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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 mortality, temperature, interaction strength, Snail Kite, ontogeny, predator-prey

# Abstract:

Juvenile survival and growth rates are commonly studied demographic rates with consequences for population growth. For species that can grow to achieve a size refuge from juvenile predators, the time spent at vulnerable sizes is acknowledged to affect population dynamics, but the interaction between juvenile survival and growth has not been illustrated theoretically and most studies of the concept have been controlled experiments. We used a published size-indexed demographic model of an annual gastropod (Florida Apple Snail, *Pomacea paludosa*) to construct a zero-population growth isocline from 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 two wetlands twice during the recruitment period, incorporating variable predator assemblages and seasonal environmental conditions. 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 ectothermic predators in the dry season produced higher mortality despite the cooler temperatures. Juvenile growth was faster in the warmer wet season. Parameter combinations of juvenile growth and survival in the dry season predicted 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 experimental and natural 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-dynamic context to quantified demographic rates and identified important temporal variation in survival and growth for the population. 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 qualitative prediction from the isocline should be generalizable. More importantly, the use of a population growth isocline from a size-indexed demographic model provided a framework for making meaningful interpretations about field-measured rates.

# Introduction

Population growth dynamics for many species are recognized to be influenced by stage- or size-specific growth and mortality rates (e.g., predation; Werner and Gilliam 1984, De Roos et al. 2003, Craig et al. 2006). Forty years ago in their review paper, Werner and Gilliam (1984) wrote about the importance of using size-indexed demographic models because a) size is a key feature affecting vital rates, and b) growth rates drive the relationship between size and age:

“A size-indexed demography,… 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 sub-models 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)

For many species, juvenile growth determines the amount of time an individual spends in a vulnerable size class, such that fast growth can be a type of defense against stage-specific juvenile predators (Werner and Gilliam 1984, Davidson et al. 2021).

Historical research on size-structured interactions 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 recent work has focused on how individual growth rates influence cohort survival in size-structured populations (Craig et al. 2006, McCoy et al. 2011, Schmera et al. 2015, Brannelly et al. 2019). There has been less done about the specific growth and mortality conditions that determine population dynamics (growth or decline); and to our knowledge, explicit theoretical predictions, whether general or specific, are lacking. Of the two theoretical studies that have explored theoretical predictions for growth-mediated effects on prey 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 asymmetrical thermal responses to variation in temperature. Neither study explored population-dynamic consequences of the interaction between juvenile mortality and growth.

Size-indexed demographic models that track size at age, combine growth (i.e., developmental) rates and survival to make population growth projections and identify sensitive stages/ages, could be used to identify the demographic parameter space making population growth negative, zero, or positive. One way to describe the parameter space would be the use of zero-population growth isoclines. Zero-population growth isoclines have typically been used by theoreticians 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 demographic 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 rates could offer quantitative maps for interpreting the combinatorial effects of juvenile survival and individual growth on population growth. Field-measured parameters could then be compared to the isocline to identify natural spatial or temporal variation in factors influencing recruitment or population growth.

The demographic-based isocline describing the zero-population growth should be negative when quantified with daily survival and individual growth rates (Figure 1), though the exact slope will depend on reproductive rates and life history details. The negative slope indicates that populations with higher individual growth rates can achieve positive growth with lower survival rates (higher mortality; Figure 1A). In natural settings, spatiotemporal environmental factors that influence juvenile survival, juvenile growth or both will mediate where a population falls in demographic isocline space and thus the level of top-down control on a population and the populations potential for growth (Craig et al. 2006, Davidson and Dorn 2018, Davidson et al. 2021, Ma et al. 2021, Nunes et al. 2021, Meehan et al. 2022). We suggest that the relationship is rather general and that by combining field measurements with the isocline population growth or positive recruitment can be assessed (Figure 1A) along spatiotemporal environmental gradients (e.g., temperature, productivity, salinity, moisture). The importance of the relationship between the two juvenile-stage variables can be observed and/or reasonably hypothesized for several species of conservation or management interest (Figures 1B-C) and we illustrate three examples conceptually from the published literature. By considering these examples from different ecosystems under the same framework we do not mean to over-simplify the ecological details of recruitment but rather conceptually illustrate the similar issue of the demographic rate combination that can help population biologists, whether involved in conservation, resource management, or pest management, assess the potential for population growth using a model and field measured rates.

First, in a freshwater rock pool system a spatial temperature gradient simultaneously affects growth rates of larval mosquitoes (*Aedes atropalpus*) and their survival with dragonfly (*Pantala* spp.) naiad predators (per-capita foraging rates of dragonflies increase with temperature; Figure 1B; Davidson et al. 2021, 2024). When measured by the researchers, the net effect of both rate changes was such that at lower temperatures the mosquito populations would not recruit well even though survival was high because daily growth was too low (left side of Figure 1B). With higher temperatures the short-term survival decreased but increased daily growth rate more than compensated for the lower daily survival rates, and mosquito populations could recruit and grow (right side of Figure 1B). In a contrasting, but similar invertebrate study of ant predator-caterpillar prey interactions in a terrestrial system, increases in caterpillar growth with higher temperatures were unable to compensate for increased ant predation (Pepi et al. 2018).

In a well-studied terrestrial ecosystem, recruitment (sucker to sapling) of quaking aspen (*Populus tremuloides*) that are browsed by elk (*Cervus canadensis*) are both hypothesized and known to be influenced by elk numbers and environmental variation in moisture (Figure 1C; Kauffman et al. 2010, Brice et al. 2024). After wolves (*Canus lupis*) were extirpated from the Greater Yellowstone Ecosystem (USA) and elk abundance was high, the browsing pressure on aspen stands was high everywhere regardless of the available moisture, resulting in non-recruiting stands (bottom of Figure 1C). Following wolf reintroduction the elk declined and browsing pressure was reduced (Kauffman et al. 2010, Brice et al. 2024), but aspen stand regrowth has been variable (Ripple and Beschta 2007, Kauffman et al. 2010, Beschta and Ripple 2016). Recent evidence indicates that the patchy recruitment of aspen suckers from different stands maybe from spatiotemporal variability in moisture allowing aspen suckers to grow to sizes large enough to escape the browsing pressure (top of Figure 1C; Brice et al. 2024). While no comparison of browsing and sucker growth has been conducted to our knowledge, this understanding of spatially patchy aspen recruitment in GYE was proposed by Kauffman et al. (2010) and the work by Brice et al. (2024) appears to confirm the importance of the interaction from the aspect of spatiotemporal variation in moisture. Examinations of the two rates in combination across spatiotemporal gradients, rather than being considered as alternative explanations (i.e., top-down vs. bottom-up factors), could improve the understanding of the patchy regrowth of aspen and other plants in response to wolf reintroductions and elk declines (Beschta and Ripple 2016).

In a marine ecosystem, multiple environmental gradients appear to affect one or both rates for oysters (e.g., *Crassostrea virginica* or *Saccostrea glomerata*); salinity gradients have been shown to influence eastern oyster growth rates (Munroe et al. 2017) and cause outbreaks of drilling snails (*Stramonita haemastoma*; Kimbro et al. 2013) at higher salinity levels than those observed by Munroe et al., (2017). Assuming oyster growth rates increase linearly at salinity levels above those observed by Munroe et al., (2017) then decreased survival by the outbreak of drilling snails at high salinity would likely overwhelm the benefits of quicker growth (Figure 1D). Alternatively, if oyster growth rates declined at salinity levels above those observed by Munroe et al., (2017) (i.e., unimodal growth response; Figure 1D), then the declines in growth would exacerbate the decreased survival by the outbreak of drilling snails (Figure 1D). Additionally, intertidal depths also influence the abundance of other juvenile-stage predators (e.g., crabs, snails, and fish; Figure 1D; Baillie and Grabowski 2019) and would increase survival rate in shallower locations. In another marine system combining juvenile survival and growth identified source-sink habitats for cleaner shrimp populations (*Stenopus hispidus;* Chockley et al. 2008).

While the specific slopes of the isoclines for these examples from freshwater, marine and terrestrial ecosystems are unknown, the qualitative description of the isocline should be generalizable to any species with high juvenile mortality and stage- or size-dependent predators (e.g., plants, vertebrates, invertebrates), and this approach has great potential for explaining and predicting patterns of population growth and recruitment in natural systems. In this paper, we use the case study of the Florida Apple Snail (*Pomacea paludosa;* hereafter FAS), an annual freshwater gastropod of conservation concern, and demonstrate the utility of a demographic based zero population growth isocline. We used a previously parameterized age-structured model for an annual freshwater gastropod, to identify theoretical combinations of juvenile-stage parameters predicting population stasis, growth, or decline. 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 predicted population growth during the annual reproduction/recruitment period (spring vs. early summer) in different wetlands. Using the isocline approach the measured values in the field become interpretable from a population-dynamic perspective and provide material for generation of novel hypotheses about population limitation.

# 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; Appendix S2: Figure S1). 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), which experienced significant declines within the ridge-slough landscape 2001-2010. The decline in Snail Kite populations within the ridge-slough landscape is at least partly explained by declines in FAS, so improving the conditions within the ridge-slough landscape 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, Kesler and Munns 1989), may also depredate juvenile FAS and lives in the Everglades, but the relationship had not been identified. Juvenile FAS outgrow most common fish and invertebrate predators when they reach ~10-11 mm SL (Valentine-Darby et al. 2015, Davidson and Dorn 2017, Supplemental). There had been no investigation on the factors that influence top-down control by these predators within natural systems partly because tracking cohorts of juvenile snails is notoriously difficult, thus we developed an isocline approach to investigate these factors using a FAS demographic model.

## 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 Appendix S1). The model tracks annual cohorts on daily time steps where the size structure is determined by growth parameters and daily mortality depends on size. Cohorts are produced seasonally in the spring months and depend upon adult numbers and water depths. The model was re-coded in R using the original parameters (Darby et al. 2015) with a few parameters adjusted to reflect recent changes in understanding of FAS life history (see Appendix S1: Table S1). Zero population growth isoclines were constructed by combinatorial simulations of the parameters for juvenile survival and growth under two different hydrologic conditions which produced depth-dependent differences in reproduction (i.e., “Good Reproduction” or “Poor Reproduction”; Appendix S1). For each combinatorial simulation, we measured population growth rate (λ) after a stable size distribution was achieved. The juvenile growth and mortality combinations for which population growth was constant (λ = 1) were identified and plotted as an isocline for each hydrologic scenario.

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

Once the isocline was constructed, we then measured survival and growth parameters in the field and plotted the results on the isocline state space. Using *in situ* experimental techniques (detailed further below and in Appendix S2) we calculated juvenile 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 the parameters are average experienced throughout the year. The season-dependent predictions from the field measures 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 make an annual estimate of growth and survival. 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; Appendix S2: Figure S1) 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 (Appendix S2: Figure S1B). Both wetlands have seasonally varying water levels but the water levels in LILA are under tighter control by pumps and culverts to perform landscape-scale hydrologic experiments. 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 (Appendix S2: Figure S1: 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, including 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. Tethering can inflate mortality rates of animals capable of escape (Baker and Waltham 2020), but FAS are relatively less mobile than their typical predators and rely on retracting into their shell to avoid predation rather than escape. For prey with little escape capability, tethering should give reliable information about prey survival particularly across gradients of predation as it measures encounter rate variation (Rochette and Dill 2000, Ruehl and Trexler 2013). Additionally, prior experimental work with this species did not indicate any measurable anti-predator response, either morphological or behavioral, to chronic exposure to crayfish (Davidson and Dorn 2017).

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 also observed tethering artefacts of different predators that allowed us to identify common predators (see further discussion in Appendix S2).

We measured growth either using *in-situ* 1-m2 mesh cages or with a regression that predicted wet season juvenile snail growth using total phosphorus (TP) concentrations in metaphytic mats (R2 = 0.85; Barrus et al., 2023). The metaphyton (sometimes called periphyton) in the Everglades is a floating calcareous mat composed 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 at WCA3A site 3, we measured the TP of metaphytic mats to predict FAS growth 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 lower mortality (higher survival) to persist or grow (λ≥1). Better reproduction (more eggs/female), produced in this model by different hydrologic conditions in the spring, 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 juvenile survival rates of 0.80; Appendix S1: Figure S2). The effects of higher reproduction on the isocline strengthened with faster growth and lower survival (Appendix S1:Figure S2).

## Empirical Survival and Growth related to the Isocline

We observed variation in the measured survival and growth parameters across sites and seasons (Figure 3). Tethering snails from hatchling to adults sizes indicated that survival was strongly size-dependent in the dry season with snails (<10 mm SL) heavily depredated (Appendix S2: Figure S2, Appendix S2:Table S1). Examination of the artefacts of deceased snails (<10 mm SL) suggested that the predators were primarily native invertebrates (*Belostoma lutarium*, *Procambarus fallax*) and salamanders (Appendix S2) and predator surveys indicated that abundances were also compositionally variable across seasons and sites (Appendix 2).

Across both field sites the juvenile growth was faster in the warmer wet season than the dry season (Figure 3, Appendix S3: Figure S2). The dry season had lower survival and slower growth with combinations falling below and to the left of the isocline (Figure 3). In contrast, the wet season had higher survival rates and faster growth; with average combinations falling on the isocline (LILA wetlands) or even above and to the right (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 egg production distributions, resulted in annual mortality and growth parameters that predicted a declining population for LILA, and confidence intervals that slightly overlapped the zero-growth isocline in WCA3 site 2 (Figure 3). The overlap of the confidence region with the isocline (indicating potential replacement) can only be observed when the isocline reflects good (hydrologic) conditions for egg-laying in WCA3A site 2 (Figure 3). While we present here only field parameters from the two sites which had growth rates measured from both seasons, the parameters from WCA3A site 3, and survival measured from the predator exclusion cages are plotted in Appendix S1: Figure S3.

# 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 that faster juvenile growth can offset higher mortality. Our work was specific to an annual freshwater gastropod with size-dependent survival, but 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. Field combinations of similar rates have been examined for other invertebrates (e.g., Chockley et al. 2008), but they were not compared against model-based population dynamic 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 (spring: Feb-April) which overlapped with most of the reproductive period of FAS. The results produce novel hypotheses about environmental variation and predator control that might limit the FAS populations in the Everglades.

*Growth-Survival Isocline*

A few theoretical studies (e.g., Rice et al. 1993) and extensive empirical studies have explored how growth mediates juvenile mortality rates (Jeyasingh and Weider 2005, Craig et al. 2006, Davidson and Dorn 2018, Pepi et al. 2018, Ma et al. 2021, Meehan et al. 2022, Davidson et al., 2024). Yet, studies on how interactions between growth and survival scale up to influence population dynamics remain rare, with only one theoretical study exploring changes in equilibrium densities between predator and prey (Pepi et al. 2023). We suggest that our zero-population growth isocline from a size-indexed demographic model is the first to illustrate the population dynamic predictions of growth-mediated predator limitation through juvenile mortality. The resulting isocline between juvenile survival and growth illustrates and confirms the logic that faster growth can allow populations to withstand higher mortality (Figure 2). This result held for a variety of hydrologic conditions that affect reproduction (Figure 2) including when hydrologic conditions were held constant at the best depth for reproduction (Appendix S1: Figure S3). Although shown in a specific case, we expect this negative slope isocline would hold for species with size-dependent survival, particularly species with annual life cycles and type III survivorship. How the two rates vary in time and space with increased system productivity or other environmental factors could be an important area of future theoretical investigations with a generalized model. Using an isocline may help illustrate and interpret the expectations.

The isocline also seems to indicate that altering reproduction can change the magnitude of the negative slope of the isocline (i.e., better reproduction makes the slope more negative) suggesting that populations disproportionately benefit from increased reproductive rates when conditions for growth are better than when they are worse. The steeper slope was likely a numerical response from juvenile snails hatching earlier and growing to maturity before the end of the summer reproductive season (i.e., early onset breeders). To the best of our knowledge, this is possible under the current understanding of FAS biology, but has not been demonstrated, thus indicating an emergent theoretical prediction for this system that could be tested further. In the FAS population model, water depth was an environmental condition that influenced reproductive rates, but other environmental conditions that influence reproduction could produce similar results. Indeed, temperature effects on reproductive rates have been extensively studied for many organisms (Dougherty et al. 2024), and temperature has been shown to influence multi-voltinism in moths in Boreal systems (Pöyry et al. 2011). The result that populations disproportionately benefit from increased reproductive rates at higher growth needs to be further corroborated with future theoretical work, but our suggestion demonstrates at least one reason for the need to explore the theoretical backing of population dynamic outcomes of size, and therefore growth-mediated juvenile mortality.

*Interpreting empirical measures of survival and growth*

Including an isocline analysis of survival and growth allowed us to interpret natural empirically-measured parameters in a population dynamic perspective and offers insights about how environmental variation might influence predator-prey interaction strength (Davidson et al. 2021, Pepi et al. 2023). Current temperature-dependent studies conclude that consumer-resource interaction strength should weaken or strengthen depending on the asymmetries in the thermal responses of the prey growth rate and predator per-capita foraging (Davidson et al. 2021, Pepi et al. 2023). Florida apple snail juveniles grow 1.4 times faster in the warmer wet season (Figure 5, Appendix S3: Figure S2) consistent with general responses of ectotherms (Kingsolver and Woods 2016, Pepi et al. 2018). So, overall prey survival might be expected to be greater, as we observed, in the wet season, except estimates of the per capita foraging rates of common (ectothermic) predators also increased in the warmer wet season (calculation in Appendix S2: Figure S4). The largest change between seasons seems to have been lower predator abundances after the wetlands reflooded (Appendix S2: Figure S4) which lowered overall mortality; the predator community changes seem to have overwhelmed any changes in survival that might have been mediated by temperature (Appendix S2). Studies that isolate the effects of variable environmental conditions on predator-prey interactions 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 (Davidson et al. 2024). Environmentally mediated changes in predator abundances may be more important to survival than the per-capita rates, but also could counteract or exacerbate the temperature-mediated changes to per-capita foraging rates.

*Novel Hypotheses for Population Management*

The hydrologic conditions within the Everglades are heavily managed with the goal of restoring conditions for wildlife and biodiversity. Improved conditions for the FAS in the Everglades will be necessary to make their populations rebound and support nesting populations of the Federally endangered Everglades Snail Kite. 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 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 (Appendix S1: Figure S3). 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 what conditions could be favorable for populations of FAS in the Everglades.

First, seasonal variation in growth, reproduction and survival have important implications for FAS populations. The dry season parameters were worse than the wet season for recruitment which seems counterintuitive because most egg-laying occurs during the dry season (spring) before the water reaches its annual minimum depth (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 hydrologic conditions that shift more of the egg laying to the wet season, would also shift the weighting of the parameter average towards stasis (Figure 3). Current management goals are to keep depths ideal for reproduction for as long as possible, but management strategies that could shift more reproduction to later in the wet season when growth and survival conditions are favorable could be fruitful. Although more research is needed to understand how populations respond in this manner, one observation suggests that shifts in reproduction to July-August can occur in shorter-hydroperiod locations outside the ridge-slough landscape (O’Hare 2010).

Spatial variation in productivity (i.e., total phosphorus, TP) or perhaps restoration of historic flow could encourage growth rates. 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 TP 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. Perhaps more promisingly, the Everglades was historically a flowing system (the River of Grass) with velocities > 2 cm/s, and recent work has shown that increasing water flow velocity, increases growth of *Pomacea* apple snails through changes to microbial food quality (Hansen et al. 2022). Therefore, an Everglades restored with more discharge might improve growth of the juvenile FAS.

Finally, the predation rates in the Everglades might currently be higher than historical levels as a function of non-native fishes or perhaps hydrologic conditions 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 of diets and tethering remnants 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 like Mayan cichlids. One option might be to study hydrologic covariates of 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 and it remains unclear how floods or hydrologic droughts could fundamentally shift juvenile predators (low water and drying encourages crayfish; Dorn and Cook 2015, Sinnickson and Dorn 2024). 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 better survival (e.g., depths of 10-15 cm).

*Conclusion*

The joint effects of juvenile growth and survival on recruitment is well-understood in ecology (e.g., population studies of fish, mosquitoes, aspen, shrimp), but using a demographic isocline approach to studying spatiotemporal recruitment variation in populations is novel and could have utility for understanding and managing populations. We created a zero-population isocline using a size-indexed demographic model that illustrated the negative relationship between juvenile growth and survival; populations with faster-growing juveniles can withstand greater mortality (lower survival) and still grow. Our application operationalized the concept for use in a field setting making it possible to interpret field-based demographic rates and incorporate variable reproduction. Measured rates for the snail we studied indicated that seasonally-averaged conditions could not support positive population growth but that conditions were better in the summer (warmer season) than in the spring (cooler season). Seasonal changes in the predator community overwhelmed a simpler prediction based on thermal-responses of predators and prey. Finally, this approach combining a theoretical isocline with field-derived parameters offered new hypotheses about the conditions needed to restore a historical prey population of an endangered species. We encourage others working on any species with high juvenile mortality and stage- or size-dependent predators (e.g., plants, vertebrates, invertebrates) to develop isoclines from size-indexed demographic models, obtain field-based parameters, and interpret the factors producing positive or negative population growth of the field-based parameters.

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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

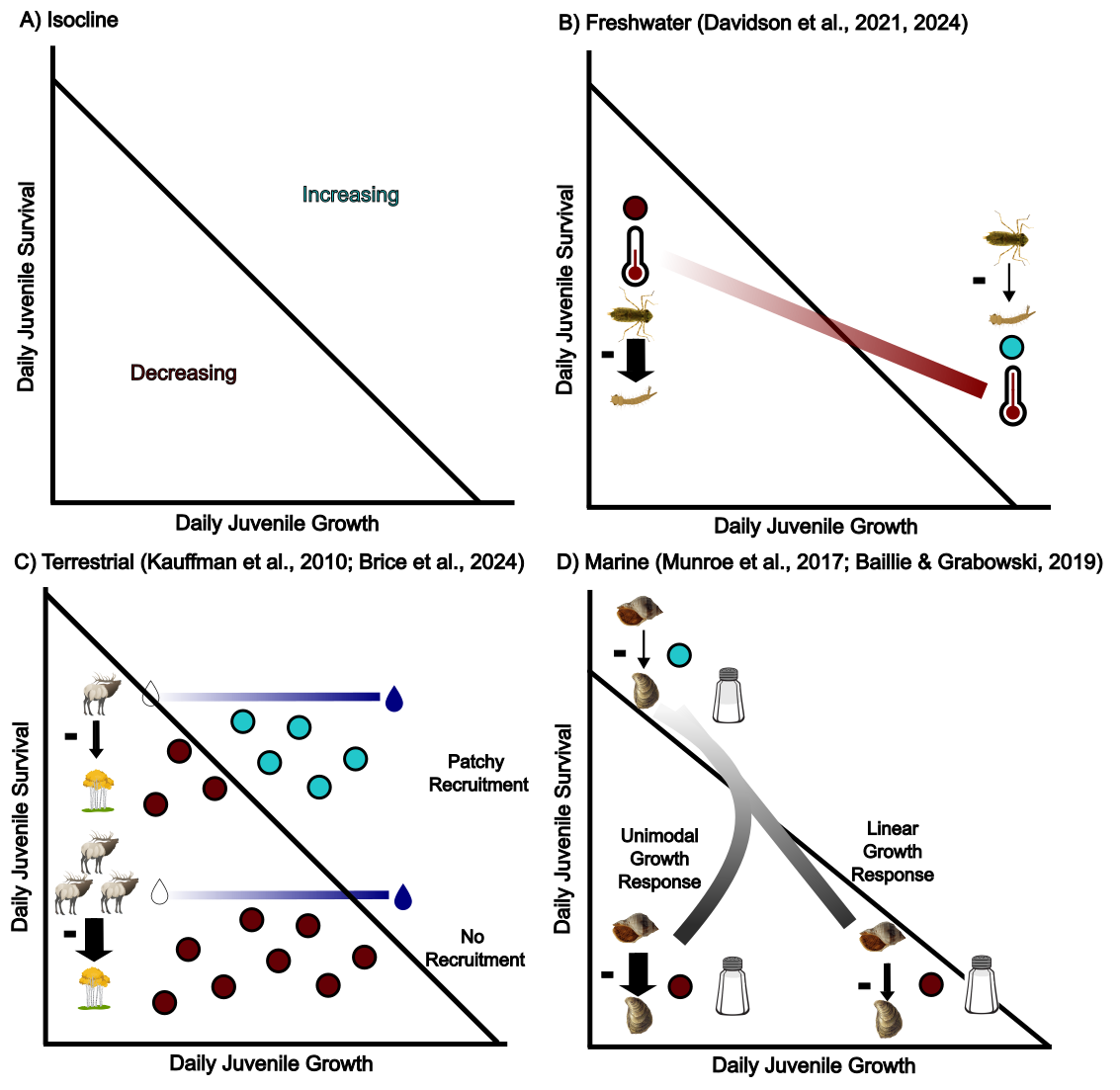


Figure 1. A) Zero-population growth isocline illustrating the expected joint impact of juvenile growth rates and mortality to consumers. Areas to the left and below the isocline indicate prey populations are decreasing/not recruiting while areas above and to the right indicate populations are increasing/recruiting. B-D) Demonstrated or hypothetical examples of populations spanning freshwater, terrestrial and marine ecosystems for which the demographic isocline could give conceptual meaning to population dynamics and predictive value for field measured rates. Points colored red indicate populations are declining/not recruiting while points colored blue indicate populations are increasing/recruiting. B) The relationship between mosquito (*Aedes atropalpus*) population with predatory dragonflies (*Pantala* spp.) depends on temperature mediation of both consumption rates (mosquito survival) and mosquito growth rates so that warmer conditions produce greater mosquito recruitment. C) Quaking aspen (*Populus tremuloides*) stand recruitment depends on moisture/precipitation gradients and elk (*Cervus canadensis*) population sizes that determine browsing rates and sucker survival. D) Oyster (*Crassostrea virginica*) growth and mortality to predators drilling snails are affected by salinity gradients, though the combinatorial impacts on population recruitment cannot be easily predicted conceptually.

A graph of growth and decline

Description automatically generated

Figure 2 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.

A screenshot of a computer game

Description automatically generated

Figure 3. Zero-population growth isocline illustrating the expected joint impact of juvenile growth rates and mortality to consumers. Areas to the left and below the isocline indicate prey populations are decreasing/not recruiting while areas above and to the right indicate populations are increasing/recruiting. Blue points represent wet season parameters, brown points represent dry season parameters, and open circles represent weighted averages of the two seasons. Numbers indicate new hypotheses for management and further research to improve conditions for FAS.