Received: 11 March 2022 | Revised: 23 November 2022 | Accepted: 1 December 2022

DOI: 10.1002/ecy.3991

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Source–sink dynamics within a complex life history

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Funding information
National Science Foundation, Grant/Award Numbers: DEB-1637685, DEB-1655653, DEB-1050459, DEB-1114804

Handling Editor: Mark C. Urban

Abstract

Source–sink patch dynamics occur when movement from sources stabilizes sinks by compensating for low local vital rates. The mechanisms underlying source–sink dynamics may be complicated in species that undergo transitions between discrete life stages, particularly when stages have overlapping habitat requirements and similar movement abilities. In these species, for example, the demographic effects of movement by one stage may augment or offset the effects of movement by another stage. We used a stream salamander system to investigate patch dynamics within this form of complex life history. Specifically, we tested the hypothesis that the salamander *Gyrinophilus porphyriticus* experiences source–sink dynamics in riffles and pools, the dominant geomorphic patch types in headwater streams. We estimated stage-specific survival probabilities in riffles and pools and stage-specific movement probabilities between the two patch types using 8 years of capture–recapture data on 4491 individuals, including premetamorphic larvae and postmetamorphic adults. We then incorporated survival and movement probabilities into a stage-structured, two-patch model to determine the demographic interactions between riffles and pools. Monthly survival probabilities of both stages were higher in pools than in riffles. Larvae were more likely to move from riffles to pools, but adults were more likely to move from pools to riffles, despite experiencing much lower survival in riffles. In simulations, eliminating interpatch movements by both stages indicated that riffles are sinks that rely on immigration from pools for stability. Allowing only larvae to move stabilized both patch types, but allowing only adults to move destabilized pools due to the demographic cost of adult emigration. These results indicated that larval movement not only stabilizes riffles, but also offsets the destabilizing effects of maladaptive adult movement. Similar patch dynamics may emerge in any structured population in which movement and local vital rates differ by age, size, or stage. Addressing these forms of internal demographic structure in patch dynamics analyses will help to refine and advance general understanding of spatial ecology.

KEYWORDS
amphibian, capture–mark–recapture, geomorphology, life history, movement ecology, salamander, stream, survival

INTRODUCTION

Patch dynamics are a product of variation in local demographic rates and interpatch movement probabilities (Harrison, 1991; Levin et al., 2012; Pulliam, 1988). Stable patch dynamics may result from many combinations of these parameters, but we often reduce this complexity by categorizing patches as sources or sinks. In temporally stable environments, sources are patches that maintain stable populations and produce emigrants without relying on immigration, whereas sinks are patches that rely on immigration from sources for persistence (Boughton, 1999; Dias, 1996). Sources and sinks can, therefore, be identified based on spatial variation in local demographic rates (i.e., births and deaths), or—for greater accuracy—by removing the demographic effects of movement (i.e., immigration and emigration) and assessing patch stability (Watkinson & Sutherland, 1995).

Stable source–sink dynamics occur when immigration from sources is sufficient to maintain species occurrence in sinks. But source–sink dynamics are also characterized by maladaptive habitat selection because, on average, movement into sinks reduces individual fitness relative to fitness in sources (Delibes et al., 2001; Kristan, 2003; Remeš, 2000). These maladaptive movements can be maintained by density- or trait-mediated interactions within sources that promote emigration (Harman et al., 2020; Severns & Breed, 2018), or by habitat characteristics that lure individuals into sinks, despite fitness costs (Hale & Swearer, 2016; Schlaepfer et al., 2002). Without these mechanisms, evolution should act to eliminate movement from sources to sinks, maximizing individual fitness and population growth in sources (McPeek & Holt, 1992; Wilson, 2001).

Generally, the same expectations should apply to source–sink dynamics in species with complex life histories that include transitions between discrete life stages. In animals, these life-stage transitions often occur at metamorphosis, accompanied by changes in habitat and mobility that may be dramatic, resulting in stage-specific habitat requirements and capacities for habitat selection (Lowe et al., 2021; Wilbur, 1980). In many metamorphic species, therefore, an individual source or sink is a patch that encompasses the habitat requirements of all stages, but patch dynamics are driven by the stage with the mobility required to move among these patches (Figure 1a). For example, in insects with aquatic larvae and short-lived aerial adults, patches are defined by aquatic habitat structure (e.g., ponds or lakes), and sinks are maintained by the movements of postmetamorphic adults (Caudill, 2003; Harabiš & Dolný, 2012; Resetarits et al., 2019). Mobile, terrestrial adults play a similar role in the patch dynamics of pond-breeding amphibians with aquatic larvae (Cayuela et al., 2020). In these species, however, individual patches must include both aquatic and terrestrial habitat components to meet the habitat requirements of larvae and adults (e.g., a pond surrounded by a terrestrial buffer; Petranka et al., 2004; Semlitsch, 2000).

The behavioral and demographic mechanisms underlying patch dynamics may be more complicated when life stages have overlapping habitat requirements and similar movement abilities, which is the case for many metamorphic vertebrates and invertebrates (Montgomery et al., 2001; Resh & Rosenberg, 1984; Wilbur, 1980). In these species, habitat-selection behaviors may differ among stages, and may be independent of fitness consequences for other stages (i.e., variation in local, stage-specific vital rates). Consequently, maladaptive habitat selection by one stage

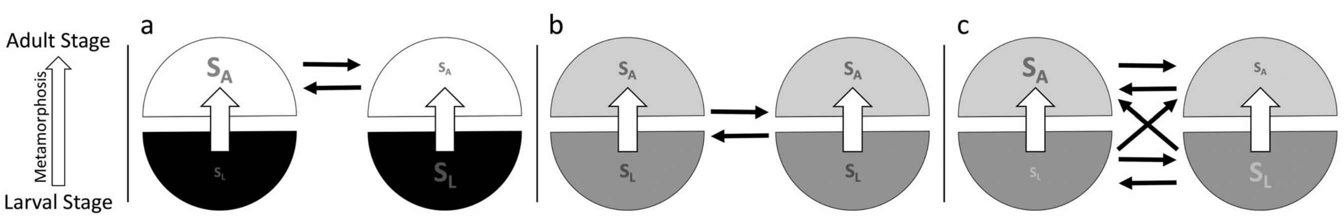

FIGURE 1 Conceptual illustration of variation in the demographic components of patch dynamics in species with complex life histories that include a transition between discrete larval and adult stages at metamorphosis. Circles represent patches and semicircles represent the two stages within each patch. Semicircles are shaded to represent the general habitat requirements of each stage (e.g., similar shading = greater habitat overlap). S_L and S_A represent stage-specific survival probabilities in each patch; font size scales with hypothetical survival probability. Per capita recruitment probabilities of new larvae are assumed to be similar across patches. In many metamorphic species, stages have distinct habitat requirements and one stage (often adults) is capable of active movement among patches (a). In these cases, demographic interactions among patches will be mediated by movements of the mobile stage, irrespective of variation in stage-specific survival probabilities. In other species, stages have overlapping habitat requirements and similar capacities for movement among patches (b, c). If stages have similar local survival probabilities (b), then stage structure should have little effect on patch dynamics. But if stages differ in local survival probabilities (c), then uncovering the demographic and behavioral mechanisms underlying patch dynamics requires stage-specific analyses of survival and movement.

does not preclude adaptive habitat selection by another stage, and vice versa (Lecchini et al., 2007; Nakazawa, 2015). More generally, distinguishing adaptive from maladaptive habitat selection must be on a stage-specific basis, also requiring stage-specific assessment of the movements underlying patch dynamics.

Likewise, when life stages have similar habitat requirements and movement abilities, the demographic mechanisms maintaining patch dynamics will depend on local variation in stage-specific vital rates. If stages experience similar vital rates within patches and similar movement rates among patches, then stage structure should have little effect on patch dynamics (Figure 1b). But if, instead, vital rates differ by stage within and among patches, then stage-specific movements will contribute differentially to patch stability (Figure 1c). For example, if one stage experiences significantly lower survival in a putative sink than in the source, then immigration by that stage may contribute little to stability, while imposing a high emigration cost on the source. In this case, stable source–sink dynamics would require that movements by another stage stabilize sinks while also compensating for this emigration cost in sources.

Our stream salamander study system offers an opportunity to investigate the patch dynamics that emerge when multiple stages within a complex life history are capable of active habitat selection. In streams, habitat patches are commonly delineated by channel gradient and water flow conditions (e.g., pools, runs, riffles, cascades; Frissell et al., 1986; Gordon et al., 1992; Hawkins et al., 1993), and previous analyses indicated that survival of the stream salamander *Gyrinophilus porphyriticus* differs between riffles and pools, the two dominant patch types in our study streams (Lowe & Addis, 2019). Riffles are characterized by high velocity, turbulent flows and high channel gradients; pools are characterized by low velocity, circulating flows and low channel gradients (modified from Montgomery & Buffington, 1998). Based on 4 years of capture–recapture data, the monthly survival probability of *G. porphyriticus* individuals—pooling across life stages—was lower in riffles than in pools (riffles $\pm$ 1 SE $=$ 0.77 $\pm$ 0.13, pools $\pm$ 1 SE $=$ 0.96 $\pm$ 0.01). But, despite this difference in survival probability, individuals move between pools and riffles, and riffles remain occupied over time (Lowe, 2005; Lowe et al., 2019).

These observations led us to hypothesize that riffles act as sinks within streams, where *G. porphyriticus* persistence is maintained by movements from pools. Here we tested this hypothesis by quantifying survival and movement separately for the strictly aquatic larval stage and semiaquatic adult stage of *G. porphyriticus*. Specifically, we used 8 years of capture–recapture data from three headwater streams to quantify stage-specific survival probabilities in riffles and pools, and stage-specific probabilities of movement between these two patch types. These estimates allowed us to assess stage-specific fitness consequences of interpatch movements. We then incorporated these empirical survival and movement probabilities into a stage-structured, two-patch model to assess demographic interactions between riffles and pools by simulating the elimination of interpatch movements by larvae and adults, in combination and separately.

MATERIALS AND METHODS

Study species and site

Gyrinophilus porphyriticus, a lungless salamander in the family Plethodontidae, is found in small, cool, well oxygenated streams along the Appalachian uplift (Petranka, 1998). Larvae are exclusively aquatic, with external gills for respiration. At our study sites, adults are mainly aquatic, but can forage and use moist refuges on land (Greene et al., 2008). Larvae and adults are found in spaces among rocks and wood in the streambed during the day, when our surveys were conducted. In our study streams in New Hampshire, USA, larval size is 26–80 mm snout-to-vent length (SVL) and adults can reach 120 mm SVL. Growth models indicate that the larval period can last for up to 7 years in these streams, and individuals can live for more than 18 years (Cochrane et al., in review). Sexing *G. porphyriticus* in the field is difficult, but previous studies have found no differences in the probability or distance of movement by females and males that were positively sexed (Addis & Lowe, 2022; Lowe & McPeek, 2012). Past studies have also shown that movements by *G. porphyriticus* larvae and adults are not consistently downstream biased (Addis et al., 2019; Lowe, 2003), so we did not expect passive drift to be the primary mechanism of movement between patches. Of animals recaptured more than once over a 6-year period, <1% moved from a capture location (i.e., meter of stream channel, measured as distance from the downstream end of a survey each) and subsequently returned to that location (Lowe, 2009), indicating that the majority of movements are discrete, unidirectional dispersal events, not migratory movements (Semlitsch, 2008). Additionally, our data indicated that dispersal (i.e., movements that result in settlement at a new location) ranges in distance from ≈2 m (accounting for 1-m sampling resolution) to >400 m, and that home ranges are generally <3 m in channel length (Addis & Lowe, 2020). Both larvae and adults showed a wide range of dispersal distances, and distance distributions do not differ between stages (Addis et al., 2019; Lowe, 2003), indicating that the spatial scale of habitat sampling does not differ greatly between the stages.

This research took place in three headwater streams (1st to 3rd order) in the Hubbard Brook Experimental Forest (HBEF), in central New Hampshire (43°56′ N, 71°45′ W): Bear Brook, Paradise Brook, and Zigzag Brook. These three streams are hydrologically independent, and all flow into the mainstem of Hubbard Brook, a tributary of the Pemigewasset River. The study streams are typical of most streams in the HBEF, with low conductivity (12.0–15.0 μS), slight acidity (pH of 5.0–6.0), high dissolved oxygen content (80%–90% saturation), and moderate mid-day summer temperatures (13.0–17.0°C). Hydrology of the HBEF streams is characterized by high spring discharge due to melting snow. High-discharge events may also occur throughout the year due to isolated storms. Base flow conditions usually occur in August and September. The study streams are high-gradient mountain headwaters with cobble, boulder, and bedrock substrates. These chemical and physical characteristics are common to mountain streams of the northeastern USA. The spatial dimensions of flow-delineated habitats (i.e., riffles and pools) generally scale with the size of streams, where size is based on discharge, bank-full width, stream order, or related measures (Frissell et al., 1986). As a result, these habitats may differ between meters of channel length in headwaters, as they do in our study streams (see Figure 1 in Lowe & Addis, 2019), or at larger scales (10–100 m) in mainstem streams and rivers. The dominant tree species in the surrounding forests are *Acer saccharum*, *Fagus grandifolia*, *Betula alleghaniensis*, *Picea rubens*, *Abies balsamea*, and *B. papyrifera*.

Field surveys

Capture–recapture surveys were conducted from mid-June through to mid-September of 2012–2015 and 2018–2021. We surveyed two 500-m long reaches in each stream: downstream reaches started at the confluence with the Hubbard Brook mainstem; upstream reaches ended at weirs where long-term water quality data were collected (Bormann & Likens, 1979). Distances between downstream and upstream reaches, measured along the stream, were 400 m in Bear Brook, 250 m in Paradise Brook, and 500 m in Zigzag Brook.

Each stream was surveyed nine times in each field season, for a total of 72 surveys per stream over the 8 years of sampling. We conducted three surveys of each stream during three 14–21-day survey sessions distributed evenly throughout the field season. In each survey, we maintained a constant search effort by turning one cover object per meter of stream length (Heyer et al., 1994). Salamanders were marked individually with visible implant elastomer (2012–2015; Northwest Marine Technologies, Washington, USA) and PIT tags (2018–2021; Hecere Electronic Col, Ltd., Quanzhou, CN), then returned to the same cover object where they were found. We could not mark larvae smaller than 35 mm SVL. We recorded the patch type (riffle, pool) where each salamander was captured based on flow and gradient conditions 0.5 m upstream and downstream of a salamander's location (see "*Introduction*" for criteria; Lowe & Addis, 2019).

Estimating survival and movement probabilities

We used empirical estimates of survival and movement probabilities to quantify demographic interactions between pools and riffles and assess source–sink dynamics. Multistate capture–recapture models estimated monthly recapture (p), survival (S), and pairwise transition probabilities (ψ) for four states defined by life stage and patch type: larva-pool (lp), larva-riffle (lr), adult-pool (ap), adult-riffle (ar). 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. Survival probability is the probability that an animal alive at time t in one state will be alive at time $t+1$, independent of state at $t+1$. The transition probability is the conditional probability that an animal in one state at time t will be in another state at $t+1$, given that the animal is alive at $t+1$ (e.g., $\psi^{lp \to lr}$, $\psi^{lr \to ap}$, $\psi^{ar \to ap}$). Consequently, one minus the sum of all transition probabilities out of one state is the conditional probability that an animal in that state at time t will be in the same state at $t+1$ (e.g., $\psi^{lp \to lp} = 1 - [\psi^{lp \to lr} + \psi^{lp \to ap} + \psi^{lp \to ar}]$). Transitions from larval states to adult states represent metamorphosing animals (e.g., $\psi^{lp \to ap}$, $\psi^{lr \to ap}$) (Lowe et al., 2019). Impossible transitions from adult states to larval states were fixed at 0 (e.g., $\psi^{ap \to lp}$). Independent estimates of survival and transition probabilities were used to calculate monthly joint survival-transition probabilities (e.g., $\Phi^{lp \to lp}$, $\Phi^{lp \to lr}$), representing the probability of an animal surviving from t to $t+1$ and either moving to another state (e.g., $\Phi^{lp \to lr} = S^{lp}\psi^{lp \to lr}$) or remaining in the same state (e.g., $\Phi^{lp \to lp} = S^{lp}\psi^{lp \to lp}$; Williams et al., 2002).

To increase the precision of parameter estimates, we pooled data across the three study streams and collapsed the three surveys in each 14–21-day survey session into a single observation for each month of the field season (e.g., mid-June, mid-July, mid-August), resulting in a total of 24 sampling occasions over the 8 years of sampling. Estimates of survival probability confound mortality with permanent emigration, but we believe that emigration did not strongly bias our analyses because the weirs above our study reaches probably prevented most upstream emigration, and only two individuals were detected moving between downstream and upstream reaches over the 10 years of this project. Overland emigration is likely to be rare, considering the highly aquatic habits and morphology of *G. porphyriticus* at our sites. Multistate capture–recapture models accommodate variable time intervals between successive surveys (e.g., 1 month during the field season, 10 months between field seasons, etc.), which are explicitly incorporated during model parameterization. This allowed us to use the entire 8-year data set in demographic analyses, despite the gap between the 2015 and 2018 field seasons.

We expected recapture probabilities to vary over time due to variations in stream flow, temperature, and other abiotic conditions that might influence detection rates over the 8 years of sampling (Bailey et al., 2004). Therefore, we modeled recapture probabilities as a variable by time (month) and used model selection to determine a parsimonious structure for survival and transition probabilities (Grant et al., 2010; Lebreton et al., 1992). We modeled survival and transition probabilities as constant or variable by state, time, and state × time. We held transition probabilities constant to identify the most parsimonious structure for survival, then used the resulting parameterization for survival probability to identify the best structure for transition probabilities.

We used Akaike's information criterion (AIC; Akaike, 1973) to select the most parsimonious model structure from these candidate model sets. Models were ranked by second-order AIC differences (ΔAIC_c; Burnham & Anderson, 2002). The relative likelihood of each model in a candidate set was then estimated with AIC_c weights (Buckland et al., 1997). Model evaluation and selection were performed with RMark (Laake, 2013). Prior to model selection, we used Program U-CARE (Choquet et al., 2009) to perform goodness-of-fit tests on the saturated multistate model. None of the five lack-of-fit tests performed on the saturated model were significant, indicating that the multistate framework was appropriate for the data set.

Demographic analyses

We assessed whether stage-specific movements were adaptive by comparing stage-specific interpatch movement probabilities (e.g., $\psi^{lp \rightarrow lr}$ vs. $\psi^{lr \rightarrow lp}$) to stage-specific survival probabilities in riffles and pools (e.g., S^{lp} vs. S^{lr}). If stage-specific movements were adaptive, we predicted that individuals within a life stage would be more likely to move into the patch type where that stage experienced higher survival (e.g., $\psi^{lp \rightarrow lr} > \psi^{lr \rightarrow lp}$ if $S^{lr} > S^{lp}$). We expected probabilities of remaining within a patch type (e.g., $\psi^{lp \rightarrow lp}$, $\psi^{lr \rightarrow lr}$) to be greater than interpatch movement probabilities due to the cumulative risks associated with movement (Bonte et al., 2012), and because previous studies had shown that individuals were more likely to remain at their initial location than to move away (Addis & Lowe, 2020; Lowe, 2003), but we had no basis for predicting the magnitude of these differences.

We used a stage-structured, two-patch model to simulate demographic interactions between riffles and pools (Figure 1c). Specifically, we used this model to assess source–sink dynamics by simulating the elimination of all interpatch movements (i.e., by both larvae and adults), then evaluated the consequences for species persistence in each patch type. If pools and riffles were found to exhibit source–sink dynamics, we evaluated the contributions of stage-specific movements by simulating the elimination of movements by a single life stage, then assessing the consequences for species persistence in each patch type. We used geometric mean lambda in each patch type over a 10-year period to assess the consequences for species persistence under these different movement scenarios (Mills, 2013).

Our model was parameterized with joint survival-transition probabilities (Φ) derived from the best-fitting capture–recapture models, then seeded with initial abundances of 25 individuals in each of the four states. To simulate the elimination of movements, we reduced the relevant transition probabilities to 0 (e.g., $\psi^{lp \rightarrow lr}$, $\psi^{ar \rightarrow ap}$), increased the corresponding probabilities of remaining in the same state by the same amount (e.g., $\psi^{lp \rightarrow lp}$, $\psi^{ar \rightarrow ar}$), then recalculated joint survival-transition probabilities based on these changes. Multistate capture–recapture models cannot estimate recruitment probabilities of new individuals into the population (Lebreton et al., 2009); therefore, we assumed that per capita recruitment probabilities of new larvae into pools and riffles were equal. We set these recruitment probabilities to 0.08, which—in combination with empirical survival-transition probabilities—stabilized abundances in riffles and pools over a simulated period of 10 years (Figure 2a).

The assumption of equal and stabilizing larval recruitment probabilities in pools and riffles is supported by our observation that both patch types are consistently occupied in the study streams and in a stream in northern New Hampshire that has been surveyed annually for 22 years (Lowe & Addis, 2019; Lowe et al., 2019). However, we also evaluated this assumption by testing whether pools and riffles differed in larvae:adult ratios, size distributions of larvae, and adult female body sizes. If per capita recruitment probabilities differed between patch types, then we expected larvae:adult ratios to be higher in the patch type where per capita recruitment probability was higher. We tested for this difference by quantifying the total numbers of larvae and adults captured in each year, calculating yearly larvae:adult ratios

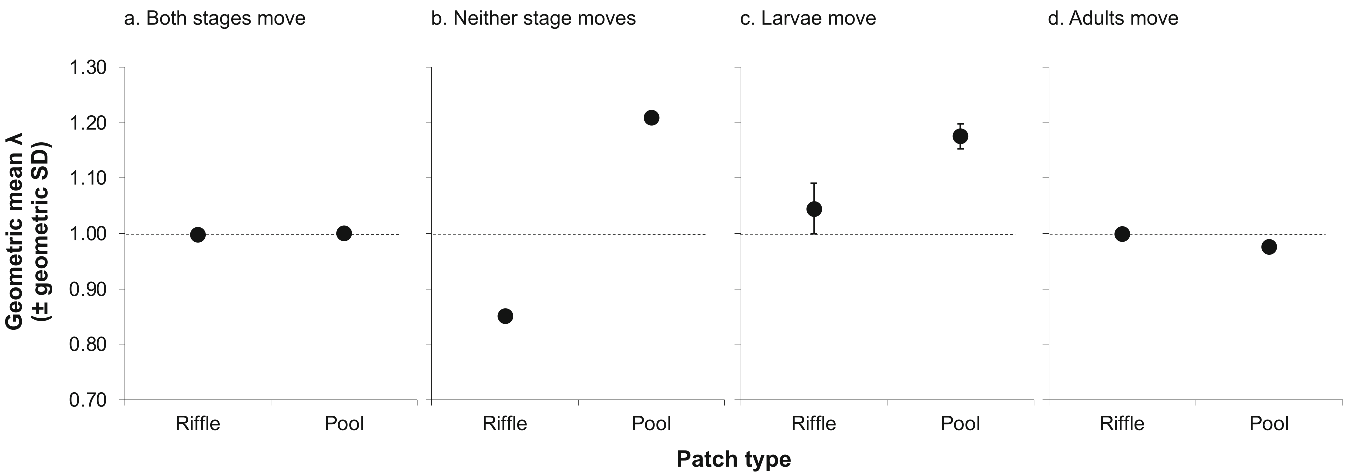

FIGURE 2 Estimates of geometric mean lambda (λ, ± geometric standard deviation) in riffles and pools from a stage-structured two-patch model parameterized with survival and transition probabilities from capture–recapture analyses of *Gyrinophilus porphyriticus* individuals in three streams in the Hubbard Brook Experimental Forest, New Hampshire, USA (Table 2). Lambda estimates were derived from simulations that differed in the life stage(s) moving between riffle and pool patch types: (a) both stages, (b) neither stage, (c) larvae only, and (d) adults only. Patches were seeded with initial populations of 25 larvae and 25 adults. Larval recruitment probabilities were assumed to be equal in riffles and pools, and stabilizing under estimated survival and transition probabilities (Table 2; simulation a). Geometric mean lambdas and geometric standard deviations were calculated for a 10-year period. Standard deviations ≤0.01 are not visible. The dashed line shows λ = 1.0. Patches are self-sustaining at λ ≥ 1.0.

for each patch type, then testing for an effect of patch type on yearly larvae:adult ratio in a mixed-effects analysis of variance (ANOVA) with year as a random effect. Larvae:adult ratios were log-transformed for this analysis (Isles, 2020). We also expected that larvae in the smaller size classes would occur at higher frequencies in the patch type where per capita recruitment probability was higher, causing larval size distributions to differ. We used a Kolmogorov–Smirnov test to compare body size distributions (SVL, mm) of all new larvae marked in pools and riffles over the 8 years of sampling. Finally, we expected that a difference in average female body size (SVL, mm) between pools and riffles could lead to a difference in per capita larval recruitment because female fecundity increases with body size in *G. porphyriticus* (Bruce, 1972). We used a mixed-effects ANOVA, with year as a random effect, to test for a difference between pools and riffles in the average annual body size of adult females. For this analysis, we used adults that were positively identified as female over 6 years of sampling (2014, 2015, 2018–2021; $N = 564$). Sex was assessed in the field based on the presence of papillae in the cloaca of males (Noble, 1954).

RESULTS

Field surveys

Over 8 years of sampling, we marked 4491 *G. porphyriticus* individuals in the three study streams: 1625 individuals in Bear Brook (1142 larvae, 483 adults), 1653 individuals in Paradise Brook (1173 larvae, 480 adults), and 1213 individuals in Zigzag Brook (809 larvae, 404 adults). Across the three streams, the frequency of individuals in riffles was 0.46 and the frequency of individuals in pools was 0.54. Based on our survey method (i.e., turning one cover object per meter of channel length) and our method for assigning individuals to patch type (i.e., flow and gradient conditions 0.5 m upstream and downstream of the capture location), these frequencies indicate that the overall areas of riffle and pool habitat occupied were also very similar. Within streams, frequencies of individuals in riffles and pools were, respectively, 0.53 and 0.47 in Bear Brook, 0.39 and 0.61 in Paradise Brook, and 0.46 and 0.54 in Zigzag Brook. Quantifying the dimensions of individual riffles and pools would have required mapping each stream repeatedly within and across field seasons. Unfortunately, this was beyond the scope of our funding and not possible with the time constraints imposed by the salamander surveys (27 surveys during each 3-month field season).

Demographic parameters

Analyses of larvae:adult ratios, larval size distributions, and adult female body size supported our assumption that per capita recruitment probabilities of larvae did not differ between pools and riffles. Mixed-effects ANOVAs showed no difference between patch types in larvae:adult (L:A) ratios (mean L:A [±SD]: pools = 4.98 [±5.22], riffles = 2.42 [±2.33]; $F_{1,13} = 2.03$, $p = 0.18$) or average female body size (mean average female SVL [±SD]: pools = 77.25 mm [± 1.27], riffles = 80.18 mm [±3.91]; $F_{1,9} = 2.80$, $p = 0.13$). When we added fixed effects of the stream and the stream × patch type interaction to these models neither was significant ($F < 0.60$, $p > 0.55$), indicating that these relationships did not differ among streams. A Kolmogorov–Smirnov test also failed to reject the hypothesis that larval body sizes in pools and riffles were drawn from the same distribution (mean larval SVL [±SD]: pools = 51.70 mm [±9.77], riffles = 51.01 mm [±10.09]; $D = 0.04$, $p = 0.12$).

In the best-fitting multistate model, survival and transition probabilities varied by state, not by time or the state × time interaction (Table 1). Support for the top survival and transition models was unambiguous, with AIC_c weights of >0.99. To assess how pooling data from the three streams influenced these results, we re-ran the top multistate capture–recapture models allowing S and ψ to vary by state and stream. Neither model with variation among streams received greater support (i.e., lower AIC_c) than the model without variation among streams (S: AIC_c = 12,440.65 vs. 12,439.85; ψ: AIC_c = 12,023.17 vs. 12,022.88), indicating that any among-stream variation in S and ψ was minor, and supporting our a priori approach. Monthly survival probabilities of larvae and adults were higher in pools than in riffles (Table 2). Converted to yearly probabilities, larval survival was ~13% higher in pools than in riffles (0.69 vs. 0.61, respectively) and adult survival was ~64% higher in pools than in riffles (0.69 vs. 0.42). Larvae were more likely to move from riffles to pools than from pools to riffles (Table 2). Adults, however, were more likely to move from pools to riffles than from riffles to pools, despite experiencing much lower survival in riffles. Standard error estimates on all parameters were very small (Table 2), increasing our confidence that survival and transition probabilities differed by life stage and patch type. Time-variable recapture probabilities (p, ±SE) ranged from 0.02 ± 0.00 to 0.13 ± 0.01.

Patch dynamics

When we simulated the elimination of interpatch movements by larvae and adults in our two-patch model, geometric mean lambda (± 1 SE) over a 10-year period was 1.21 ± 0.00 in pools and 0.85 ± 0.00 in riffles (Figure 2b).

TABLE 1 Multistate capture–recapture models assessing variation in monthly survival probabilities (a) and transition probabilities (b) of *Gyrinophilus porphyriticus* individuals in three streams at the Hubbard Brook Experimental Forest, New Hampshire, USA.

Model	AIC_c	ΔAIC_c	AIC_c wt	K
(a) Monthly survival probabilities				
$S_{(state)}, p_{(time)}, \psi_{(\bullet)}$	12,439.85	0.00	1.00	28
$S_{(state \times time)}, p_{(time)}, \psi_{(\bullet)}$	12,475.88	36.03	0.00	116
$S_{(time)}, p_{(time)}, \psi_{(\bullet)}$	12,497.22	57.38	0.00	47
$S_{(\bullet)}, p_{(time)}, \psi_{(\bullet)}$	12,507.84	67.99	0.00	25
(b) Transition probabilities				
$S_{(state)}, p_{(time)}, \psi_{(state)}$	12,022.88	0.00	1.00	36
$S_{(state)}, p_{(time)}, \psi_{(state \times time)}$	12,085.35	62.46	0.00	234
$S_{(state)}, p_{(time)}, \psi_{(time)}$	12,398.56	375.68	0.00	50
$S_{(state)}, p_{(time)}, \psi_{(\bullet)}$	12,439.85	416.97	0.00	28

Note: Survival and transitions probabilities (S and ψ, respectively) were modeled as constant or variable by state, time (survey month), and the state × time interaction. The four states were defined by life stage and patch type: larva-pool, larva-riffle, adult-pool, adult-riffle. Models incorporated 8 years of data on 4491 individual salamanders. Monthly recapture probabilities (p) were modeled as variable by time to account for variation in stream flow, temperature, and other abiotic conditions that might influence detection rates over the 8 years of sampling. 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 given in parentheses, where "•" = constant.

TABLE 2 State-specific monthly survival probabilities (S) and pairwise transition probabilities (ψ) for *Gyrinophilus porphyriticus* in three streams at the Hubbard Brook Experimental Forest, New Hampshire, USA.

Parameter	Estimate	1 SE	Note
S^{lp}	0.97	0.00	
S^{lr}	0.96	0.01	
S^{ap}	0.97	0.01	
S^{ar}	0.93	0.01	
$\psi^{lp \to lr}$	0.25	0.03	
$\psi^{lp \to ap}$	0.05	0.01	
$\psi^{lp \to ar}$	0.01	0.01	
$\psi^{lr \to lp}$	0.36	0.04	
$\psi^{lr \to ap}$	0.04	0.02	
$\psi^{lr \to ar}$	0.02	0.01	
$\psi^{ap \to lp}$	0.00	0.00	Fixed at 0.0
$\psi^{ap \to lr}$	0.00	0.00	Fixed at 0.0
$\psi^{ap \to ar}$	0.50	0.05	
$\psi^{ar \to lp}$	0.00	0.00	Fixed at 0.0
$\psi^{ar \to lr}$	0.00	0.00	Fixed at 0.0
$\psi^{ar \to ap}$	0.37	0.05	

Note: Superscripts refer to the four states, defined by life stage and patch type: larva-pool (lp), larva-riffle (lr), adult-pool (ap), adult-riffle (ar). Probability estimates are taken from a multistate capture–recapture model incorporating 8 years of data on 4491 individual salamanders (Table 1).

Eliminating interpatch movements by adults, so that only larvae moved between patches, resulted in a geometric mean lambda in pools of 1.18 ± 0.02 and a geometric mean lambda in riffles of 1.05 ± 0.05 (Figure 2c). Eliminating interpatch movements by larvae, so that only adults moved between patches, resulted in a geometric mean lambda in pools of 0.98 ± 0.01 and a geometric mean lambda in riffles of 1.00 ± 0.01 (Figure 2d). Changing the initial abundance of individuals in each state did not qualitatively change these results, other than influencing the rate of convergence on stable values of lambda.

DISCUSSION

By parameterizing a stage-structured, two-patch model with survival and movement estimates from over 4000 marked salamanders, we were able to generate novel insight into the role of population stage structure in source–sink interactions. When we simulated the elimination of interpatch movements by both life stages of *G. porphyriticus*, premetamorphic larvae and postmetamorphic adults, lambda in riffles dropped to 0.85 and lambda in pools increased to 1.21. This result supported our hypothesis that riffles are demographic sinks in streams where *G. porphyriticus* occurrence is maintained by immigration from pools (Figure 2b). Pools appear to be demographic sources where *G. porphyriticus* occurrence is not dependent on immigration.

These demographic outcomes changed considerably when we simulated the elimination of movement by one of the two life stages, illustrating the complex demographic interactions that emerge when multiple stages are capable of active habitat selection within a complex life history. When movement by *G. porphyriticus* adults was eliminated, lambdas in both riffles and pools were greater than 1.0, indicating that larval movement—in combination with local survival probabilities (Table 2)—stabilized both patch types. Pools are net recipients of larvae and the patch type where larval survival is highest, both of which sustain a larval subsidy to riffles that compensates for lower larval and adult survival there. In contrast, when movement by *G. porphyriticus* larvae was eliminated, and only adults moved between patches, lambda in riffles remained at 1.0 and declined to 0.98 in pools. This indicated that, in the absence of larval immigration, adult emigration destabilizes pools, causing total abundance in pools to decline and leading to a decline in the numerical subsidy to riffles. Adult immigration is sufficient to stabilize riffles in the short term, resulting in geometric mean lambda of 1.0 over a 10-year interval (Figure 2d), but realized lambda in riffles dropped to 0.99 by year three of this simulation.

Taken together, these results demonstrated that source–sink structure is maintained in this system despite conflicting demographic effects of stage-specific movements. Based on our simulations, interpatch movements by larvae not only stabilize pools and riffles, but also offset the destabilizing effects of adult movements from pools to riffles. This represents a novel form of stage-structured source–sink dynamics, in which the stability of sinks depends not on a net immigrant subsidy from sources, but on the balance of stage-specific rates of emigration and immigration. These stage-structured source–sink dynamics may be common among metamorphic species with life stages that share habitat requirements and capacities for interpatch movement (Figure 1c), including many species of insects, amphibians, marine invertebrates, and fish (Belles, 2020; Lowe et al., 2021; Wilbur, 1980). But similar patch dynamics may emerge in any structured population in which vital rates differ by age, size, or stage within patches, and rates of movement among patches also differ by age, size, or stage. Addressing these forms of internal demographic structure in patch dynamics analyses will help to refine and advance general understanding of spatial ecology (Barfield et al., 2011; Caswell, 2001; Manly, 1990).

Our results also show the importance of considering population stage structure when assessing individual and population-level consequences of habitat selection. Survival of larvae and adults is lower in riffles than in pools, and the drop in adult survival is particularly large (Table 2). Larval behavior is well matched to this difference in survival: larvae are more likely to move into pools than into riffles. Adults, however, appear to exhibit maladaptive habitat selection, in which individuals are more likely to move into riffles than into pools, despite experiencing much lower survival in riffles. Regardless of the proximate mechanism underlying movement probabilities, these results show that focusing on a single stage—or pooling individuals across stages—would misrepresent the fitness consequences of habitat selection, and that adaptive habitat selection by one stage (e.g., larvae) does not preclude source–sink dynamics.

There are several proximate mechanisms that could cause the net flux of adults into riffles, including negative interactions among adults in pools (e.g., aggression, chemically mediated avoidance; Nowicki & Vrabec, 2011) or attractive habitat conditions in and along riffles (e.g., lower substrate embeddedness, higher soil moisture; Delibes et al., 2001; Hale & Swearer, 2016; Harmon et al., 1986). In an a posteriori analysis, we tested whether the relative growth rates of recaptured larvae and adults differed between riffles and pools. We used the growth model developed by Cochrane et al. (in review), which applies a von Bertalanffy growth function to individual body size data using a Bayesian hierarchical approach that accounts for measurement error. The von Bertalanffy growth function is derived from basic metabolic principles (West et al., 2001) and fits plethodontid growth better than a logistic function due to its marked deceleration of growth rate over time (Staub, 2016). The relative growth rate was calculated as the difference between observed SVL at the last capture and model-predicted SVL at last capture based on SVL at the first capture and the time interval between the first and last capture (days). In ANOVA, with stream as a random effect, there was no significant difference between patch types in relative growth rates of larvae ($F_{1,276} = 0.01$, $p = 0.91$) or adults ($F_{1,111} = 2.75$, $p = 0.10$), suggesting that movements between patch types were not related to prey availability and growth conditions. Also, in a prior study based at a different field site, we found that larvae and adults displayed similar associations with pools and riffles—matching our observations from the Hubbard Brook streams—and that adults had no effect on survival, growth, or activity of larvae in a mesocosm experiment (Lowe, 2005), indicating that negative interactions between the two stages did not influence survival or interpatch movement probabilities. We acknowledge, however, that moving into riffles may have fitness benefits to adults that we could not quantify (e.g., related to mate availability or nest site quality).

Our stage-structured, two-patch model relied on an assumption of equal and stabilizing per capita recruitment probabilities of new larvae into riffles and pools. This assumption was supported by analyses of larvae:adult ratios, larval size distributions, and adult female body size, as well as by our observation that the two patch types are consistently occupied by *G. porphyriticus* in our study streams (Lowe, 2005; Lowe & Addis, 2019; Lowe et al., 2019). Nevertheless, we were unable to quantify larval recruitment probabilities directly because multistate capture–recapture models cannot estimate the recruitment of new individuals (Lebreton et al., 2009). Considering the overlap of larvae:adult ratios, larval size distributions, and adult female body size in riffles and pools, it seems unlikely that any difference in recruitment is great enough to stabilize riffles (or destabilize pools) under the no-movement scenario (Figure 2b). However, a smaller increase in recruitment in pools could stabilize both patch types under adults-only movement (Figure 2d), and reduced recruitment in riffles could be destabilizing under larvae-only movement (Figure 2c).

It is also important to acknowledge that our simulations do not account for density-dependent responses to changes in interpatch movement rates. We have not found evidence of density-dependent vital rates in prior analyses (Addis & Lowe, 2022; Lowe, 2009), but it is likely that the changes in patch-specific lambdas under the no-movement scenario (Figure 2b) would illicit some form of density-dependent response. These and other uncertainties underscore the wisdom of Watkinson and Sutherland (1995), who first concluded that the only unambiguous method for assessing source–sink dynamics is by experimentally eliminating interpatch movements and observing the demographic consequences directly. This approach would be challenging in our study system because *G. porphyriticus* occurs at low densities (Lowe et al., 2004) and detection probabilities are also low (Lowe et al., 2019), making small-scale experimental manipulations difficult to apply, with low power to detect demographic responses. Our study design—with long-term data on thousands of individuals across three streams and three kilometers of channel length—may be the only option for characterizing spatial dynamics in this species. Because of this design, vital rate estimates (Table 2) should be interpreted as representing the predominant demographic interaction between riffles and pools throughout the sampling area. We have no doubt that these vital rates vary within the system, both spatially and temporally, but our approach—by necessity—helps to reveal the emergent consequences of habitat variability.

Integrating across fine-scale variation in habitat structure and associated vital rates, our results indicated that *G. porphyriticus* distribution along streams is maintained by source–sink interactions between pools and riffles, showing a fundamental connection between demography and geomorphology. This study is not the first to find variation in demographic rates among geomorphic patch types (Goldberg et al., 2022; Labbe & Fausch, 2000; Schlosser, 1991), and modern stream ecology is built on the well justified assumption that geomorphology and correlated environmental conditions (e.g., water velocity, substrate size, channel slope) play a central role in ecological processes (Frissell et al., 1986; Poole, 2010; Townsend, 1989). But we are not aware of other studies that have documented spatial population dynamics occurring among geomorphic units with the precision that our long-term data provide (Table 2). Geomorphically structured source–sink dynamics may be common across stream organisms, including algae, microbes, invertebrates, and fish. Many stream organisms are associated with geomorphic patch types or with proximate habitat conditions defining patch types (Bergey, 1999; Bond & Lake, 2003; Ledger et al., 2008; Ward, 1992). But movement among patches and settlement in suboptimal patches is nearly unavoidable due to the fine-scale geomorphic complexity of streams (Pringle et al., 1988; Winemiller et al., 2010). Source–sink dynamics may, therefore, be a defining attribute of the population biology of many stream organisms, with similar—yet largely unexplored—ecological and evolutionary implications across taxa (Bolnick & Nosil, 2007; Holt, 1996; Kawecki, 2004).

ACKNOWLEDGMENTS

We thank Ian Halm (US Forest Service), Don Buso, Geoff Wilson, and Gene Likens for logistical and intellectual support. We thank Jon Davenport, Mariah Childs, Jessica Hernandez, Jarred Jones, Laurel Low, Jenn McKenzie, Nick Steijn, Tyler Hodges, Ryan Wagner, Megan Delamont, Anna Willig, Kai Barreras, Riley Waters, Sarah McPeek, and Max Chung for field assistance. Leah Joyce and Eric Lyons gave us helpful comments on this manuscript. This research was funded by the United States National Science Foundation (DEB-1114804, DEB-1050459, DEB-1655653, DEB-1637685) and was conducted under Montana State Institutional Care and Use Protocol No. 003-14WLDBS-012714. This work is a contribution of the Hubbard Brook Ecosystem Study. Hubbard Brook is part of the Long Term Ecological Research (LTER) network, which is supported by the United States National Science Foundation. HBEF is operated and maintained by the United States Department of Agriculture, Forest Service, Northern Research Station.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Lowe et al., 2023) are available in the Environmental Data Initiative (EDI) Data Portal at https://doi.org/10.6073/pasta/a31de7704466bc78061ee332704f6f18.

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How to cite this article: Lowe, Winsor H., Brett R. Addis, Madaline M. Cochrane, and Leah K. Swartz. 2023. "Source–Sink Dynamics Within a Complex Life History." *Ecology* 104(4): e3991. https://doi.org/10.1002/ecy.3991