

## LINKING DISPERSAL TO LOCAL POPULATION DYNAMICS: A CASE STUDY USING A HEADWATER SALAMANDER SYSTEM

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**Abstract.** Dispersal can strongly influence local population dynamics and may be critical to species persistence in fragmented landscapes. Theory predicts that dispersal by resident stream organisms is necessary to offset the loss of individuals to downstream drift. However, there is a lack of empirical data linking dispersal and drift to local population dynamics in streams, leading to uncertainty regarding the general demographic significance of these processes and the power of drift to explain observed dispersal patterns. I assessed the contribution of dispersal along a first-order stream to population dynamics of the headwater salamander *Gyrinophilus porphyriticus* (Plethodontidae). I conducted mark–recapture surveys of two contiguous 500 m long sections of a study stream in June, July, and August of 1999, 2000, and 2001. Movement by *G. porphyriticus* larvae and adults showed a strong upstream bias in the study stream, as well as in 11 other streams that I surveyed. Using mark–recapture models and Akaike’s information criterion for model selection, monthly probability of dispersal from the downstream section to the upstream section of the study stream (mean  $\pm$  1 SE) was estimated to be  $0.02 \pm 0.01$ . The probability of dispersal from the upstream section to the downstream section was  $0.00 \pm 0.00$ . Monthly survival probabilities did not differ between sections. Estimated monthly population growth rates were  $1.01 \pm 0.01$  in both sections. Net dispersal from the downstream section to the upstream section contributed to the equality of population growth rates. Additionally, reproduction and individual condition were lower in the upstream section, suggesting that population stability and growth there (i.e.,  $\lambda \geq 1.0$ ) may have been dependent on immigration from downstream. Similar interactions between dispersal and variation in local demographic rates along the stream continuum may underlie the distribution and abundance patterns of other organisms at multiple spatial scales. Greater empirical understanding of these interactions will improve conservation of stream biota. The strong upstream bias of *G. porphyriticus* movement suggests that dispersal is not a response to downstream drift. I propose an alternative model for the evolution of directionally biased dispersal based on the landscape-scale distribution of headwater habitats.

**Key words:** amphibian; body condition; demography; dispersal; drift; evolution; *Gyrinophilus porphyriticus*; habitat quality; Plethodontidae; population biology; salamander; stream.

### INTRODUCTION

Local population dynamics are a function of survival and reproductive rates within a focal area and rates of dispersal into and out of that area. Growing interest in the causes and consequences of animal dispersal stems from basic ecological and evolutionary investigation (McPeck and Holt 1992, Hastings 1993, Dieckmann et al. 1999, Byers 2001, Kawecki and Holt 2002) and from increased awareness that dispersal may be critical to species persistence in fragmented landscapes (Zwick 1992, Kareiva and Wennergren 1995, Mills and Allendorf 1996, Hanski and Ovaskainen 2000). This interest has generated a large body of theory in need of direct, empirical evaluation (Ferriere et al. 2000, Clobert et al. 2001, Nathan 2001), both to test the generality of

existing theory and to direct future theoretical work toward questions pertaining to natural systems.

To resolve what has become known as the “drift paradox,” theory predicts that compensatory dispersal is critical to population persistence in resident stream organisms exposed to the advective force of the flowing water and associated loss of individuals to downstream drift (Müller 1982, Anholt 1995, Speirs and Gurney 2001). Although directional trends in movement along the stream corridor have been documented in a variety of stream taxa, including invertebrates (Müller 1954, Hershey et al. 1993, Elliott 2002), amphibians (Petranka et al. 1987, Storer and Sih 1998, Ferguson 2000), and fish (Aparicio and De Sostoa 1999, Chenuil et al. 2000, Skalski and Gilliam 2000), restriction of these data to one segment of the population (e.g., larvae or adults) and a lack of complementary data on local demography have precluded the assessment of population-scale consequences of observed movement patterns. Therefore, while downstream drift and active dispersal may be widespread phenomena among stream

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organisms (Palmer et al. 1996), we currently have no empirical evidence that these are demographically significant processes, or, therefore, that they are causally linked.

Among amphibians, the lack of understanding of the demographic significance of dispersal in stream-associated species is underscored by abundant evidence for the importance of this process in the population biology of pond-associated species (e.g., Sjogren-Gulve 1994, Skelly et al. 1999, Trenham et al. 2001). Studies of stream amphibians have usually selected the stream reach as the unit of observation, a relatively small longitudinal segment of the stream (typically  $\leq 100$  m) defined by homogeneous physical features. This scale of observation has been extremely important in identifying mechanisms of species interaction (Hairston 1987, Resetarits 1991, Storfer and Sih 1998), documenting local effects of habitat perturbation (Hawkins et al. 1983, Corn and Bury 1989, Welsh and Ollivier 1998), and describing changes in population size over time (Tilley 1980, Hairston 1987). However, by not considering the contribution of larger scale patterns of movement along the stream corridor to local population dynamics, this approach may have failed to provide a complete picture of the controls on amphibian distribution, abundance, and demography in streams.

The objective of this study was to directly assess the role of downstream and upstream movement in the population biology of the headwater salamander *Gyrinophilus porphyriticus* (Plethodontidae). Larvae of this species are strictly aquatic and adults are highly aquatic, but can be found along the stream bank on wet nights (Bishop 1941, Petranksa 1998). I used mark-recapture methods to quantify the frequency, directionality, and temporal pattern of movement along the stream corridor by *G. porphyriticus* larvae and adults, and to analyze the contribution of longitudinal dispersal to local population dynamics in a first-order study stream. To control for another potential mediator of *G. porphyriticus* population dynamics, I also tested the prediction that variation in local demographic rates (i.e., survival and reproduction) along the stream continuum corresponds to variation in habitat quality, as represented by individual condition.

## METHODS

### *Study species and site*

*G. porphyriticus* belongs to the family Plethodontidae, the lungless salamanders. It is a large salamander (up to 112 mm snout-vent length [SVL]) usually found in cool, well-oxygenated, low-order streams. Females lay eggs deep in the streambed, and oviposition occurs from May through September in the northeastern US (Bishop 1941; W. H. Lowe, unpublished data). Past studies have estimated larval size at hatching to be up to 26 mm SVL (Pope 1915, Bishop 1941). The larval

period is 3–4 yr, and sexual maturation occurs within one year of metamorphosis (Bishop 1941, Bruce 1980).

I conducted this study in Merrill Brook, a fishless, first-order stream in Dartmouth College's Second College Grant, Coos County, New Hampshire, USA. Merrill Brook flows into the fourth-order Dead Diamond River. A wetland at the confluence serves as a barrier to brook trout. I designed this study around two contiguous 500 m long sections of Merrill Brook encompassing the entire perennial portion of the stream. The downstream section began where the stream joins the outflow wetland, and the upstream section started 500 m upstream and continued to a distance of 1000 m from the confluence. No *G. porphyriticus* individuals were found in yearly sampling of the outflow wetland, adjacent Dead Diamond River, and upper ephemeral portion of Merrill Brook. Therefore, I assumed that movement out of the study section was minimal, and, because the nearest occupied stream was 3 km away, that immigration into Merrill Brook from other populations did not occur at a demographically significant rate over the course of this study.

The predominant tree species in the Merrill Brook drainage were *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, *Betula papyrifera*, *Populus tremuloides*, *Picea rubens*, and *Abies balsamea*. Undisturbed headwater streams in New Hampshire display low conductivity (12.0–15.0  $\mu$ S), slight acidity (pH of 5.0–6.0), high dissolved oxygen content (80–90% saturation), and moderate midday temperatures in the summer (13.0°–17.0°C) (Lowe and Bolger 2002). Results of sampling throughout Merrill Brook before and during this study matched these data. Predominant reach types in Merrill Brook were riffles, characterized by moderate gradient and turbulent flow, and pool-drop cascades, characterized by high gradient and highly turbulent flow (Montgomery and Buffington 1998). Other salamanders encountered in Merrill Brook included *Eurycea bislineata* and *Desmognathus fuscus* (both Plethodontidae).

### *Field methods*

Salamander surveys of each section of Merrill Brook were conducted during 3-d periods in mid-June, mid-July, and mid-August of 1999, 2000, and 2001. A cover-controlled active search sampling method was used (Heyer et al. 1994). Moving upstream, I turned rocks between 64 and 256 mm in diameter (cobble; Platts et al. 1983) within the channel and along the edge. Surveys continued until 600 cover objects had been turned in each section. An even distribution of cobble within both study sections allowed me to maintain a constant effort of just over one cover object per meter of stream length. I used an aquarium dip net to capture salamanders, including those flushed by the current. All unmarked *G. porphyriticus* larvae and adults encountered were individually marked by subcutaneous injection of a fluorescent elastomer (Northwest Marine Technolo-

gies, Shaw Island, Washington, USA), and marked individuals were recorded. The longitudinal position (distance from the confluence, meters), length (SVL, millimeters), and mass (milligrams) of all individuals encountered were recorded.

#### *Analysis of movement*

Movement of recaptured individuals was measured as distance along the stream (meters) from the position of last capture. Movement was quantified using histograms of the frequency distribution of distances moved, arbitrarily assigning negative values to downstream moves and positive values to upstream moves. To assess directional bias, I tested for skewness of the movement distribution (Zar 1984). To determine if directional bias was consistent across time, I divided movement data into three groups differentiated by recapture interval: 1–2 mo, 10–14 mo, and 22–26 mo. I then tested for skewness of the movement distribution of each group.

To further examine the relationship between time and movement distance, I tested the hypothesis that the variance of distance moved increased linearly with time, a characteristic of movement by simple diffusion (Skellam 1951, Turchin 1998). For this analysis, I regressed the estimated variance of distance moved (weighted by sample size) on time (months) using the polynomial equation  $y = c_0 + c_1t + c_2t^2$ , where  $y$  is the variance and  $t$  is time. The hypothesis predicts  $c_0 = 0$ ,  $c_1 > 0$ , and  $c_2 = 0$ . This analysis describes the spread of animals from a hypothetical single release point.

To assess the generality of any directional bias in *G. porphyriticus* movement in Merrill Brook, I also investigated movement patterns in 11 other first-order streams located throughout New Hampshire. These streams varied in brook trout abundance and fine sediment accumulation resulting from logging activities, two factors found to predict *G. porphyriticus* abundance (Lowe and Bolger 2002). Mark–recapture surveys of 100 m long reaches of these streams were conducted in June, July, and August of 2000 and 2001 using the same methods described in *Field methods* and turning 100 cover objects per survey. I tested for skewness of the movement distribution of all individuals recaptured in these surveys, pooling data across streams and sampling dates.

#### *Mark–recapture analyses*

Monthly *G. porphyriticus* survival ( $S^d$  and  $S^u$ ) and recapture ( $p^d$  and  $p^u$ ) probabilities in the downstream (d) and upstream (u) sections of Merrill Brook, transition probability from the downstream to the upstream section ( $\Psi^{du}$ ), and transition probability from the upstream to the downstream section ( $\Psi^{ud}$ ) were estimated with a multistrata model (Brownie et al. 1993, Nichols et al. 1993, Schwarz et al. 1993) using the MARK computer program (White and Burnham 1999). The

survival probability represents the probability that an animal alive at time  $t$  in one stratum (i.e., stream section) will be alive at time  $t + 1$ , independent of stratum at  $t + 1$ . With two strata, the transition probability is the conditional probability that an animal in one stratum at time  $t$  will be in the other stratum at  $t + 1$ , given that the animal is alive at  $t + 1$ . Transition probability estimates are based on the assumption that survival from time  $t$  to  $t + 1$  does not depend on stratum at  $t + 1$ . Recapture probability is the probability that a marked animal at risk of capture at time  $t$  is captured at  $t$ . Recapture probability is not estimable for the first sampling date in multistrata models.

Survival probabilities were modeled as either constant within strata, variable over time (sampling date), variable by life-history stage (larva and adult), or variable over both time and stage. The inclusion of time and stage variables in modeling  $\Psi^{du}$  and  $\Psi^{ud}$  was informed by results of the analysis of *G. porphyriticus* movement. According to the a priori expectation that recapture probabilities would vary unpredictably in the two stream sections as a function of stream discharge,  $p^d$  and  $p^u$  were modeled as variable over time. Estimates of  $S^d$ ,  $S^u$ ,  $\Psi^{du}$ , and  $\Psi^{ud}$  were used to calculate monthly survival/transition probabilities ( $\phi^{dd}$ ,  $\phi^{uu}$ ,  $\phi^{du}$ , and  $\phi^{ud}$ ), representing the probability of an animal surviving from  $t$  to  $t + 1$  and either moving to the other stratum (e.g.,  $\phi^{du} = S^d\Psi^{du}$ ) or remaining in the same stratum (e.g.,  $\phi^{dd} = S^d[1 - \Psi^{du}]$ ).

To assess how differences in survival and inter-section dispersal probabilities affected local population dynamics in the two stream sections, monthly realized population growth rates ( $\lambda$ ) were estimated using a Pradel model (Pradel 1996). This model also includes monthly survival ( $\phi$ ) and recapture ( $p$ ) probability parameters. Variability in  $\lambda$  by stream section was modeled to explicitly test the prediction that realized population growth rates differed between the downstream and upstream sections. I modeled variability in  $\phi$  to be consistent with multistrata model results. I modeled  $p$  to be variable over time in each stream section. Because the Pradel model cannot incorporate transitions between strata, individuals that dispersed between sections had two recapture histories, each specific to a section. This model estimated recapture probabilities for all sampling dates. Because MARK allows for variable time intervals between successive surveys (e.g., June 2000 to July 2000 = 1 month, August 2000 to June 2001 = 10 months), I was able to use information from all surveys in both multistrata and Pradel models.

I used Akaike's information criterion (AIC; Akaike 1973, Burnham and Anderson 1998) to identify the multistrata and Pradel model that represented the data adequately with as few parameters as possible, thus making a trade-off between potential bias caused by having too few parameters and poor precision of parameter estimates caused by having too many parameters. Models in the candidate set were

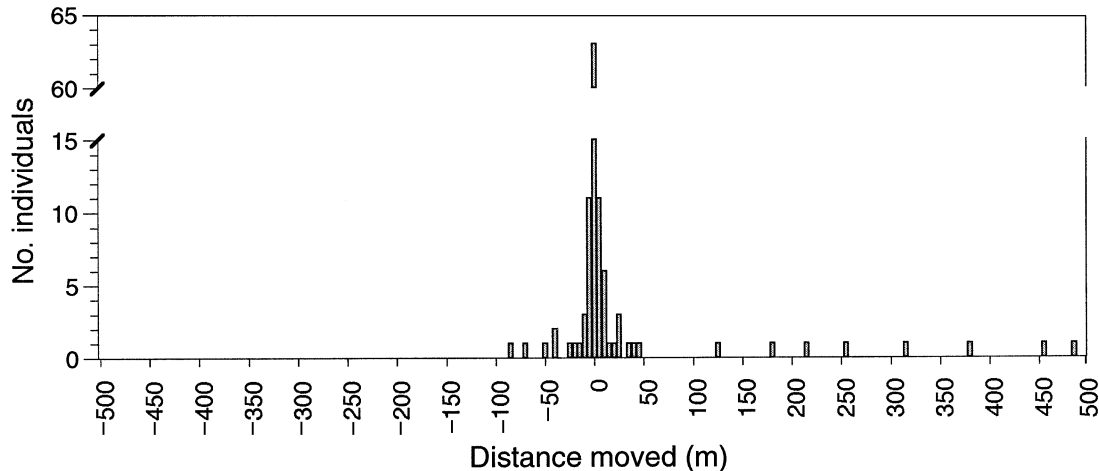


FIG. 1. Movement distribution of *Gyrinophilus porphyriticus* individuals recaptured in Merrill Brook, New Hampshire, USA;  $N = 118$ . Positive values represent upstream moves, and negative values represent downstream moves. Data are pooled over all recaptured intervals.

first ranked by second-order AIC ( $AIC_c$ ) differences ( $\Delta AIC_c$ ; Burnham and Anderson 1998), the difference between  $AIC_c$  for each model, and that for the model with the lowest observed  $AIC_c$ : the best-fitting model. Relative likelihood of each model in the candidate set was then estimated with  $AIC_c$  weights (Buckland et al. 1997). The  $AIC_c$  weights for all models in a candidate set sum to 1.

In calculations of  $AIC_c$ , the variance inflation factor ( $\hat{c}$ ) corrects for overdispersion, or extra binomial variation in the data (Lebreton et al. 1992, Burnham and Anderson 1998). The equation for  $\hat{c}$  is

$$\hat{c} = \chi^2/df \quad (1)$$

where the  $\chi^2$  statistic is derived from an independent test of model fit and  $df$  is the model degrees of freedom. When  $\hat{c} = 1.0$ , the model fits the data. When  $\hat{c} > 1.0$ , then overdispersion, or lack of fit is indicated. A generally agreed upon independent test of fit for multistrata and Pradel models is not currently available, and the default value of  $\hat{c}$  used by MARK to calculate  $AIC_c$  is 1.0. However, MARK allows the user to change the value of  $\hat{c}$  used in calculating  $AIC_c$ . Cooch and White (2001) suggest that confidence in the best-fitting model

should increase if the model retains its rank across a range of  $\hat{c}$  values. I assessed the rank stability of the best-fitting multistrata and Pradel models by entering  $\hat{c}$  values between 1.0 and 6.0. Lebreton et al. (1992) suggest that  $\hat{c} \leq 3.0$  is a good general criterion for assessing adequacy of model fit.

#### Analysis of body condition

Log-transformed SVL and mass measurements from previously unmarked individuals were used to calculate size-corrected mass, an index of body condition (Jakob et al. 1996, Green 2001). The functional relationship between log SVL and log mass among *G. porphyriticus* individuals was linear (W. H. Lowe, unpublished data), and there was no correlation between log SVL and the residuals from this regression (Pearson product-moment correlation:  $R < 0.0001$ ,  $N = 509$ ,  $P = 1.0$ ) (Green 2001). Analysis of covariance (ANCOVA) was used to assess variation between stream sections in size-corrected mass. Stream section, survey month, survey year, and all interactions were initially entered as sources of variability. SVL was entered as a continuous covariate. Only significant sources were included in the final ANCOVA model ( $P < 0.05$ ).

## RESULTS

### Movement

*G. porphyriticus* individuals in Merrill Brook displayed a strong upstream bias in movement that was consistent across life-history stage, stream section, and time (Fig. 1, Table 1). There was no difference between the movement distributions of larvae and adults ( $N = 23$  and 95, respectively) or individuals in the downstream and upstream sections ( $N = 69$  and 49, respectively) (Kolmogorov-Smirnov tests:  $P > 0.05$ ). Movement by animals marked in 1999 and recaptured in 1999 and 2000, and by those marked in 2000 and re-

TABLE 1. Estimates of the skewness of movement distributions (frequency distribution of meters moved) for *Gyrinophilus porphyriticus* individuals in Merrill Brook, New Hampshire, USA.

Data set	$N$	Skewness (mean $\pm$ 1 SE) <sup>†</sup>	$P$ (skewness = 0)
All intervals	118	4.07 $\pm$ 0.22	<0.002
1–2 months	61	2.70 $\pm$ 0.31	<0.002
10–14 months	38	2.67 $\pm$ 0.38	<0.002
22–26 months	19	2.19 $\pm$ 0.52	<0.002

Notes: Data were pooled over all recapture intervals and divided into three groups differentiated by recapture interval.

<sup>†</sup> Positive values indicate upstream bias.

TABLE 2. Multistrata models of monthly survival ( $S$ ), recapture ( $p$ ), and transition ( $\Psi$ ) probabilities for *Gyrinophilus porphyriticus* populations in the downstream (d) and upstream (u) sections of Merrill Brook.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC weight	K
$S^d, S^u, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	876.25	0.00	0.55	20
$S^d, S^u_{stage}, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	878.37	2.12	0.19	21
$S^d_{stage}, S^u, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	878.40	2.15	0.19	21
$S^d_{stage}, S^u_{stage}, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	880.53	4.28	0.06	22
$S^d, S^u_{time}, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	884.83	8.58	0.01	27
$S^d_{stage}, S^u_{time}, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	887.03	10.78	0.00	28
$S^d_{time}, S^u_{stage}, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	890.08	13.83	0.00	28
$S^d_{time}, S^u_{time}, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	896.85	20.59	0.00	34
$S^d, S^u_{stage \times time}, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	898.72	22.47	0.00	35
$S^d_{stage}, S^u_{stage \times time}, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	900.99	24.74	0.00	36
$S^d_{stage \times time}, S^u, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	905.40	29.15	0.00	35
$S^d_{stage \times time}, S^u_{stage}, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	907.64	31.39	0.00	36
$S^d_{time}, S^u_{stage \times time}, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	911.08	34.83	0.00	42
$S^d_{stage \times time}, S^u_{time}, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	914.81	38.55	0.00	42
$S^d_{stage \times time}, S^u_{stage \times time}, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	929.58	53.33	0.00	50
$S^d_{time}, S^u, p^d_{time}, p^u_{time}, \Psi^{du}, \Psi^{ud}$	992.43	116.17	0.00	27

Notes: Second-order Akaike’s information criterion values (AIC<sub>c</sub>), AIC<sub>c</sub> differences (ΔAIC<sub>c</sub>), AIC<sub>c</sub> weights, and number of estimable parameters (K) are provided for all models. Subscripts give parameterization for  $S$ ,  $p$ , and  $\Psi$ : no subscript = constant over stage and time variables; “stage” = variation by life-history stage (larva and adult); “time” = variation by sampling data. Subscripts joined by “×” indicate a factorial model.

captured in 2000 and 2001, showed upstream bias (1999–2000: skewness [mean ± 1 SE] = 3.39 ± 0.41,  $N = 32$ ,  $P$  [skewness = 0] < 0.002; 2000–2001: skewness = 5.22 ± 0.34,  $N = 49$ ,  $P < 0.002$ , where positive skewness represents upstream bias), indicating that movement bias did not vary by year. Distance moved was not correlated with individual size (Spearman rank correlation:  $R_s = -0.16$ ,  $N = 118$ ,  $P = 0.08$ ). There was also no correlation between distance moved in the first recapture interval and distance moved in the second interval among individuals recaptured twice (Spearman rank correlation:  $R_s = -0.20$ ,  $N = 18$ ,  $P = 0.42$ ). All animals encountered in surveys were marked. The size range of marked animals was 28–112 mm SVL.

Variance in distance moved increased linearly with time (linear regression:  $F_{1,5} = 38.96$ ,  $P < 0.01$ ,  $R^2 = 0.86$ ), consistent with a model of simple diffusion. The estimated intercept of the variance in distance by time polynomial regression did not differ from zero ( $t = -1.71$ ,  $P = 0.16$ ), the slope was significantly positive ( $t = 4.50$ ,  $P = 0.01$ ), and the quadratic term did not differ from zero ( $t = 1.75$ ,  $P = 0.15$ ).

Individuals in the 11 additional streams surveyed also displayed a strong upstream bias in movement (skewness = 2.19 ± 0.37,  $N = 42$ ,  $P$  [skewness = 0] < 0.002). The number of recaptured individuals per stream ranged from 1 to 10 (mean number of recaptured individuals = 3.82) and was positively correlated with the total number of marked animals in each stream (Pearson product-moment correlation:  $R = 0.86$ ,  $N = 11$ ,  $P < 0.001$ ) and the mean number of animals encountered per survey ( $R = 0.86$ ,  $N = 11$ ,  $P < 0.001$ ), indicating that variation in recapture rates was a function of variation in *G. porphyriticus* abundance among

streams. There was no difference between the movement distributions of larvae and adults ( $N = 21$  and 21, respectively) recaptured in these surveys (Kolmogorov-Smirnov test:  $P > 0.05$ ). Among individuals in these streams that moved more than 1.0 m ( $N = 21$ ), mean distance moved (± 1 SE) was 9.1 ± 2.8 m.

Mark-recapture analyses

Based on the results of analyses of *G. porphyriticus* movement, inter-section transition probabilities ( $\Psi^{du}$  and  $\Psi^{ud}$ ) were modeled as constant over time and life-history stage. In the best-fitting multistrata model,  $S^d$  and  $S^u$  were also constant over time and life-history stage (Table 2). This model fit the data more than twice as well as the second-best-fitting model and maintained its rank up to  $\hat{c} = 6.0$ . Standard error estimates around monthly survival probabilities for the downstream and upstream sections overlapped (Table 3). Recapture probabilities were low and variable over time in both sections. Modeling recapture probabilities as variable by life-history stage did not improve model fit. Consistent with the directional trend in *G. porphyriticus* movement (Fig. 1), the estimate of  $\Psi^{ud}$  was extremely low. Fixing  $\Psi^{ud}$  at 0 had no effect on estimates of  $S^d$ ,  $S^u$ , or  $\Psi^{du}$ . Therefore, I set  $\Phi^{ud}$  at 0 to calculate  $\phi^{uu}$  and  $\phi^{ud}$ . Values of  $\phi^{dd}$ ,  $\phi^{uu}$ ,  $\phi^{du}$ , and  $\phi^{ud}$  were 0.94, 0.98, 0.02, and 0.00, respectively.

The Pradel model with  $\lambda$  constant by stream section was more than twice as well supported by the data as the model with variable  $\lambda$  (Table 4) and maintained its rank up to  $\hat{c} = 6.0$ . Estimated  $\lambda$  (mean ± 1 SE) for both the downstream and upstream sections of Merrill Brook was 1.01 ± 0.01 (Table 5). Modeling  $\lambda$  as variable over time did not improve model fit. Pradel model

TABLE 3. Monthly survival (*S*), recapture (*p*), and transition ( $\Psi$ ) probability estimates for *Gyrinophilus porphyriticus* populations in the downstream (d) and upstream (u) sections of Merrill Brook from the best-fitting multistrata model (Table 2).

Parameter	Estimate	1 SE	95% CI	
			Lower	Upper
$S^d$	0.96	0.02	0.91	0.98
$S^u$	0.98	0.02	0.88	1.00
$P^d_{July\ 1999}$	0.05	0.03	0.02	0.15
$P^d_{August\ 1999}$	0.09	0.03	0.04	0.18
$P^d_{June\ 2000}$	0.06	0.03	0.02	0.16
$P^d_{July\ 2000}$	0.11	0.03	0.06	0.20
$P^d_{August\ 2000}$	0.05	0.02	0.02	0.10
$P^d_{June\ 2001}$	0.07	0.03	0.03	0.16
$P^d_{July\ 2001}$	0.10	0.03	0.05	0.19
$P^d_{August\ 2001}$	0.02	0.01	0.01	0.07
$P^u_{July\ 1999}$	$0.75 \times 10^{-13}$	$0.13 \times 10^{-6}$	0.00	$0.25 \times 10^{-6}$
$P^u_{August\ 1999}$	0.04	0.03	0.01	0.21
$P^u_{June\ 2000}$	0.02	0.02	0.00	0.15
$P^u_{July\ 2000}$	0.06	0.03	0.02	0.15
$P^u_{August\ 2000}$	0.15	0.04	0.09	0.24
$P^u_{June\ 2001}$	0.09	0.04	0.04	0.19
$P^u_{July\ 2001}$	0.08	0.03	0.04	0.16
$P^u_{August\ 2001}$	0.03	0.02	0.01	0.08
$\Psi^{du}$	0.02	0.01	0.01	0.06
$\Psi^{ud}$	$0.57 \times 10^{-14}$	$0.12 \times 10^{-7}$	0.00	$0.23 \times 10^{-7}$

Notes: Standard errors (SE) and 95% confidence intervals (CI) are provided for all estimates. Subscripts on *p* refer to sampling dates.

estimates of  $\phi^d$  and  $\phi^u$  were nearly identical to multistrata model estimates of  $\phi^{dd}$  and  $\phi^{uu}$ .

*Body condition*

Size-corrected mass of *G. porphyriticus* individuals was greater in the downstream section than in the upstream section across all years ( $F_{1,504} = 25.58, P < 0.0001$ ). The small overall proportion of dispersers in the stream (Fig. 1, Table 3) suggests that this difference was not due to the dispersal histories of individuals in the two sections. There was also a significant effect of survey year on size-corrected mass ( $F_{2,504} = 67.60, P < 0.001$ ; Tukey's HSD: 1999 < 2000 < 2001).

DISCUSSION

*Stream-scale spatial population dynamics*

I found that dispersal along the stream corridor contributed to the equality of *G. porphyriticus* population growth rates in the downstream and upstream sections of Merrill Brook. In the downstream section, the estimated monthly population growth rate of 1.01 was a

function of local survival, local reproduction, and net emigration to the upstream section. Monthly population growth rate in the upstream section was also estimated to be 1.01 over the study period, but there it was a function of local survival, local reproduction, and net immigration from the downstream section. While these data agree with the results of past research showing that the growth rates of stream amphibian populations are stable over time (Tilley 1980, Hairston 1987), mine is the first study to explicitly examine and confirm the contribution of dispersal to this stability.

Given the strong upstream bias of *G. porphyriticus* dispersal and the similarity of survival estimates for the two stream sections, the equality of population growth rates indicates that local reproduction was considerably higher in the downstream section than in the upstream section of Merrill Brook, which is consistent with variation in individual condition. Longitudinal variation in reproduction may have produced source-sink spatial population dynamics in this stream (Puliam 1988), where population stability and growth in

TABLE 4. Pradel models of monthly survival ( $\phi$ ) and recapture probabilities (*p*) and realized population growth rates ( $\lambda$ ) for *Gyrinophilus porphyriticus* populations in the downstream and upstream sections of Merrill Brook.

Model	AIC <sub>c</sub>	$\Delta AIC_c$	AIC weight	<i>K</i>
$\phi_{section} p_{section \times time} \lambda$	3039.22	0.00	0.74	21
$\phi_{section} p_{section \times time} \lambda_{section}$	3041.35	2.14	0.26	22

Notes: Second-order Akaike's information criterion values (AIC<sub>c</sub>), AIC<sub>c</sub> differences ( $\Delta AIC_c$ ), AIC<sub>c</sub> weights, and number of estimable parameters (*K*) are provided for both models. Subscripts give parameterization for  $\phi, p$ , and  $\lambda$ : no subscript = constant over section and time variables; "section" = variation by stream section (downstream and upstream); "time" = variation by sampling date. Subscripts joined by "×" indicate a factorial model.

TABLE 5. Monthly survival probability ( $\phi$ ), recapture probability ( $p$ ), and realized population growth rate ( $\lambda$ ) estimates for *Gyrinophilus porphyriticus* populations in the downstream (d) and upstream (u) sections of Merrill Brook from the best-fitting Pradel model (Table 4).

Parameter	Estimate	1 SE	95% CI	
			Lower	Upper
$\phi^d$	0.94	0.02	0.90	0.96
$\phi^u$	0.97	0.02	0.91	0.99
$p^d_{\text{June 1999}}$	0.14	0.04	0.08	0.23
$p^d_{\text{July 1999}}$	0.07	0.02	0.04	0.11
$p^d_{\text{August 1999}}$	0.07	0.02	0.04	0.13
$p^d_{\text{June 2000}}$	0.13	0.03	0.09	0.19
$p^d_{\text{July 2000}}$	0.11	0.02	0.07	0.16
$p^d_{\text{August 2000}}$	0.05	0.01	0.03	0.09
$p^d_{\text{June 2001}}$	0.12	0.03	0.07	0.20
$p^d_{\text{July 2001}}$	0.10	0.03	0.06	0.16
$p^d_{\text{August 2001}}$	0.03	0.01	0.02	0.06
$p^u_{\text{June 1999}}$	0.02	0.01	0.01	0.06
$p^u_{\text{July 1999}}$	0.06	0.02	0.03	0.11
$p^u_{\text{August 1999}}$	0.07	0.02	0.04	0.14
$p^u_{\text{June 2000}}$	0.07	0.02	0.04	0.12
$p^u_{\text{July 2000}}$	0.11	0.03	0.06	0.17
$p^u_{\text{August 2000}}$	0.09	0.02	0.05	0.14
$p^u_{\text{June 2001}}$	0.10	0.03	0.06	0.17
$p^u_{\text{July 2001}}$	0.08	0.02	0.05	0.15
$p^u_{\text{August 2001}}$	0.04	0.01	0.02	0.08
$\lambda$	1.01	0.01	0.98	1.03

Notes: Standard errors (SE) and 95% confidence intervals (CI) are provided for all estimates. Subscripts on  $p$  refer to sampling dates.

the upstream section (i.e.,  $\lambda \geq 1.0$ ) were dependent on high reproduction in the downstream section and immigration from that section. Alternatively, immigration from the downstream section may have reduced local reproduction in the upstream section through a density-dependent mechanism (Boughton 1999). The temporal trend in individual condition in both stream sections (1999 < 2000 < 2001) was consistent with the stability of population growth rates at above-replacement levels, suggesting that *G. porphyriticus* population dynamics were also responding to yearly variation in factors acting at the whole-stream or landscape scale, such as precipitation and temperature.

Longitudinal gradients in abiotic and biotic conditions occur in streams at multiple levels of organization, from the reach, to the stream, to the watershed (Frissell et al. 1986), and these conditions are widely acknowledged to regulate demographic rates in stream biota (Vannote et al. 1980, Schlosser 1991). Therefore, longitudinally structured spatial population dynamics similar to those documented here may underlie both local and large-scale patterns of distribution and abundance in other stream organisms. Set within stream networks, these dynamics may result in emergent ecological properties (e.g., levels of population stability, species diversity, food web complexity) that apply to other systems exhibiting fractal-like spatial structure (Grevstad and Klepetka 1992, Milne et al. 1992, Wiens et al. 1995). Working to expand the scale and taxonomic breadth of our understanding of interactions

among species movement, demography, and habitat quality will lead to novel research questions (Cuddington and Yodzis 2002, Power and Dietrich 2002) and methods (Fausch et al. 2002) that strengthen basic knowledge of stream ecology, and increase the contribution of this discipline to general ecological theory (Fisher 1997). Progress toward an empirically based, multiscale understanding of stream ecology will also improve conservation and management by closing the gap between the traditional scale of ecological investigation ( $\leq$  reach) and the scale of human impact to these systems (stream, drainage network) (Lowe 2002).

#### Dispersal in streams

What initiates movement in *G. porphyriticus* individuals? The fit of movement data to a model of simple diffusion and the temporal consistency of the movement distribution (Table 1) indicate that movement along the stream corridor was not periodic, but initiated either at random or with constant probability over time (Skellam 1951, Clobert et al. 2001). This pattern is very different from the seasonal breeding migrations of other amphibians (Gill 1978, Berven and Grudzien 1990, Dodd and Cade 1998, Trenham et al. 2001), a difference that is likely related to the hydrologic stability of the stream environment relative to that of the ponds where many amphibians breed (Wellborn et al. 1996, Skelly et al. 1999).

Consistent with this lack of periodicity, movement may be initiated by the occurrence of a temporally independent event, such as exposure to a threshold in conspecific density (Hastings 1993, Travis et al. 1999) or to a predation threat (Gilliam and Fraser 2001, Weisser 2001). The leptokurtosis of the movement distribution ( $N = 118$ , kurtosis =  $17.24 \pm 0.44$  [mean  $\pm$  1 SE],  $P < 0.002$ ; Fig. 1) suggests that movement may also be regulated by a behavioral polymorphism (Fraser et al. 2001), either independent of or interacting with a specific cue. According to this interpretation, the shape of the movement distribution reflects the behaviors of two morphotypes: "stayers," represented by values close to the 0-m mark, and "movers," which form the tails of this distribution. In future research, behavioral assays of members of these two groups will be used to test this hypothesis.

At the population level, upstream movement greatly overcompensated for downstream movement by *G. porphyriticus* individuals in Merrill Brook, both in frequency and distance (Fig. 1). Based on data from the 11 additional streams that I surveyed, this upstream bias appears to be a general characteristic of *G. porphyriticus* movement. It is especially surprising to see this bias in Merrill Brook, where it resulted in the flow of individuals from high-quality habitat (i.e., the downstream section) into low-quality habitat (i.e., the upstream section). Discharge data collected at a USGS station 3 km downstream of the confluence of Merrill

Brook and the Dead Diamond River (available online)<sup>2</sup> indicate that multiple extreme high-flow events (relative to maximum mean daily flows since 1941) occurred during the study period, yet there is little evidence that these events caused *G. porphyriticus* individuals to drift downstream (Fig. 1). Additionally, the minimal difference between the size of recently hatched larvae and the size of the smallest larvae observed and marked in this study (26 and 28 mm SVL, respectively) suggests that drift was not occurring in an unrepresented size class. Therefore, my interpretation of these results is that upstream-biased movement by *G. porphyriticus* is not a response to downstream drift. These results also suggest that the selective forces that produced the upstream bias acted over a broad geographical area, and were strong enough to withstand counteracting conditions like those in Merrill Brook. Consequently, selection for upstream movement in *G. porphyriticus* was likely driven by a consistent characteristic of its habitat, and one capable of significantly influencing individual fitness.

In addition to the flowing water, a second absolutely consistent characteristic of stream systems is the hierarchical structure, where smaller, lower order streams join to form larger, higher order streams in a pattern similar to the branching of a tree (Strahler 1952). Within this structure, the likelihood that a headwater specialist will either remain in suitable habitat (e.g., when local density of competitors or predators initiates movement) or encounter suitable habitat (e.g., during periods of potential range expansion, when selection favors colonization ability) is dependably higher when movement is biased in the upstream direction rather than the downstream direction. In species subject to fish predation, like *G. porphyriticus* (Resetarits 1991), the optimality of upstream-biased movement is reinforced by the tendency of fish to become more abundant in higher order streams and rivers (Schlosser 1991).

I propose that the upstream bias of *G. porphyriticus* movement is a result of natural selection for traits that increase the probability that the individual will locate suitable, headwater habitat within the stream continuum. Recent research by K. H. Macneale, G. E. Likens, and B. L. Peckarsky (*unpublished manuscript*) at the Hubbard Brook Experimental Forest, West Thornton, New Hampshire, USA, shows a similar upstream bias in movement by a population of the stonefly *Leuctra ferruginea*, another headwater specialist. To my knowledge, this is the first model for the evolution of dispersal predicting that a directional bias can be maintained at the species level by the landscape-scale spatial structure of a specific type of habitat. This model represents a much-needed alternative to those linking the dispersal patterns of stream organisms to drift (Chamberlin 1897). By elucidating a previously unrecognized mechanism for the evolution of directionally biased

dispersal, my results also underscore the value of empirical data on animal dispersal as a source of direction for future theoretical work.

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