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Stage-specific demographic effects of hydrologic variation in a stream salamander

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Title: Stage-specific demographic effects of hydrologic variation in a stream salamander

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Abstract

We lack a strong understanding of how organisms with complex life histories respond to climate variation. Many stream-associated species have multi-stage life histories that are likely to influence the demographic consequences of floods and droughts. However, tracking stage-specific demographic responses requires high-resolution, long-term data that are rare. We used eight years of capture-recapture data for the headwater stream salamander *Gyrinophilus porphyriticus* to quantify the effects of flooding and drying magnitude on stage-specific vital rates and population growth. Drying reduced larval recruitment but increased the probability of metamorphosis (i.e., adult recruitment). Flooding reduced adult recruitment but had no effect on larval recruitment. Larval and adult survival declined with flooding but were unaffected by drying. Annual population growth rates (lambda, λ) declined with flooding and drying. Lambda also declined over the study period (2012 – 2021), although mean λ was 1.0 over this period. Our results indicate that *G. porphyriticus* populations are resilient to hydrologic variation due to compensatory effects on recruitment of larvae vs. adults (i.e., reproduction vs. metamorphosis). Complex life cycles may enable this resilience to climate variation by creating opportunities for compensatory demographic responses across stages. However, more frequent and intense hydrologic variation in the latter half of this study contributed to a decline in λ over time, suggesting that increasing environmental variability poses a threat even when demographic compensation occurs.

Introduction

Earth's climate, a key force governing the distribution and demography of animal populations, is becoming more variable (IPCC 2021). This intensifying climate variability includes more severe and frequent extreme events, including floods and droughts (IPCC 2021). Understanding the effects of climate variability on natural populations is a crucial challenge facing ecologists and conservation biologists in the Anthropocene (Vázquez et al. 2017). More specifically, effective management and conservation will rely on identifying how demographic rates respond to climatic variation, and the species traits that lead to population resilience in the face of extremes (Munoz et al. 2016, Amburgey et al. 2018).

Isolating the demographic effects of climate variation is particularly challenging in species with complex life cycles, which include the majority of animals on Earth (Wilbur 1980, Laudet 2011). These organisms undergo metamorphosis or other discrete life stage transitions that entail major changes in physical and physiological traits, in addition to changes to vital rates (Kingsolver et al. 2011, Rose et al. 2021). Because of these abrupt ontogenetic changes, animals may be particularly vulnerable to climate variation during metamorphosis (Geffen et al. 2007, Lowe et al. 2021). However, organisms with complex life cycles also have greater life history flexibility than those with simple life cycles, creating more opportunities for demographic compensation across life stages (Doak and Morris 2010, Denoël and Ficetola 2014, Villellas et al. 2015). Teasing out these stage-specific responses to environmental variation is necessary for a complete understanding of the demographic effects of climate change in organisms with complex life cycles.

Most species that inhabit streams and rivers have complex life histories, and these species are likely to be affected directly by floods and droughts associated with changing precipitation regimes. However, the magnitude and directionality of these responses is not easy to predict. For example, floods may kill or displace organisms (Gibbins et al. 2007, Veith et al. 2019), or reduce population growth rates by limiting food resources or habitat availability (Lake et al. 2006). But floods also alter the geomorphological template of streams and rivers, which can increase habitat complexity, benefitting flood-tolerant species and increasing biodiversity (Death et al. 2015, Hauer et al. 2016, Larson et al. 2018). Droughts have largely negative effects on stream organisms (Boulton 2003), including reducing survivorship due to dehydration (Spotila 1972) and increasing crowding and the intensity of negative interactions among species (Lake 2003, Kupferberg et al. 2021). Yet, the strengths of these responses vary depending on historic flow regimes and associated phenotypic and life history adaptations (Lytle and Poff 2004, Walls et al. 2013, Weinbach et al. 2018). As floods and droughts continue to increase in severity, isolating the demographic mechanisms underlying population-level responses will become more crucial.

We have a rare opportunity to assess the effects of hydrologic variation throughout the complex life cycle of a headwater stream salamander. Most stream salamanders have a biphasic life cycle (Petranka 1998). Larvae respire with external gills and are thus exclusively aquatic. Individuals then go through metamorphosis, where larvae transform into their adult form, lose their external gills, and begin breathing cutaneously, allowing them to use terrestrial habitats (Greene et al. 2008, Campbell Grant et al. 2010). Stream salamander diversity is also highest in headwater systems (Hairston and Hairston 1987, Petranka 1998), where they experience dynamic hydrologic environments that range from ephemeral conditions during droughts, to floods that may occur seasonally or following precipitation events (Datry et al. 2014). Our goal was to advance basic understanding of the demographic and life history mechanisms by which species with complex life cycles, like stream salamanders, respond to hydrologic variation.

We used eight years of intensive capture-recapture data on *Gyrinophilus porphyriticus*, the northern spring salamander, to determine how stage-specific vital rates respond to variation in the magnitude of stream flooding and drying over time, and how these vital rate responses influence population growth rates. We tested the overarching prediction that larger magnitude flooding and drying reduce recruitment and survival of *G. porphyriticus* larvae and adults, reducing population growth. Specifically, we predicted that larger floods would cause the most vulnerable individuals, including hatchling larvae and individuals undergoing metamorphosis, to experience increased mortality due to physical disturbance, thereby reducing larval and adult recruitment. We also predicted that drying would increase mortality of all larvae due to the risk of desiccation in dry stream channels. Because adult stages can survive terrestrially and larval stages cannot, we expected more intense hydrologic conditions to have larger negative effects on larval survival than adult survival. Finally, we expected this combination of responses to cause population growth rates to decline in years with severe flooding or drying.

Methods

Study organism

Gyrinophilus porphyriticus is a lungless salamander (family Plethodontidae) that lives in small, cool, well-oxygenated streams along the Appalachian uplift in the eastern United States (Petranka 1998). This species has a biphasic life cycle: larvae are exclusively aquatic (Bruce 1972), and adults are predominantly aquatic but can leave the stream in humid conditions

(Greene et al. 2008). Larvae feed on aquatic invertebrates and smaller larval salamanders (Burton 1976), whereas adults also feed on terrestrial invertebrates (Lowe et al. 2005). *G. porphyriticus* exhibit slow and variable growth rates (Bonett et al. 2014, Beachy et al. 2017), metamorphosing at 2 – 10 years in age, and living up to 20 years (M. M. Cochrane, unpublished data). Aquatic predators include *Salvelinus fontinalis* (brook trout; Resetarits 1995) and terrestrial predators include *Thamnophis sirtalis* (common garter snakes; Petranka 1998). Previous research has shown that changing precipitation and discharge regimes in the northeastern USA are associated with changes in *G. porphyriticus* survival through metamorphosis and adult abundance (Lowe 2012, Lowe et al. 2019), but previous studies have not assessed the specific hydrologic conditions affecting survival (e.g., droughts v. floods) or the population-level consequences of these effects.

Study site

We conducted this research at the Hubbard Brook Experimental Forest (HBEF) in New Hampshire, USA (43°56′N, 71°45′ W). We sampled three hydrologically independent headwater streams within the 32-km^2 HBEF: Bear Brook, Paradise Brook, and Zigzag Brook (fig. S1). We surveyed two 500-m long reaches in each stream. Downstream reaches started at the confluence with Hubbard Brook, a fifth-order stream flowing into the Pemigewasset River. Upstream reaches ended at weirs where long-term water quality and discharge data are collected and beyond which sampling is prohibited (Bormann and Likens 1979). Distances between downstream and upstream reaches, measured along stream channels, were 400 m in Bear Brook, 250 m in Paradise Brook, and 500 m in Zigzag Brook (Addis and Lowe 2020). *S. fontinalis* occur in all downstream reaches.

Discharge in the HBEF streams typically peaks in the spring due to snowmelt, but flood events can occur throughout the year after isolated rainstorms. Base flows usually occur in late summer and early fall (Likens and Bormann 1995). The study streams drain small, high-gradient watersheds with watershed areas ranging from 0.14 to 3.53 km^2 and gradients ranging from 4° to 25°, based on measurements every 100 m along the stream channels. The majority of stream habitats are characterized as step-pools (Montgomery and Buffington 1997). Streams have low conductivity (12.0 – 15.0 µS), slight acidity (pH of 5.0 – 6.0), and high dissolved oxygen content (80 – 90% saturation; Likens and Bormann 1995). Stream water temperatures range from 0 – 20°C throughout the year (M. M. Cochrane, unpublished data). Other stream salamanders include *Eurycea bislineata* and *Desmognathus fuscus* (both Plethodontidae). The HBEF landscape is dominated by northern hardwood forest (Bormann and Likens 1979).

Survey Methods

Our analyses are based on six mark-recapture surveys of all reaches conducted during July and August of 2012 – 2015 and 2018 – 2021, for a total of 48 surveys per reach. In each survey, we used cover-controlled, active search sampling (Heyer et al. 1994), where one haphazardly-selected cover object was turned per meter of stream length. From 2012 – 2015, salamanders were marked with visual implant elastomer (Northwest Marine Technology, Inc., Anacortes, Washington, USA). From 2018 – 2021, salamanders were marked with 8-mm passive integrated transponders (PIT-tags; Hecere Electronic Col, Ltd., Quanzhou, China). Both marking methods have been shown to have very high retention rates in salamanders (Mitchell et al. 2017, Moon et al. 2022, Knapp et al. 2023). We recorded the stage and mass of all individuals, and snout-vent-lengths (SVL) were measured from photographs with ImageJ 1.50i software (Schneider et al. 2012).

Quantifying hydrologic variation

To characterize flooding and drying magnitude, we quantified annual peak discharge (i.e., floods) and lowest discharge (i.e., stream drying) in each stream for each year of this study (fig. S2). We also put these values in the context of Hubbard Brook’s long term discharge record, which began in 1957, by calculating the recurrence interval for each annual peak and lowest discharge of each stream. All calculations were based on daily discharge data collected at weirs immediately upstream of our upstream survey reaches on each stream (USDA Forest Service 2022). Discharge data were normalized by dividing by the drainage area at the weir where the data were collected and are thus reported as specific discharge, in units of depth per unit time (mm/day; Bailey et al. 2003), although hereafter we refer to these specific discharges simply as discharge. To then account for variable increases in watershed area (and thus stream volume) between upstream and downstream reaches in each stream, we included watershed area in all models. Watershed areas were calculated every 100 m along each reach from 1-m Digital Elevation Models (University of New Hampshire, Durham, NH) using ArcMap Version 10.8 (Environmental Systems Research Institute, Inc., Redlands, CA). Years were defined as the 12-month period preceding salamander surveys (July 1 – June 30). To characterize annual flood magnitude for each stream, we calculated Q99, which is the discharge exceeded only 1% of the year. To quantify annual stream drying magnitude for each stream, we calculated the minimum 7-day lowest discharge for each year (Olden and Poff 2003, Ries et al. 2016).

Analyses overview

We used two different capture-recapture models to calculate all stage-specific vital rates and test for effects of flooding and drying magnitude on those vital rates. First, we used a reverse-time Pradel model to test our predictions that larval recruitment and population growth decline with flooding and drying magnitude. Pradel models invert capture histories to estimate the probability of entry into a population (i.e., larval recruitment; Pradel 1996). We also used this model to estimate annual population growth rates (lambda, λ), because it quantifies both gains and losses in a population. Next, we used a multi-state Cormack-Jolly-Seber (CJS) model to test our predictions that larval survival and adult recruitment are reduced by flooding and drying magnitude. The multi-state CJS model allowed us to estimate annual survival probabilities of larvae and adults separately, as well as the probability of transitioning between those life stages (i.e., metamorphosis or adult recruitment; Lebreton et al. 2009). Both models accommodate variable time intervals between surveys, including the interval between surveys in 2015 and 2018.

Pradel model

The Pradel model estimates annual recruitment probability (f), annual apparent survival probability (ϕ), and capture probability (p), but can also be used to derive population change (λ) across years. We included both larval and adult individuals in these analyses, so f estimates include any new individuals entering the population, both young-of-the year (larval recruitment) and immigrating individuals from outside the study reach. However, we assumed that the majority of recruitment was in the form of new larvae because previous analyses suggest that immigration from outside of study reaches is very low (Lowe et al. 2006, Addis and Lowe 2020). Apparent survival is defined as the probability of any individual (larvae or adult) surviving and staying within the study reach between sampling occasions. Population growth is the sum of f and ϕ. Capture probability is the probability that a marked individual is available for detection (i.e., present) and is captured during the sampling period.

We implemented a robust design version of the Pradel model that used our six surveys in late summer of each year to estimate p, and the period between years to estimate f and ϕ (Pradel 1996). This parameterization assumes a population is closed to demographic changes between July and August (i.e., secondary intervals) but open between years (i.e., primary intervals). This design is more robust to heterogeneity in capture and demographic rates than closed or open-population methods alone (Kendall 2006). Within the closed population model structure, we used the Otis (1978) full likelihood formulation to estimate population size (White and Burnham 1999).

Multi-state Cormack-Jolly-Seber Model

Multi-state CJS models estimate apparent survival and recapture probabilities for larval and adult stages separately, in addition to the probability of initiating and surviving the transition from larva to adult (Ψ_{LA}; adult recruitment). In our model, this transition probability is the conditional probability that a larval individual stays alive and is available for capture, but transitions into an adult life stage by the next year. Because individuals cannot transition from adults back to larva, we set $\Psi_{AL} = 0$ in all models.

We used a robust design version of the multi-state CJS model to increase the precision of parameter estimates (Bailey et al. 2010). Because this model assumes that individuals cannot change states within secondary capture sessions, we only included the stage at initial capture for the seven individuals (< 0.01% of all recaptures) that began to transition from larvae to adults during the two-month closed sampling window (July – August).

Model selection

We implemented all models in Program MARK (White and Burnham 1999), accessed through RStudio (Version 1.4.1716; R Development Core Team 2021) using the RMark interface (Laake 2013). To assess goodness of model fit and potential overdispersion, we calculated the variance inflation factor ($\hat{c}$) for this dataset (program RELEASE global test: TEST 2 + TEST 3; Anderson and Burnham 2002, Perret et al. 2003, Muths et al. 2017). Calculated $\hat{c}$ was < 1, but because underdispersion is not biologically meaningful, we conducted our model selection assuming a value of $\hat{c} = 1$ (White and Burnham 1999, Lebreton et al. 2012).

To first account for variability in capture rates in both Pradel and CJS models, we selected the best covariate structure for *p* by allowing capture rates to vary based on capture occasion (i.e., time), stream, reach (i.e., upstream vs. downstream), or none of the above, while keeping a full time-varying structure for survival and recruitment parameters (Doherty et al. 2012, Muths et al. 2017). We assumed capture and recapture rates were equivalent because we do not expect any type of trap response. In multi-state CJS models, we also allowed *p* to vary by stage (larva, adult). Next, we forced all survival and recruitment covariate structures to include stream and watershed area to account for unknown sources of variability among streams (Addis and Lowe 2020), consistent differences in flow magnitude as watershed area increases from upstream to downstream reaches within streams (M. M. Cochrane, unpublished data), and increased occurrence of *S. fontinalis* at larger watershed areas (Warren et al. 2008).

For both Pradel and CJS models, we used a logit transformation to test if and how flooding and drying magnitude influenced recruitment and survival parameters. Discharge covariates were scaled and centered prior to model fitting, and we used a Pearson's correlation test to ensure they were not significantly correlated with one another. Candidate models – which included effects of flooding magnitude, drying magnitude, both, and neither on recruitment and survival parameters (see table S1 for complete list of models) – were ranked by second-order AIC differences, corrected for small sample sizes (ΔAIC_c; Burnham and Anderson 2002). When $\Delta AIC_c < 2$, we used pairwise likelihood ratio tests (LRTs) to compare model fit. We assumed a significant LRT result ($P \leq 0.05$) indicated support for the model with more parameters, whereas a nonsignificant LRT result indicated equal support for both models, so we selected the model with fewer parameters (White and Burnham 1999). We also estimated the relative likelihood of each model with AIC_c weights (AIC_c wt; Anderson and Burnham 2002).

To summarize how the *G. porphyriticus* population at Hubbard Brook changed from 2012 – 2021, we calculated geometric mean λ from stream specific λ estimates. We used geometric mean λ because it is the appropriate average for stochastic population growth (White and Burnham 1999). To approximate standard errors for λ (a derived demographic parameter), we used the delta method (Powell 2007). To determine if there was a trend in λ over time we also calculated the Theil-Sens slope (Ohlson and Kim 2015). We considered flooding and drying magnitude to affect λ significantly if 95% confidence intervals for λ did not overlap when comparing λ at minimum and maximum flooding magnitude, and at minimum and maximum drying magnitude. Minimum and maximum values were calculated annually for each stream between 2012 – 2021. Similarly, to quantify effect sizes of flooding and drying magnitude on all stream-specific demographic rates, we compared rate estimates (and 95% confidence intervals) following the annual minimum and maximum measures of flooding and drying magnitude observed between 2012 – 2021.

Results

Salamander surveys

We marked 3307 individual salamanders across all streams and years. The total number of captures was 4094, including new individuals and recaptures. This included 2767 larvae and 1327 adults. Total number of captures by stream were 1515 in Bear, 1511 in Paradise, and 1068 in Zigzag.

Hydrologic variation

The mean Q99, representing peak annual discharge (i.e., largest flood) across all years and streams was 62 mm/day (SD = 20; range = 32 – 97) and typically occurred on March 20th (SD = 75 days; fig. S2). The mean recurrence interval for all peak discharge values was 5 y (SD = 5, min = 1, max = 16; fig. S2). The minimum 7-day lowest discharge, our index of drying magnitude, across all years and streams was 0.05 mm/day (SD = 0.05; range = 0.00 – 0.18) and typically occurred between August 10th – 16th (SD = 25 days). The mean recurrence interval for all lowest discharge values was 5 y (SD = 12, min = 1, max = 65). Annual drying and flooding magnitudes were not correlated ($r = -0.05$, P = 0.83, df = 19).

Pradel model

Our data were not overdispersed ($\hat{c} = 0.39$), and the final covariate structure for capture probability (p) included stream and reach (table S2). The top two Pradel models included an effect of flooding magnitude on annual apparent survival (ϕ) and an effect of drying magnitude on annual larval recruitment (*f*), but differed in the inclusion of an effect of flooding magnitude on *f* (table 1). Support for these two models was somewhat ambiguous ($\Delta AIC_c = 1.69$); however, the LRT was not significant ($\chi^2 = 0.33$, $P = 0.57$), indicating that the model with fewer parameters was more parsimonious. In that model, drying reduced *f* by 20% (95% CI: 12 – 24) when comparing the highest 7-day lowest discharge (0.16 mm/day) to the lowest 7-day lowest discharge (0.00 mm/day; fig. 1a; table S3). Flooding decreased ϕ by 52% (95% CI: 43 – 57) when comparing the smallest flood (40 mm/day) to the largest flood (97 mm/day). Based on these rate estimates, drying reduced λ by 15% (95% CI: 14 – 16) and flooding reduced λ by 32% (95% CI: 31 – 33) when comparing minimum to maximum measures across the 8-yr study period (fig. 2). Geometric mean population growth (λ) across all streams and years was 1.00 (SD = 0.09; fig. 3). Yet, λ declined over the study period (Theil-Sens slope = -0.02, P = 0.004, DF = 5). Mean annual *f* for all streams and years was 0.57 (SD = 0.03). Mean annual ϕ across all streams and years was 0.44 (SD = 0.09).

Multi-state Cormack-Jolly-Seber Model

The final Cormack-Jolly-Seber (CJS) capture probability (*p*) covariate structure included stream, reach, and life stage. The top two CJS models included the effect of flooding magnitude on stage-specific survival and the effect of drying magnitude on Ψ_{LA}, but differed in the inclusion of the effect of flooding magnitude on Ψ_{LA} (table 2). Support for these two was somewhat ambiguous ($\Delta AICc = 1.74$), however the LRT was significant ($\chi^2 = 3.76$, $P = 0.05$), indicating that the model with more parameters was just barely preferred. In that model, flooding reduced ϕ_L by 70% (95 CI: 63 – 75) and reduced ϕ_A by 33% (95% CI: 23 – 46) when comparing the smallest to the largest floods across the 8-yr study period (fig. 4; table S4). Drying increased Ψ_{LA} by 1190% (95% CI: 183 – 5893) when comparing the lowest and highest 7-day lowest discharges across this 8-yr period (fig. 1b; table S4). Flooding reduced Ψ_{LA} by 73% (95% CI: 43 – 87) when comparing the smallest to the largest floods across this 8-yr period (fig. S3; table S4). Mean annual Ψ_{LA} across all streams and years was 0.29 (SD = 0.12). Mean ϕ_L and mean ϕ_A across all streams and years was 0.43 (SD = 0.13) and 0.49 (SD = 0.07), respectively.

Discussion

We found that severe floods and drier streams reduce *G. porphyriticus* population growth rates (fig. 2), but differential demographic responses to these disturbances across this species' complex life cycle provide resiliency. Stage-specific survival and recruitment rates responded differently to flooding and drying (table 3), dampening the net effect of hydrologic variation on population growth. For instance, the positive effects of drying on adult recruitment (i.e., the probability of larvae initiating and surviving metamorphosis) helped to offset the negative effects of drying on larval recruitment. A negligible change in larval and adult survival in response to drying, in contrast to the strong negative effect of flooding, also aided in this resilience. The mean population growth rate (λ) was 1.0 between 2012 – 2021 across all streams, with considerable year-to-year variation (min = 0.84, max = 1.17). However, severe flooding and drought in 2017 and 2020 caused λ to decline across the study period (2012 – 2021; fig. 3). Our results suggest that that increasing environmental variability associated with climate change poses a significant threat to species with complex life cycles, even when those species are capable of demographic compensation among stage-specific vital rates.

Drying reduced recruitment of *G. porphyriticus* larvae (fig. 1a) – the first documentation of this response in a stream salamander. The mechanisms driving this result may include breeding failure due to limited water availability (Taylor et al. 2006), increased competition for breeding sites (Berven 1990), or reduced survival rates for the smallest and most vulnerable life stages (Price et al. 2012, Cayuela et al. 2015). It is not possible to distinguish among these mechanisms with our current data because we find few visibly gravid females or egg masses during our surveys, and the smallest larvae (< 35 mm) cannot be tagged with current methods. It is also possible that females skip breeding in drought years, reducing larval recruitment (Kinkead and Otis 2007). *G. porphyriticus* is known to oviposit every year in the southern part of its range (Bruce 1972); however, breeding intervals may be more plastic in the northern portion of the range where the active season is shorter (Church et al. 2007). Predation on larvae by *S. fontinalis* and conspecifics may also increase during droughts, as stream reaches dry and both prey and predators become concentrated in isolated pools (Lake 2003). We also acknowledge that this parameter received moderate support in model selection (ΔAIC = 2.08), and should be interpreted cautiously, in addition to having a small net effect in comparison to other responses, including the effect of drying on adult recruitment.

Adult recruitment, the probability of larvae initiating and surviving metamorphosis to become adults, increased dramatically with drying (fig. 1b). This is likely due to an increase in the proportion of larvae initiating metamorphosis during droughts to avoid desiccation in drying streambeds. Pond breeding amphibians are known to exhibit plasticity in the duration of the larval period, and to accelerate metamorphosis to avoid pond drying (Denver 1997, Székely et al. 2017), often initiated by stress hormones (Bonett et al. 2010, Denver 2021). However, ours is the first study of stream amphibians to document this response directly. Importantly, this response will increase the size of the breeding population, providing demographic compensation for reduced larval recruitment after droughts (fig. 1a). Because our estimate of adult recruitment (Ψ_{LA}) incorporates both the probability of initiating metamorphosis and the probability of surviving the transition from larva to adult, it is also possible that drying increases rates of survival through the transition. This would be surprising considering that metamorphosis is an inherently vulnerable life stage (Székely et al. 2020, Lowe et al. 2021), and drought is unlikely to mitigate that vulnerability (Zylstra et al. 2015).

Flooding reduced survival of larvae and adults (fig. 4), and adult recruitment (fig. S3). This result matched our predictions, and it is consistent with studies showing that flooding – including higher discharge and debris transport – causes declines in other stream amphibians (Barrett et al. 2010, Cover et al. 2010) and in aquatic invertebrates (Gibbins et al. 2007). Of the three demographic rates, larval survival was the most sensitive to variation in peak discharge. *G. porphyriticus* adults can leave the stream to avoid high flows, which likely accounts for the stronger effect of flooding on larval mortality. Individuals undergoing metamorphosis (i.e., adult recruitment) may also be particularly vulnerable to floods as they undergo abrupt and major physiological and physical transformations (Kingsolver et al. 2011, Rose et al. 2021), all while they are not able to leave the stream to escape flooding. In addition to direct physical effects on individuals, flooding and associated shear stresses can mobilize instream wood and remove allochthonous material from the stream channel, reducing secondary production (i.e., in-stream prey resources; Bilby and Likens 1980, Wallace et al. 1997, Wohl 2010). This reduction in prey resources may exacerbate intraspecific competition and predation in the nutrient-limited headwater streams of Hubbard Brook (Hall et al. 2001, McGuire et al. 2014), ultimately reducing survival rates, particularly in *G. porphyriticus* larvae (Resetarits 1995). High-discharge events can also provide opportunities for fish to move upstream into new areas (David & Closs 2002), which could increase predation pressure on larval salamanders (Resetarits 1995). We did not find a strong effect of drying on larval or adult survival, suggesting that both stages have access to refuges in the streambed and riparian zone with sufficient water availability during droughts (Feral et al. 2005, Bonett and Chippindale 2006).

Overall, our results show that high hydrologic variability, resulting from larger floods and drier streams, reduces annual population growth rates, and led to a decline in population growth between 2012 – 2021. In the Northeast, where this study occurred, a major impact of climate change is increased precipitation intensities and peak flows, particularly in the winter and spring (Demaria et al. 2016, Siddique and Palmer 2021). Based on this research, these changes will be particularly detrimental to *G. porphyriticus* survival, particularly larval stages, and consequently population growth. We expect these challenges to be similar across other freshwater species with complex life cycles, including other stream amphibians and invertebrates. We also acknowledge that continued monitoring will be necessary to differentiate climate-related effects from natural fluctuations in λ, especially given the relatively limited duration of our study (8 y) in comparison to the long-life span of *G. porphyriticus* (20 y; M. M. Cochrane unpublished data).

This study provides a blueprint to understand the demographic mechanisms driving population change in taxa with complex life cycles – the majority of animals on Earth – during this era of increasing environmental variability. Regardless of the form of environmental variation, isolating stage-specific demographic rates is critical to assessing demographic compensation, which may be more common in species with complex life cycles than previously acknowledged (Radchuk et al. 2013, Cayuela et al. 2022). However, complex life cycles can also allow for compounding negative responses to disturbance, accelerating population declines (Kissel et al. 2019). Consequently, detailed understanding of which mechanisms and conditions have the greatest leverage on population growth will be crucial in this age of increasing climate extremes (IPCC 2021), when effective management and conservation rely on nuanced insights on population regulation that intensive demographic analyses provide. Here, we were able to identify which stage-specific vital rates are susceptible to specific aspects of hydrologic variation, and we recommend the same approach in other long-term monitoring programs that aim to track demographic responses to climate-associated changes in environmental variability.

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Statement of Authorship

M.M.C. conceptualized the ideas. All authors participated in method development. W.H.L. acquired the funds. M.M.C. and B.R.A. performed data collection. M.M.C. analyzed the data and performed data visualization. M.M.C. wrote the original draft while B.R.A. and W.H.L. reviewed and edited the manuscript.

Data Availability: Data supporting the results of this study are available from the Environmental Data Initiative Data Portal at https://doi.org/10.6073/pasta/cd5f5a03df194930bf87eb12157b8182 (Lowe 2022) and https://doi.org/10.6073/pasta/15b300e96c2d2f9785d0155b3e18b0e9 (USDA Forest Service 2022). The R script used for these analyses is deposited in Zenodo (https://zenodo.org/records/10214926).

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Tables

Table 1: The top four robust design Pradel models assessing support for effects of flooding and drying magnitude on annual larval recruitment (*f*) and apparent survival probability (ϕ) for *Gyrinophilus porphyriticus* in the Hubbard Brook Experimental Forest, New Hampshire, USA.

Model	k	AICc	ΔAIC	AICc wt
ϕ(flooding) *f* (drying)	22	8630.98	0.00	0.35
ϕ(flooding) *f* (drying, flooding)	23	8632.67	1.69	0.15
ϕ(drying, flooding) *f* (drying)	23	8632.95	1.97	0.13
ϕ(flooding) *f* (.)	21	8633.06	2.08	0.13

Note: Estimates are from 4094 captures across three streams over eight years (2012 – 2015, 2018 – 2021). All models included effects of stream and watershed area on ϕ and *f*, in addition to stream and reach effects on capture probability. Parameterization for ϕ and *f* to vary by flooding or drying magnitude are in parentheses; a period indicates no effect of either flooding or drying on that parameter. Number of estimated parameters (k), second-order Akaike's information criterion values (AIC_c), AIC_c differences (ΔAIC_c), and AIC_c weights (AIC_c wt) for all models are shown.

Table 2: The top four robust design multi-state Cormack-Jolly-Seber models assessing support for effects of flooding and drying magnitude on stage-specific annual apparent survival probability (ϕ) and annual adult recruitment (Ψ_{LA}) for *Gyrinophilus porphyriticus* in the Hubbard Brook Experimental Forest, New Hampshire, USA.

Model	**k**	**AICc**	**ΔAIC**	**AICc wt**
ϕ(flooding*stage) Ψ_{LA}(drying, flooding)	26	-402.96	0.00	0.47
ϕ(flooding*stage) Ψ_{LA}(drying)	25	-401.22	1.74	0.20
ϕ(flooding*stage, drying*stage) Ψ_{LA}(drying, flooding)	28	-400.81	2.15	0.16
ϕ(flooding*stage, drying*stage) Ψ_{LA}(drying)	27	-398.79	4.17	0.06

Note: Estimates are from 4094 captures across three streams over eight years (2012 – 2015, 2018 – 2021). All models included effects of stream and watershed area on ϕ and Ψ_{LA}, in addition to stream and reach effects on capture probability (*p*). Parameterization for ϕ or Ψ_{LA} to vary by flooding or drying magnitude are in parentheses; a period indicates no effect of either flooding or drying on that parameter. Number of estimated parameters (k), second-order Akaike's information criterion values (AIC_c), AIC_c differences (ΔAIC_c), and AIC_c weights (AIC_c wt) for all models are shown.

Table 3: Summary of the negative (-), positive (+), or non-significant (NS) effects of discharge conditions (i.e., flooding and drying) on larval recruitment (*f*), adult recruitment (Ψ_{LA}), larval survival (ϕ_L), adult survival (ϕ_A), combined survival (ϕ), and overall population growth rate (λ) for *Gyrinophilus porphyriticus* in the Hubbard Brook Experimental Forest, New Hampshire, USA.

Parameter	Flooding	Drying	Model
f	NS	-	Pradel
Ψ_{LA}	-	+	CJS
ϕ_L	-	NS	CJS
ϕ_A	-	NS	CJS
ϕ	-	NS	Pradel
λ	-	-	Pradel

Note: Estimates were derived from a robust design reverse-time Pradel model (table 1) or robust design multi-state Cormack-Jolly-Seber models (table 2), using *G. porphyriticus* capture-recapture and stream discharge data collected in three streams over eight years (2012 – 2015, 2018 – 2021).

Figure Legends

Figure 1. Relationships (bold lines) between the minimum 7-day lowest discharge (i.e., stream drying) and annual larval recruitment (a) and annual adult recruitment (b) for *Gyrinophilus porphyriticus* across three streams (Bear, Paradise, and Zigzag) in the Hubbard Brook Experimental Forest, New Hampshire, USA. Points are year- and stream-specific recruitment estimates. The colored ribbons represent the 95% confidence interval in mean responses. Larval recruitment was estimated with a robust-design Pradel model (table 1). Adult recruitment was estimated with a robust-design multi-state Cormack-Jolly-Seber model (table 2).

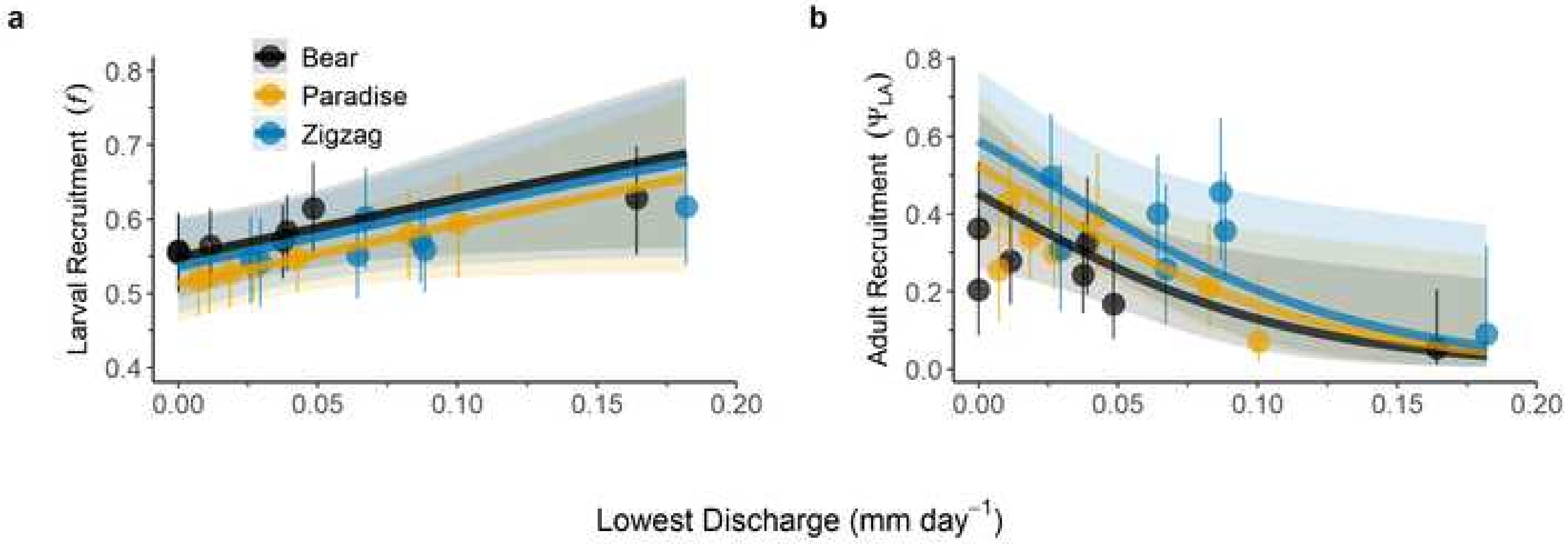
Figure 2. Relationships (bold lines) between peak annual discharge (a) and minimum 7-day lowest discharge (b) and population growth (λ) for *Gyrinophilus porphyriticus* across three streams (Bear, Paradise, and Zigzag) in the Hubbard Brook Experimental Forest, New Hampshire, USA. Colored points represent year- and stream-specific population growth estimates. The colored ribbons represent the 95% confidence intervals in mean responses. Population growth rates were derived from the top robust-design Pradel model estimating the effects of discharge variation on larval recruitment and apparent survival rates of all individuals (i.e., pooling larvae and adults; table 1).

Figure 3. Estimated annual population growth (λ) for *Gyrinophilus porphyriticus* across three streams (Bear, Paradise, and Zigzag) from 2012 – 2021 in the Hubbard Brook Experimental Forest, New Hampshire, USA. Colored points represent year- and stream-specific λ estimates derived from a robust-design Pradel model (table 1). Bars represent the 95% confidence intervals in mean responses. Colored lines represent the Theil-Sens slope for λ across this study period.

Figure 4: Relationships (bold lines) between peak annual discharge and annual larval apparent survival (a) and annual adult apparent survival (b) for *Gyrinophilus porphyriticus* across three streams (Bear, Paradise, and Zigzag) in the Hubbard Brook Experimental Forest, New Hampshire, USA. Colored points represent year- and stream-specific survival estimates. The colored ribbons represent the 95% confidence intervals in mean responses. Survival estimates are from a robust-design multi-state Cormack-Jolly-Seber model (table 3).

End-of-Article Figure: Photo of an adult *Gyrinophilus porphyriticus*, captured during mark-recapture surveys in the Hubbard Brook Experimental Forest, New Hampshire, USA. Photographer: Madaline Cochrane.

Figure 1



a
b
Bear
Paradise
Zigzag
Larval Recruitment (f)
Adult Recruitment (Ψ_{LA})
0.8
0.7
0.6
0.5
0.4
0.8
0.6
0.4
0.2
0.0
0.00
0.05
0.10
0.15
0.20
0.00
0.05
0.10
0.15
0.20
Lowest Discharge (mm day^{-1})

Figure 2

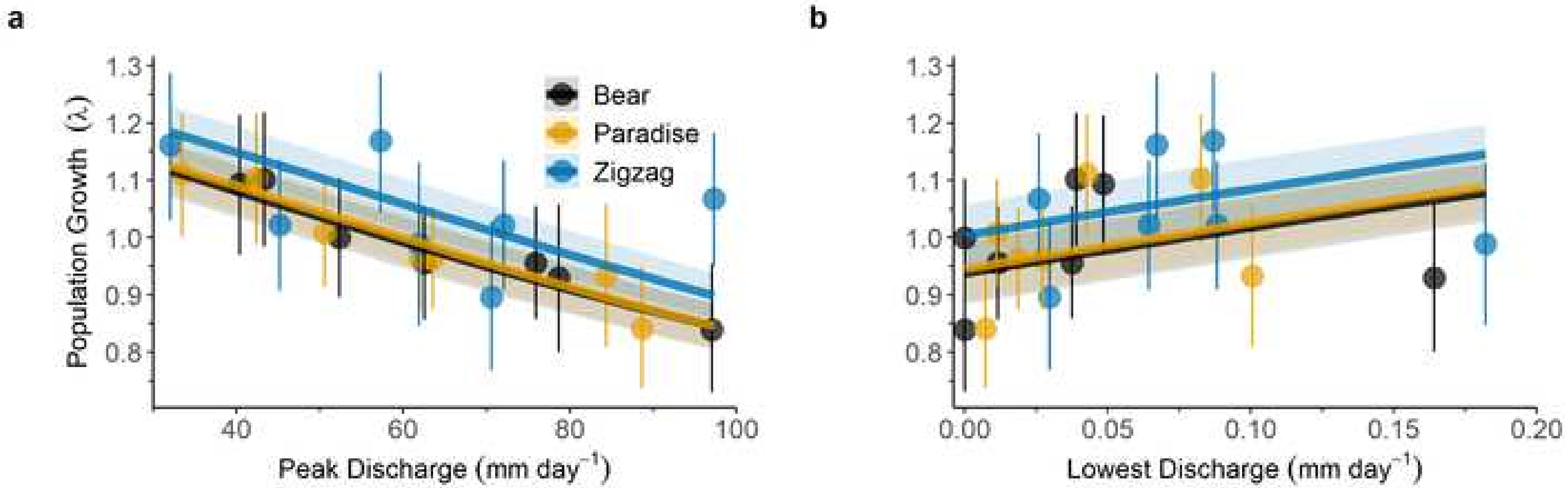

a
b
Population Growth (λ)
1.3
1.2
1.1
1.0
0.9
0.8
40
60
80
100
Peak Discharge (mm day^{-1})
Bear
Paradise
Zigzag
0.00
0.05
0.10
0.15
0.20
Lowest Discharge (mm day^{-1})

Figure 3

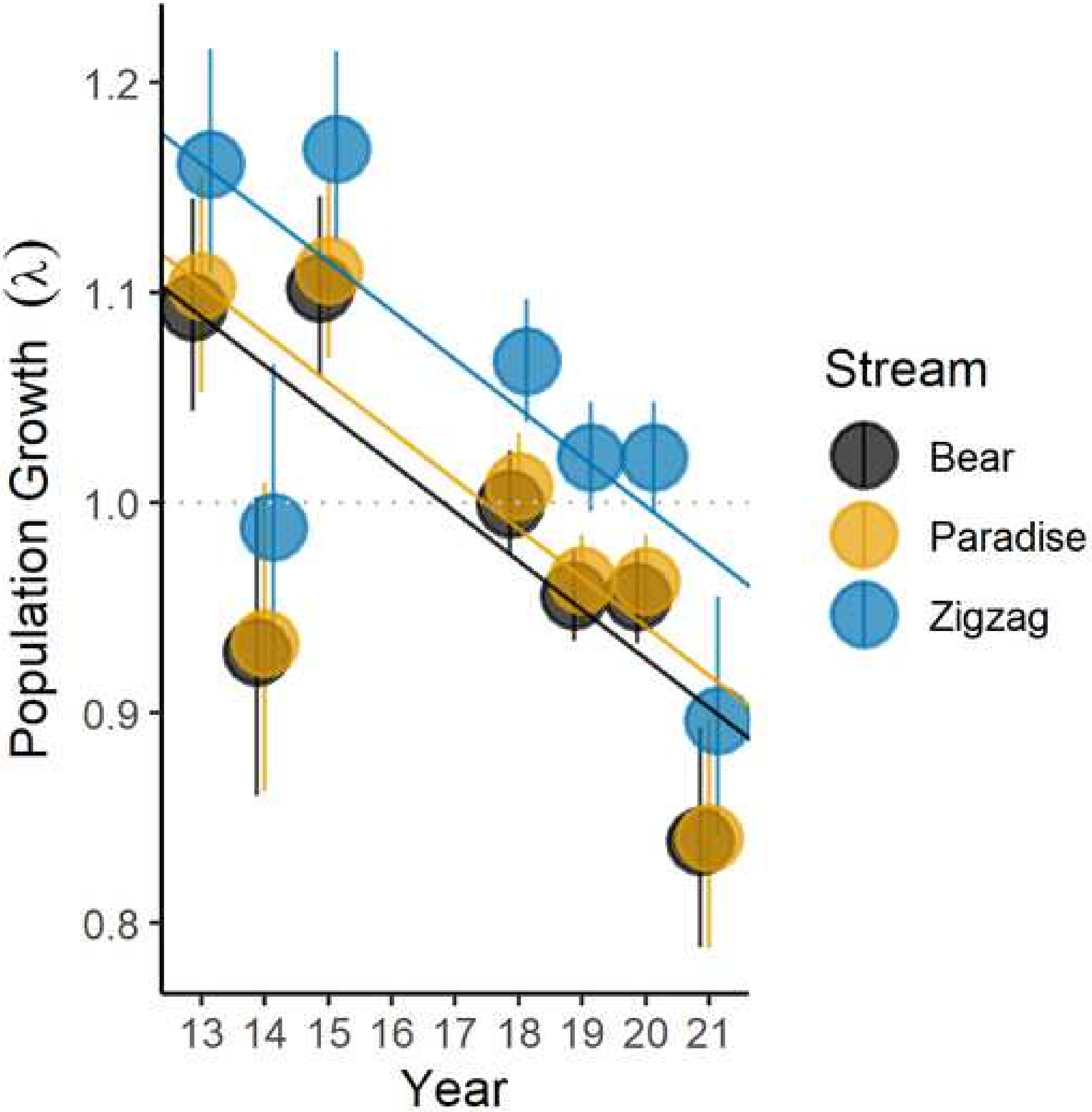
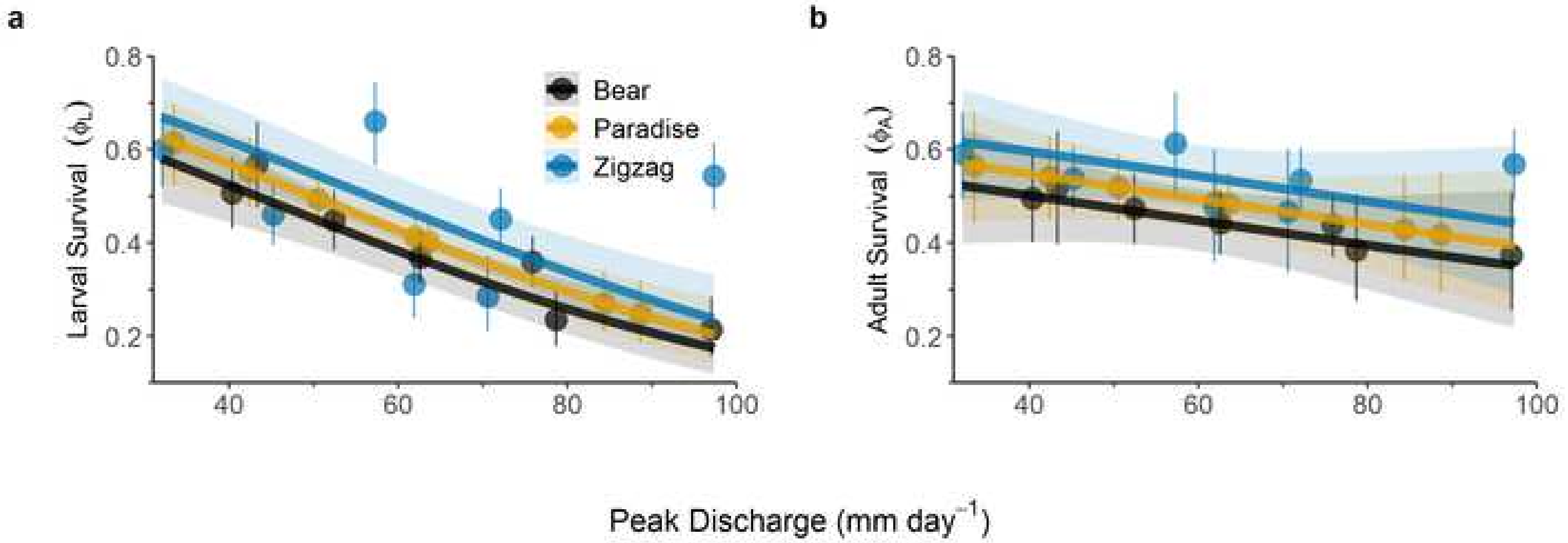

Population Growth (λ)
1.2
1.1
1.0
0.9
0.8
13
14
15
16
17
18
19
20
21
Year
Stream
Bear
Paradise
Zigzag

Figure 4


a
b
Larval Survival (ϕ_L)
Adult Survival (ϕ_A)
0.8
0.6
0.4
0.2
40
60
80
100
Bear
Paradise
Zigzag
Peak Discharge (mm day^{-1})

End of Article Figure

Supplement to

Stage-specific demographic effects of hydrologic variation in a stream salamander

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Table S1. List of candidate models tested to describe the effect of flooding magnitude, drying magnitude, or neither on larval recruitment (*f*; Pradel model set), adult recruitment (Ψ_{LA}; CJS model set), and stage-specific survival (ϕ; CJS model set). Stream and watershed area were also included to describe all survival and recruitment parameters. Recapture rates varied by stream and reach for both model types, and by stage in CJS models.

Model Type	**Parameter(s) of Interest**	**Model Number**	**Survival Parameter**	**Recruitment Parameter**
Pradel	larval recruitment (*f*)	1	ϕAll(.)	*f*(.)
		2	ϕAll(.)	*f*(flooding)
		3	ϕAll(.)	*f*(drying)
		4	ϕAll(.)	*f*(flooding, drying)
		5	ϕAll(flooding)	*f*(.)
		6	ϕAll(flooding)	*f*(flooding)
		7	ϕAll(flooding)	*f*(drying)
		8	ϕAll(flooding)	*f*(flooding, drying)
		9	ϕAll(drying)	*f*(.)
		10	ϕAll(drying)	*f*(flooding)
		11	ϕAll(drying)	*f*(drying)
		12	ϕAll(drying)	*f*(flooding, drying)
		13	ϕAll(flooding, drying)	*f*(.)
		14	ϕAll(flooding, drying)	*f*(flooding)
		15	ϕAll(flooding, drying)	*f*(drying)
		16	ϕAll(flooding, drying)	*f*(flooding, drying)
CJS	adult recruitment (ΨLA) & stage-specific survival (ϕ)	1	ϕ(.)	ΨLA(.)
		2	ϕ(stage)	ΨLA(.)
		3	ϕ(flooding*stage)	ΨLA(.)
		4	ϕ(drying*stage)	ΨLA(.)
		5	ϕ(drying*stage, flooding*stage)	ΨLA(.)
		6	ϕ(.)	ΨLA(flooding)
		7	ϕ(stage)	ΨLA(flooding)
		8	ϕ(flooding*stage)	ΨLA(flooding)
		9	ϕ(drying*stage)	ΨLA(flooding)
		10	ϕ(drying*stage, flooding*stage)	ΨLA(flooding)
		11	ϕ(.)	ΨLA(drying)
		12	ϕ(stage)	ΨLA(drying)

13	ϕ(flooding*stage)	ΨLA(drying)
14	ϕ(drying*stage)	ΨLA(drying)
15	ϕ(drying*stage, flooding*stage)	ΨLA(drying)
16	ϕ(.)	ΨLA(drying, flooding)
17	ϕ(stage)	ΨLA(drying, flooding)
18	ϕ(flooding*stage)	ΨLA(drying, flooding)
19	ϕ(drying*stage)	ΨLA(drying, flooding)
20	ϕ(drying*stage, flooding*stage)	ΨLA(drying, flooding)

Table S2. The top four robust design Pradel models to describe the best covariate structure for capture probability (*p*) for *Gyrinophilus porphyriticus* in the Hubbard Brook Experimental Forest, New Hampshire, USA.

Model	k	AICc	ΔAIC	AICc wt
p (reach + stream)	26	8594.11	0.00	0.87
p (reach + stream + time)	33	8597.84	3.73	0.13
p (reach + time)	31	8657.64	63.53	0.00
p (reach)	24	8658.72	64.61	0.00

Note: Parameterization for *p* to vary by reach, stream, or time are in parentheses. Apparent survival (ϕ) and larval recruitment (*f*) varied by time in all models. Number of estimated parameters (k), second-order Akaike’s information criterion values (AIC_c), AIC_c differences (ΔAIC_c), and AIC_c weights (AIC_c wt) for all models are shown.

Table S3. Parameter estimates from the top robust design Pradel model assessing support for effects of flooding and drying magnitude on annual larval recruitment (*f*) and apparent survival probability (ϕ) for *Gyrinophilus porphyriticus* in the Hubbard Brook Experimental Forest, New Hampshire, USA.

Parameter	Estimate	SE	LCL	UCL
ϕ				
Intercept	-0.44	0.10	-0.64	-0.24
StreamParadise	0.18	0.13	-0.07	0.43
StreamZigzag	0.32	0.15	0.03	0.61
Watershed area	-0.11	0.07	-0.24	0.03
Flooding	-0.36	0.07	-0.49	-0.22
f				
Intercept	0.37	0.11	0.15	0.59
StreamParadise	-0.15	0.13	-0.40	0.11
StreamZigzag	-0.05	0.15	-0.35	0.25
Watershed area	0.14	0.07	0.00	0.28
Drying	0.16	0.08	0.00	0.33
p				
Intercept	-2.82	0.05	-2.91	-2.72
StreamParadise	-0.01	0.04	-0.08	0.06
StreamZigzag	-0.30	0.04	-0.38	-0.22
Downstream reach	-0.53	0.03	-0.59	-0.46

Note: Standard error (SE), lower confidence limit (LCL), and upper confidence limit (UCL) provided for all parameter estimates. Models were forced to include the effects of stream (Bear, Paradise, and Zigzag) and watershed area on ϕ and *f*, and stream and reach effects on capture probability.

Table S4. Parameter estimates from the top robust design multi-state Cormack-Jolly-Seber model assessing support for effects of flooding and drying magnitude on stage-specific annual apparent survival probability (ϕ) and annual adult recruitment (Ψ_{LA}) for *Gyrinophilus porphyriticus* in the Hubbard Brook Experimental Forest, New Hampshire, USA.

Parameter	Estimate	SE	LCL	UCL
ϕ				
Intercept	-0.23	0.14	-0.50	0.04
StreamParadise	0.19	0.13	-0.07	0.44
StreamZigzag	0.38	0.15	0.08	0.69
Area	-0.11	0.07	-0.25	0.02
Flooding	-0.21	0.16	-0.53	0.10
Larvae	-0.31	0.14	-0.60	-0.03
Flooding*larvae	-0.35	0.20	-0.74	0.04
Ψ_{LA}				
Intercept	-1.57	0.36	-2.28	-0.86
StreamParadise	0.29	0.36	-0.42	1.00
StreamZigzag	0.55	0.43	-0.30	1.40
Area	-0.05	0.20	-0.45	0.35
Drying	-0.86	0.37	-1.58	-0.13
Flooding	-0.44	0.23	-0.90	0.01
p				
Intercept	-3.15	0.06	-3.26	-3.03
Fish	-0.50	0.03	-0.57	-0.44
StreamParadise	-0.01	0.04	-0.09	0.06
StreamZigzag	-0.28	0.04	-0.36	-0.20
Larvae	0.58	0.03	0.51	0.65

Note: This model also includes a parameter for apparent annual survival (ϕ). Standard error (SE), lower confidence limit (LCL), and upper confidence limit (UCL) provided for all parameter estimates. Models were forced to include the effects of stream (Bear, Paradise, and Zigzag) and watershed area on ϕ and Ψ_{LA}, and stream and reach effects on capture probability

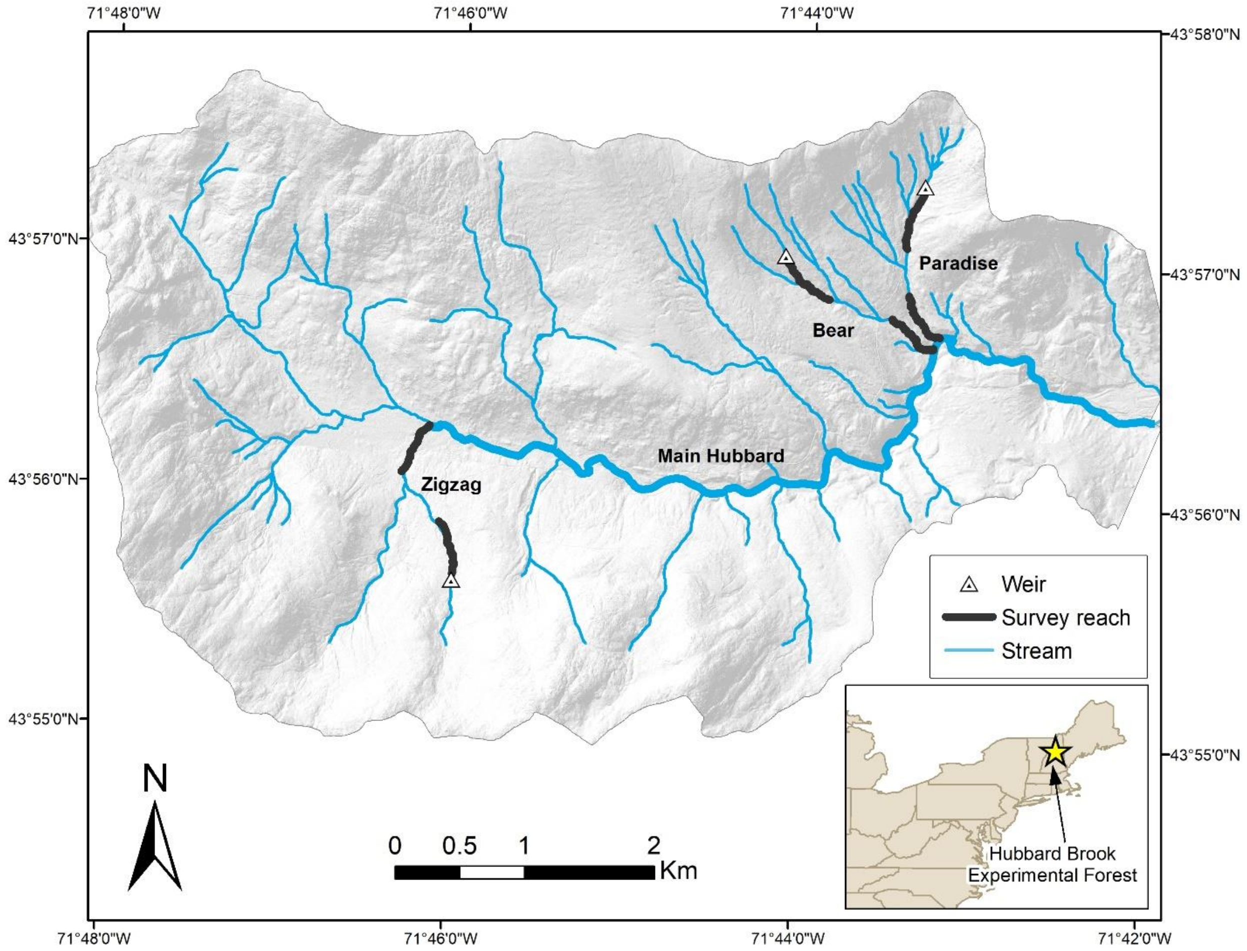

Figure S1. Map of the six study reaches (black lines) across three streams (Bear, Paradise, and Zigzag Brooks) in the Hubbard Brook Experimental Forest in New Hampshire, USA where capture-recapture data was collected for *Gyrinophilus porphyriticus* from 2012 – 2015, 2018 – 2021. Map also includes locations of gauged weirs (triangles) that recorded discharge data for each stream.

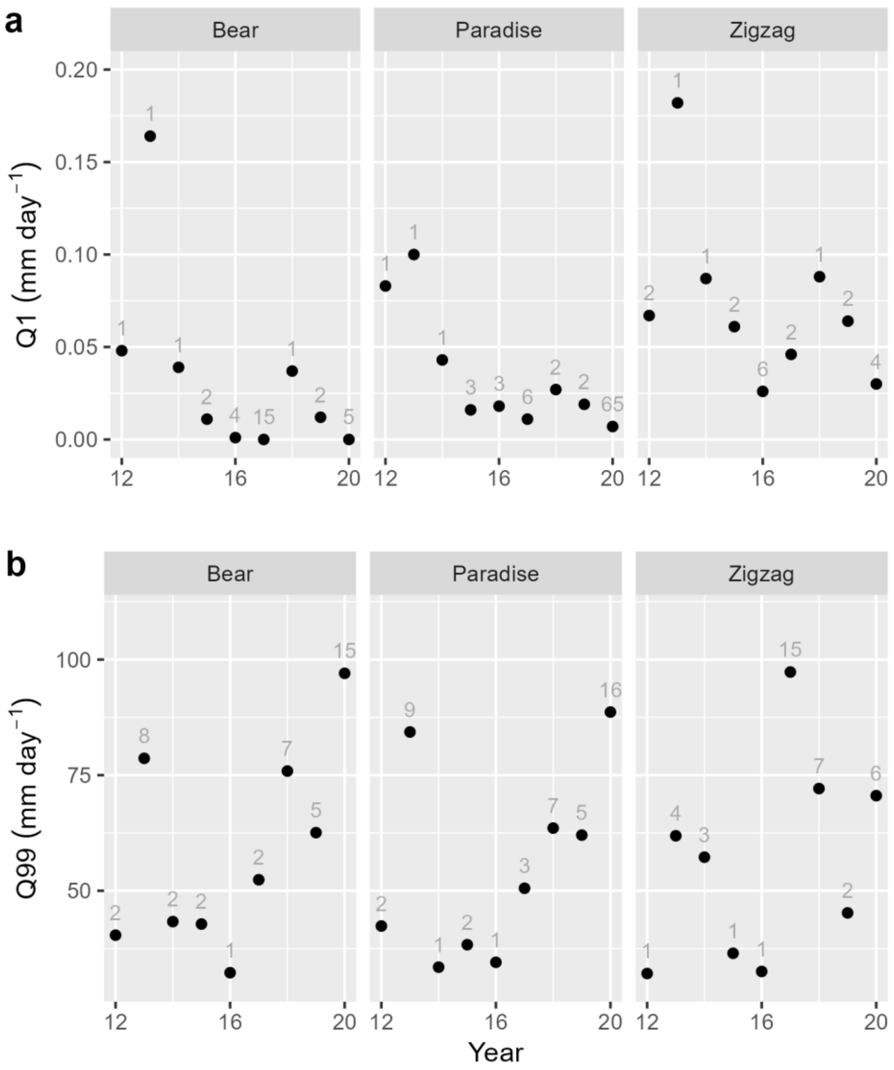

Figure S2: Lowest (Q1) and peak (Q99) discharges (black dots; mm/day) for our three study streams (Bear, Paradise, and Zigzag Brooks) in the Hubbard Brook Experimental Forest, New Hampshire, USA from 2012 to 2020. Years were defined as the 12-month period preceding salamander surveys, so for example, Q1 for 2012 was calculated from daily lowest discharge values from July 1, 2011 – June 30, 2012. We also included the site-specific recurrence intervals (in years) for each lowest or peak discharge value (grey values above each black dot). For example, the most extreme lowest discharge event for Paradise Brook occurred in 2020 and had a recurrence interval of 65 y.

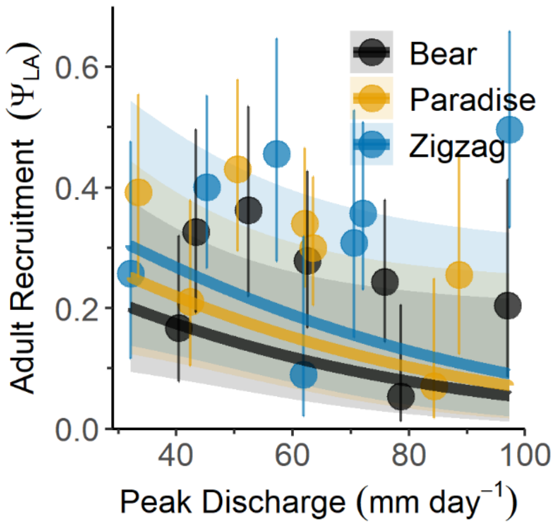

Figure S3. Relationships (bold lines) between peak annual discharge and annual adult recruitment for *Gyrinophilus porphyriticus* across three streams (Bear, Paradise, and Zigzag) in the Hubbard Brook Experimental Forest, New Hampshire, USA. Points are year- and stream-specific recruitment estimates. The colored ribbons represent the 95% confidence intervals in mean responses. Adult recruitment was estimated with a robust-design multi-state Cormack-Jolly-Seber model (table 2).