

The spatial structure of variation in salamander survival, body condition and morphology in a headwater stream network

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Abstract

1. Understanding the spatial structure of individual variation is critical to assessing the mechanisms and scale of species-level ecological and evolutionary responses. But the continuity and complexity of streams can make it difficult to discern spatial structure, and data on individual variation spanning spatial scales are rare.
2. Our goal was to objectively resolve the scale of ecological and evolutionary processes affecting the salamander *Gyrinophilus porphyriticus* by testing for spatial structure in individual variation across a headwater stream network. We used 3 years of spatially explicit capture–mark–recapture data from four headwater streams in the Hubbard Brook Experimental Forest, New Hampshire, USA, to test for individual variation in survival at three scales: (a) among c. 2-km² watersheds, (b) in 500-m downstream and upstream reaches within watersheds and (c) in riffle and pool habitats along reaches. We also tested for corresponding spatial variation in individual body condition and morphology to gain insight on the causes and implications of variation in survival.
3. Survival of *G. porphyriticus* larvae was constant among watersheds, but differed by reach and habitat. Larval survival was higher in upstream reaches than downstream reaches, matching the distribution of predatory brook trout (*Salvelinus fontinalis*), which were restricted to downstream reaches. Larval survival was also higher in pools than riffles. Survival of *G. porphyriticus* adults was constant at all scales.
4. Larval body condition was higher in downstream reaches than upstream reaches. Both larvae and adults differed in morphology at the habitat scale: individuals in pools had longer limbs than individuals in riffles.
5. Negative covariation in larval survival and body condition at the reach scale suggests that there is a trade-off between fitness and proximate performance along streams. The surprising differences between habitats in survival and morphology show the potential for fine-scale ecology–evolution interactions in streams, potentially driven by differences in flow and gradient conditions in riffles and pools.
6. Our results suggest that the larval stage is key to understanding individual, population and community-level processes affecting *G. porphyriticus*. More broadly, this research provides a novel empirical link between traditional studies of fine-scale ecological complexity in streams and recent studies showing consistent spatial dynamics at the network scale. By documenting differences in survival, body

condition and morphology at reach and habitat scales, we hope this work shows the feasibility and value of spatially explicit approaches to species-level ecological and evolutionary questions in streams.

KEYWORDS

amphibian, fitness, morphology, salamander, spatial ecology

1 | INTRODUCTION

We now have access to diverse conceptual and empirical tools for exploring spatial processes affecting ecology and evolution (Hand, Lowe, Kovach, Muhlfeld, & Luikart, 2015; Hanski, Mononen, & Ovas-kainen, 2011; Holyoak, Leibold, & Holt, 2005). But to take advantage of these tools, researchers must have some understanding of the spatial structure of key ecological and evolutionary processes (Addicott et al., 1987; Wiens, 1989). These spatial boundaries are rarely discrete, whether due to the movement of individuals (Baxter, Fausch, & Saunders, 2005; Lenormand, 2002) or fluxes of energy and nutrients (Likens & Bormann, 1974; Marczak, Thompson, & Richardson, 2007). Nevertheless, research on spatial processes—whether observational or experimental (Cottenie & De Meester, 2004; Fitzpatrick, Gerberich, Kronenberger, Angeloni, & Funk, 2014)—is much more justifiable and interpretable when focal species, populations or communities are associated with distinct spatial units (e.g., ponds, fields, forest patches). Likewise, understanding spatial processes can be challenging without clear spatial delineations, leading to bias in the systems that are the focus of spatial studies (Hanski & Gilpin, 1997; Richardson, Urban, Bolnick, & Skelly, 2014) and in the interpretation of results (Hewitt, Thrush, Dayton, & Bonsdorff, 2007; Levin, 1992).

The continuity and environmental complexity of streams can make it particularly difficult to discern the spatial structure of ecological and evolutionary processes. Physical, chemical and biological heterogeneity occurs across scales in stream systems, from individual rocks in the streambed to entire watersheds (Likens & Bormann, 1995; Palmer, Swan, Nelson, Silver, & Alvestad, 2000; Schlosser, 1991; Stanford, Lorang, & Hauer, 2005). But, due to the lack of clear spatial delineations and other logistical constraints, most ecological and evolutionary research is limited to relatively fine spatial scales, leaving the true spatial scope of these processes unresolved (Cooper, Diehl, Kratz, & Sarnelle, 1998; Lowe, Likens & Power, 2006; Wine-miller, Flecker, & Hoeinghaus, 2010). Population genetic studies have been useful in this context, where the relative ease of collecting tissue samples has enabled researchers to test for hierarchical structure across spatial scales (Hughes, Schmidt, & Finn, 2009; Mullen, Woods, Schwartz, Sepulveda, & Lowe, 2010; Selkoe, Scribner, & Galindo, 2016). However, genetic structure may not match the structure of key ecological and evolutionary processes (Kokko et al., 2017; Lowe, Kovach, & Allendorf, 2017), reinforcing the need for alternative approaches to resolve the spatial structure of these processes.

To confront the challenging continuity and complexity of streams, researchers have developed conceptual models distinguishing key scales of spatial variability. Broadly, these models can be broken into three categories based on the scale proposed as most relevant to understanding ecological variation: watershed, reach and habitat (Figure 1). We know that interactions with upland terrestrial habitats affect ecological processes throughout entire tributaries (Bernhardt et al., 2005; Bormann & Likens, 1979; Richards, Johnson, & Host, 1996), creating ecological variation among hydrologically independent watersheds. At an intermediate scale, stream ecologists have long recognised that gradients in physical, chemical and biological conditions produce predictable ecological variation among reaches arrayed along stream channels—an observation at the core of the river continuum concept (Minshall et al., 1983; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). At the finest scale, hydrogeomorphic models view local flow and gradient conditions as key environmental variables, leading to predictable abiotic and biotic variation among bedform units within stream reaches (e.g., pools, runs, riffles, cascades; Frissell, Liss, Warren, & Hurley, 1986; Gordon, McMahon, & Finlayson, 1992; Hawkins et al., 1993; Montgomery & Buffington, 1997). Stream ecologists commonly refer to these bedform units as “habitats” (e.g., Bisson, Sullivan, & Nielsen, 1988; Iwata, 2007; Senay, Boisclair, & Peres-Neto, 2015).

These models have guided spatial analyses of stream ecosystem and community data (e.g., nutrient concentrations, species diversity; Resetarits, 1997; Brown & Swan, 2010; McGuire et al., 2014; Tonkin, Heino, & Altermatt, 2018). In contrast, our understanding the structure of spatial variation in individual attributes—whether within or among populations—remains weak, despite the importance of these individual-level data for resolving the mechanisms and implications of species-level ecological and evolutionary responses (Chaput-Bardy, Pays, Lode, & Secondi, 2007; Landguth et al., 2014; Letcher, Coombs, & Nislow, 2011). This is not to suggest that we lack evidence that ecological and evolutionary processes shape individual variation in streams, which is clearly not the case for fish (Fitzpatrick et al., 2014; Lively, Craddock, & Vrijenhoek, 1990; Travis et al., 2014; Vrijenhoek, 1989) and a few other taxa (Jackrel & Wootton, 2014; Storfer & Sih, 1998). In these studies, however, the scale of observation is imposed by researchers (e.g., focal pools distributed along a study reach), rather than by *a priori* analysis of the spatial structure of variation in individual attributes, leaving the spatial scope of inference unresolved (Levin, 1992; Messier, McGill, & Lechowicz, 2010).

Our goal was to objectively resolve the scale of ecological and evolutionary processes affecting the salamander *Gyrinophilus porphyriticus* by testing for spatial structure in survival across a headwater stream network. Specifically, we used 3 years of spatially explicit capture–mark–recapture data from four headwater streams to test for watershed, reach and habitat-scale variation in survival—a key component of fitness and fundamental index of ecological response. Much of our past work in this system has focused on dispersal by *G. porphyriticus*, but we have never attempted to determine the scale of environmental variation relevant to dispersal decisions (e.g., emigration, vagrancy, settlement; Ronce, 2007). The high spatial resolution and broad spatial scope of this data set created an opportunity to characterise the “fitness landscape” that governs these dispersal decisions and their consequences. For example, the scale of variation in survival is likely to affect emigration propensities (i.e., stay versus leave), dispersal distances and settlement probabilities, thereby also determining the scale(s) at which we might expect genetic and demographic effects of dispersal. Perhaps more importantly, we hoped to uncover the spatial structure of ecological and evolutionary processes that determine the fate of nondispersers, which represent the majority of individuals in our study populations (e.g., Lowe, 2003).

To gain insight on the causes and implications of spatial variation in individual survival, we also tested for spatial variation in (a) body condition and (b) body morphology. Correspondence of spatial

variation in body condition and survival would suggest that variation in survival is caused—at least in part—by factors affecting an individual's performance during its lifetime, as opposed to discrete sources of mortality (e.g., predation, floods), which may reduce survival without affecting individual performance. If mechanism(s) producing spatial variation in survival also contribute to morphological diversity, whether via plasticity and/or selection, we expected spatial structure of morphological variation to match that of survival.

2 | METHODS

2.1 | Study species and sites

Gyrinophilus porphyriticus belongs to the family Plethodontidae, the lungless salamanders, and is found in small, cool, well-oxygenated streams along the Appalachian uplift in the eastern United States (Petranka, 1998). Larvae are exclusively aquatic (Bruce, 1980); adults are mainly aquatic but can forage terrestrially at night (Deban & Marks, 2002; Degraaf & Rudis, 1990; Greene, Lowe, & Likens, 2008). During the day, larvae and adults are found in interstitial spaces among the larger substrate particles of the streambed. In the northern Appalachians, larvae range in size from 26 to 80 mm snout-to-vent length (SVL) and adults can reach 120 mm SVL (Lowe, 2003). The larval period lasts 3–5 years (Bruce, 1980), and adults can live to be 14 years (W. H. Lowe, unpublished data).

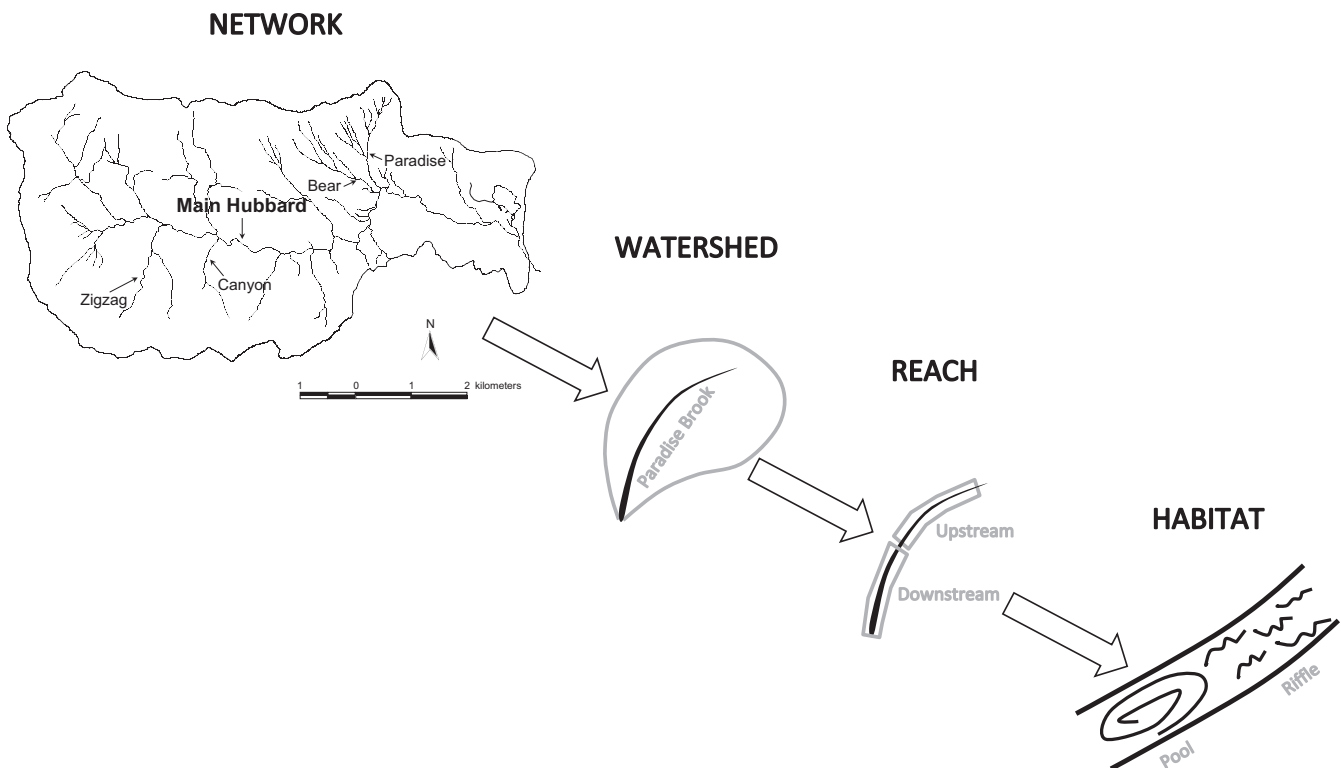


FIGURE 1 Four spatial scales emphasised in conceptual models of environmental heterogeneity in stream systems, and which guided our analysis of the spatial structure of individual variation in the stream salamander *Gyrinophilus porphyriticus*. We sampled across four watersheds in the Hubbard Brook stream network, New Hampshire, USA. Within each watershed, we sampled downstream and upstream reaches and characterised the habitat (riffle, pool) where each individual was encountered

This research took place in four hydrologically independent first-order streams in the Hubbard Brook Experimental Forest (HBEF), in the White Mountains of central New Hampshire (43°56'N, 71°45'W). All four streams flow into the mainstem of Hubbard Brook (Figure 1), a tributary of the Pemigewasset River. Typical of headwater streams in New Hampshire, the study streams have low conductivity (12.0–15.0 μS), slight acidity (pH of 5.0–6.0), high dissolved oxygen content (80%–90% saturation) and moderate midday summer temperatures (13.0–17.0°C). Hydrology of HBEF streams is characterised 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 August and September. The study streams are high gradient mountain headwaters with cobble, boulder and bedrock substrate. The dominant tree species in forests surrounding these streams were *Acer saccharum*, *Fagus grandifolia*, *Betula alleghaniensis*, *Picea rubens*, *Abies balsamea*, *B. papyrifera*.

2.2 | Study design

To resolve the spatial scale of variation in survival, body condition and body morphology in *G. porphyriticus*, we designed our sampling regime to encompass three spatial scales: watershed, reach and habitat (Figure 1). To assess watershed-scale variation, we conducted spatially explicit capture–mark–recapture surveys throughout the four study streams (Bear Brook, Canyon Brook, Paradise Brook, Zigzag Brook) over 3 years (2012–2014). Each stream was divided into two 500-m-long reaches (downstream and upstream). Locations of these reaches along stream channels were selected to encompass as much longitudinal variation in environmental conditions as possible, given other sampling constraints at the HBEF. Downstream reaches started at the confluence with Hubbard Brook and weirs set the upstream end of the upstream reaches. Because long-term water quality data are collected at the weirs, sampling is restricted upstream of the weirs (Bormann & Likens, 1979). 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.

To assess habitat-scale variation in salamander survival, condition and morphology, we categorised the habitat where each salamander was initially encountered during surveys. Habitat type was based on flow and gradient conditions 0.5 m upstream and downstream of the salamander's location and was categorised as riffle or pool (modified from Montgomery & Buffington, 1998). Riffles were defined by moderate gradient and turbulent flow. Pools were defined by low gradient, circulating flow and evidence of obstruction or constriction at the downstream end of the pool.

2.3 | Survey methods

Capture–mark–recapture (CMR) surveys were conducted mid-June through mid-September of 2012–2014. Each stream was surveyed nine times each field season, for a total of 27 surveys per stream over the 3-year study period. We conducted three surveys of each

stream during three two-week periods distributed evenly throughout the field season; streams were surveyed in a random order within each of these two-week sampling periods. In each survey, a constant search effort was maintained by turning one haphazardly selected cover object per metre of stream length. Salamanders were individually marked with visible implant elastomer (Northwest Marine Technologies, Washington, USA; Grant, 2008). All *G. porphyriticus* individuals were photographed to quantify body morphology. Animals were placed on a level stage with the camera approximately 20 cm above the stage, which allowed us to capture the entire dorsal surface of the animal in the photograph, along with a ruler. The ruler was used to calibrate morphological measurements in millimetre. We used these photographs to measure head, trunk and leg morphology, as well as SVL, the standard measure of body size in amphibians (Heyer, Donnelly, McDiarmid, Hayek, & Foster, 1994). We measured body mass in the field to quantify body condition (Schulte-Hostedde, Zinner, Millar, & Hickling, 2005).

We also surveyed to determine the distribution of brook trout (*S. fontinalis*) in the study streams. Brook trout occur within the HBEF (Warren, Likens, Buso, & Kraft, 2008) and are known to prey on *G. porphyriticus* larvae (Lowe, Nislow, & Bolger, 2004; Resetarits, 1991, 1995). Therefore, we expected that brook trout distribution could strongly affect *G. porphyriticus* survival, body condition and possibly body morphology (Benard, 2004). Between mid-June and mid-August of 2013, the four study streams were trapped once every 10 days, for a total of three trapping sessions per stream. In each fish survey, vinyl-coated minnow traps (Frabill, Plano, IL) were placed every 25 m along downstream and upstream reaches, ensuring that trapping effort was equal across streams. Traps were placed in both riffles and pools and open for 18–20 hr. All fish received a unique tag behind the eye with visual elastomer so that we could accurately count the number of individuals captured.

2.4 | Survival estimation

We used multistate CMR models to test for watershed, reach and habitat-scale variation in individual survival probabilities. Monthly survival (S) and recapture (p) probabilities of *G. porphyriticus* larvae and adults, and transition probabilities from the larval to the adult stage ($\psi^{\text{larva} \rightarrow \text{adult}}$) were estimated with a multistate model using Program MARK (Lebreton, Nichols, Barker, Pradel, & Spindelov, 2009; White & Burnham, 1999). For this analysis, the three surveys in each two-week survey session were collapsed into a single observation for each month of the field season (e.g., mid-June to mid-July, etc.). Program MARK accommodates variable time intervals between successive surveys (e.g., 1 month during the field season, 10 months between field seasons), so we were able to include all 3 years of data in CMR models. This approach allowed us to derive monthly parameter estimates and, relative to models where all 27 surveys were included, increased the accuracy and precision of parameters of interest (e.g., Grant, Nichols, Lowe, & Fagan, 2010).

Survival probability represents the probability that an animal alive at time t in one state (i.e., life-history stage) will be alive at time

$t + 1$, independent of state at $t + 1$. With two states, the transition probability is the conditional probability that an animal in one state at time t will be in the other state at $t + 1$, given that the animal is alive at $t + 1$. Recapture probability is the probability that a marked animal at risk of capture at time t is captured at t , conditional on being alive and available for recapture.

Estimates of survival probability confound mortality with permanent emigration from the population. We assumed that weirs immediately above upstream reaches would prevent most upstream emigration, and movement data from the study streams supported this assumption (B. R. Addis, unpublished data). We also assumed that downstream emigration into the fifth-order Hubbard Brook was minimal due to the dramatic habitat change below the confluence, and previous surveys where no *G. porphyriticus* individuals were found in the mainstem. Extensive overland dispersal is unlikely considering the highly aquatic habits and morphology of *G. porphyriticus* adults. Finally, we have shown significant genetic divergence among streams in the HBEF (Lowe, Likens, McPeck, & Buso, 2006), suggesting that rates of immigration and emigration are low, and increasing our confidence that survival estimates were not heavily biased by emigration.

We first used model selection to determine a parsimonious structure of recapture probabilities (p^{larva} , p^{adult}) and transitions from the larval to adult stage ($\psi^{\text{larva} \rightarrow \text{adult}}$), while retaining a consistent structure of apparent survival (Grant et al., 2010; Lebreton, Burnham, Clobert, & Anderson, 1992). We modelled recapture probabilities as constant or variable by time (month), watershed and time \times watershed. This candidate set of models was justified by variation in stream flow that could cause recapture probabilities to vary over time (e.g., as salamanders change patterns of habitat use to avoid exposure to high flows), and differences in geomorphology among streams that might affect recapture probabilities directly and via interactions with temporal variation in flow (Bailey, Simons, & Pollock, 2004). We modelled $\psi^{\text{larva} \rightarrow \text{adult}}$ as constant or variable by time, watershed and time \times watershed. These candidate models were based on a previous study documenting temporal variation in $\psi^{\text{larva} \rightarrow \text{adult}}$ in a stream outside of the HBEF (Lowe, 2012). Because transitions from the adult to larval stage are impossible, we fixed $\psi^{\text{adult} \rightarrow \text{larva}}$ at 0. The four watersheds were represented as attribute groups in Program MARK (Cooch & White, 2007).

Using the most parsimonious model structure for recapture and transition probabilities, we then tested for spatial structure in individual survival probabilities. This analysis was conducted in stages corresponding to the three spatial scales of variation. First, we modelled survival as constant or variable at the watershed scale, again representing the four study watersheds as attribute groups. Starting with the most parsimonious models of watershed-scale variation, we then modelled survival as constant or variable at the reach scale (downstream versus upstream) and as constant or variable at the habitat scale (riffle versus pool). Reach and habitat were modelled as individual covariates so that we could retain watershed groups where necessary (Pollock et al., 2002).

This approach allowed for spatially nested variation in survival, such as variation among watersheds and between habitat types within watersheds. It is also important to note that these multistate models estimated survival for larvae and adults separately, providing valuable insight on variation in survival over the life history, but also increasing model parameterisation. We did not test for temporal variation in survival or interactions between spatial scales because these additional levels of model parameterisation compromised estimation of our focal parameters. For example, the watershed \times reach interaction would have required 16 estimates of survival, in addition to p and ψ estimates.

We used Akaike's information criterion, or AIC (Akaike, 1973), to identify models that best represented the data with as few parameters as possible. Models were ranked by second-order AIC (AIC_c) differences (ΔAIC_c ; Burnham & Anderson, 2002). Relative likelihood of each model in the candidate set was then estimated with AIC_c weights (Buckland, Burnham, & Augustin, 1997). Prior to model selection, we used program U-CARE (Choquet, Reboulet, Lebreton, Gimenez, & Pradel, 2003) to perform goodness-of-fit tests on the saturated multistate model. Cooch and White (2007) suggest that confidence in the best-fitting multistate model should increase if the model retains its rank across a range of values for the variance inflation factor (\hat{c}). Therefore, to further assess model fit, we tested the rank stability of the best-fitting multistate models by entering \hat{c} values between 1.0 and 4.0 in Program MARK. Lebreton et al. (1992) suggest that $\hat{c} \leq 3.0$ is a good general criterion for assessing adequacy of model fit.

2.5 | Body condition and morphology

We used log-transformed SVL and mass measurements from all individuals to calculate size-corrected mass (log mg) with ordinary least squares (OLS) linear regression. Size-corrected mass is a common index of body condition (Green, 2001; Jakob, Marshall, & Uetz, 1996; Schulte-Hostedde et al., 2005). The use of OLS linear regression was justified by the lack of statistical support for more complex models of the functional relationship between log SVL and log mass, and by the lack of correlation between log SVL and residuals from these regressions ($r < 0.01$; Green, 2001).

To quantify body morphology, we used measurements of head, trunk and leg morphology to generate size-adjusted morphological characters with principal component analysis (PCA). We extracted seven principal components from the larval and adult trait covariance matrices, which were comprised of log-transformed SVL, head length and width, trunk length and width, humerus length and femur length. The first principal components (PC1) represented generalised size because SVL was positively correlated with all morphological measurements and was expected to account for the highest proportion of overall morphological variation. The remaining six principal components were size-adjusted morphological characters (Adams & Beachy, 2001; Bookstein, 1989; Jungers, Falsetti, & Wall, 1995). We used the second principal components (PC2) for analyses.

2.6 | Statistical analyses

Support for alternative scales of variation in individual survival was assessed based on CMR model ranking. Specifically, ranking showed whether models with variation in survival at a particular scale (e.g., between habitat types) fit the data better than those with constant survival at that scale. With the top ranked models, we then derived estimates of apparent survival probability (and *SE*) for each group (e.g., pools versus riffles).

Our *a priori* objective was to use data on salamander body condition and morphology to gain insight on the causes and implications of spatial variation in survival, rather than describing spatial variation in condition and morphology independently. Therefore, we used analysis of variance (ANOVA) to test how body condition and morphology varied at the spatial scales identified as significant in the analysis of survival. Scales that did not explain spatial variation in survival were included as random effects in these ANOVA models, thereby accounting for variation in condition and morphology that was unrelated to variation in survival. We also tested for interactions among main effects in these ANOVA models. Sample sizes for body condition and morphology analyses differed because mass measurements were not collected for 37 individuals and 65 digital photos were unusable for morphology measurements.

3 | RESULTS

Over the 3-year study period, we captured 729 *G. porphyriticus* in Bear Brook, 390 in Canyon Brook, 678 in Paradise Brook and 375 in Zigzag Brook. Ratios of larvae to adults in the four streams were 2.35:1, 2.16:1, 2.26:1 and 1.74:1, respectively. We captured brook trout throughout the downstream reaches of all four streams; no brook trout were captured in upstream reaches. Across all sampling events in the downstream reaches of Bear, Canyon, Paradise and Zigzag Brooks, we caught 17, 10, 15 and 16 brook trout, respectively.

3.1 | Survival

In the best-fitting model, recapture probability for larvae (p^{larva}) varied by watershed, recapture probability for adults (p^{adult}) varied by time, and transition probability from the larval to the adult stage ($\psi^{\text{larva} \rightarrow \text{adult}}$) varied by watershed (Table 1). Only parameterisation of $\psi^{\text{larva} \rightarrow \text{adult}}$ differed in the three top models, which had a combined AIC_c weight of >0.99 . This gave us high confidence in recapture probability parameterisation.

Model ranking indicated that apparent survival probabilities of larvae and adults (S^{larva} , S^{adult}) were constant across watersheds (Table 2a). There was some support for the model with variation in larval survival among watersheds ($\Delta AIC_c = 0.48$). However, 95% confidence intervals of larval survival estimates for the four watersheds were broadly overlapping, which increased our confidence that the top model—with no variation in survival among watersheds—was the most accurate and conservative. Model ranking indicated

that larval survival differed by reach (upstream $>$ downstream) and by habitat (pool $>$ riffle; Tables 2b,c; Figure 2a). There was no support for variation in adult survival by reach or habitat (Tables 2b,c; Figure 2a). None of the five lack-of-fit tests performed on the saturated model with program U-CARE were significant, indicating that the multistate framework was appropriate for the data set (Choquet et al., 2003), and all best-fitting models retained their ranks up to $\hat{c} = 4.0$.

3.2 | Body condition

The ANOVA of larval body condition showed a significant effect of reach (Table 3), where larvae had higher body condition in downstream reaches than upstream reaches (Figure 2b). There was no effect of habitat on larval body condition, and the interaction of reach and habitat was also not significant. The ANOVA of adult body condition showed no effect of reach, habitat, or the interaction of reach and habitat (Table 3). Because CMR models indicated that survival did not differ among watersheds, watershed was included as a random effect in ANOVAs of larval and adult body condition.

3.3 | Body morphology

Head, trunk and leg measurements of *G. porphyriticus* larvae and adults were positively correlated with SVL ($r = 0.54\text{--}0.96$). In separate analyses of larvae and adults, first principal components were positively weighted by all seven variables, accounting for 81.7% of total variation in larval body morphology and 74.4% of total variation in adult body morphology. Second principal components (PC2) accounted for 8.7% of total variation in larval body morphology and 11.8% of total variation in adult body morphology. Each of the remaining five principal components accounted for $\leq 5.7\%$ and 4.5% of variation in larval and adult morphology, respectively. In both larvae and adults, PC2s were negatively weighted by head length, head width, trunk length and trunk width, and positively weighted by humerus length and femur length. However, absolute values of loadings for head length, head width, trunk length and trunk width were ≤ 0.22 , whereas loadings for humerus and femur lengths were ≥ 0.44 , indicating that PC2 values predominantly reflected variation in limb lengths.

ANOVAs of larval and adult morphology PC2s showed no effect of reach, significant effects of habitat, and no effect of the reach \times habitat interaction (Table 4). In both larvae and adults, PC2 values were greater in pools than riffles, indicating that individuals in pools had relatively longer humerus and femur lengths than individuals in riffles (Figure 2c). Here again, because CMR models indicated that survival did not differ among watersheds, watershed was included as a random effect in morphology ANOVAs.

4 | DISCUSSION

This study provides an empirical link between traditional studies of fine-scale ecological complexity in streams and recent evidence of

TABLE 1 Multistate capture–mark–recapture models of monthly larval and adult recapture probabilities (p^{larva} , p^{adult}) and larva→adult transition probability ($\psi^{\text{larva} \rightarrow \text{adult}}$) for *Gyrinophilus porphyriticus* in the four study streams, based on data from 2012–2014. We compared 64 candidate models and show the five best-fitting models here (AIC weights > 0.00002). Larval and adult survival probabilities (S^{larva} , S^{adult}) were held constant for this analysis

Model	AIC _c	ΔAIC _c	AIC _c wt	K
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(w)$	3456.00	0.00	0.58	19
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(\cdot)$	3456.87	0.88	0.38	16
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(t)$	3461.50	5.50	0.04	23
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(w), p^{\text{adult}}(w \times t), \psi^{\text{larva} \rightarrow \text{adult}}(\cdot)$	3473.52	17.52	0.00	40
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(t), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(\cdot)$	3476.37	20.38	0.00	20

Notes. Second-order Akaike's information criterion values (AIC_c), AIC_c differences (ΔAIC_c), AIC_c weights (AIC_c wt) and number of estimable parameters (K) are provided for all models. Parameterization for S, p and ψ is in parentheses: “·” = constant by time (month) and watershed, “w” = variation by watershed, “t” = variation by time.

TABLE 2 Multistate capture–mark–recapture models assessing variation in monthly survival probabilities of *Gyrinophilus porphyriticus* larvae and adults (S^{larva} , S^{adult}) at the watershed scale (a), reach scale (b) and habitat scale (c). Recapture probabilities (p^{larva} , p^{adult}) and larva→adult transition probability ($\psi^{\text{larva} \rightarrow \text{adult}}$) were parameterized based on results in Table 1

Model	AIC _c	ΔAIC _c	AIC _c wt	K
(a)				
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(w)$	3456.00	0.00	0.40	19
$S^{\text{larva}}(w), S^{\text{adult}}(\cdot), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(w)$	3456.48	0.48	0.31	22
$S^{\text{larva}}(w), S^{\text{adult}}(w), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(w)$	3458.00	2.01	0.15	25
$S^{\text{larva}}(\cdot), S^{\text{adult}}(w), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(w)$	3458.06	2.06	0.14	22
(b)				
$S^{\text{larva}}(r), S^{\text{adult}}(\cdot), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(w)$	3451.18	0.00	0.65	20
$S^{\text{larva}}(r), S^{\text{adult}}(r), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(w)$	3453.00	1.80	0.26	21
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(w)$	3456.00	4.81	0.06	19
$S^{\text{larva}}(\cdot), S^{\text{adult}}(r), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(w)$	3457.56	6.38	0.03	20
(c)				
$S^{\text{larva}}(h), S^{\text{adult}}(\cdot), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(w)$	3451.06	0.00	0.64	20
$S^{\text{larva}}(h), S^{\text{adult}}(h), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(w)$	3452.72	1.66	0.28	21
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(w)$	3456.00	4.94	0.05	19
$S^{\text{larva}}(\cdot), S^{\text{adult}}(h), p^{\text{larva}}(w), p^{\text{adult}}(t), \psi^{\text{larva} \rightarrow \text{adult}}(w)$	3457.37	6.31	0.03	20

Notes. Second-order Akaike's information criterion values (AIC_c), AIC_c differences (ΔAIC_c), AIC_c weights (AIC_c wt) and number of estimable parameters (K) are provided for all models. Parameterization for S, p and ψ is in parentheses: “·” = constant by time (month) and across all spatial scales, “w” = variation by watershed, “r” = variation by reach, “h” = variation by habitat.

consistent spatial processes at the network scale. At local scales, we know that streams are highly heterogeneous in abiotic and biotic conditions, suggesting that spatial processes affecting stream organisms are likely to be context-specific (Downes, Lake, & Schreiber, 1995; Fausch, Torgersen, Baxter, & Li, 2002; Lowe, Likens, & Power, 2006). In the last decade, however, theory and empirical research has shown that the dendritic structure of stream networks—a universal attribute of these systems—can impose consistent spatial constraints on populations, communities and ecosystem processes (e.g., Altermatt, Seymour, & Martinez, 2013; Brown & Swan, 2010; McGuire et al., 2014; Munepeperkul et al., 2008). The generality of these network-scale dynamics is, in theory, dictated by the branching structure of stream networks, irrespective of fine-scale spatial complexity within networks (i.e., along individual channels; Fagan, 2002;

Grant, Lowe, & Fagan, 2007; Peterson et al., 2013). Our study bridges these two lines of research by showing consistent spatial variation in survival, body condition and morphology of salamanders across a network of interconnected watersheds (Figure 1), thereby highlighting the potential for broadly informative, multiscale understanding of the spatial ecology of streams.

We found reach and habitat-scale structure in salamander survival, body condition and morphology across four watersheds in the Hubbard Brook network. Our analysis was based on existing models of spatial variation in streams (Figure 1; Bormann & Likens, 1979; Vannote et al., 1980; Hawkins et al., 1993). Until now, however, the lack of individual-level data with sufficiently high spatial resolution and extent has precluded explicit tests of these alternative models. Based on a unique, multiyear CMR data set spanning watershed,

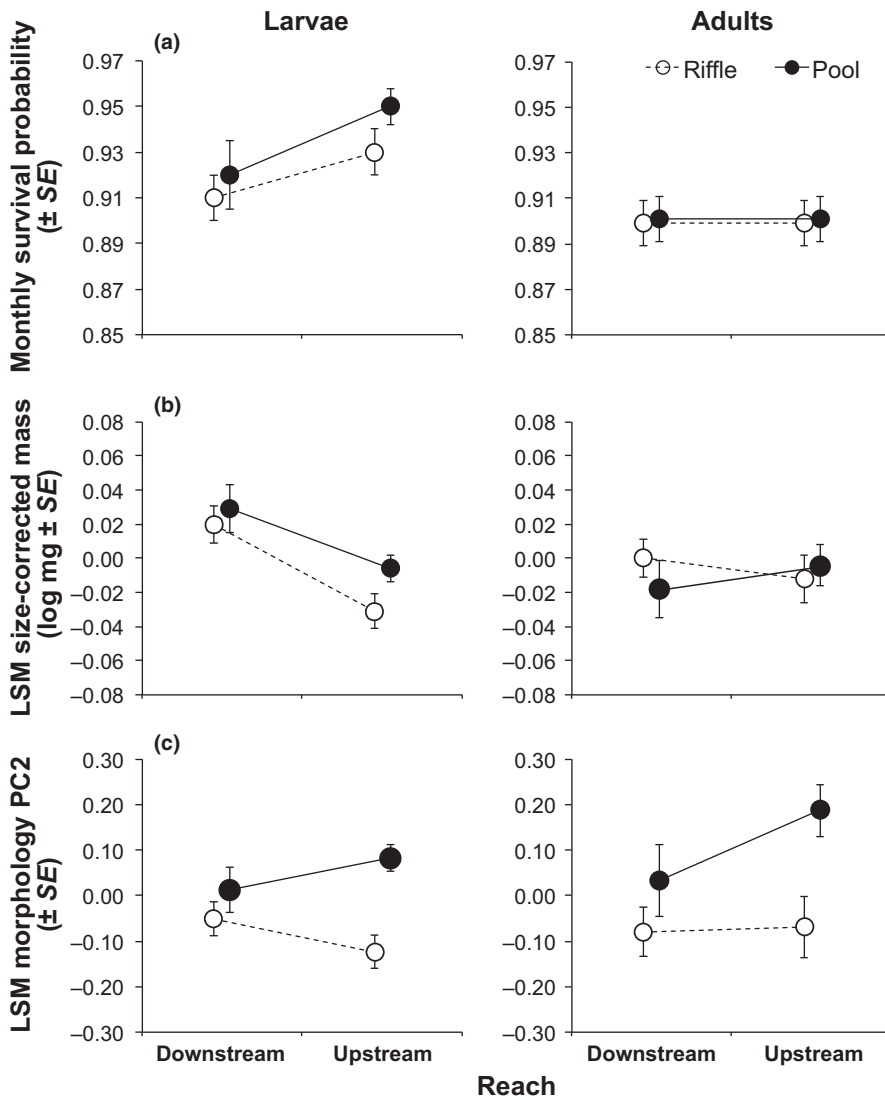


FIGURE 2 Reach and habitat-scale variation in monthly survival probability (a), body condition (b) and morphology (c) of *Gyrinophilus porphyriticus* larvae (left column) and adults (right column) in four study streams in the Hubbard Brook Experimental Forest, New Hampshire, USA. Survival probabilities are from best-fit capture–mark–recapture models (Table 2); body condition and morphology data are least squares means (LSM) from ANOVA models (Tables 3 and 4)

reach and habitat scales, our results provide an empirical framework for understanding spatial processes affecting *G. porphyriticus* fitness, population and community dynamics, habitat selection and phenotypic variation (Messier et al., 2010; Violle et al., 2012). Perhaps more importantly, these results show that consistent spatial structure can emerge from the continuity of stream systems, independent of perceptual, logistical and other biases that we researchers may impose (Frissell et al., 1986; Levin, 1992).

Survival probability of *G. porphyriticus* larvae was lower in downstream reaches than in upstream reaches (Figure 2a), matching the distribution of brook trout, which were restricted to downstream reaches in all four streams. Negative effects of brook trout on survival of *G. porphyriticus* larvae are well documented in experimental studies (Lowe et al., 2004; Resetarits, 1991, 1995). In observational studies, Resetarits (1997) found that abundance of *G. porphyriticus* larvae was reduced downstream of a brook trout barrier in a Virginia stream, and larval abundance declined with increasing brook trout abundance across 15 New Hampshire streams (Lowe et al., 2004). Our results link these experimental and observational studies by

showing an association between brook trout distribution and larval survival across multiple streams. We found no difference between reaches in survival of *G. porphyriticus* adults, consistent with results from surveys throughout New Hampshire showing no relationship between adult abundance and brook trout abundance (Lowe et al., 2004). These field-based estimates of larval and adult survival are, therefore, a new line of evidence for the importance of size-structured interactions in allowing *G. porphyriticus* to persist with brook trout (Resetarits, 1995). It is important to acknowledge, however, that we cannot isolate the effects of brook trout from other biotic and abiotic conditions that may differ between downstream and upstream reaches.

Body condition of *G. porphyriticus* larvae was higher in downstream reaches than upstream reaches, opposite to the pattern of survival (Figure 2b). This suggests that increased survival in upstream reaches—likely due to the absence of predatory brook trout—comes at the cost of other biotic or abiotic conditions that reduce individual performance. We found the same difference in body condition between downstream and upstream reaches in a stream

TABLE 3 Results of ANOVAs testing for differences in the body condition of larval and adult *Gyrinophilus porphyriticus* in downstream and upstream reaches, and in riffle and pool habitats. Watershed was included as a random effect in both ANOVA models

Source	df	MS	F	p
Larvae				
Reach	1	0.71	15.62	<0.0001
Habitat	1	0.12	2.58	0.11
Reach × Habitat	1	0.03	0.57	0.45
Error	1,878	0.05		
Adults				
Reach	1	0.00005	0.002	0.97
Habitat	1	0.005	0.14	0.71
Reach × Habitat	1	0.035	0.98	0.32
Error	851	0.04		

TABLE 4 Results of ANOVAs testing for differences in the morphology of larval and adult *Gyrinophilus porphyriticus* between downstream and upstream reaches, and between pool and riffle habitats. Watershed was included as a random effect in both ANOVA models

Source	df	MS	F	p
Larvae				
Reach	1	0.005	0.008	0.93
Habitat	1	7.09	11.85	<0.0006
Reach × Habitat	1	2.17	3.63	0.06
Error	1,858	0.60		
Adults				
Reach	1	1.27	1.59	0.21
Habitat	1	6.68	8.37	0.004
Reach × Habitat	1	0.95	1.19	0.28
Error	843	0.80		

approximately 120 km northeast of the HBEF (Lowe, 2003), pointing to a consistent attribute of headwater streams as the underlying driver. Gradients in water chemistry and temperature are highly variable along the HBEF streams, both in the range and spatial scale of variation (Likens & Buso, 2006; McGuire et al., 2014), suggesting that these conditions are not the cause of reduced body condition in upstream reaches. In contrast, all streams have gradients in discharge that lead to lower base flows and more frequent drying in upstream reaches, potentially reducing salamander performance by increasing the risk of desiccation or reducing invertebrate prey availability (Datry, Bonada, & Boulton, 2017; Duellman & Trueb, 1986). We are currently processing benthic invertebrate samples to assess changes in prey availability along these channels and will use corticosterone assays to compare physiological stress in downstream and upstream reaches (Becker, Breedlove, Crews, & McCarthy, 2002; Romero & Wikelski, 2001).

Perhaps our most surprising results were differences in *G. porphyriticus* survival and morphology between riffle and pool habitats (Figure 2c). The difference in survival was restricted to larvae (pool > riffle; Table 2c) and appears to be greater in upstream reaches than downstream reaches (Figure 2a). Both stages showed the same morphological differences between habitat types (Table 4). Specifically, individuals in pools had longer limbs than individuals in riffles, with a trend of greater morphological divergence in upstream reaches than downstream reaches (Figure 2c). The consistency of these morphological differences in the two life-history stages suggests that the underlying mechanism acts at the larval stage, although there is the potential for reinforcement at the adult stage (Ebenman & Persson, 1988; Van Allen, Briggs, McCoy, & Vonesh, 2010; Wilbur, 1980). More generally, these results show that consistent variation in fitness and phenotype can occur at very fine spatial scales along headwater streams (c. 1 m of channel length).

We do not know the genetic versus environmental contributions to these habitat-scale morphological differences; nevertheless, our results suggest that selection regimes of riffles and pools differ greatly. Hydrogeomorphic models emphasise the importance of flow and gradient conditions in structuring stream habitat (Frissell et al., 1986; Gordon et al., 1992; Hawkins et al., 1993), and these conditions are shown to affect demographic rates, morphology and ecological interactions in stream organisms (e.g., Cobb, Galloway, & Flannagan, 1992; Imre, Mclaughlin, & Noakes, 2002; Senay et al., 2015). Likewise, there are numerous direct and indirect pathways by which flow and gradient conditions could produce variation in *G. porphyriticus* survival and morphology. It is notable, however, that *G. porphyriticus* limb lengths (longer in pools, shorter in riffles) appear well matched to flow conditions in the two habitat types: nonturbulent, circulating flow in pools; turbulent flow and high maximum water velocities in riffles (Montgomery & Buffington, 1998; Vogel, 1994). Flume experiments and biomechanical models show that drag increases significantly with limb length in *G. porphyriticus* individuals (B.R. Addis, unpublished data). The energetic cost of longer limbs is, therefore, likely to be greater in riffles than pools, whereas the locomotory benefits of long limbs may be greater in pools than riffles (e.g., for walking under water and terrestrially; Ashley-Ross & Bechtel, 2004; Pontzer, 2007).

Movement of *G. porphyriticus* individuals along the stream channel could contribute to habitat-scale morphological divergence in two (nonexclusive) ways. If most individuals remain in the same habitat over their lifetimes, it would increase the potential for morphological differences to be maintained by local adaptation or plasticity (Endler, 1986; Ghalambor, McKay, Carroll, & Reznick, 2007; Richardson et al., 2014). Alternatively, individuals may self-sort into the two habitat types based on morphological phenotype, producing the same pattern of divergence without a direct effect of habitat conditions on morphology (i.e., habitat matching; Edelaar, Siepielski, & Clobert, 2008; Edelaar, Jovani, & Gomez-Mestre, 2017). Data on *G. porphyriticus* movement from previous studies show that the majority of individuals remain within 3 m of their initial capture location (Lowe, 2003). This scale of movement would

allow for transitions between habitat types, and longer limbs have been linked to dispersal in this species (Lowe & Mcpeek, 2012), supporting the self-sorting hypothesis. However, strong selection for habitat-specific phenotypes could produce the same morphological difference, even with random movement of individuals between habitat types (Fitzpatrick et al., 2014). To isolate these mechanisms, future studies will test for effects of morphology on individual survival within pools and riffles, and on movement between habitat types.

We hope this work helps to advance the broader discipline of stream ecology by encouraging other researchers to approach the challenge of spatial scale more explicitly, such as by assessing the scale of variation in response variables before initiating more focused, mechanistic research. Mechanistic studies of ecology and evolution are invaluable, but the scope of inference of these studies increases dramatically when results are placed within an explicit spatial framework (Hewitt et al., 2007; Levin, 1992). In our study system, this analysis provided critical information on the spatial structure of ecological and evolutionary processes affecting *G. porphyriticus*. We now know that ecological variation along channels (e.g., occurrence of predatory fish, availability of invertebrate prey) affects larval survival and body condition—a proximate index of individual performance. This reach-scale structure is likely to mediate population dynamics within the watershed and fitness consequences of long-distance dispersal (Anderson, Nisbet, Diehl, & Cooper, 2005; Labbe & Fausch, 2000; Melbourne & Chesson, 2005). Habitat-scale structure in *G. porphyriticus* survival and morphology shows the potential for very localised ecology–evolution interactions, as well as the spatial context of short-distance movement (Fitzpatrick et al., 2014; Richardson et al., 2014; Storfer & Sih, 1998). Independent of this insight on spatial structure, we also have strong evidence that larvae represent the critical life-history stage for understanding individual, population and community-level processes affecting *G. porphyriticus*.

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