Hydrologic variability contributes to reduced survival through metamorphosis in a stream salamander

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Changes in the amount, intensity, and timing of precipitation are increasing hydrologic variability in many regions, but we have little understanding of how these changes are affecting freshwater species. Stream-breeding amphibians—a diverse group in North America—may be particularly sensitive to hydrologic variability during aquatic larval and metamorphic stages. Here, we tested the prediction that hydrologic variability in streams decreases survival through metamorphosis in the salamander *Gyrinophilus porphyriticus*, reducing recruitment to the adult stage. Using a 20-y dataset from Merrill Brook, a stream in northern New Hampshire, we show that abundance of *G. porphyriticus* adults has declined by ∼50% since 1999, but there has been no trend in larval abundance. We then tested whether hydrologic variability during summers influences survival through metamorphosis, using capture–mark–recapture data from Merrill Brook (1999 to 2004) and from 4 streams in the Hubbard Brook Experimental Forest (2012 to 2014), also in New Hampshire. At both sites, survival through metamorphosis declined with increasing variability of stream discharge. These results suggest that hydrologic variability reduces the demographic resilience and adaptive capacity of *G. porphyriticus* populations by decreasing recruitment of breeding adults. They also provide insight on how increasing hydrologic variability is affecting freshwater species, and on the broader effects of environmental variability on species with vulnerable metamorphic stages.

climate change | demography | headwater streams | long-term monitoring | Plethodontidae

Mounting evidence suggests that changes in environmental variability are affecting natural populations and communities as much as changes in mean climate conditions (1–5). Changes in the variability of precipitation and streamflow are likely to have particularly strong effects on freshwater biodiversity (6–8). In the northeastern United States, current and projected hydrologic changes include increased annual precipitation, reduced snow coverage, and increased frequency and intensity of extreme precipitation events (9–14). These changes are expected to further increase hydrologic variability (15), and similar trends are occurring and predicted in other regions (16–18). Currently, however, we have little empirical understanding of how changes in hydrologic variability influence the demography of freshwater species, leading to population- and community-level effects (19–21).

Many amphibians have complex life cycles tightly tied to water availability, making them vulnerable to changing hydrologic regimes (22–24). Broadly, life cycles of amphibians with free-living larvae can be divided into 3 posthatching stages: (1) an immature larval stage during which many species are restricted to aquatic environments (i.e., ponds, lakes, streams) and respire cutaneously or with external gills; (2) metamorphosis, when larvae transform to the adult body form, which includes the loss of external gills in many species; and (3) an adult stage when reproduction occurs, usually after further growth and sexual maturation following metamorphosis, and respiration is cutaneous or assisted with lungs and other internal respiratory surfaces (25). Amphibian species differ in many aspects of this general life cycle, including the duration of larval, metamorphic, and postmetamorphic stages (26); the extent of morphological and physiological change during metamorphosis (27); the timing of sexual maturation (28); and adult associations with aquatic vs. terrestrial habitats (29). Across species, however, larval survival and adult recruitment are closely tied to the hydrology of aquatic habitats (30–32).

Intensive and long-term demographic data show that changing hydrologic regimes are affecting pond-breeding amphibians (33–35), but a lack of similar data for stream and terrestrial amphibians has limited our ability to assess their response to climate change (36). Stream-breeding amphibians may be sensitive to hydrologic change because many have prolonged larval and metamorphic stages, during which they are restricted to stream channels, and behavioral, morphological, and ecological traits adapted to historical hydrologic conditions (37–41). Consistent with this expectation, stream amphibians were virtually absent from California streams exposed to catastrophic debris floods (42), unpredictable dam releases increased mortality in 2 river-breeding frogs (43), and occupancy of larval salamanders in North Carolina streams dropped by 30% during an extended drought (44).

We used 20 y of data from Merrill Brook, a stream in northern New Hampshire (44°92′N, 71°08′W), to understand the demographic effects of hydrologic variability on the stream salamander *Gyrinophilus porphyriticus*. *G. porphyriticus* is in the Plethodontidae, a diverse family of lungless salamanders, many of which breed in streams (29, 45). This species is found in small, cool, well-oxygenated streams along the Appalachian uplift in eastern North America. Larvae are exclusively aquatic and have external

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Significance

Streamflows are becoming more variable over time in many regions, but we have little understanding of how this variability affects species that live in streams. We studied how streamflow variability affects populations of the salamander *Gyrinophilus porphyriticus*, a headwater species with aquatic larvae and semiaquatic adults. In a stream in northern New Hampshire, abundance of *G. porphyriticus* adults has declined by ∼50% over the last 20 y, but there has been no trend in larval abundance. This suggests that fewer individuals are surviving metamorphosis to the adult stage. Based on intensive studies in 5 streams, we found that increasing streamflow variability reduces survival through metamorphosis in *G. porphyriticus*, resulting in a decline in the number of breeding adults.

Author contributions: W.H.L., B.R.A., and G.E.L. designed research; W.H.L., L.K.S., and B.R.A. performed research; W.H.L. and L.K.S. analyzed data; and W.H.L., L.K.S., and G.E.L. wrote the paper.

Reviewers: L.L.B., Colorado State University; and S.J.K., University of California, Berkeley.

The authors declare no conflict of interest.

Data deposition: The data reported in this paper have been deposited in the Environmental Data Initiative, available at the Long-Term Ecological Research Network Data Portal, https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter.144.

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gills; the larval period lasts 3 to 5 y (46). External gills are reabsorbed during metamorphosis, along with other morphological changes that include the loss of a keeled tail and horizontally compressed head. There is little published information on the timing and rate of metamorphosis in *G. porphyriticus*, but Bishop (47) observed larvae transforming from March through October in New York populations. Our observations also indicate that metamorphosis is gradual in northern populations, extending over multiple months. Adults rely on cutaneous respiration and remain highly aquatic, but can leave the stream to forage terrestrially at night (48–50). During the day, *G. porphyriticus* individuals are found in interstitial spaces among the larger substrate objects of the streambed and bank.

In a previous analysis, we found that abundance of *G. porphyriticus* adults in Merrill Brook declined between 1999 and 2010, but there was no trend in larval abundance over that period (51). The same study showed that larval and adult survival probabilities were constant across years (1999 to 2004), but adult recruitment from the larval population varied by year. These results led us to predict that climate-related changes in hydrology may be decreasing survival through metamorphosis, causing adult recruitment and abundance to decline. Our objectives here were (1) to determine whether abundance of *G. porphyriticus* adults continued to decline in Merrill Brook through 2018 and (2) to assess the demographic mechanism for this decline by testing if survival through metamorphosis declined with increasing variation in stream discharge during the summer, thereby reducing adult recruitment. For our first objective, we used 20 y of survey data from Merrill Brook (1999 to 2018) to test for long-term trends in abundance of *G. porphyriticus* larvae and adults. We used 2 approaches to accomplish our second objective. First, we tested whether survival through metamorphosis was related to variation in stream discharge during the summer over the first 6 y of sampling at Merrill Brook (1999 to 2004). We conducted intensive capture–mark–recapture surveys in that first 6-y period, allowing for direct estimation of survival through metamorphosis. As a second, independent assessment of this demographic mechanism, we tested whether survival through metamorphosis was related to variation in summer discharge in 4 gauged streams in the Hubbard Brook Experimental Forest (HBEF), located in central New Hampshire (43°56′N, 71°45′W), 120 km southwest of Merrill Brook. We expected a priori that salamanders would be most vulnerable to discharge variability during the summer, when they are active in and along stream channels (52, 53).

Results

Long-Term Trends in Abundance. Between 1999 and 2018, counts of *G. porphyriticus* larvae in July surveys of the 1,000-m study section of Merrill Brook ranged from 20 to 122 and counts of adults ranged from 9 to 70. After correcting for stage-specific recapture probabilities (51), estimates of larval abundance ranged from 268 to 943 and estimates of adult abundance ranged from 60 to 467. There was no trend in larval abundance over the 20-y sampling period ($n = 20$, Kendal's $\tau = 0.07$, $P = 0.67$; Fig. 1*A*), but adult abundance declined significantly ($n = 20$, $\tau = -0.45$, $P = 0.01$; Fig. 1*B*). Larval and adult abundances were not correlated ($n = 20$, $r = -0.07$, $P = 0.78$) and there was no significant trend in total *G. porphyriticus* abundance when larval and adult abundances were combined ($n = 20$, $\tau = -0.16$, $P = 0.31$).

Hydrologic Variability. Between 1999 and 2018, summer discharge coefficients of variation (CVs) in the Dead Diamond River, 9.2 km downstream of the Merrill Brook confluence, ranged from 70 to 197 (Fig. 1*C*). The maximum discharge CV was 178.05 over the 5 summers included in our analysis of survival through metamorphosis (Fig. 2*A*), well within the range of hydrologic variability over the 20-y study period. Summer discharge CVs were not correlated with summer discharge means ($n = 20$, $r = -0.14$, $P = 0.55$) or with discharge CVs for the preceding and subsequent nonsummer periods (i.e., September 1 to May 31; $n = 20$, $|r| < 0.24$, $P > 0.28$). Summer discharge CVs were positively correlated with the number of summer days below the fifth percentile of mean daily discharge values ($n = 20$, $r = 0.67$, $P < 0.01$), but not significantly correlated with the number of summer days above the 95th percentile of mean daily discharge values ($n = 20$, $r = -0.04$, $P = 0.56$). There was no significant temporal trend in summer discharge CVs ($n = 20$, $\tau = -0.21$, $P = 0.21$).

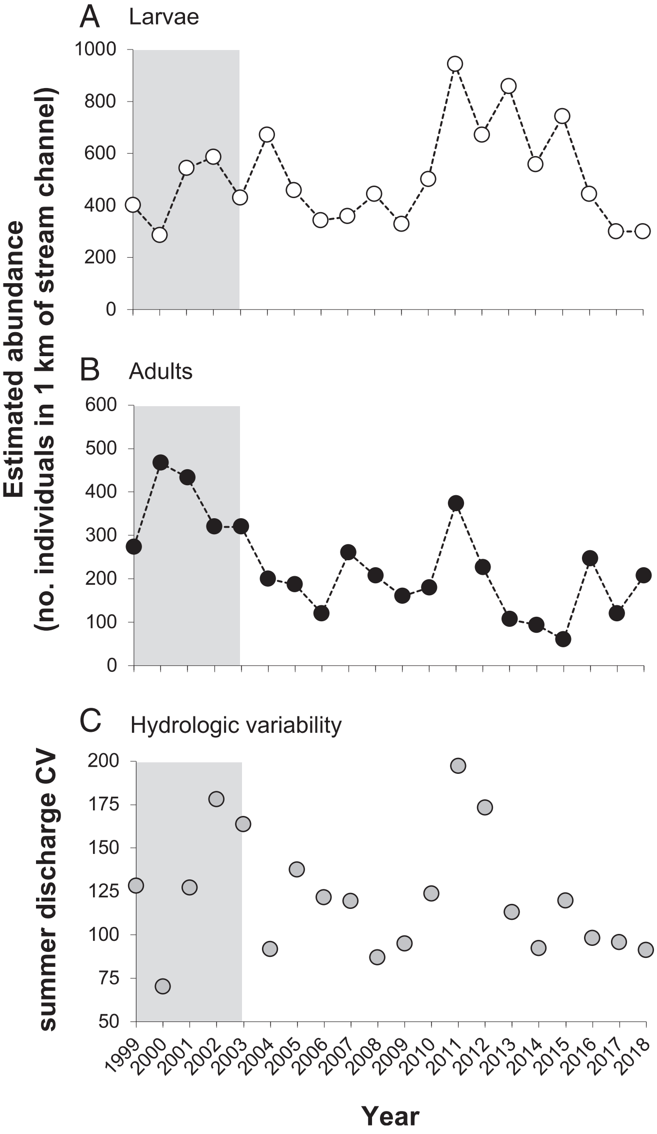

Fig. 1. Trends in abundance of *G. porphyriticus* larvae (*A*) and adults (*B*) in Merrill Brook, New Hampshire, and CVs of summer discharge in the Dead Diamond River (*C*) over the 20-y sampling period (1999 to 2018). Abundance estimates are based on counts from surveys in mid-July of each year, corrected for stage-specific detection probabilities. There was no trend in larval abundance ($n = 20$, $\tau = 0.07$, $P = 0.67$), but adult abundance declined significantly over the 20-y period ($n = 20$, $\tau = -0.45$, $P = 0.01$). The discharge gauge on the Dead Diamond River is 9.2 km downstream of the Merrill Brook confluence. There was no trend in summer discharge CVs in the Dead Diamond River ($n = 20$, $\tau = -0.21$, $P = 0.21$). Shaded areas show the years during which intensive capture–mark–recapture surveys were conducted, which allowed us to estimate survival through metamorphosis.

Despite their close proximity to one another, the HBEF streams differed in discharge CVs over the summers of 2013 and 2014 (Fig. 2*B*). North-facing Zigzag and Canyon Brooks had

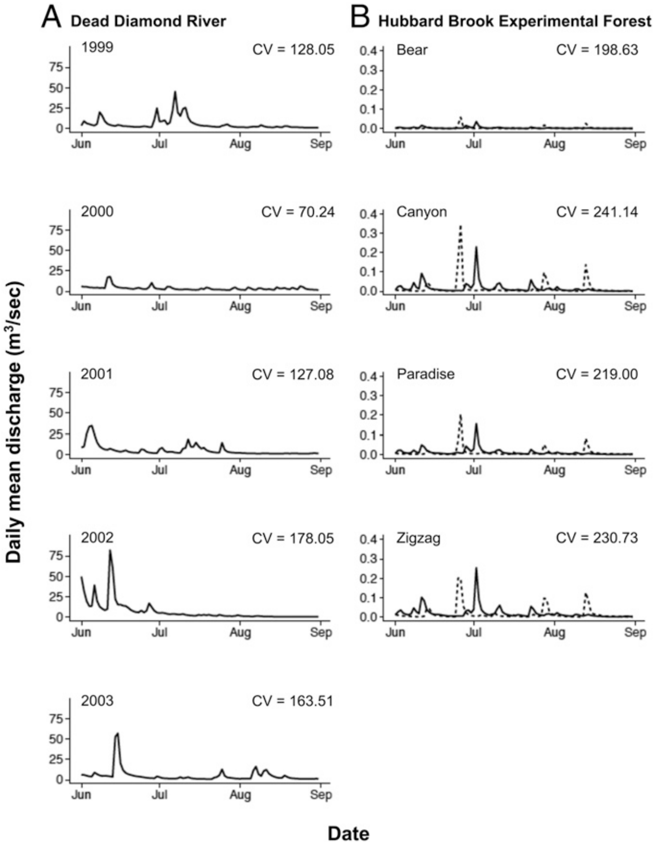

Fig. 2. Hydrographs of summer discharge (June 1 to August 31) in the Dead Diamond River (*A*) and 4 streams in the HBEF (*B*), New Hampshire. Dead Diamond plots show discharge data for the summers of 1999 to 2003, the summers included in our analysis of survival through metamorphosis in Merrill Brook. The discharge gauge on the Dead Diamond River is 9.2 km downstream of the Merrill Brook confluence. Hubbard Brook plots show discharge data from the summers of 2013 (solid line) and 2014 (dashed line), the 2 summers during the study period (2012 to 2014) when discharge sampling occurred at regular 5-min intervals. The CV of daily mean discharge is shown in the upper right portion of each panel.

higher summer discharge CVs, whereas south-facing Paradise and Bear Brooks had lower summer discharge CVs. The difference between south- and north-facing slopes suggests that evapotranspiration contributes to stream discharge variability, in addition to differences in precipitation regimes, catchment area, and other hydrogeomorphic factors. Summer discharge CVs for 2013 and 2014 were not correlated with summer discharge means ($n = 4$, $\boldsymbol{\tau} = 0.55$, $P = 0.28$) or with discharge CVs for the intervening nonsummer period ($n = 4$, $\boldsymbol{\tau} = 0.67$, $P = 0.17$). Summer discharge CVs in the HBEF streams were not significantly correlated with the number of summer days below the fifth percentile of mean daily discharge values ($n = 4$, $\boldsymbol{\tau} = 0.20$, $P = 0.12$) or above the 95th percentile of mean daily discharge values ($n = 4$, $\boldsymbol{\tau} = -0.36$, $P = 0.80$).

Effects of Hydrologic Variability on Survival through Metamorphosis. Support for the top 2 transition probability models for Merrill Brook was somewhat ambiguous (differences in Akaike's information criterion corrected for small sample sizes [$\Delta\mathrm{AIC_c}$] = 1.88; Table 1), but the likelihood ratio test (LRT) result was not significant ($\chi^2 = 4.21$, $P = 0.38$), indicating that the model with fewer parameters was more parsimonious (i.e., with larva-to-adult transition probabilities [$\psi^{\text{larva}\rightarrow\text{adult}}$] a linear function of summer discharge CV). Unbiased estimates of annual survival through metamorphosis (i.e., $\psi^{\text{larva}\rightarrow\text{adult}}$ with $S^{\text{larva}} = 1.0$) showed a strong negative relationship with summer discharge CVs for the Dead Diamond River between 1999 and 2003 ($\hat{\beta} \pm \mathrm{SE} = -0.02 \pm 0.008$; Fig. 3*A* and Table 2). There was unambiguous support for the top transition probability model for the HBEF streams, with $\psi^{\text{larva}\rightarrow\text{adult}}$ a linear function of summer discharge CV ($\Delta\mathrm{AIC_c} > 2.0$; Table 1). Like in Merrill Brook, unbiased estimates of monthly survival through metamorphosis showed a strong negative relationship with summer discharge CVs for the HBEF streams ($\hat{\beta} \pm \mathrm{SE} = -0.04 \pm 0.01$; Fig. 3*B* and Table 2).

Discussion

Abundance of *G. porphyriticus* adults in Merrill Brook declined by ∼50% between 1999 and 2018, but there was no trend in larval abundance (Fig. 1). This result indicates that adult survival or adult recruitment has declined over the last 20 y; however, adult survival appears to be constant across years (51, 54) (Table 2), pointing to metamorphosis as the critical stage for understanding this trend. Here, we tested whether hydrologic variability during the summer, when *G. porphyriticus* individuals are active in and along stream channels, reduces adult recruitment by decreasing survival through metamorphosis. Using intensive capture–mark–recapture data from the first 6 y of sampling in Merrill Brook (1999 to 2004) and from 4 HBEF streams (2012 to 2014), we found that the probability of individuals surviving through metamorphosis declined with increasing hydrologic variability during the summer (Table 1 and Fig. 3). Summer discharge CVs were not correlated with summer discharge means or discharge CVs for nonsummer periods, and not consistently correlated with the frequency of extreme low- or high-flow events, suggesting that overall hydrologic variability during summers (i.e., both relatively low and high flows) reduces survival through metamorphosis.

Despite small sample sizes, clear relationships between hydrologic variability and $\psi^{\text{larva}\rightarrow\text{adult}}$ in Merrill Brook and the 4 HBEF streams show the vulnerability of *G. porphyriticus* individuals during metamorphosis. Likewise, previous analyses showing a lack of variation in larval and adult survival probabilities in Merrill Brook and the HBEF streams (51, 55) indicate that pre- and postmetamorphic individuals are resistant to the effects of hydrologic variability. These results add to mounting evidence that metamorphic stages are vulnerable to abiotic and biotic stressors (56–58), while also underscoring the need for more research on this topic in light of climate-related increases in environmental variability worldwide (9, 59, 60). Metamorphosis is an inherently vulnerable, transitional life stage, and many species have physiological, phenological, and behavioral strategies to reduce exposure to environmental variation during this stage (61–64). It is reasonable to expect, therefore, that increases in spatial and temporal environmental variability are testing the limits of these strategies, and may be affecting survival through metamorphosis more broadly than currently recognized.

We did not observe a decline in total *G. porphyriticus* abundance over the study period because larval abundance—although highly variable among years—showed no long-term trend, buffering the decline in adult abundance (Fig. 1). This lack of correlation between larval and adult abundances suggests that adult recruitment is, at least in part, independent of larval density. It is also consistent with a potential mechanism for the decline in adult recruitment: the inability of metamorphs to access refuges during low and high flows. Small larvae can burrow deep into the streambed to avoid physical disturbance during high flows and to access subsurface water during low flows, whereas the large body size of metamorphs likely limits access to these deep interstitial refuges (65, 66). Adults are larger than metamorphs, but can move to streambank refuges to avoid high flows and to access moist microsites during low flows (48, 67). Metamorphs, in contrast, are likely restricted to the stream channel due to continued use of

Table 1. Multistate capture–mark–recapture models assessing support for variation in $\psi^{\mathrm{larva}\rightarrow\mathrm{adult}}$ of *G. porphyriticus* individuals in Merrill Brook and 4 streams in the HBEF, New Hampshire, as a linear function of CVs of summer discharge

Model	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	$\mathrm{AIC_c}$ wt	K
Merrill Brook				
$S^{\mathrm{larva}}_{(\mathrm{fixed})}$, $S^{\mathrm{adult}}_{(\cdot)}$, $p^{\mathrm{larva}}_{(\cdot)}$, $p^{\mathrm{adult}}_{(\cdot)}$, $\psi^{\mathrm{larva}\rightarrow\mathrm{adult}}_{(\mathrm{discharge\ CV})}$	1,363.95	0.00	0.68	5
$S^{\mathrm{larva}}_{(\mathrm{fixed})}$, $S^{\mathrm{adult}}_{(\cdot)}$, $p^{\mathrm{larva}}_{(\cdot)}$, $p^{\mathrm{adult}}_{(\cdot)}$, $\psi^{\mathrm{larva}\rightarrow\mathrm{adult}}_{(\mathrm{time})}$	1,365.83	1.88	0.27	8
$S^{\mathrm{larva}}_{(\mathrm{fixed})}$, $S^{\mathrm{adult}}_{(\cdot)}$, $p^{\mathrm{larva}}_{(\cdot)}$, $p^{\mathrm{adult}}_{(\cdot)}$, $\psi^{\mathrm{larva}\rightarrow\mathrm{adult}}_{(\cdot)}$	1,369.09	5.14	0.05	4
HBEF				
$S^{\mathrm{larva}}_{(\mathrm{fixed})}$, $S^{\mathrm{adult}}_{(\cdot)}$, $p^{\mathrm{larva}}_{(\mathrm{stream})}$, $p^{\mathrm{adult}}_{(\mathrm{time})}$, $\psi^{\mathrm{larva}\rightarrow\mathrm{adult}}_{(\mathrm{discharge\ CV})}$	4,765.58	0.00	0.68	15
$S^{\mathrm{larva}}_{(\mathrm{fixed})}$, $S^{\mathrm{adult}}_{(\cdot)}$, $p^{\mathrm{larva}}_{(\mathrm{stream})}$, $p^{\mathrm{adult}}_{(\mathrm{time})}$, $\psi^{\mathrm{larva}\rightarrow\mathrm{adult}}_{(\cdot)}$	4,767.76	2.18	0.23	14
$S^{\mathrm{larva}}_{(\mathrm{fixed})}$, $S^{\mathrm{adult}}_{(\cdot)}$, $p^{\mathrm{larva}}_{(\mathrm{stream})}$, $p^{\mathrm{adult}}_{(\mathrm{time})}$, $\psi^{\mathrm{larva}\rightarrow\mathrm{adult}}_{(\mathrm{stream})}$	4,769.61	4.03	0.09	17

Transition probabilities represent the probability of larvae surviving from time t to $t+1$ and metamorphosing to the adult stage. Summer discharge CVs for Merrill Brook were based on mean daily discharge values from a gauge station on the Dead Diamond River, 9.2 km downstream of the confluence. Discharge data for the Hubbard Brook streams are from weirs on the streams themselves. Parameterization of larval and adult recapture probabilities (p) was based on prior analyses (51, 55). S^{larva} was fixed to 1.0 to ensure that transition probabilities were unbiased estimates of survival through metamorphosis by removing the assumption that survival is dependent on the state of an individual at time t. Transition probabilities were modeled as constant, variable by year (Merrill Brook) and stream (Hubbard Brook), or as a linear function of summer discharge CV. Second-order Akaike's information criterion values ($\mathrm{AIC_c}$), $\mathrm{AIC_c}$ differences ($\Delta\mathrm{AIC_c}$), $\mathrm{AIC_c}$ weights ($\mathrm{AIC_c}$ wt), and number of estimated parameters (K) for all models are shown. Parameterization for S, p, and ψ is shown in parentheses. •, constant; discharge CV, variation as a linear function of summer discharge CV; fixed, fixed to 1.0; stream, variation by stream; time, variation by time.

external gills (68), although exactly how reliance on external gills changes during metamorphosis is unknown. We would not expect this mechanism to be dependent on the density of larvae, which should be far less limited by refuge availability than metamorphs due to their small size, on average, thus reducing interactions between the 2 stages (65, 66). The maximum size of larvae (snout-to-vent length) declined by ∼10 mm in Merrill Brook between 1999 and 2018 ($n = 20$, $\tau = -0.39$, $P = 0.01$), further indicating size-specific effects of aquatic refuge availability. There was no trend in maximum adult size ($n = 20$, $\tau = -0.12$, $P = 0.47$). Nevertheless, we acknowledge that more work is needed to test the mechanism of metamorph mortality directly, and we have begun observational and experimental studies of refuge use for that purpose.

The larger question of how reduced survival through metamorphosis affects demographic viability depends on the sensitivity of the population growth rate to changes in adult recruitment (69). *G. porphyriticus* clutch sizes range from 15 to 66 ova, but appear to decline moving northward (45). Based on this low annual reproductive output, life history theory predicts that the population growth rate should be more sensitive to changes in adult survival than equivalent changes in recruitment (70, 71). However, our data show that adult survival is relatively invariant (51, 55), suggesting that other vital rates (e.g., adult recruitment) may play a larger role in population viability. Larval recruitment in Merrill Brook also remains largely independent of adult density (Fig. 1): There were no correlations between adult abundance in year t and larval abundances in years t through $t + 5$ ($n = 15$ to 20, $|r| < 0.34$, $P > 0.2$). The same pattern occurs in streams throughout New Hampshire (72), suggesting that factors other than adult density limit larval recruitment (e.g., nest sites, parental condition, predation). These complexities underscore the need for additional demographic modeling and, more generally, the importance of evaluating species vulnerability to increased environmental variability using a stage-based approach to understand compounding or compensatory effects among life history stages (73).

Models and data show that hydrologic variability is increasing in the northeastern United States (9, 10, 15), including at the HBEF (13). Our results suggest that this climatic trend may be causing the long-term decline of adult *G. porphyriticus* abundance in Merrill Brook (Fig. 1) by decreasing survival through metamorphosis (Fig. 3). However, there was no long-term trend in summer discharge CVs in the Dead Diamond River, possibly due to other sources of hydrologic variability in the Dead Diamond watershed (74–76). In a posteriori analysis, we did detect a significant increase in the Dead Diamond's Richards–Baker Flashiness Index (1999 to 2018; $n = 20$, $\tau = 0.48$, $P < 0.01$), which reflects the frequency and speed of short-term changes in streamflow, and has greater power to detect long-term trends than the CV (77). We also would not expect hydrologic variability in Merrill Brook, a first-order stream, to match that of the fifth-order Dead Diamond River exactly (78), and this mismatch may account for a lack of a direct correlation between summer discharge CVs and adult *G. porphyriticus* abundances ($n = 20$, $r = 0.27$, $P = 0.25$). In the 4 HBEF streams, where discharge is measured in the streams themselves, adult abundances (July counts adjusted by recapture probabilities for adults [p^{adult}]; Table 2) declined with summer discharge CVs ($n = 4$, $\tau = 0.04$, $P < 0.01$). We limited our analyses to discharge CVs based on a priori predictions about the effects of overall hydrologic variability, thus avoiding exploratory analyses of alternative hydrologic variables. However, we acknowledge that discharge CVs are a coarse measure of hydrologic variability, and plan further analyses of these hydrologic data to isolate proximate components of variability associated with *G. porphyriticus* demography (79–81).

This study assesses hydrologic correlates and population-level consequences of variation in survival through metamorphosis, but also underscores the challenge of drawing this connection in species with complex life cycles. Despite a significant decline in the adult population in Merrill Brook over the last 20 y (Fig. 1*B*), there has been no temporal trend in total *G. porphyriticus* abundance or larval abundance (Fig. 1*A*). Based on abundance alone, then, we cannot conclude that increasing hydrologic variability poses a direct risk to *G. porphyriticus* populations. We can conclude, however, that the trend in Merrill Brook makes the population less resilient to other perturbations by increasing demographic reliance on a single life history stage: larvae (71, 82, 83). The variability of larval abundances over the last 20 y underscores this risk to *G. porphyriticus* populations (Fig. 1*A*), while a long-term decline in abundance of a terrestrial plethodontid at the HBEF, *Plethodon cinereus* (12), raises the possibility of broader threats to this diverse family of salamanders. It is also likely that the shift in stage structure has caused the number of breeding

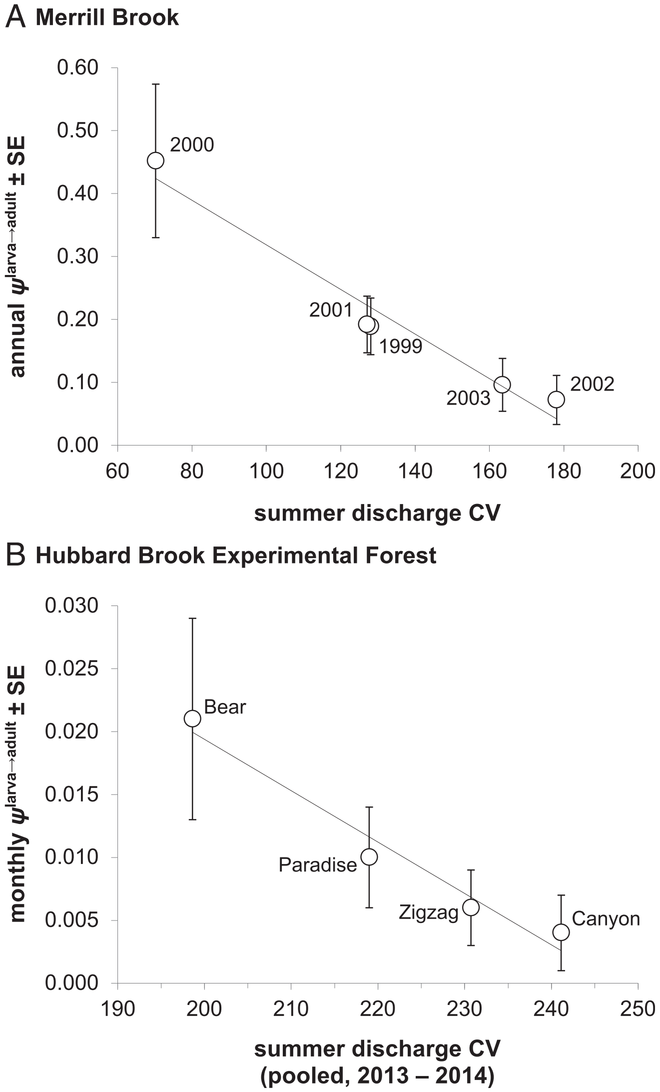

Fig. 3. Relationships between CVs of summer discharge and $\psi^{\mathrm{larva}\rightarrow\mathrm{adult}}$ in Merrill Brook (*A*) and 4 streams in the HBEF (*B*), New Hampshire. Transition probabilities represent the probability of larvae surviving from time t to $t + 1$ and metamorphosing to the adult stage, estimated on an annual interval for Merrill Brook and on a monthly interval for the Hubbard Brook streams (Tables 1 and 2). Summer discharge CVs for Merrill Brook were based on mean daily discharge values from a gauge station on the Dead Diamond River, 9.2 km downstream of the confluence. Discharge data for the Hubbard Brook streams are from weirs on the streams themselves. Hubbard Brook summer discharge CVs were calculated by pooling mean daily discharge values from the summers of 2013 and 2014, when sampling occurred at regular 5-min intervals. Linear regression lines are plotted to illustrate trends. Labels adjacent to Merrill Brook points are years; labels adjacent to Hubbard Brook points are stream names.

G. porphyriticus adults to decline, reducing effective population size and, therefore, the capacity for adaptive response to future conditions (84–86). We hope this study promotes additional research on these direct and indirect effects of increasing hydrologic variability on freshwater species, and on the broader effects of changing patterns of environmental variability on species with vulnerable metamorphic stages.

Methods

Study Sites. The primary study site was Merrill Brook, a fishless, first-order stream in Dartmouth College's Second College Grant, in northern New Hampshire. A wetland at the confluence with the Dead Diamond River acts as a barrier to brook trout (*Salvelinus fontinalis*) that might enter Merrill Brook from the larger river. We sampled throughout a 1,000-m section of Merrill Brook that started at the confluence with the outflow wetland, encompassing the perennial portion of the stream (54).

We also sampled 4 hydrologically independent first-order streams in the 32-km^2 HBEF: Bear Brook, Canyon Brook, Paradise Brook, and Zigzag Brook. All 4 streams flow into the mainstem of Hubbard Brook, a tributary of the Pemigewasset River. Sampling occurred along two 500-m long reaches in each stream. Downstream reaches started at the confluence with Hubbard Brook, and upstream reaches ended at weirs where long-term water quality data are collected (87). Distances between downstream and upstream reaches, measured along stream channels, were 400 m in Bear Brook, 0 m in Canyon Brook, 250 m in Paradise Brook, and 500 m in Zigzag Brook (55). We pooled *G. porphyriticus* individuals across the 2 reaches so that our unit of replication was a 1,000-m section of each stream, matching the scale of the Merrill Brook data. Unlike Merrill Brook, predatory brook trout (*S. fontinalis*) are present in the lower reaches of the HBEF streams (88).

Hydrology of Merrill Brook and the HBEF streams is characterized by high spring discharge due to melting snow and high discharge events throughout the year associated with isolated storms. Base flow conditions usually occur in late summer and early fall (13). The study streams drain small, high-gradient headwater watersheds, with catchment areas ranging from 0.96 to 3.32 km^2 and average slopes ranging from 18.73 to 27.04°. Bank-full channel widths range from 2 to 4 m; the majority of stream habitats are categorized as riffles and pools (89, 90); and the dominant substrate types are cobble, boulder, and bedrock, with low embeddedness and little fine sediment (e.g., sand, silt). Dominant tree species in forests surrounding these streams are *Acer saccharum*, *Fagus grandifolia*, *Betula alleghaniensis*, *Picea rubens*, *Abies balsamea*, and *Betula papyrifera* (54). The streams have low conductivity (12.0 to 15.0 μS·cm^{-1}), slight acidity (pH of 5.0 to 6.0), high dissolved oxygen content (80 to 90% saturation), and moderate midday temperatures in the summer (13.0 to 17.0 °C) (13, 54, 91). Other salamanders encountered in Merrill Brook and the HBEF streams were *Eurycea bislineata* and *Desmognathus fuscus* (both Plethodontidae).

Survey Methods. We used a cover-controlled, active search sampling method in all surveys (92). Moving upstream, we turned rocks within the channel and along the edge measuring 64 to 256 mm in diameter (cobble). In each survey, a constant search effort was maintained by turning just over 1 haphazardly selected cover object per meter of stream length. We used aquarium dipnets to capture salamanders, including those flushed by the current (54, 55). The life history stage (larva vs. adult) was recorded for all individuals based on the presence of external gills (47, 93), so metamorphosing individuals were recorded as larvae until external gills were lost, and then as adults. Salamanders were individually marked with visible implant elastomer from Northwest Marine Technologies (94).

We conducted capture–mark–recapture surveys of Merrill Brook during 3-d periods in mid-June, mid-July, and mid-August of 1999 to 2004. We continued single annual abundance surveys of Merrill Brook in mid-July of 2005 to 2018. Methods were identical to those used in the earlier surveys, but animals were not examined for existing marks and no new animals were marked (51, 54). In the HBEF streams, capture–mark–recapture surveys were conducted mid-June through mid-September of 2012 to 2014. Each stream was surveyed 9 times each field season, for a total of 27 surveys per stream over the 3-y study period. We conducted 3 surveys of each stream during three 2-wk periods distributed evenly throughout the field season, for a total of 9 surveys per stream each summer and 27 surveys per stream over the 3-y study period. Streams were surveyed in a random order within each of these 2-wk sampling periods (55).

Quantifying Hydrologic Variability. To quantify variability of stream discharge in Merrill Brook, we obtained mean daily discharge data from the nearest US Geological Survey gauge on the Dead Diamond River, 9.2 km downstream of the confluence with Merrill Brook (95). We then calculated the mean and CV of summer discharge (June 1 to August 31) for each year of our study, as well as the discharge CVs for the intervening nonsummer periods (September 1 to May 31). The CV is the ratio of the SD to the mean, a unitless measure of relative variability that can be compared across samples with different means. To assess the contributions of extreme low and high flows to summer discharge CVs, we calculated the number of days each summer below the fifth percentile and above the 95th percentile of mean daily discharge values over the entire study period.

Stream discharge has been monitored at the HBEF since as early as 1956 (96). However, a switch to electronic sensors in 2013 made continuous flow data available at 5-min intervals, whereas readings were recorded at irregular intervals prior to 2013. We only used data from 2013 and 2014 to quantify discharge variability in the HBEF streams to ensure that inconsistent sampling intervals and rates did not bias our analyses. We calculated mean daily discharge for each stream and used these values to calculate means

Table 2. Stage-specific survival (*S*) and recapture (*p*) probabilities, and $\psi^{\text{larva}\rightarrow\text{adult}}$ for *G. porphyriticus* populations in Merrill Brook and 4 streams in the HBEF, New Hampshire

Site	S^{larva}	S^{adult}	p^{larva}	p^{adult}	$\psi^{\text{larva}\rightarrow\text{adult}}$
Merrill Brook					
1999	1.000 (0.000)	0.715 (0.049)	—	—	0.189 (0.045)
2000	1.000 (0.000)	0.715 (0.049)	0.066 (0.012)	0.146 (0.022)	0.452 (0.122)
2001	1.000 (0.000)	0.715 (0.049)	0.066 (0.012)	0.146 (0.022)	0.192 (0.045)
2002	1.000 (0.000)	0.715 (0.049)	0.066 (0.012)	0.146 (0.022)	0.072 (0.039)
2003	1.000 (0.000)	0.715 (0.049)	0.066 (0.012)	0.146 (0.022)	0.096 (0.042)
2004	—	—	0.066 (0.012)	0.146 (0.022)	—
HBEF					
Bear	1.000 (0.000)	0.895 (0.012)	0.056 (0.005)	0.018 (0.013)–0.266 (0.078)	0.021 (0.008)
Canyon	1.000 (0.000)	0.895 (0.012)	0.017 (0.004)	0.018 (0.013)–0.266 (0.078)	0.004 (0.003)
Paradise	1.000 (0.000)	0.895 (0.012)	0.044 (0.005)	0.018 (0.013)–0.266 (0.078)	0.010 (0.004)
Zigzag	1.000 (0.000)	0.895 (0.012)	0.056 (0.008)	0.018 (0.013)–0.266 (0.078)	0.006 (0.003)

Estimates are from best-fit capture–mark–recapture models (Table 1), with $\psi^{\text{larva}\rightarrow\text{adult}}$ a linear function of CVs of summer discharge. Merrill Brook estimates are annual, and Hubbard Brook estimates are monthly. S^{larva} was fixed at 1.0 to generate unbiased estimates of $\psi^{\text{larva}\rightarrow\text{adult}}$, representing the probability of larvae surviving from time t to $t+1$ and metamorphosing to the adult stage. Merrill Brook estimates are from the first 6 y of sampling (1999 to 2004), when we conducted intensive capture–mark–recapture surveys there. Estimates for the Hubbard Brook streams are from surveys in 2012 to 2014. Adult recapture probability varied by time in the Hubbard Brook streams, so minimum and maximum estimates for each stream are provided. Values in parentheses are SEs.

and CVs of summer discharge, pooling discharge data across summers. We also calculated the discharge CV for the period between summers 2013 and 2014 (i.e., September 1, 2013 to May 31, 2014).

Estimating Demographic Parameters. To test for long-term population trends in Merrill Brook, we generated indices of larval and adult abundance by correcting annual count data from July surveys for stage-specific recapture (i.e., detection) probabilities (97, 98). Previous analysis of the first 6 y of data showed that recapture probabilities (*p*) differed between larvae and adults, but did not differ by year (51). Because detection did not differ over time, counts (C^{larva} and C^{adult}) were reliable indices of relative abundances of each stage, but converting counts to total abundance estimates (i.e., $\hat{N}^{\text{larva}} = C^{\text{larva}}/\hat{p}^{\text{larva}}$) better reflects the stage structure of the population.

We implemented multistate capture–mark–recapture models in Program MARK to estimate survival through metamorphosis in Merrill Brook and the HBEF streams (99, 100). Multistate models estimate apparent survival (*S*) and recapture (*p*) probabilities of larvae and adults, and $\psi^{\text{larva}\rightarrow\text{adult}}$. Transition probability is the conditional probability that an individual in one state (i.e., stage) at time t will be in the other state at $t+1$, given that the animal is alive at $t+1$. Best-fitting multistate models for Merrill Brook (1999 to 2004) and the 4 HBEF streams (2012 to 2014) were identified in previous analyses (model selection results are provided in refs. 51, 55), and we used these models as the foundation for the current analysis. For Merrill Brook, the best-fitting model had time-invariant larval and adult survival and recapture probabilities (S^{larva}, S^{adult}, p^{larva}, and p^{adult}), and $\psi^{\text{larva}\rightarrow\text{adult}}$ varied by year. In the best-fitting model for the HBEF streams, larval and adult survival probabilities (S^{larva} and S^{adult}) were constant across streams, p^{larva} varied by stream, p^{adult} varied by time, and $\psi^{\text{larva}\rightarrow\text{adult}}$ varied by stream.

Building on these best-fitting model structures, we assessed support for relationships between stream discharge CVs and survival through metamorphosis in Merrill Brook and the HBEF streams. Specifically, we used Akaike's information criterion corrected for small sample sizes (AIC_c) (101) to select the most parsimonious model structure from candidate models where $\psi^{\text{larva}\rightarrow\text{adult}}$ was either constant, variable by year (Merrill Brook) and stream (HBEF), or a linear function of summer discharge CV. We fixed S^{larva} at 1.0 in these models, which ensures that $\psi^{\text{larva}\rightarrow\text{adult}}$ is an unbiased estimate of survival through metamorphosis by removing the assumption that survival is dependent on the state of an individual at time t (102). Candidate models were ranked by second-order AIC differences (ΔAIC_c) (103). Relative likelihood of each model in a candidate set was then estimated with AIC_c weights (104). When rankings of the top models were ambiguous [i.e., $\Delta\text{AIC}_c < 2.0$ (103)], we used pairwise LRTs to compare model fit. A significant LRT result ($P < 0.05$) indicates greater support for the model with more parameters; a nonsignificant LRT result indicates equal support for both models, in which case the model with fewer parameters is more parsimonious (105).

Demographic probabilities in Merrill Brook were estimated on an annual interval by collapsing data from the 3 surveys each summer into a single observation for each individual (i.e., captured, not captured), representing that individual's overall capture history for the summer [mid-June through mid-August (106)]. Therefore, transition probabilities ($\psi^{\text{larva}\rightarrow\text{adult}}$) apply to the interval from mid-June of year t through mid-June of year $t+1$, spanning both summer and nonsummer periods. For the HBEF streams, observations from the 3 surveys in each 2-wk survey session were collapsed into a single observation for each month of the field season (e.g., mid-June, mid-July, mid-August) and transition probabilities were estimated for a monthly interval. These monthly probabilities apply throughout the sampling period, from mid-June of 2012 to mid-August of 2014, spanning both summer and nonsummer periods, like the Merrill Brook estimates.

Statistical Analyses. We used nonparametric Mann–Kendall tests to assess long-term trends in *G. porphyriticus* abundance estimates and summer discharge CVs over the entire study period in Merrill Brook (1999 to 2018). Mann–Kendall tests control for temporal autocorrelation in the dependent variable (107). We also used Mann–Kendall tests in other analyses where sample sizes were too small to justify parametric Pearson product-moment correlation analyses (108).

ACKNOWLEDGMENTS. We are grateful for support from Lorraine Turner, Ian Halm, Don Buso, Tammy Wooster, Amey Bailey, Scott Bailey, John Campbell, Geoff Wilson, Scott Decker, Kevin Evans, Jenny Tollefson, Will Lowe, and Iris Lowe. We thank Linda Greene, Cheryl Shannon, Christina Glastris, Anne Margolis, Bert Fisher, Mariah Childs, Jessica Hernandez, Laurel Low, Jenn McKenzie, Jamie Rasor, Tommy Mitchell, Leah Nagel, Jill Newman, and Jon Davenport for field assistance. This is a contribution to the Hubbard Brook Ecosystem Study. The HBEF is operated and maintained by the Northeastern Forest Research Station, US Department of Agriculture Forest Service, Newtown Square, PA, and we are particularly grateful for the hydrologic dataset maintained by the station. This research was conducted under Montana State Institutional Care and Use Protocol 003-14WLDBS-012714. This research was funded by the Sweet Water Trust, the National Science Foundation (Grants DEB-0105091, DEB-1114804, DEB-1050459, DEB-1637685, and DEB-1655653), and The Andrew W. Mellon Foundation.

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