**Journal**: Ecology

**Manuscript type**: Article

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

Nathan T. Barrus1,2,4; ORCID: 0000-0001-7503-3120

Mark I. Cook3,

and Nathan J. Dorn2,4; ORCID: 0000-0001-5516-0253

1 Corresponding Author: Nathan T. Barrus, nbarrus1@gmail.com

2 Current affiliation: Institute of Environment and Dept. of Biological Sciences, Florida International University, Miami, FL, USA

3 Applied Sciences Bureau, South Florida Water Management District. West Palm Beach, FL, USA

4 Department of Biological Sciences, Florida Atlantic University, Boca Raton, FL, USA

# 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**

Consumptive effects, size-dependent mortality, demographic rates, interaction strength, predator-prey, top-down vs bottom up.

# 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 smaller vulnerable sizes is expected to affect population dynamics, but the combinatorial effect of juvenile growth and survival has not been illustrated theoretically and most studies of the interaction have been in experimental settings. The combinatorial effects of the two rates have applications to field studies of recruitment variation for a diversity of species that could be assessed with demographic models and isoclines. We conceptually illustrate the potential of using demographic isoclines for marine, terrestrial and freshwater examples in the literature, and then demonstrate the use of a demographic isocline in a case study for an annual freshwater gastropod (Florida Apple Snail, *Pomacea paludosa*). Using a published size-indexed demographic model, we constructed a zero-population growth isocline for theoretical combinations of juvenile growth and survival rates. We then quantified daily juvenile survival and growth in two wetlands twice during the recruitment period, incorporating variable predator assemblages and seasonal environmental conditions (i.e., water depth and temperature). Daily juvenile survival rates were lower in the cooler dry season than in the warmer wet (rainy) season. Juvenile growth was faster in the warmer wet season. Parameter combinations of juvenile growth and survival in the dry season predicted declining populations (λ < 1), 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 qualitative predictions were robust to variation in hydrologic conditions affecting reproductive rates, but with better hydrologic conditions one lambda was near one (i.e., at replacement). Our demographic isoclines gave population-dynamic context to field measured demographic rates, identified important temporal variation in survival and growth for the population and generated new hypotheses for future investigation and management. We encourage others to consider developing demographic isocline to interpret variation of stage-sensitive demographic rates across spatiotemporal environmental conditions.

# Introduction

Population growth dynamics for many species are 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). In a review paper 40 years ago, Werner and Gilliam (1984) wrote that size-indexed demographic models are important because a) size is a key feature affecting vital rates, and b) growth rates determine the relationship between size and age. Because growth determines the amount of time an individual spends in vulnerable sizes, faster growth can be a type of defense against stage-specific consumers (Werner and Gilliam 1984, Davidson et al. 2021). Research on size-structured interactions has historically 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). More recently studies of the interaction have 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), but only two studies have examined the theoretical juvenile growth and mortality conditions of populations dynamics (e.g., fish recruitment-Rice et al. 1993, equilibrium densities of caterpillars-Pepi et al. 2023). To our knowledge, explicit theoretical predictions about population growth or declines are lacking and no effort has been made to use theoretical predictions to interpret the combinations of measured field demographic rates on population growth.

Size-indexed demographic models track size at age, combining growth (i.e., developmental) rates and per-capita survival rates to make population growth projections. Such models can also be used to identify the demographic parameter space making population growth negative, zero, or positive and we suggest the parameter combinations can be profitably be illustrated with zero population growth isoclines. Zero population growth isoclines have typically been used theoretically to predict population dynamics and/or coexistence outcomes for interacting species under variable parameter values and assumptions about the interactions (MacArthur and Levins 1964, Vance 1985), but zero-growth isoclines could. 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 survival and growth of a sensitive stage on population growth. Field measured parameters could then be compared to the isocline to identify natural spatial or temporal variation influencing recruitment or population growth. Here we describe examples from marine, terrestrial, and freshwater ecosystems that can be conceptualized using demographic isoclines and demonstrates the use of an isocline with a case study of a freshwater gastropod of conservation concern.

Demographic-based isoclines can be created by identifying specific combinations of individual survival and growth rates of a sensitive stage (hereafter “juvenile”) that produce populations at dynamic equilibrium (λ = 1) and plotting the rate combinations in demographic rate space (Figure 1A). Populations grow (λ>1) when a population experiences demographic conditions that fall above and to the right of the isocline. In contrast to individual survival, cohort survival is the product of the individual survival rate and growth rate which sets the time spent in the vulnerable juvenile stage. The exact shape (i.e., steepness, linearity) of the isocline will depend on life history traits, but the negative slope indicates that populations in places or times with faster individual growth rates can persist or increase with higher rates of daily mortality (lower survival) (Figure 1A). In natural settings, spatiotemporal environmental factors that influence survival and growth of a sensitive stage will combine to mediate where the population falls in demographic state space (Craig et al. 2006, Davidson and Dorn 2018, Davidson et al. 2021, Ma et al. 2021, Nunes et al. 2021, Meehan et al. 2022). If most of the variation in per capita survival can be attributed to stage-specific consumers (Werner and Gilliam 1984) then the rate locations in demographic state space also indicates the degree of consumer control on the population and environmental mediation of such top-down control (Figure 1B-D).

The general utility of this isocline approach can be demonstrated using several species of conservation concern that span terrestrial, marine, and freshwater ecosystems. For these examples the specific isoclines are not known but details of the recruitment or population growth are described in relevant ways to make the approach appropriate. In all three cases demographic parameters related to environmental gradients have been studied and the qualitative predictions about where conditions might fall can be reasonably hypothesized (Figures 1B-D). By describing these three examples from published literature under the same framework we do not intend to over-simplify the ecological details of recruitment, but rather to conceptually illustrate the similar issue of the demographic rate combinations that can help population biologists, whether involved in conservation, resource 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 (i.e., per-capita foraging rate of the predator increases with temperature; Figure 1B; Davidson et al. 2021, 2024). The net effect of both rate changes was such that at cooler temperatures the mosquito populations would not recruit well even though survival was high because daily growth was too slow; rate combinations were below and left of the isocline (Figure 1B). With higher temperatures the average daily survival decreased, but the increased daily growth rate with warmer temperatures shortened the time spent in the larval stage even further so that mosquito populations could recruit and grow; joint rates moved down, but also to the right of the isocline (Figure 1B). In a contrasting invertebrate system (not shown) of ant predator-caterpillar prey interactions in a terrestrial system, warmer temperatures affected both rates in the same manner, but increases in caterpillar growth with higher temperatures were unable to compensate for lower survival from 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 influenced by elk numbers and environmental variation (Figure 1C; Brice et al. 2024). After wolves (*Canus lupis*) were extirpated from the Greater Yellowstone Ecosystem, USA (GYE) and elk abundance was high, the browsing pressure on aspen stands was high everywhere regardless of the available moisture, resulting in widespread recruitment failure (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 was 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 may be from spatiotemporal variability in moisture allowing aspen suckers to grow to sizes large enough to escape the browsing pressure (upper points in Figure 1C; Brice et al. 2024). While no comparison of browsing rates 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) 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 predator reintroductions and herbivore densities (Beschta and Ripple 2016).

In a marine ecosystem, multiple environmental gradients (e.g., depth, salinity; Munroe et al. 2017, Baillie and Grabowski 2019) appear to affect one or both demographic rates of small settling oysters (e.g., *Crassostrea virginica* or *Saccostrea glomerata*) which are considered foundation species. Higher salinity produces faster growth of small oysters (Munroe et al. 2017), but high salinity can also encourage outbreaks of predaceous drilling snails (Kimbro et al. 2013). How the two rates change together in state space with increased salinity is unclear from the literature, but salinity-mediated changes to survival and a subsequent population collapse (illustrated in Figure 1D) in an estuary was observed by Kimbro et al. (2013).

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 mortality from stage- or size-dependent predators (e.g., plants, vertebrates, invertebrates) and we examined the Florida Apple Snail (*Pomacea paludosa;* hereafter FAS), as a case study to demonstrate the utility of a demographic-based zero population growth isoclines. The FAS is an annual gastropod of conservation concern, and we used a previously parameterized age-structured model to identify theoretical combinations of juvenile-stage parameters predicting population stasis (λ = 1), growth (λ > 1), or decline (λ < 1). We then quantified size- and season-dependent daily survival rates and growth rates in the field to 1) test for size-dependent survival and 2) interpret the combined effects that juvenile growth and survival have on predicted population growth during the annual 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 generating 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 in the wet season 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 wetlands (Gutierre et al. 2019). Snails grow from 3–4 mm shell length (SL) at hatching to > 40 mm SL as 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 from 2001–2010. The decline in Snail Kite populations in the Everglades 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). Giant water bugs (Belostomatidae, Kesler and Munns 1989) live in the Everglades, are known to eat snails but had not been studied. 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, Appendix 2: Figure S2). There has been no investigation of the factors that influence survival of juvenile snails after hatching or the population-dynamic impacts within natural systems partly because tracking cohorts of small juvenile snails is logistically infeasible, thus we developed an isocline approach to investigate spatiotemporal variation in mortality and growth using a 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 (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 to summer months and depend upon adult numbers and water depths. The model was re-coded in R using most of the original parameters from Darby et al. (2015) but excluded carrying capacity and included a few adjusted parameters to reflect recent changes in the 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 (16/m2) in mesh predator-exclusion cages (Barrus et al. 2023), we considered negative density-dependent growth to be irrelevant to our model evaluations which were more simply trying to identify parameters that would produce an increasing or decreasing population.

Once the isocline was constructed, we quantified 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 the isocline state space assumed that the parameters were averages experienced throughout the year. The season-dependent predictions from the field measures were therefore expected snail recruitment assuming the rates measured each season. To combine the seasonal parameters for each population into annual average values, we calculated the weighted averages of the seasonal parameters. Because ~70% of reproduction (egg laying) 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

We measured survival and growth in wetlands at the Loxahatchee Impoundment Landscape Assessment (LILA) and in 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 wetland impoundments at LILA 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 previously supported Snail Kite nesting (Cattau et al. 2016).

We tethered snails by attaching monofilament to the apex of the shell using super glue, then attaching the other end of the monofilament to 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).

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). Prior experimental work with this species did not find any measurable anti-predator response, either morphological or behavioral, to chronic exposure to crayfish (Davidson and Dorn 2017).

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 mesocosms 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.

# Results

Zero-population growth isoclines created from the age-structured population model produced a declining isocline consistent with the expected interaction between daily growth and survival (Figure 2). Combinations of the two parameters above and to the right of the isocline predict growing populations (λ > 1) while combinations below the isocline predict 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). Hydrologic conditions that improved reproductive conditions (i.e., eggs laid/female) moved the isocline down and left (gray isocline in Figure 2), making the population slightly 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; Figure 2). The separation between the isoclines was greatest for conditions with faster growth and lower survival (Figure 2).

## 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 adult 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 variable across seasons and sites (Appendix S2).

Across both field sites the juvenile growth was faster in the warmer wet season than the dry season (Figure 2, 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 2). 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 2). Snails in WCA3A site 2 had faster growth than those in LILA (Figure 2). The combined effects, weighted by seasonal egg production distributions, resulted in average mortality and growth parameters that predicted a declining population for both sites, though confidence intervals slightly overlapped the zero-growth isocline for WCA3 site 2 (Figure 2). The overlap of the confidence region with the isocline (indicating potential replacement) could only be observed when the isocline reflected good hydrologic conditions for egg-laying in WCA3A site 2 (Figure 2).

# Discussion

Using a size-indexed age-structured population model we produced zero-population growth isoclines illustrating the combinatorial effects of growth and survival of a sensitive stage on population growth. The expected effect that faster juvenile growth can offset higher mortality was illustrated. Our work was specific to an annual freshwater gastropod with size-dependent survival, but the approach is conceivably applicable to any size-structured consumer-resource interaction. Field combinations of demographic rates for a marine shrimp were examined for multiple populations by Chockley et al. (2008), but they were not compared against population dynamic predictions. The isocline from the demographic model allowed us to interpret field measured rates and conclude that the populations should be static or declining. Seasonal parameters further indicated that both survival and growth were poorer in the dry season (spring: Feb–April) which overlaps with most of the reproductive period of FAS. The results produce novel hypotheses about environmental variation and predator control that might limit the FAS in the Everglades. Creating similar demographic isoclines for other species could offer insights into the spatiotemporal conditions producing population growth and recruitment.

*Growth-Survival Isocline*

A few theoretical studies (e.g., Rice et al. 1993) and extensive empirical studies have explored how growth mediates mortality rates of a sensitive stage (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 one theoretical study exploring fish recruitment (Rice et al. 1993), and one theoretical study exploring changes in equilibrium densities between predator and prey (Pepi et al. 2023). 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 any species with size-dependent survival. 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.

Adjusting conditions for better FAS reproduction steepened the slope and effectively increased the combinatorial parameter space that produced increasing populations. This suggests that populations would disproportionately benefit from increased reproductive rates when juvenile growth rates were faster than when they were slower. The steeper slope was probably caused by the simulated juvenile snails hatching earlier and growing to maturity before the end of the summer reproductive season. 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 hypothesis 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 might 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 interpretation that populations disproportionately benefit from increased reproductive rates in times and places with higher juvenile growth needs to be further corroborated, but our work demonstrates the need to explore the theoretical expectations of population dynamic outcomes of size- and growth-mediated juvenile mortality.

To employ demographic based isoclines in population research would require the development of a size-indexed demographic model that allows the isolation of the growth and survival of sensitive juvenile stages. The time steps in the model should be relevant to the sensitive stages (size-dependent mortality) and the measurements in the field should be measured commensurately to match the predictions.

*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 consumer-resource interaction strength (Davidson et al. 2021, Pepi et al. 2023). Recent studies of temperature-dependence conclude that consumer-resource interaction strength should weaken or strengthen depending on asymmetries between thermal responses of the resource growth rate and consumer per-capita foraging (Davidson et al. 2021, Pepi et al. 2023). For our wetlands, the per capita foraging rates of ectothermic predators increased in the warmer wet season (calculation in Appendix S2: Figure S4), which should strengthen interactions between FAS and their predators (Figure 2) except that lower predator abundances after the wetlands reflooded also changed between seasons (Appendix S2: Figure S4). The predator community (abundance) changes appear to have overwhelmed any changes in snail survival that were mediated by temperature on per-capita foraging (Appendix S2). Studies that isolate the effects of variable environmental conditions on predator-prey interactions have typically controlled predator densities 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 consideration of natural seasonal variation in predator abundances that could covary with temperature (Davidson et al. 2024). Environmentally mediated changes in predator communities may be more important to survival than the per-capita rates and could conceivably 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, historic habitats, biodiversity, and safe-guarding drinking water (National Academies of Sciences, Engineering, and Medicine 2021). Improved conditions for the FAS populations in the Everglades will be necessary to support nesting 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, at best, only maintain the already small populations of FAS. For FAS population growth to become positive, we offer three hypotheses (see numbers in Table 1 and Figure 3) about the spatiotemporal environmental conditions that could shift the average daily survival and growth conditions experienced by juveniles (open circles Figure 3).

The dry season parameters were combinatorially worse than the wet season parameters which is particularly problematic 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. If females can store their resources and hydrologic conditions can conceivably shift more of the egg laying to the wet season, then the average demographic parameters would move up and right towards stasis or growth (Hypothesis 1; Table 1). Although more research is needed to understand how water levels might mediate this response, one observation suggests that shifting reproduction to the wet season (July–August) can occur in shorter-hydroperiod wetlands outside the ridge-slough landscape (O’Hare 2010).

Improved food quality could also move parameters to the right in state space (Hypothesis 2; Table 1). The Everglades is phosphorus-limited ecosystem and periphyton total phosphorus ranges between 30–1000 µg·g-1 with natural 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 in the periphyton (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), and it was the only site that had wet season growth and survival parameter combinations that predicted population growth. Nevertheless, restoration and management actions expressly avoid eutrophication of the Everglades (citation). Perhaps more promisingly, the pre-drainage Everglades was a flowing ecosystem (the “River of Grass”) with water velocities > 2 cm/s. Recent work showed that increasing flow velocity increased growth of *Pomacea* apple snails through changes to microbial food quality (Hansen et al. 2022). Therefore, flow restorion might improve growth rates of juvenile FAS (Hypothesis 2; Table 1).

Finally, the predation rates in the Everglades might currently be higher than historical levels as a function of non-native fishes (Pintar et al. 2023) or hydrologic conditions supporting higher densities of juvenile predators (e.g., invertebrates) in the sloughs (Hypothesis 3;Table 1). Some non-native fishes introduced to the Everglades have molluscivorous tendencies, 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 mortality patterns than non-native species like Mayan cichlids (*Mayaheros uropthalmus*). Because the predator assemblage feeding on juvenile snails included native species existing across a wide range of the hydroperiod gradient, it remains unclear how floods or hydrologic droughts would fundamentally shift survival rates (e.g., low water and drying encourage crayfish populations; Dorn and Cook 2015, Sinnickson and Dorn 2024).

*Conclusion*

We demonstrated the first demographic isocline approach to studying spatiotemporal recruitment variation in populations that could be used in studying and managing size-structured consumer-resource interactions across terrestrial, marine and freshwater ecosystems. The isocline was derived from combinations of daily survival and growth of sensitive sizes within a size-indexed demographic model and illustrated a negative relationship between juvenile growth and survival. The negative relationship indicates that populations with faster-growing juveniles can withstand greater mortality (lower survival) and still grow. When this approach is operationalized in a field setting, the local population dynamics can be interpreted from field-based demographic rates. Our case study indicated that seasonal changes in the predator community were more important in determining interaction strength than simpler physiological expectations based on thermal responses of predators and prey. This demographic isocline approach provided novel hypotheses about the conditions needed to restore a historical resource of an endangered species.

# Acknowledgments:

J. Sommer and E. Cline were instrumental in completing the fieldwork and maintaining the wetland hydrologic conditions. K. Buckman, S. Olayon, J. Aymonin, and K. Chehab also participated in field work. The thoughtful comments of this work from the Aquatic ecology lab in Florida International University significantly improved this work. This work was made possible by a contract between the South Florida Water Management District and Florida Atlantic University (#4600003950) and Florida International University (#4500013351). It was also made possible through the cooperative agreement between Florida International University and National Park Service (#P21AC10856). This paper is contribution ## the Institute of Environment at Florida International University.

# Author Contributions

All authors contributed 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.

# References

Baker, R., and N. Waltham. 2020. Tethering mobile aquatic organisms to measure predation: A renewed call for caution. Journal of Experimental Marine Biology and Ecology 523:151270.

Barrus, N. T., D. Drumheller, M. I. Cook, and N. J. Dorn. 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 850:841–860.

Beschta, R. L., and W. J. Ripple. 2016. Riparian vegetation recovery in Yellowstone: The first two decades after wolf reintroduction. Biological Conservation 198:93–103.

Brannelly, L. A., M. E. B. Ohmer, V. Saenz, and C. L. Richards‐Zawacki. 2019. Effects of hydroperiod on growth, development, survival and immune defences in a temperate amphibian. Functional Ecology 33:1952–1961.

Brice, E. M., E. J. Larsen, D. R. Stahler, and D. R. MacNulty. 2024. The primacy of density‐mediated indirect effects in a community of wolves, elk, and aspen. Ecological Monographs:e1627.

Cattau, C. E., P. C. Darby, R. J. Fletcher, and W. M. Kitchens. 2014. Reproductive responses of the endangered snail kite to variations in prey density: Effects of Prey Density on Kite Reproduction. The Journal of Wildlife Management 78:620–631.

Cattau, C. E., R. J. Fletcher, B. E. Reichert, and W. M. Kitchens. 2016. Counteracting effects of a non‐native prey on the demography of a native predator culminate in positive population growth. Ecological Applications 26:1952–1968.

Craig, J. K., B. J. Burke, L. B. Crowder, and J. A. Rice. 2006. Prey growth and size-dependent predation in juvenile estuarine fishes: experimental and model analyses. Ecology 87:2366–2377.

Darby, P. C., D. L. DeAngelis, S. S. Romañach, K. Suir, and J. Bridevaux. 2015. Modeling apple snail population dynamics on the Everglades landscape. Landscape Ecology 30:1497–1510.

Davidson, A. T., and N. J. Dorn. 2017. Life history traits determine the differential vulnerability of native and invasive apple snails (Pomacea spp.) to a shared juvenile-stage predator. Aquatic Ecology 51:331–341.

Davidson, A. T., and N. J. Dorn. 2018. System productivity alters predator sorting of a size-structured mixed prey community. Oecologia 186:1101–1111.

Davidson, A. T., E. A. Hamman, M. W. McCoy, and J. R. Vonesh. 2021. Asymmetrical effects of temperature on stage‐structured predator–prey interactions. Functional Ecology 35:1041–1054.

Davidson, A. T., C. R. Stunkle, J. T. Armstrong, E. A. Hamman, M. W. McCoy, and J. R. Vonesh. 2024. Warming and top‐down control of stage‐structured prey: Linking theory to patterns in natural systems. Ecology 105:e4213.

De Roos, A. M., L. Persson, and E. McCauley. 2003. The influence of size‐dependent life‐history traits on the structure and dynamics of populations and communities. Ecology Letters 6:473–487.

Dougherty, L. R., F. Frost, M. I. Maenpaa, M. Rowe, B. J. Cole, R. Vasudeva, P. Pottier, E. Schultner, E. L. Macartney, I. Lindenbaum, J. L. Smith, P. Carazo, M. Graziano, H. Weaving, B. Canal Domenech, D. Berger, A. Meena, T. R. Bishop, D. W. A. Noble, P. Simões, J. Baur, M. C. Breedveld, E. I. Svensson, L. T. Lancaster, J. Ellers, A. N. De Nardo, M. A. Santos, S. A. Ramm, S. M. Drobniak, M. Redana, C. Tuni, N. Pilakouta, Z. V. Zizzari, G. Iossa, S. Lüpold, M. Koppik, R. Early, C. Gasparini, S. Nakagawa, M. Lagisz, A. Bretman, C. Fricke, R. R. Snook, and T. A. R. Price. 2024. A systematic map of studies testing the relationship between temperature and animal reproduction. Ecological Solutions and Evidence 5:1–17.

Drumheller, D. K., M. I. Cook, and N. J. Dorn. 2022. The role of direct chemical inhibition in the displacement of a native herbivore by an invasive congener. Biological Invasions 24:1739–1753.

Gaiser, E. E., P. V. McCormick, S. E. Hagerthey, and A. D. Gottlieb. 2011. Landscape Patterns of Periphyton in the Florida Everglades. Critical Reviews in Environmental Science and Technology 41:92–120.

Gaiser, E. E., J. C. Trexler, and P. R. Wetzel. 2012. The Florida Everglades. Pages 231–252 Wetland Habitats of North America. University of California Press, Los Angeles California.

Gutierre, Darby, Valentine-Darby, Mellow, Therrien, and Watford. 2019. Contrasting Patterns of Pomacea maculata Establishment and Dispersal in an Everglades Wetland Unit and a Central Florida Lake. Diversity 11:1–20.

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

Hansen, C., S. Newman, C. J. Saunders, E. K. Tate-Boldt, and N. J. Dorn. 2022. Flow-mediated growth of an aquatic herbivore. Hydrobiologia 849:3161–3173.

Jeyasingh, P. D., and L. J. Weider. 2005. Phosphorus availability mediates plasticity in life-history traits and predator-prey interactions in *Daphnia*: Phosphorus alters life-history and predation. Ecology Letters 8:1021–1028.

Kauffman, M. J., J. F. Brodie, and E. S. Jules. 2010. Are wolves saving Yellowstone’s aspen? A landscape‐level test of a behaviorally mediated trophic cascade. Ecology 91:2742–2755.

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

Kimbro, D. L., B. S. Cheng, and E. D. Grosholz. 2013. Biotic resistance in marine environments. Ecology Letters 16:821–833.

Ma, G., C. Bai, V. H. W. Rudolf, and C. Ma. 2021. Night warming alters mean warming effects on predator–prey interactions by modifying predator demographics and interaction strengths. Functional Ecology 35:2094–2107.

MacArthur, R., and R. Levins. 1964. Competition, habitat selections, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences 51:1207–1210.

McCoy, M. W., B. M. Bolker, K. M. Warkentin, and J. R. Vonesh. 2011. Predicting Predation through Prey Ontogeny Using Size-Dependent Functional Response Models. The American Naturalist 177:17.

McVoy, C. W., W. P. Said, J. Obeyseker, J. A. VanArman, and T. W. Dreschel. 2011. Landscapes and Hydrology of the Predrainage Everglades. University Press of Florida.

Meehan, M. L., K. F. Turnbull, B. J. Sinclair, and Z. Lindo. 2022. Predators minimize energy costs, rather than maximize energy gains under warming: Evidence from a microcosm feeding experiment. Functional Ecology 36:2279–2288.

Munroe, D., S. Borsetti, K. Ashton-Alcox, and D. Bushek. 2017. Early Post-Settlement Growth in Wild Eastern Oyster (Crassostrea virginica Gemlin 1791) Populations. Estuaries and Coasts 40:880–888.

National Academies of Sciences, Engineering, and Medicine. 2021. Progress Toward Restoring the Everglades: The Eighth Biennial Review - 2020. Page 25853. National Academies Press, Washington, D.C.

Nunes, L. T., D. R. Barneche, N. S. Lastrucci, A. A. Fraga, J. A. C. C. Nunes, C. E. L. Ferreira, and S. R. Floeter. 2021. Predicting the effects of body size, temperature and diet on animal feeding rates. Functional Ecology 35:2229–2240.

O’Hare, N. K. 2010. Pomacea paludosa (Florida Apple Snail) Reproduction in Restored and Natural Seasonal Wetlands in the Everglades. Wetlands 30:1045–1052.

Pepi, A., P. Grof-Tisza, M. Holyoak, and R. Karban. 2018. As temperature increases, predator attack rate is more important to survival than a smaller window of prey vulnerability. Ecology 99:1584–1590.

Pepi, A., T. Hayes, and K. Lyberger. 2023. Thermal asymmetries influence effects of warming on stage and size-dependent predator–prey interactions. Theoretical Ecology 16:105–115.

Pöyry, J., R. Leinonen, G. Söderman, M. Nieminen, R. K. Heikkinen, and T. R. Carter. 2011. Climate-induced increase of moth multivoltinism in boreal regions: Climate-induced increase in moth multivoltinism. Global Ecology and Biogeography 20:289–298.

Rice, J. A., T. J. Miller, K. A. Rose, L. B. Crowder, E. A. Marschall, A. S. Trebitz, and D. L. DeAngelis. 1993. Growth Rate Variation and Larval Survival: Inferences from an Individual-Based Size-Dependent Predation Model. Canadian Journal of Fisheries and Aquatic Sciences 50:133–142.

Richardson, C. J. 2010. The Everglades: North America’s subtropical wetland. Wetlands Ecology and Management 18:517–542.

Ripple, W. J., and R. L. Beschta. 2007. Restoring Yellowstone’s aspen with wolves. Biological Conservation 138:514–519.

Rochette, R., and L. M. Dill. 2000. Mortality, behavior and the effects of predators on the intertidal distribution of littorinid gastropods. Journal of Experimental Marine Biology and Ecology 253:165–191.

Ruehl, C. B., and J. C. Trexler. 2013. A suite of prey traits determine predator and nutrient enrichment effects in a tri‐trophic food chain. Ecosphere 4:1–21.

Ruetz, C. R., J. C. Trexler, F. Jordan, W. F. Loftus, and S. A. Perry. 2005. Population dynamics of wetland fishes: spatio‐temporal patterns synchronized by hydrological disturbance? Journal of Animal Ecology 74:322–332.

Schmera, D., A. Baur, and B. Baur. 2015. Size-dependent shell growth and survival in natural populations of the rock-dwelling land snail *Chondrina* *clienta*. Canadian Journal of Zoology 93:403–410.

Sklar, F. H., M. J. Chimney, S. Newman, P. McCormick, D. Gawlik, S. Miao, C. McVoy, W. Said, J. Newman, C. Coronado, G. Crozier, M. Korvela, and K. Rutchey. 2005. The ecological–societal underpinnings of Everglades restoration. Frontiers in Ecology and the Environment 3:161–169.

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

Vance, R. R. 1985. The Stable Coexistence of Two Competitors for One Resource. The American Naturalist 126:72–86.

Werner, E. E., and J. F. Gilliam. 1984. The Ontogenetic Niche and Species Interactions in Size-Structured Populations. Annual Review of Ecology and Systematics 15:393–425.

Zweig, C. L., and W. M. Kitchens. 2008. Effects of landscape gradients on wetland vegetation communities: Information for large-scale restoration. Wetlands 28:1086–1096.

# Tables

Table 1: Three hypothesized changes in spatiotemporal conditions that could shift FAS annual survival and growth parameters from the left of the isocline to the right of the isocline.

|  |  |
| --- | --- |
| Hypothesis | Description of Environmental Change Hypothesis |
| 1 | Seasonal depth/hydro-patterns that shift more of the egg production to the wet season expose more juveniles to favorable wet season parameters. |
| 2 | Hydrologic conditions that improve growth rates (e.g., flow or flow-loading of nutrients) through improved food quality or water quality (oxygenation). |
| 3 | Hydrologic patterns that disfavor important predators could improve survival for juvenile snails (especially in the dry season). |

# Figure Captions

Figure 1. A) Zero-population growth isocline illustrating the expected joint impact of growth rates and mortality to consumers at a sensitive stage (diagonal black line). Resource populations are decreasing/recruiting in areas to the left and below the isocline shaded purple) while areas above and to the right indicate populations that are increasing/recruiting (shaded green). The strength of consumer control is represented by the gradient from dark green to dark purple. B-D) Demonstrated or hypothetical examples of populations spanning freshwater, terrestrial and marine ecosystems for which assumed demographic isocline could provide conceptual meaning to population dynamics and predictive values for field measured rates. The color of points corresponds to their position along the gradient in A). B) The relationship between mosquito (*Aedes atropalpus*) population with predatory dragonflies (*Pantala* spp.) depends on joint temperature mediation of survival (driven by dragonfly consumption) and growth of mosquitos. C) Quaking aspen (*Populus tremuloides*) stand recruitment depends on moisture/precipitation gradients and elk (*Cervus canadensis*) browsing rates driving sucker survival. D) Oyster (*Crassostrea virginica*) growth and mortality to predators drilling snails are affected by salinity gradients, though growth rate declines as seen from low to intermediate level have not been described at high salinity levels and could follow linear or unimodal relationships.

Figure 2 Isoclines illustrating the combinatorial effects of juvenile growth and survival that produce zero net population growth for a size-structured model of a freshwater gastropod (*Pomacea paludosa*) under two different hydrologic regimes that affect reproduction (black isocline = lower reproduction, gray isocline = higher reproduction). Points are mean daily survival (snails < 10mm SL) and growth (kgrowth) quantified in LILA wetlands and site 2 in Water Conservation Area 3A. Error bars represent 95% confidence intervals for each parameter estimate based on field variation at the site. The combined parameters (open symbols) were calculated by a weighted average reflecting greater juvenile snail production (egg laying and hatching) in the dry season.