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Interpreting field measurements of juvenile growth and survival rates with population growth isoclines.

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# Open Research Statement

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

# **Key words**

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

# Abstract (350 words):

Juvenile survival and growth rates are commonly measured performance metrics with population-level consequences. For species that can grow to achieve a size refuge from predators, the time spent at vulnerable sizes is acknowledged to affect population dynamics, but the interaction between juvenile survival and growth has rarely been illustrated theoretically or quantified under natural conditions. We used a published demographic model of an annual gastropod (Florida Apple Snail, *Pomacea paludosa*) to construct a zero-population growth isocline for combinations of juvenile growth and survival. The resulting isocline illustrated the expected result that faster juvenile growth could offset greater mortality. We then quantified daily juvenile survival and growth in wetlands twice during the recruitment period, incorporating variable predator assemblages and seasonal environmental conditions (e.g., temperature). Seasonal and averaged rates were interpreted relative to the isocline. Daily juvenile survival rates were lower, and more clearly size-dependent, in the cooler dry season than in the warmer wet (rainy) season. Higher abundances of generalist predators in the dry season caused higher mortality. Juvenile growth was faster in the warmer wet season. Parameter combinations of growth and survival in the dry season would predict declining populations, while rates from wet season predicted populations at replacement (λ = 1) or increasing. When parameters were combined for the full annual recruitment window, populations were projected to decline in both wetlands. The predictions were robust to water depths affecting reproductive rates, but with better hydrologic conditions one population was near replacement. The use of the null isoclines gave population-level context to quantified rates and identified important temporal variation in survival and growth of the snail. Our isocline illustrates the growth-mediated predator impacts for a species with type III survivorship and stage- or size-specific predators and we suggest that the shape of the isocline could be a general. More importantly, the use of a population growth isocline from a size-indexed demographic population model provide a framework for making meaningful interpretations about field-measured rates. We encourage population ecologists to consider such an approach for species of management interest, including those that are in steady decline.

# Introduction

Population dynamics for many species with stage or age structure are widely recognized to be influenced by stage- or size-specific growth and mortality factors (e.g., predation; Werner and Gilliam 1984, De Roos et al. 2003, Craig et al. 2006). Forty years ago, Werner and Gilliam (1984) made this point about the importance of individual growth to demographic models:

“A size-indexed demography, however, includes three vital rates: size-specific mortality and fecundity rates, plus individual growth rates. The explicit inclusion of individual growth rates is a natural mathematical consequence of indexing by size rather than by age. If we can determine how these vital rates scale with body size, these relationships can be used as basic submodels for the parameters of a size-based demography. A size-based demography, in turn, would permit us to explore the population-dynamic consequences of various types of interactions.” (pp 401-402)

Historical research on size-structured interactions have focused on theoretical and empirical treatments of density-dependent growth rates, competition, ontogenetic habitat switching, population size-structure, and juvenile bottlenecks (e.g., fish: Werner and Gilliam 1984, De Roos et al. 2003), while less has been done with population dynamics (growth or decline) as mentioned at the end of the quote. What is known is that for many species juvenile growth determines the time a prey animal spends in a vulnerable size class, such that fast growth can be a type of defense against stage-specific juvenile predators; the importance of mortality to population dynamics therefore is partly environmentally mediated (Craig et al. 2006, Davidson and Dorn 2018, Davidson et al. 2021, Ma et al. 2021, Nunes et al. 2021, Meehan et al. 2022). Environmental mediation of predator-prey interactions in natural systems, could be caused by variation in resources or temperature affecting juvenile growth rates (Jeyasingh and Weider 2005, Davidson and Dorn 2018, Pepi et al. 2018, Davidson et al. 2021). Additionally, multiple factors in natural systems are also producing variation natural predation regimes in time and space (McPeek and Peckarsky 1998, McCoy et al. 2011, Soomdat et al. 2014, Dorn and Cook 2015). Taken together, spatial and temporal variation in growth or mortality or both may provide windows of opportunity (i.e., favorable combinations of the two parameters) for population growth.

Studies of size-structured interactions are often conducted experimentally (e.g., Jeyasingh and Weider 2005, McCoy et al. 2011, Davidson and Dorn 2018, Pepi et al. 2018, Davidson et al. 2021, Ma et al. 2021) with careful control to limit the interacting species and densities. But studies of population dynamics for species that either grow rapidly (outbreaks) or those experiencing steady declines require ecologists to understand how parameters combine to drive variable population growth (λ) under natural conditions. Furthermore, while size-dependent mortality is well known (Craig et al. 2006, McCoy et al. 2011, Schmera et al. 2015, Brannelly et al. 2019) and population-dynamic consequences of the interaction between juvenile growth and mortality are logical, they have only been generally alluded to (De Roos et al. 2003); theoretical predictions, whether general or specific, are lacking. Of the two studies that have explored theoretical predictions for growth-mediated effects on prey survival from predation in size-structured populations, Rice et al. (1993) examined how variation in growth rates influenced the numbers and proportions of surviving juveniles while Pepi et al. (2023) focused on changes in equilibrium densities of predator and prey due to mismatches in thermal responses to variation in temperature while holding prey reproduction constant.

Size-indexed demographic models, combining growth (i.e., developmental) rates and survival can makepopulation growth projections and identify sensitive stages/ages (e.g., Chockley et al. 2008), but could also be used to identify combinations of parameters making population growth negative, zero, or positive. Zero-population growth isoclines are typically used to predict population dynamics and coexistence outcomes for interacting species with variable population parameters, resources, and environmental variation (MacArthur and Levins 1964, Vance 1985), but zero-growth isoclines can also be derived from stage- or size- structured population models to identify parameter combinations producing zero population growth. To our knowledge this has not been done, but isoclines from demographic models that include growth ratescould offer quantitative maps for understanding the combinatorial effects juvenile survival and growth on population growth. Field-measured parameters could then be compared to the isocline and predict natural spatio-temporal variation in recruitment or population growth.

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

# Materials and methods

## System and study species

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

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

## Zero-Population Growth Isocline

We used a published age-structured population model (Darby et al. 2015) to create zero-population growth isoclines from theoretical combinations of two parameters, juvenile growth and survival (FAS < 10 mm SL) holding all other variables stable (more details in Supplemental). The model tracks the annual cohorts (size and numbers) on daily time steps using daily mortality and growth parameters with cohorts produced seasonally dependent upon adult numbers and water depths. The Darbe et al. 2015 model was re-coded in R using the original parameters with a few parameters adjusted to reflect recent changes in understanding of FAS life history (see Table S1). ). Isoclines were constructed by combinatorial simulations of the parameters for juvenile survival growth under two hydrologic conditions which produced depth-dependent differences in reproduction (“Good Reproduction” or “Poor Reproduction” below; Figure 2). For each combinatorial ach simulation we measured population growth rate (r) measured after a stable size distribution was achieved. The combinations for which population growth was constant (r = 0) were identified and plotted as an isocline.

The isoclines graphically represent theoretical combinations of the two parameters that stop growth of the population (λ = 1). Under the assumption of annually unchanging growth and survival rates the isoclines are boundary conditions between a growing or a declining population. Because juvenile FAS densities are so low in our study wetlands (typically <0.1/m2) and yet can survive and grow at high densities in mesh predator-exclusion cages (Barrus et al. 2023) we considered traditional density dependence in the parameters to be irrelevant to our model evaluations which were simply trying to identify parameters that would produce an increasing or decreasing population year over year.

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

## Survival and Growth in the field

Our measures of survival and growth were made in two locations within the Everglades ecosystem;the Loxahatchee Impoundment Landscape Assessment (LILA) wetlands and two sites in the western portion of Water Conservation Area 3A (WCA3A; Figure 1) in Florida, USA. LILA consists of four 8 ha impounded wetlands with ridge and slough elevation features and hydro-patterns that mimic the wetlands of the Everglades (Figure 1B). Both wetlands have seasonally varying water levels but the water levels in LILA are under partial control by pumps and culverts to perform landscape-scale hydrologic experiments (see Supplemental). We worked in two wetlands impoundments that had hydrologic conditions deemed good for FAS reproduction (Barrus et al. 2023). The two sites near the western boundary of WCA3A near Big Cypress National Park (Figure 1; Sites 2 and 3 in Ruetz et al. 2005) were embedded within a 1240 km2 contiguous portion of the Everglades. The WCA3A sites were chosen because they were near locations of higher FAS densities in the recent past; sites that also supported Snail Kite nesting (Cattau et al. 2016).

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

We measured growth either using *in-situ* 1-m2 mesh cages or with a regression that predicted wet season snail growth using total phosphorus (TP) concentrations in metaphytic mats (R2 = 0.85; Barrus et al., 2023). The metaphytic (periphyton) in the Everglades are composites of floating calcareous mats of algae, cyanobacteria, other microbes, and algal detritus (Gaiser et al. 2011). For all cages, algae was allowed to accumulate in the cages two weeks prior to the experiment, and two liters of metaphyton was placed inside the cages as a food source (Drumheller et al. 2022, Barrus et al. 2023). Juvenile snails were individually marked and placed in cages to grow for 4-5 weeks. We placed 8 cages in LILA during both seasons and 3 cages in WCA3A site 2 in the dry season. To estimate wet season growth WCA3A site, we measured the TP of metaphytic mats to predict FAS growth of using regressions from (Barrus et al. 2023). We were only able to obtain dry season growth rates for site 2 in WCA3A because low dry season water depths at site 3 made use of cage experiments impossible. Using the growth results we then calculated the growth parameter kgrowth to relate the results to the isocline. Kgrowth is a measure of size-dependent daily growth rates that can be calculated from knowing the initial size, the final size and the maximum size. The maximum size was assumed to be 50 mm SL. Details on calculating the growth parameter (kgrowth) can be found in Appendix S2.

# Result

Zero-population growth isoclines created from the age-structured population model produced isoclines consistent with the expected interaction between growth and survival (Figure 2). Combinations of the two parameters above and to the right of the isocline produce growing populations (λ>1) while combinations below the isocline produce declining populations (λ<1). the shape of the isocline illustrates that environmental conditions favorable for faster juvenile growth will support populations that can withstand higher rates of mortality (lower survival) and populations with slower-growing juveniles need to lower mortality (higher survival) to persist or grow (λ≥1). Hydrologic conditions that improved reproduction (egg masses/female) made the population more resilient to lower survival (e.g., withstanding 3.1% lower survival at growth of kgrowth = 0.07) and/or slower juvenile growth (e.g., withstanding by 7.7% slower growth at CJS of 0.80; Appendix S1 Figure S2). The effect of better reproduction strengthened with faster growth and lower survival (Appendix S1 Figure S2). For the NAS this isocline provided a population-dynamic context for field measurements.

## Empirical Survival and Growth related to the Isocline

There was variation in the measured survival and growth parameters across sites and seasons (Figure 3). Examination of the artefacts from tethering suggested that the predators were primarily native invertebrates (Belostoma spp, *Procambarus fallax*) and salamanders (point to appendix) and quantifications of the predators indicated that they were variable across seasons and sites.

We present data from the two sites (LILA and WCA3A site 2) which had growth rates measured from both seasons, but parameters from WCA3A site 3 and survival measured from the predator exclusion cages were plotted in a single figure in Appendix S1 (Figure S3). Across both sites the juvenile growth was faster in the warmer wet season than the dry season (Figure 3, Appendix 3 Figure S2). The dry season had lower survival and slower growth with combinations falling below the isocline (Figure 3). In contrast, the wet season had higher survival rates and fasterer growth; with average combinations falling on the isocline (LILA; at replacement) or even positive population growth (WCA3A site 2; Figure 3). Snails in WCA3A site 2 had faster growth than those in LILA (Figure 3). The combined effects, weighted by seasonal differences in egg laying, resulted in annual mortality and growth parameters that predicted declining population for LILA, and confidence intervals that slightly overlapped the zero-growth isocline created with good hydrologic egg-laying conditions for WCA3A site 2 (Figure 3).

# Discussion

Using a size-indexed age-structured population model we produced zero- population growth isoclines illustrating the combinatorial effects of growth and survival on population growth . The result illustrated the expected effect; faster juvenile growth can offset higher mortality. Our work was specific to of a freshwater gastropod with size-dependent survival, but the the approach is conceivably applicable to any size-structured predator-prey interaction. The approach might be most useful for short lived species with type III survivorship and while field combinations of similar rates have been examined for other invertebrate populations (e.g., Chockley et al. 2008), they were not compared against a population model predictions. Empirical measurements allowed us to compare existing rates to the isocline and conclude that the populations we studied in the Everglades were static or declining. Seasonal parameters further indicated that both survival and growth were poorer in the dry season (Feb-April) which overlapped with most of the reproductive period of NAS. The results produced novel hypotheses about environmental variation and predator control that might limit the FAS populations in the Everglades.

*Survival and growth*

Calculating size-dependent survival for small animals like freshwater invertebrates is challenging. Traditional techniques (e.g. mark-recapture, individual tracking) are problematic because juvenile FAS are difficult to capture, cannot be individually and reliably tracked, and are typically found at exceedingly low densities in the Everglades (including LILA wetlands; Gutierre et al. 2019, Drumheller et al. 2022). Tethering is an experimental method to measure survival and could potentially inflate mortality estimates of prey but the concern is greatest for highly mobile prey for which tethers limit antipredator behaviors (Baker and Waltham 2020). Tethering offered the only feasible method for determining juvenile FAS survival. In addition, tethering less mobile prey (e.g. snails) with limited antipredator escape behaviors should produce informative survival estimates. Further, tethering across field gradients reliably estimates encounter rates with relatively more mobile predators (Rochette and Dill 2000, Ruehl and Trexler 2013). Experimental work with this species did not indicate any anti-predator response either morphological or behavioral, to chronic exposure to crayfish (Davidson and Dorn 2017).

Florida apple snail growth increased in the warmer wet season (Figure 5, Figure S2) consistent with general responses of ectotherms (Kingsolver and Woods 2016) and predator-prey experimental studies under variable ( Pepi et al. 2018, Davidson et al. 2021). .

So prey survival might be expected to be greater as we observed in the wet season, except that predators also increased foraging rates (Appendix S2 Figure S3). The largest change between seasons seems to have been a regular decline in predators abundances as that wetlands reflooded. The predator community changes seem to have overwhelmed any changes in survival that might have been mediated by temperature. The declines in abundance of predatory crayfish and bugs (Heteroptera) are explained by phenology (van der Heiden and Dorn 2017, Pintar et al. 2021) while declines in abundance of greater sirens are probably best explained by seasonal movement patterns. Greater sirens emigrate out of the wetlands into the deeper adjacent habitats to escape the low water depths (< 10 cm) at the end of the dry season, and remained in the deeper water throughout the duration of our study in the wet season (Howell 2023). Studies that isolate the effects of variable environmental conditions on predator-prey interaction have controlled predator abundance experimentally, or statistically (Jeyasingh and Weider 2005, Davidson and Dorn 2018, Pepi et al. 2018, Davidson et al. 2021, Ma et al. 2021) to measure per-capita rates, but the study of natural populations in communities requires a consideration of natural seasonal variation , because environmentally-mediated changes in predator communities could both be more important than the per-capita rates but also could counteract or exacerbate changes to per-capita foraging rates.

The dry season parameters were worse for growth than the wet season for recruitment which seems counterintuitive because most egg-laying occurs during the dry season (spring) before the water reaches its annual minimum depth (typically in May; 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. Alternatively, if females can store their resources, then conditions that shift more of the egg laying to the wet season, would also shift the weighting of the parameter average towards statsis (Fig S4). This is a novel hypothesis for the Everglades that could use exploration and currently runs counter to management goals that keep depths ideal for reproduction for as long as possible. The specific differences in hydrologic scenarios, affecting reproductive depths in the wet season, had relatively small effects on the isocline relative to the natural spatial and seasonal variation in the two juvenile parameters.

In addition to seasonal variation in predation regimes, spatial variation in productivity (i.e., TP) may also mediate predator limitation. The Everglades is phosphorus-limited ecosystem and periphyton total phosphorus ranges between 30-1000 µg·g-1 with typical oligotrophic TP concentrations between 110-400 µg·g-1 in the ridge and slough landscape (Gaiser et al. 2011).Growth of juvenile FAS varies with TP concentrations (Hansen et al. 2022, Barrus et al. 2023), and previous experimental manipulations of phosphorus showed that higher TP increased growth and juvenile apple snail survival in the presence of gape-limited crayfish (Davidson and Dorn 2018). Our results build on this finding by indicating that TP can mediate the net community level effects of predators on recruitment in the field. Periphyton total phosphorus levels were highest at WCA3A site 2 (Table S3), it was the only site to have wet season growth and survival that predicted favorable recruitment and combined parameters closer to stasis.. 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 (i.e., maintaining water levels in a shallow range of depths that encourages egg laying; Darby et al. 2015), but our results indicate that with the current levels of predation and individual growth, improving hydrologic conditions for reproduction in the Everglades can, at best, 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 molluscivorous tendencies, like mayan cichlids and african jewelfish that have invaded the Everglades and could have increased predation, but our observations suggested that native predators (e.g., crayfish, giant water bugs, greater sirens) in LILA seem to be more responsible for survival patterns than non-native species (e.g, mayan cichlids). One option might be to study controls on giant water bug predation to identify hydrologic conditions reducing their abundances in the dry season. But the observed predator community includes native species existing across a wide range of the hydroperiod gradient so it remains unclear how hydrologic variation (i.e., floods or droughts) could fundamentally shift juvenile survival. The relation between the predators and hydro-patterns may require more work, but measurements of juvenile survival and growth could also be repeated in time and space to measure variation in vital rates, especially survival, during windows of time that may produce good survival (e.g., depths of 10-15 cm). If net community-level predation has not changed from historical levels, then current hydrologic conditions could also be unfavorable for growth of the FAS (i.e., shifted to the left in Figure 5). Indeed, recent work has shown that increasing water flow velocity, increases growth of non-native *Pomacea* apple snails through changes to microbial food quality (Hansen et al. 2022). Therefore, an Everglades restored with more discharge might possibly improve growth of the juvenile FAS.

*Survival and growth Isocline*

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

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# Author Contributions

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

# Conflict of Interests

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

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# Figure Captions

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

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

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