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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 smaller vulnerable sizes is expected 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. The combinatorial effects of the two rates have applications to field studies of recruitment variation for a diversity of species species that could be assessed with demographic models and isoclines. To illustrate the utility we used a published size-indexed demographic model of an annual gastropod (Florida Apple Snail, *Pomacea paludosa*) to construct a zero-population growth isocline for theoretical combinations of juvenile growth and survival rates. The resulting isocline illustrated the expected result that faster juvenile growth rates would offset greater mortality allowing for population growth. We then quantified daily juvenile survival and growth in two wetlands twice during the recruitment period, incorporating variable predator assemblages and seasonal environmental conditions (depth and temperature). Seasonal and averaged rates were interpretable using 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 (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 conditions affecting reproductive rates, but with better hydrologic conditions one population was near replacement for the year. The use of the 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 provides a framework for making population-level interpretations about field-measured demographic 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).

Research on size-structured interactions traditionally 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 focus on the specific growth and mortality conditions that determine population dynamics (growth or decline) in the field; and to our knowledge, explicit theoretical predictions, whether general or specific, are lacking. Of the two known theoretical studies that have explored 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 fish while Pepi et al. (2023) focused on changes in equilibrium densities of predatory ants and caterpillar 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 average daily juvenile survival and growth rates (Figure 1), though the exact slope of the isocline will depend on reproductive rates and life history details. The negative slope indicates that populations with higher juvenile growth rates can achieve positive population growth (or annual recruitment) with lower survival rates (i.e., 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 state space and thus the level of top-down control on a population and the populations potential for viability or 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 general and that by combining field measurements with the isocline population growth or positive recruitment can be interpretable (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 to 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 (i.e., per-capita foraging rate of the predator increases 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 cooler temperatures the mosquito populations would not recruit well even though survival was high because daily growth was too low (below and left of isocline; Figure 1B). With higher temperatures the average daily survival decreased, but the increased daily growth rate more than compensated, and mosquito populations could recruit and grow (above and to the right side of isocline; Figure 1B). In a contrasting, invertebrate system 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 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) 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 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 maybe from spatiotemporal variability in moisture allowing aspen suckers to grow to sizes large enough to escape the browsing pressure (top points in 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 herbivore densities(Beschta and Ripple 2016).

In a marine ecosystem, multiple environmental gradients appear to affect one or both demographic rates of small settled oysters (e.g., *Crassostrea virginica* or *Saccostrea glomerata*); salinity gradients have been shown to influence eastern oyster growth rates (Munroe et al. 2017) and produce outbreaks of drilling snails (Kimbro et al. 2013). 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). Intertidal depths also influence the abundance of other juvenile-stage predators (e.g., crabs, snails, and fish; Figure 1D; Baillie and Grabowski 2019) such that survival rates may increase in shallower locations. In another marine system combined quantifications of juvenile survival and growth identified source and 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 spatiotemporal patterns of population growth and recruitment in natural systems. In this paper, we use a case study of the Florida Apple Snail (*Pomacea paludosa;* hereafter FAS), an annual freshwater gastropod of conservation concern to demonstrate the utility of a demographic-based zero population growth isocline. We used a previously parameterized age-structured model 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 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 (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 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). 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 has been no investigation of the factors that influence top-down control by these predators within natural systems partly because tracking cohorts of small juvenile snails is basically impossible, thus we developed an isocline approach to investigate these top-down 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 (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 the original parameters from Darby et al. (2015), but a few parameters were adjusted to reflect recent changes in understanding of FAS life history, and we removed carrying capacity (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 simply trying to identify parameters that would produce an increasing or decreasing population.

Once the isocline was constructed, we then 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 isocline plot assume that the parameters are averages experienced throughout the year. The season-dependent predictions from the field measures then are expected snail recruitment assuming the rates measured each season. To combine the seasonal parameters for each population into annual average values we calculated 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 wetlands 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 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).

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 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 a declining isocline consistent with the expected interaction between 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 to left, making 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; Figure2). The difference between the isoclines were 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 compositionally 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 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 only presented field parameters from the two sites which had growth rates measured from both seasons, the parameters from the other WCA3A site (site 3), and survival measured from within 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. Field combinations of similar rates have been examined for other invertebrates (e.g., Chockley et al. 2008), but they were not compared against population dynamic predictions. The isocline allowed us to interpret field measured rates and conclude that the populations were 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 populations 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 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.

Adjusting conditions for better reproduction moved the isocline (making a steeper slope) and 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 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 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 suggestion demonstrates at least one reason for the need to explore the theoretical expectations of population dynamic outcomes of size- and 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 2, Appendix S3: Figure S2) consistent with general thermal responses of ectotherms (Kingsolver and Woods 2016, Pepi et al. 2018). Overall prey survival might be expected to be greater, 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 meaningful 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 appear to have overwhelmed any changes in snail survival that might have been mediated by temperature alone (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 a consideration of natural seasonal variation covarying with temperature (Davidson et al. 2024). Environmentally mediated changes in predator communities may be more important to survival than the per-capita rates but 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. 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 FAS population growth to be positive, we offer four hypothesis (see numbers in Table 1 and Figure 3) about spatiotemporal environmental conditions could shift the average daily survival and growth conditions (open circles Figure 3).

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 (Hypothesis 1; Table 1; Figure 3). Alternatively, if females can store their resources and hydrologic conditions can 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 2; Table 1; Figure 3). Although more research is needed to understand how water levels might mediate this response one observation suggests that shifting reproduction to 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 3; Table 1; Figure 3). 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 to have wet season growth and survival parameters that predicted population growth in combination. But restoration and management actions are expressly avoiding eutrophication of the Everglades. Perhaps more promisingly, the predrainage Everglades was a flowing ecosystem (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 (Hypothesis 3; Table 1; Figure 3).

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 4; Table 1; Figure 3). 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, so it remains unclear how floods or hydrologic droughts would fundamentally shift predators (e.g., low water and drying encourage crayfish populations; Dorn and Cook 2015, Sinnickson and Dorn 2024).

*Conclusion*

The joint effects of juvenile growth and survival on recruitment is already 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 and case-study 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 were more important to seasonal rate differences than simpler physiological expectations based on thermal responses of predators and prey. Finally, the combination of 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 population growth or recruitment of any species with high juvenile mortality and stage- or size-dependent predators (e.g., plants, vertebrates, invertebrates) to consider developing isoclines from size-indexed demographic models and use the isocline to interpret measured field parameters and, thus, the spatial and temporal suitability of the environment for population growth.

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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.

# References

Baillie, C., and J. Grabowski. 2019. Factors affecting recruitment, growth and survival of the eastern oyster Crassostrea virginica across an intertidal elevation gradient in southern New England. Marine Ecology Progress Series 609:119–132.

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.

Chockley, B., C. St. Mary, and C. Osenberg. 2008. Population sinks in the Upper Florida Keys: the importance of demographic variation in population dynamics of the marine shrimp Stenopus hispidus. Marine Ecology Progress Series 360:135–145.

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: four hypothesized changes in spatiotemporal conditions that could shift FAS weighted average daily survival and growth from the left of the isocline to the right of the isocline. The numbered hypotheses correspond to the numbers in Figure 3.

|  |  |
| --- | --- |
| Hypothesis | Description |
| 1 | Hydrologic conditions that could change dry season growth and/or survival parameters would more strongly influence yearly average conditions. |
| 2 | Hydrologic conditions that shift egg laying to the more favorable wet season condition. |
| 3 | Spatiotemporal conditions that influence growth (e.g., nutrient and flow) could improve both wet season and dry season growth jointly. |
| 4 | Predators are also limited by the spatiotemporal hydrologic gradient, so there may be years or locations that have joint increases in survival. |

# Figure Captions

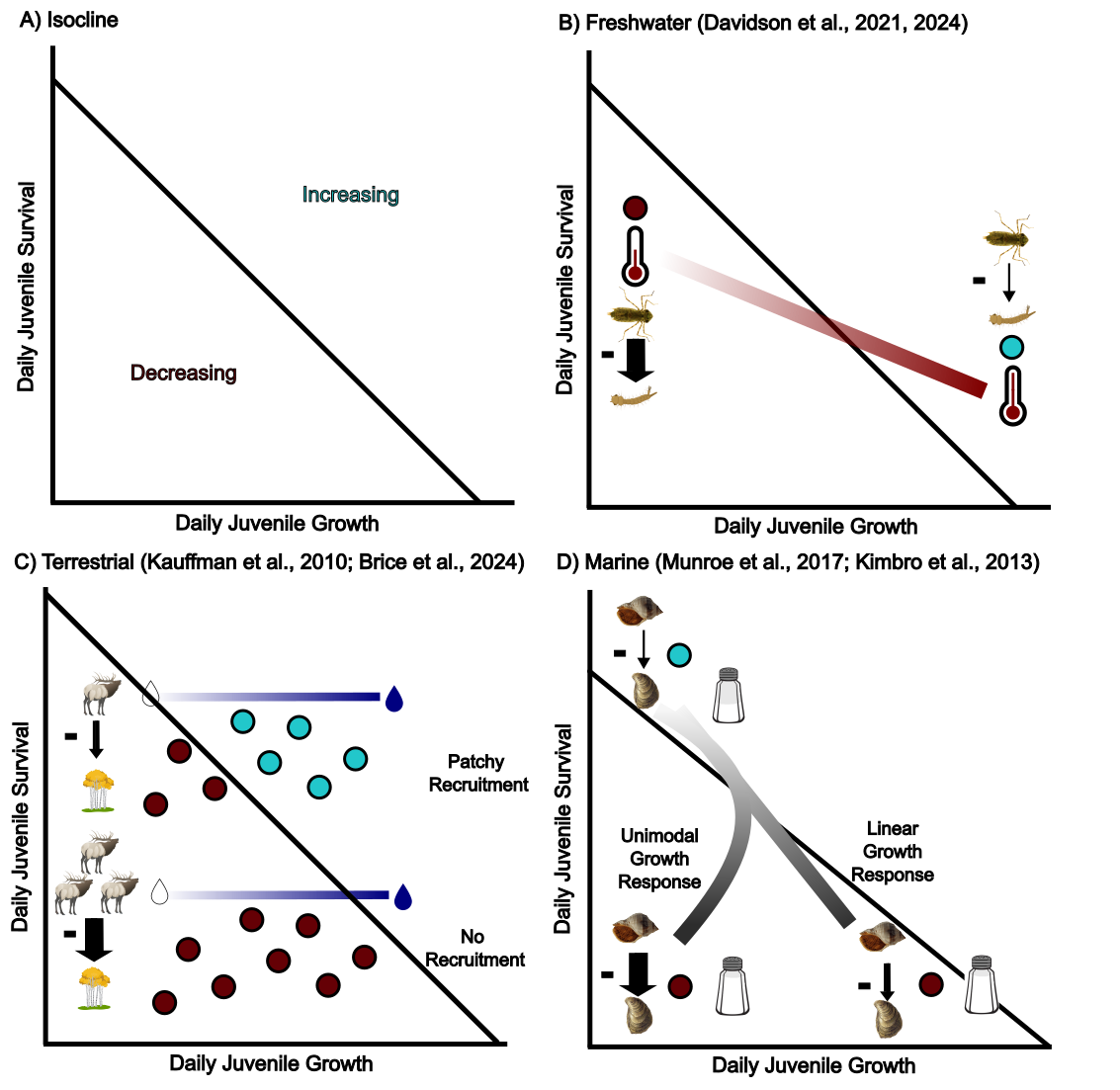


Figure 1. A) Zero-population growth isocline illustrating the expected joint impact of juvenile growth rates and mortality to consumers. Areas to the left and below the isocline indicate prey populations are decreasing/not recruiting while areas above and to the right indicate populations that are increasing/recruiting. B-D) Demonstrated or hypothetical examples of populations spanning freshwater, terrestrial and marine ecosystems for which the demographic isocline could provide 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 (black isocline = lower reproduction, gray isocline = higher reproduction). 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. 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 in the dry season.

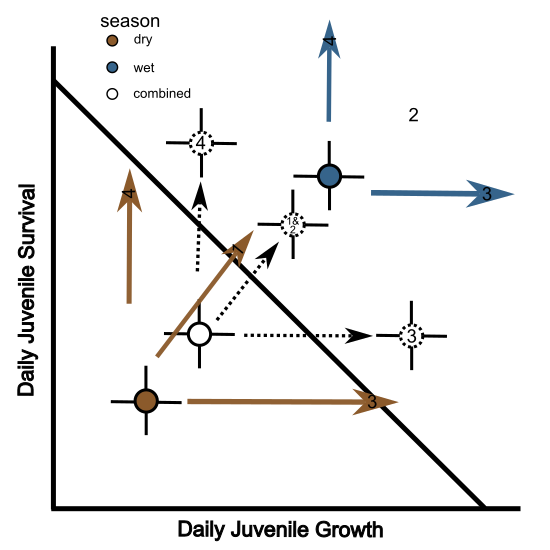


Figure 3. Zero-population growth isocline illustrating the expected joint impact of juvenile growth rates and mortality to consumers. Areas to the left and below the isocline indicate prey populations are decreasing/not recruiting while areas above and to the right indicate populations are increasing/recruiting. Blue points represent wet season parameters, brown points represent dry season parameters, and open circles represent weighted averages of the two seasons. Dashed lines and circles represent how the weighted average yearly conditions might change when spatiotemporal conditions are changed (i.e., colored arrows). The numbers represent different hypotheses with the numbers within open circles corresponding to the numbers on colored arrows. The numbered hypotheses are further described in Table 1.