

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

# References

Anderson, D. R. (2008). *Model based inference in the life sciences: A primer on evidence*. Springer, NY. https://doi.org/10.1007/978-0-387-74075-1

Baker, R., & Waltham, N. (2020). Tethering mobile aquatic organisms to measure predation: A renewed call for caution. *Journal of Experimental Marine Biology and Ecology*, *523*, 1–7.

Barrus, N. T., Drumheller, D., Cook, M. I., & Dorn, N. J. (2023). Life history responses of two co-occurring congeneric Apple Snails (Pomacea maculata and P. paludosa) to variation in water depth and metaphyton total phosphorus. *Hydrobiologia*, *850*(4), 841–860. https://doi.org/10.1007/s10750-022-05128-9

Brown, C., Oppon, K. J., & Cahill, J. F. (2019). Species‐specific size vulnerabilities in a competitive arena: Nutrient heterogeneity and soil fertility alter plant competitive size asymmetries. *Functional Ecology*, *33*(8), 1491–1503. https://doi.org/10.1111/1365-2435.13340

Cattau, C. E., Darby, P. C., Fletcher, R. J., & Kitchens, W. M. (2014). Reproductive responses of the endangered snail kite to variations in prey density. *Journal of Wildlife Management*, *78*(4), 620–631. https://doi.org/10.1002/jwmg.706

Cattau, C. E., Fletcher, R. J., Reichert, B. E., & Kitchens, W. M. (2016). Counteracting effects of a non‐native prey on the demography of a native predator culminate in positive population growth. *Ecological Applications*, *26*(7), 1952–1968. https://doi.org/10.1890/15-1020.1

Chockley, B., St. Mary, C., & Osenberg, C. (2008). Population sinks in the Upper Florida Keys: The importance of demographic variation in population dynamics of the marine shrimp Stenopus hispidus. *Marine Ecology Progress Series*, *360*, 135–145. https://doi.org/10.3354/meps07404

Cuthbert, R. N., Wasserman, R. J., Dalu, T., Kaiser, H., Weyl, O. L. F., Dick, J. T. A., Sentis, A., McCoy, M. W., & Alexander, M. E. (2020). Influence of intra‐ and interspecific variation in predator–prey body size ratios on trophic interaction strengths. *Ecology and Evolution*, *10*(12), 5946–5962. https://doi.org/10.1002/ece3.6332

Dalrymple, G. H. (1977). Intraspecific Variation in the Cranial Feeding Mechanism of Turtles of the Genus Trionyx ( Reptilia , Testudines , Trionychidae ). *Journal of Herpetology*, *11*(3), 255–285.

Darby, P. C., DeAngelis, D. L., Romañach, S. S., Suir, K., & Bridevaux, J. (2015). Modeling apple snail population dynamics on the Everglades landscape. *Landscape Ecology*, *30*(8), 1497–1510. https://doi.org/10.1007/s10980-015-0205-5

Davidson, A. T., & Dorn, N. J. (2018). System productivity alters predator sorting of a size-structured mixed prey community. *Oecologia*, *186*(4), 1101–1111. https://doi.org/10.1007/s00442-018-4099-1

Davidson, A. T., Hamman, E. A., McCoy, M. W., & Vonesh, J. R. (2021). Asymmetrical effects of temperature on stage‐structured predator–prey interactions. *Functional Ecology*, *35*(5), 1041–1054. https://doi.org/10.1111/1365-2435.13777

Dorn, N. J., & Cook, M. I. (2015). Hydrological disturbance diminishes predator control in wetlands. *Ecology*, *96*(11), 2984–2993. https://doi.org/10.1890/14-1505.1

Drumheller, D. K., Cook, M. I., & Dorn, N. J. (2022). The role of direct chemical inhibition in the displacement of a native herbivore by an invasive congener. *Biological Invasions*, *0123456789*. https://doi.org/10.1007/s10530-022-02752-3

Gaiser, E. E., Trexler, J. C., & Wetzel, P. R. (2012). The Florida Everglades. In D. P. Batzer & A. H. Baldwin (Eds.), *Wetland Habitats of North America* (pp. 231–252). University of California Press.

Gutierre, S. M. M., Darby, P. C., Valentine-Darby, P. L., Mellow, D. J., Therrien, M., & Watford, M. (2019). Contrasting patterns of pomacea maculata establishment and dispersal in an everglades wetland unit and a central florida lake. *Diversity*, *11*(10), 1–20. https://doi.org/10.3390/d11100183

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

Hansen, C., Newman, S., Saunders, C. J., Tate-Boldt, E. K., & Dorn, N. J. (2022). Flow-mediated growth of an aquatic herbivore. *Hydrobiologia*, *849*(14), 3161–3173. https://doi.org/10.1007/s10750-022-04923-8

Howell, H. J. (2023). *The Ecology, Conservation, and Management of the Everglades’ Herpetofaunal Community* [Dissertation]. University of Miami.

Jeyasingh, P. D., & Weider, L. J. (2005). Phosphorus availability mediates plasticity in life-history traits and predator-prey interactions in *Daphnia*: Phosphorus alters life-history and predation. *Ecology Letters*, *8*(10), 1021–1028. https://doi.org/10.1111/j.1461-0248.2005.00803.x

Kesler, D. H., & Munns, W. R. J. (1989). Predation by Belostoma flumineum ( Hemiptera ): An Important Cause of Mortality in Freshwater Snails Author. *Journal of the North American Benthological Society*, *8*(4), 342–350.

Kingsolver, J. G., & Woods, H. A. (2016). Beyond Thermal Performance Curves: Modeling Time-Dependent Effects of Thermal Stress on Ectotherm Growth Rates. *The American Naturalist*, *187*(3), 283–294. https://doi.org/10.1086/684786

Ma, G., Bai, C., Rudolf, V. H. W., & Ma, C. (2021). Night warming alters mean warming effects on predator–prey interactions by modifying predator demographics and interaction strengths. *Functional Ecology*, *35*(9), 2094–2107. https://doi.org/10.1111/1365-2435.13833

MacArthur, R., & Levins, R. (1964). Competition, habitat selections, and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences*, *51*(6), 1207–1210. https://doi.org/10.1073/pnas.51.6.1207

McCoy, M. W., Bolker, B. M., Warkentin, K. M., & Vonesh, J. R. (2011). Predicting predation through prey ontogeny using size-dependent functional response models. *American Naturalist*, *177*(6), 752–766. https://doi.org/10.1086/659950

McPeek, M. A., & Peckarsky, B. L. (1998). Life histories and the strengths of species interactions: Combining mortality, growth, and fecundity effects. *Ecology*, *79*(3), 867–879. https://doi.org/10.1890/0012-9658(1998)079[0867:LHATSO]2.0.CO;2

McVoy, C. W., Said, W. P., Obeysekera, J., VanArman, J. A., & Dreschel, T. W. (2011). *Landscapes and Hydrology of the Predrainage Everglades*. University Press of Florida.

Meehan, M. L., Turnbull, K. F., Sinclair, B. J., & Lindo, Z. (2022). Predators minimize energy costs, rather than maximize energy gains under warming: Evidence from a microcosm feeding experiment. *Functional Ecology*, *36*(9), 2279–2288. https://doi.org/10.1111/1365-2435.14131

Nunes, L. T., Barneche, D. R., Lastrucci, N. S., Fraga, A. A., Nunes, J. A. C. C., Ferreira, C. E. L., & Floeter, S. R. (2021). Predicting the effects of body size, temperature and diet on animal feeding rates. *Functional Ecology*, *35*(10), 2229–2240. https://doi.org/10.1111/1365-2435.13872

Osenberg, C. W., & Mittelbach, G. G. (1996). 12. The Relative Importance of Resource Limitation and Predation Limitation in Food Chains. In *Food webs* (pp. 134–148).

Pepi, A., Grof-Tisza, P., Holyoak, M., & Karban, R. (2018). As temperature increases, predator attack rate is more important to survival than a smaller window of prey vulnerability. *Ecology*, *99*(7), 1584–1590. https://doi.org/10.1002/ecy.2356

Pintar, M. R., Kline, J. L., & Trexler, J. C. (2021). The Aquatic Heteroptera (Hemiptera) of Marshes in the Florida Everglades. *Florida Entomologist*, *104*(4). https://doi.org/10.1653/024.104.0408

R Core Team. (2019). *R: A language and environment for statistical computing. R Foundation for Statistical Computing*. *URL https://www.R-project.org/*.

Richardson, C. J. (2010). The Everglades: North America’s subtropical wetland. *Wetlands Ecology and Management*, *18*(5), 517–542. https://doi.org/10.1007/s11273-009-9156-4

Rochette, R., & Dill, L. M. (2000). Mortality, behavior and the effects of predators on the intertidal distribution of littorinid gastropods. *Journal of Experimental Marine Biology and Ecology*, *253*(2), 165–191. https://doi.org/10.1016/S0022-0981(00)00253-7

Roland, J., & Embree, D. G. (1995). Biological Control of the Winter Moth. *Annual Review of Entomology*, *40*(1), 475–492. https://doi.org/10.1146/annurev.en.40.010195.002355

Ruehl, C. B., & Trexler, J. C. (2015). Reciprocal transplant reveals trade-off of resource quality and predation risk in the field. *Oecologia*, *179*(1), 117–127. https://doi.org/10.1007/s00442-015-3324-4

Sklar, F. H., Chimney, M. J., Newman, S., McCormick, P., Gawlik, D., Miao, S. L., McVoy, C., Said, W., Newman, J., Coronado, C., Crozier, G., Korvela, M., & Rutchey, K. (2005). The ecological—Societal underpinnings of Everglades restoration. *Frontiers in Ecology and the Environment*, *3*(3), 161–169. https://doi.org/10.1890/1540-9295(2005)003[0161:TEUOER]2.0.CO;2

Snyder, N. F. R., & Snyder, H. A. (1971). Defenses of the Florida Apple Snail Pomacea paludosa. *Behavior*, *40*(3), 175–215.

Soomdat, N. N., Griffin, J. N., McCoy, M., Hensel, M. J. S., Buhler, S., Chejanovski, Z., & Silliman, B. R. (2014). Independent and combined effects of multiple predators across ontogeny of a dominant grazer. *Oikos*, *123*(9), 1081–1090. https://doi.org/10.1111/oik.01579

Twardochleb, L. A., Novak, M., & Moore, J. W. (2012). Using the functional response of a consumer to predict biotic resistance to invasive prey. *Ecological Applications*, *22*(4), 1162–1171. https://doi.org/10.1890/11-0871.1

Valentine-Darby, P. L., Kell, S. E., & Darby, P. C. (2015). Predation on Florida apple snails ( Pomacea paludosa ) by native and non-native aquatic fauna , and predator-prey size relationships. *Florida Scientist*, *78*(1), 47–56.

van der Heiden, C. A., & Dorn, N. J. (2017). Benefits of adjacent habitat patches to the distribution of a crayfish population in a hydro-dynamic wetland landscape. *Aquatic Ecology*, *51*(2), 219–233. https://doi.org/10.1007/s10452-016-9612-1

Vance, R. R. (1985). The Stable Coexistence of Two Competitors for One Resource. *The American Naturalist*, *126*(1), 72–86. https://doi.org/10.1086/284397

Zweig, C. L., & Kitchens, W. M. (2008). Effects of landscape gradients on wetland vegetation communities: Information for large-scale restoration. *Wetlands*, *28*(4), 1086–1096. https://doi.org/10.1672/08-96.1

# Figures and Tables

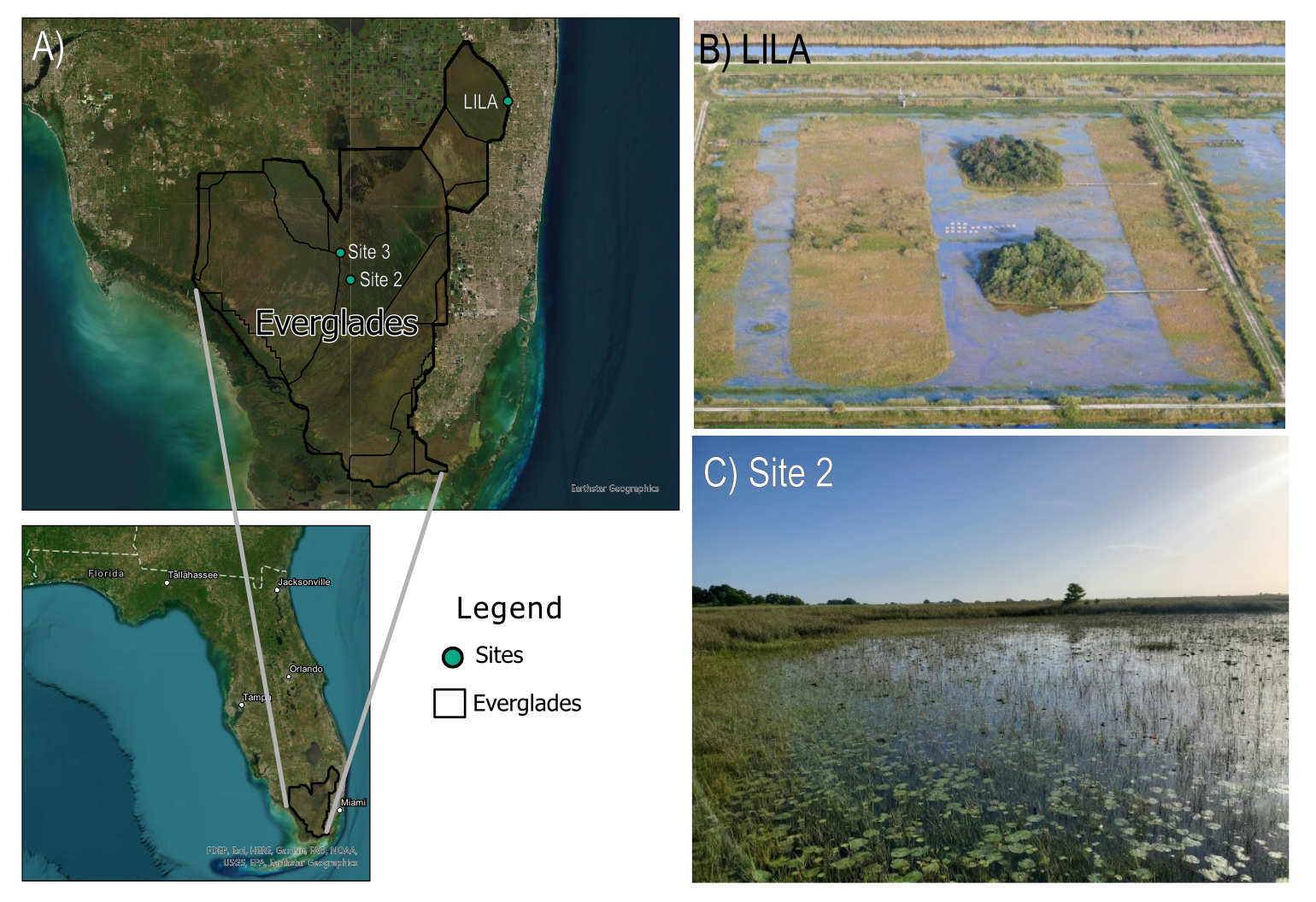


Figure 1: A) Map and images of B) LILA impoundment #2 and C) Site 2 in Water Conservation Area 3A. Photo credits to B) Mark I. Cook and C) Nathan T. Barrus.

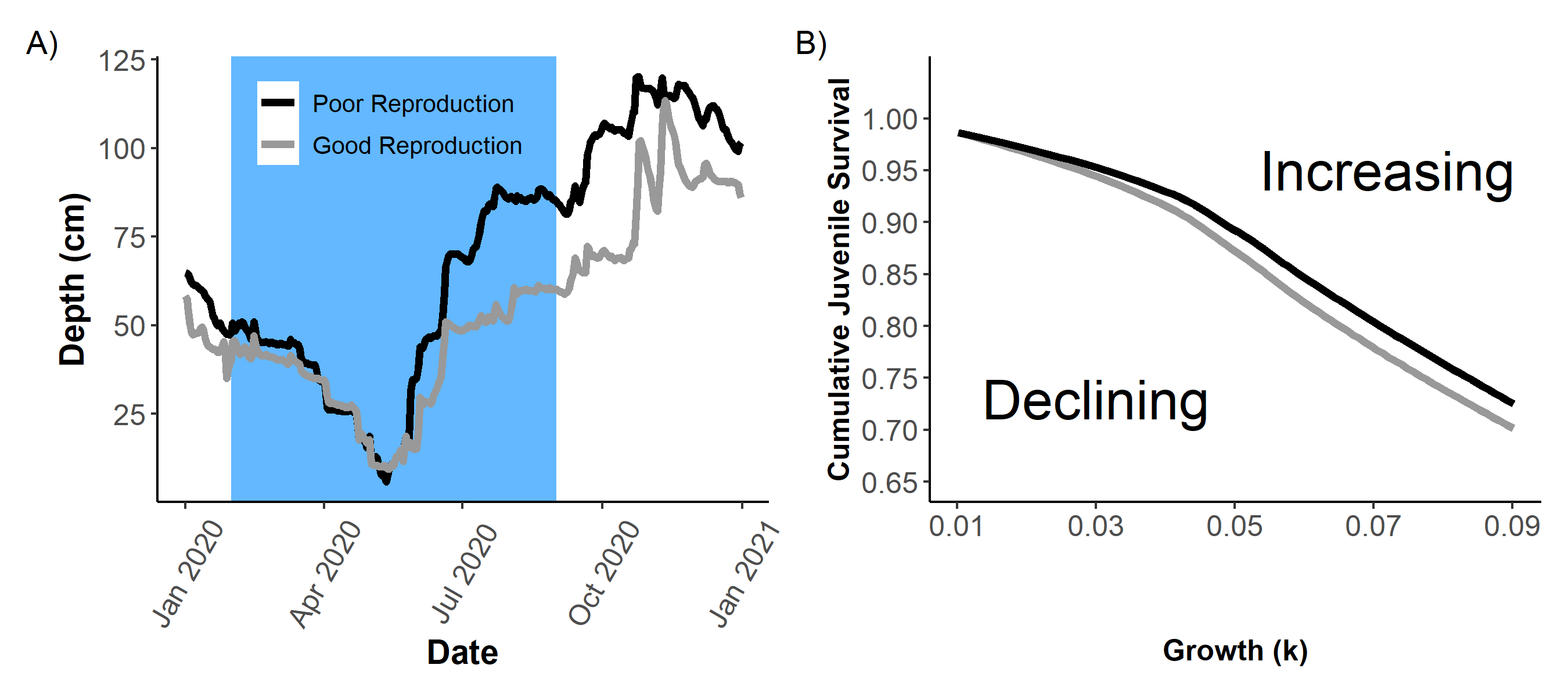


Figure 2: A) The hydrologic treatments in LILA in 2020, and B) the zero-population growth isoclines of FAS as a function of juvenile (< 10 mm SL) survival and juvenile growth rates under two hydrologic treatments (good vs. poor egg laying conditions). The FAS breeding season is represented by the blue shaded area.

A close-up of a field

Description automatically generated

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

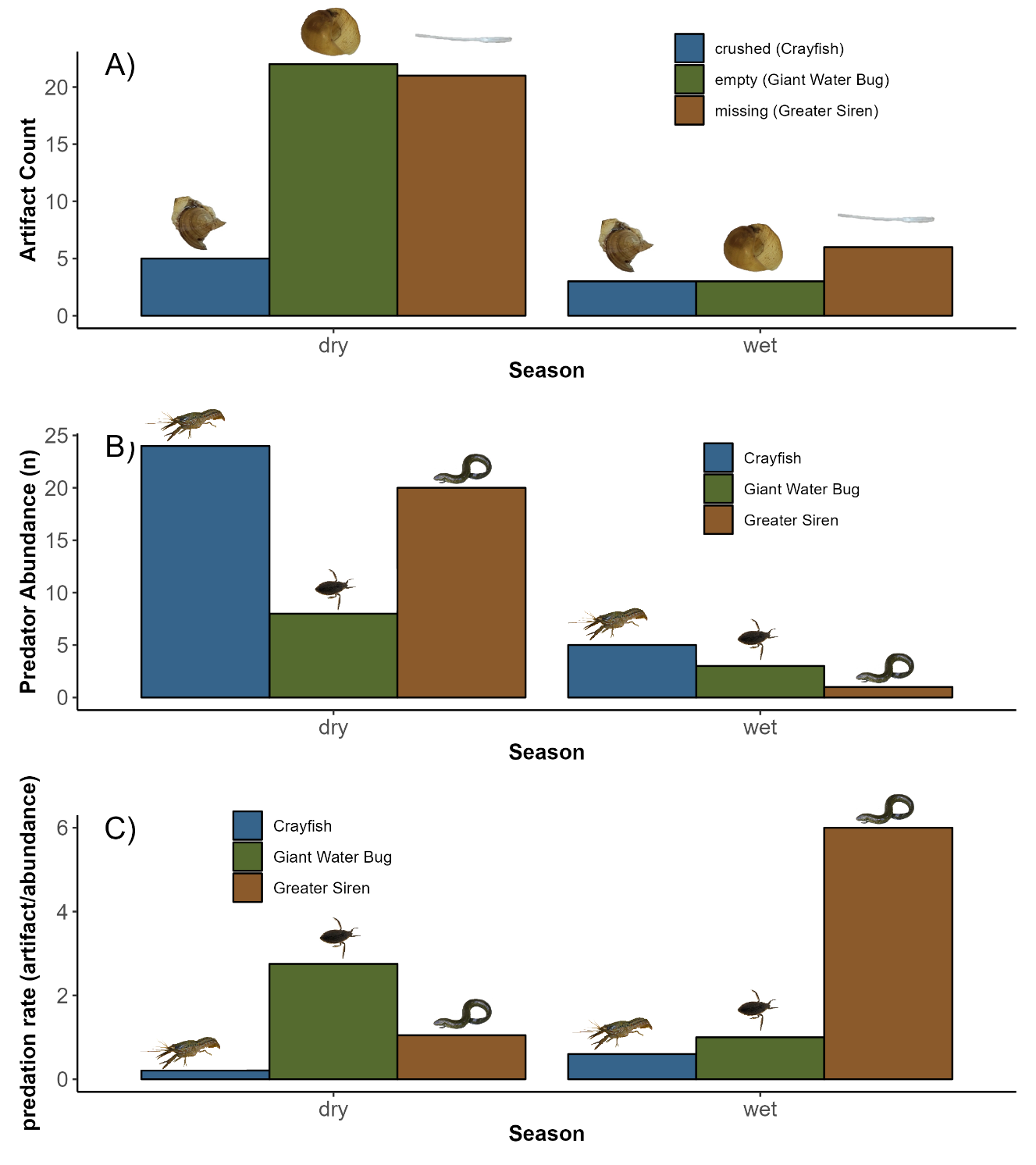


Figure 4: A) Counts of artefacts of biotic factors causing mortality of snails (< 10 mm SL) in the two seasons in the LILA wetlands, and B) seasonal abundance of predators of juvenile snails from throw-trap samples (crayfish and giant water bug), and from standard sets of trap nets (greater siren). Sampling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

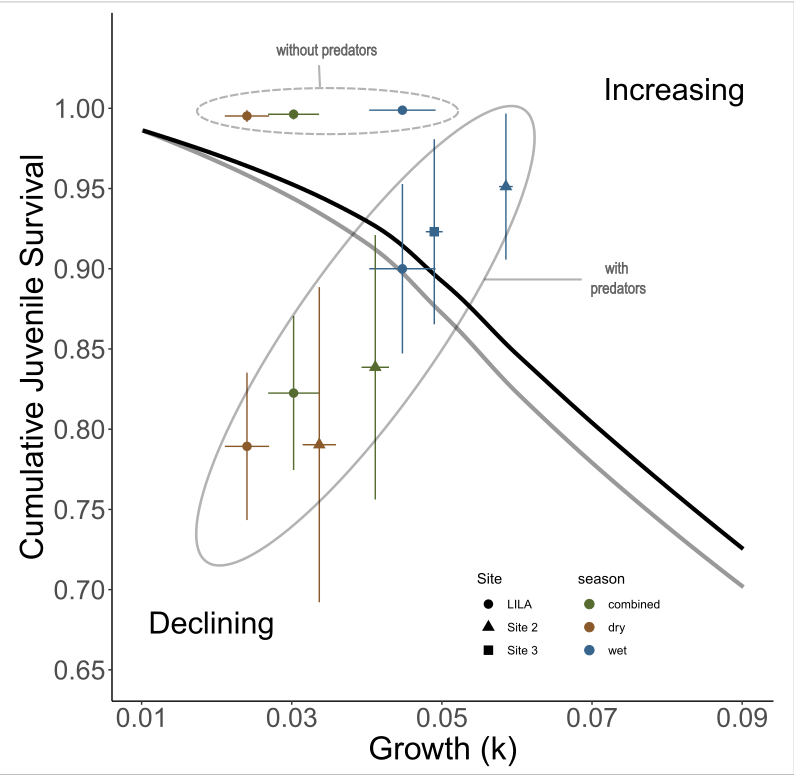


Figure 5: Isoclines illustrating the bivariate effects of juvenile growth and survival that produce zero net annual population growth for a size-structured model of a freshwater gastropod (*Pomacea paludosa*) under different hydrologic regimes that affect reproduction. The black isocline and gray isoclines represent two hydrologic scenarios producing better (Grey) and worse (Black) reproductive conditions. Mean cumulative juvenile survival (snails < 10mm SL) and growth (kgrowth) quantified in LILA and WCA3A are plotted on each panel with seasonal and combined parameters. The combined parameters were calculated by a weighted average reflecting greater juvenile snail production in the dry season.