Evaluating existing movement hypotheses in linear systems using larval stream salamanders

K.K. Cecala, S.J. Price, and M.E. Dorcas

Abstract: Because of their linear nature, streams provide a restrictive framework to understand the movement ecology of many animals. Stream movements have been characterized under two competing hypotheses. The colonization hypothesis dictates that small individuals experience passive drift, but concurrent, upstream movement by larger individuals replaces the loss of small individuals. Alternatively, the production hypothesis suggests that downstream movements are a consequence of limited resource availability. Previous research suggests that large larvae should move upstream and vice versa for small larvae, which should therefore be found downstream more often. We conducted a mark–recapture study of larval red salamanders (*Pseudotriton ruber* (Sonnini de Manoncourt and Latreille, 1801)) to assess the validity of these hypotheses. We found that no larvae exhibited downstream movement (skew = 0.361, $p = 0.019$; biased upstream), and large larvae were the only size cohort to exhibit directional movement upstream (skew = 0.901, $p = 0.035$). Contrary to predictions under the colonization hypothesis, small larvae were found upstream more frequently than large larvae ($N = 871$, $H = 16.29$, df = 2, $p < 0.001$). Our results suggest that larval movements are related to abiotic stream conditions, and we conclude that neither hypothesis fully explains stream movement. In the absence of drift, new movement hypotheses are necessary to describe persistent upstream movement in streams. These hypotheses should consider individual causes of movement and the direction of movements that will improve the fitness of the organism.

Résumé : À cause de leur structure linéaire, les cours d’eau fournissent un cadre restrictif pour comprendre l’écologie des déplacements chez plusieurs animaux. Les déplacements dans les cours d’eau ont été étudiés dans le cadre de deux hypothèses concurrentes. L’hypothèse de la colonisation veut que les petits individus subissent une dérive passive, mais qu’en même temps, le déplacement vers l’amont des individus de plus grande taille compense la perte des petits individus. Par ailleurs, l’hypothèse de la production avance que les déplacements vers l’aval sont la conséquence de la disponibilité limitée des ressources. Des études antérieures indiquent que les larves plus grandes devraient se déplacer vers l’amont et les larves plus petites vers l’aval; ces dernières devraient donc se retrouver plus fréquemment en aval. Nous avons mené une étude de marquage et de recapture de larves de salamandres rouges (*Pseudotriton ruber* (Sonnini de Manoncourt et Latreille, 1801)) pour évaluer la validité de ces hypothèses. Nous trouvons qu’aucune larve ne se déplace vers l’aval (asymétrie = 0,361, $p = 0.019$, favorisant l’amont) et les grandes larves sont la seule cohorte de taille à se déplacer en direction de l’amont (asymétrie = 0,901, $p = 0{,}035$). Contrairement aux prédictions de l’hypothèse de la colonisation, les petites larves se retrouvent plus souvent en amont que les grandes larves ($N = 871$, $H = 16{,}29$, dl = 2, $p < 0{,}001$). Nos résultats laissent croire que les déplacements des larves sont reliés aux conditions abiotiques du cours d’eau; ni l’une, ni l’autre des deux hypothèses n’explique donc complètement les déplacements dans le cours d’eau. En l’absence de dérive, il est nécessaire de formuler de nouvelles hypothèses sur la locomotion pour décrire le déplacement persistant vers l’amont dans les cours d’eau. Ces hypothèses devraient tenir compte des causes individuelles des déplacements et de la direction des déplacements qui améliorent la fitness des organismes.

[Traduit par la Rédaction]

Introduction

Streams provide a unique framework in which to examine animal movement. Although individual streams may be considered separate units, their branching structure and connectivity form dendritic ecological networks (Vannote et al. 1980; Lowe et al. 2006*c*; Campbell Grant et al. 2007). The hierarchal structure of stream networks can isolate populations within subnetworks or individual branches if community structure changes among stream orders (Fong and Culver 1994; Rissler et al. 2004; Robertson et al. 2008), thus increasing isolation and extirpation risk (Fagan 2002; Lowe 2002). Unlike typical lattice networks (patches and connectors), organisms that occupy dendritic ecological networks use the linear branches (or connectors) between nodes as primary habitat (Gilliam and Fraser 2001; Campbell Grant et al. 2007). Thus, even relatively weak directional bias in daily movements, such as those associated with foraging ac-

Received 1 August 2008. Accepted 11 February 2009. Published on the NRC Research Press Web site at cjz.nrc.ca on 12 March 2009.

K.K. Cecala[1,2] and M.E. Dorcas. Davidson College, Department of Biology, Davidson, NC 28035-7118, USA.
S.J. Price. Davidson College, Department of Biology, Davidson, NC 28035-7118, USA; Department of Biology, Wake Forest University, Winston-Salem, NC 27109, USA.

[1] Corresponding author (e-mail: cecalak@warnell.uga.edu).
[2] Present address: D.B. Warnell School of Forestry and Natural Resources, The University of Georgia, Athens, GA 30602, USA.

doi:10.1139/Z09-013

tivity or predator avoidance, and large-scale movements (i.e., dispersal) can have strong effects on genetic and demographic connectivity (Skalski and Gilliam 2000; Lowe et al. 2006*a*, 2006*b*). More generally, because dendritic ecological networks are linear, they provide a restrictive framework for movement by animals requiring aquatic habitat (Otto 1971; Gilliam and Fraser 2001; Siler et al. 2001).

Downstream drift is the primary pattern of movement described within streams (Waters 1965; Kohler 1985; Bruce 1986). There are two predominant hypotheses for this pattern described for stream organisms. The colonization hypothesis suggests that passive downstream movements by small individuals are replaced by concomitant upstream movements by large individuals or adults (Müller 1954; Anholt 1995), and is thus regarded as an evolutionarily stable strategy for population persistence (Kopp et al. 2001). Some researchers have suggested that downstream movements by smaller individuals may be a mechanism of dispersal (Bruce 1986), enabling these individuals to move upstream into different streams of the same order (Fagan 2002). However, recent research has shown upstream-biased movement in both larvae and adults of stream salamanders, insects, and fish, thus refuting the colonization hypothesis in some stream organisms (Skalski and Gilliam 2000; Lowe 2003; Macneale et al. 2004).

Alternatively, the production hypothesis suggests that drift is a density-dependent response to productivity of local stream patches and is therefore not a passive movement (Waters 1965; Williams and Levens 1988; Siler et al. 2001). Because headwater streams rely on the allochthonous input of carbon and other nutrients, resource availability and productivity may vary temporally and spatially (Rosi-Marshall and Wallace 2002). If productivity or carrying capacity of upstream patches decreases owing to seasonal and daily changes, movement from these areas in the form of drift is more likely to occur. Thus, under the production hypothesis, movements are variable and may exhibit seasonal or daily trends based on environmental factors (Iversen et al. 1982). Under the production hypothesis, upstream movements are unnecessary for local population persistence because drift is simply removing “excess” individuals from these populations. However, individuals that move upstream may have increased their reproductive success more than individuals that do not because their offspring will have farther to drift within a stream before encountering unsuitable habitat (Anholt 1995).

Although these patterns of movement exist, they are likely also influenced by abiotic factors and organismal life stage and size. Previous research in streams has identified several abiotic factors that influence movement of stream invertebrates including temperature and diel patterns (Glozier and Culp 1989; Williams and Williams 1993). Likewise, amphibian and fish activity and movement have been demonstrated to be affected by water temperature (Todd and Raben 1989; Adams and Frissell 2001; Marvin 2003; Todd and Winne 2006; Cecala et al. 2007*a*), but the consequences of these altered movements or activities have not been quantified. Furthermore, streams are areas where stage-specific movements occur that are related to foraging, predator avoidance, and dispersal. For example, larval stream salamanders are highly mobile (Lowe 2003), but size ranges can be extreme, yielding individuals that may be unable to resist drift and other individuals that are capable of moving upstream. Thus, if drift is passive, downstream movements may be more likely to occur at lower water temperatures when larvae are unable to move efficiently (Marvin 2003). Likewise, because of the strength and irregularity of increased stream flows caused by rainfall, animals may be unable to resist scour events and uncontrollable downstream movement (Bruce 1986; Lancaster et al. 1996; Elliott 2002).

To assess hypotheses of stream movement in streams and the role of abiotic factors, we examined the movements of larval red salamanders (*Pseudotriton ruber* (Sonnini de Manoncourt and Latreille, 1801)) in a first-order stream in the western Piedmont of North Carolina. Based on a previous study indicative of the colonization hypothesis in stream salamander larvae (Bruce 1986), we predicted that movement of larval stream salamanders would also follow this hypothesis. Specifically, we expected to find that small larvae would be prone to drift and therefore would exhibit downstream-biased movement. Alternatively, to counteract losses to drift, large larval *P. ruber* would exhibit upstream-biased movement. Because these movements will likely change the population size structure in upstream and downstream reaches, we expected to find that as a result of drift small larval *P. ruber* would be found most frequently in downstream reaches, while large larval *P. ruber* would be most abundant in upstream reaches to counteract losses to drift. Furthermore, if drift is passive, as predicted by the colonization hypothesis, we expected to find more downstream movement when temperatures were cooler and during rain events.

Materials and methods

Adult *P. ruber* are often stream-dwelling and typically oviposit in seeps and under refugia along headwater streams (Petranka 1998). Upon hatching, larvae are approximately 11 mm snout–vent length (SVL). *Pseudotriton ruber* has a multiyear larval period, with old larvae (e.g., 3 years) reaching sizes of 54 mm SVL (Petranka 1998). This variable size range encompasses all sizes of larvae of other coexisting stream salamander species and allowed us to examine the movement of large and small larvae of the same species. In general, larval salamanders are often much more abundant and remain in aquatic habitats throughout their larval period. Thus, their impact on a stream system is likely greater than adults (Hairston 1986; Petranka 1998; Tilley 1968). Larval stream salamanders provide an exceptional model to study an organism in stream systems that embodies many movement strategies common across taxonomic groups including swimming, crawling, and involuntary drift.

From May 2006 to April 2007, we studied movement by larval *P. ruber* in a first-order stream at Cowan’s Ford Wildlife Refuge in Huntersville, North Carolina (UTM coordinates 0503141 east, 3914881 north; zone 17). The study stream is permanent, its watershed is characterized primarily by mixed-hardwood forest, and the total length of the stream is 150 m. The stream is unbranched and originates from two seeps and drains into the Catawba River. During July and August of 2006, flow from these seeps was reduced and the uppermost reaches (1–2 m downstream from seep) were dry, but flow remained throughout the rest of the stream. During February and March of 2007, the Catawba River flooded, causing downstream reaches to become inundated (0–22 m from confluence with the Catawba River). Stream substrate varied throughout the stream, with upstream reaches characterized nearly entirely by detritus and downstream reaches by silt and some detritus. Middle reaches of the stream were characterized by a mixture of sand, detritus, and gravel.

To characterize the movement distributions of larval *P. ruber* within the study stream, we used capture–mark–recapture (CMR) methods. We sampled the entire length of the stream (150 m), from the seeps to the confluence with the Catawba River, once in May 2006, twice per month in June and July 2006, and once per month from August 2006 to April 2007. Sampling events consisted of four consecutive trapping days in May to July 2006 and three consecutive trapping days in August 2006 to April 2007. Sampling was conducted by placing two inverted bottle traps of different sizes (2 and 0.5 L bottles) in opposing directions within each metre of the stream (total of 300 traps; for more details see Willson and Dorcas 2003). Animals had to be moving within the stream to encounter traps. We also turned cover objects on the bank of the stream during each sampling period. The authors were present at each sampling event and ensured that the same cover objects were sampled each day.

After an animal was captured, we recorded its longitudinal position within the stream (distance from the confluence of the stream), size and direction of the trap in which it was captured, or whether the animal was under a cover object. Processing consisted of anesthetizing individuals with 1 g of maximum strength Orajel® per 1 L of tap water (Del Pharmaceuticals, Uniondale, New York; Cecala et al. 2007*b*), measuring SVL and total length (to the nearest millimetre), and individually marking each animal using visible implant elastomer (Bailey 2004; Northwest Marine Technology, Shaw Island, Washington). We completed all processing within 2 h of capture and released all animals within 0.5 m of their site of capture within the stream.

To assess environmental predictors of movement behaviour, we recorded stream-water temperature at 30 min intervals during our study using a temperature-sensitive datalogger (Tidbit Stowaway, Onset Computer Inc., Bourne, Massachusetts). We also used rainfall data collected from McGuire Nuclear Plant in Huntersville, North Carolina, approximately 5 km from our study site. For each analysis of these variables, we used daily mean temperature and rainfall total for each day of our sampling intervals.

To examine the effects of size on movement of recaptured individuals, we used growth rates of recaptured individuals to group all larval *P. ruber* into size classes (1st year, <37 mm SVL; 2nd year, 37–47 mm SVL; 3rd year, >47 mm SVL; Petranka 1998). We considered individuals to have moved if they were found >5 m from their previous capture location. We selected this value based on an assumption that movements of <5 m are more likely to be associated with daily foraging, rather than an active movement to occupy a different stream reach. We assumed our captured individuals were a random sample and evaluated a contingency table using a χ^2 test to determine if the frequency of movement by recaptured individuals differed among size cohorts (proportion of movers to nonmovers).

We calculated the moment coefficient of skew (g_3) and kurtosis (g_4) of each larval size cohort movement distribution (MINITAB version 12.1; Minitab Inc., State College, Pennsylvania). Using Student's *t* tests, we compared the skew and kurtosis of these movement distributions to those of the normal distribution (skew = 0, kurtosis = 3; Zar 1984). If the result of the Student's *t* tests for skew and kurtosis were significant, these results indicated that the distribution of movement was significantly different than a normal distribution. In the case of skew, significant results demonstrate that movement of *P. ruber* yielded net displacement of the *P. ruber* larval population to either upstream or downstream reaches (e.g., Skalski and Gilliam 2000). If kurtosis was judged to be different than a normal distribution, individuals had a higher probability of moving short distances (kurtosis > 3) or long distances (kurtosis < 3) than would be expected by a normal distribution of random (non-Markovian) movements (e.g., Fraser et al. 2001; Zhang et al. 2007). To assess the full distribution of movement by larval *P. ruber*, we included all movements made in the stream regardless of time between captures and included repeated movements by individuals. We used a Kruskal–Wallis test to compare the median of larval size distributions throughout the stream to test our hypothesis that individuals would be distributed non-normally.

We used two linear regressions to determine whether the net directionality of captures per day (difference of directional movement frequencies determined by the direction of the trap opening that captured an individual; arcsine-transformed; Sokal and Rohlf 1981) was influenced by temperature or rainfall. Only temperature and rainfall data collected during our salamander sampling periods (the day the traps were set until traps were removed) were used for these analyses. Mean values of temperature and rainfall were derived for each 24 h of our 3 or 4 day sampling to examine effects of abiotic factors on directionality of movement. For these analyses, we included only animals captured using funnel traps. We used an α of 0.05 to determine significance for all tests.

Results

We captured a total of 556 larval *P. ruber*; 253 individuals were recaptured at least once (29.04% recapture rate). Of those recaptures, 18% were recaptured within 1 m of their original capture location, 33% moved <5 m, and 49% of recaptured individuals moved >5 m between captures. Larger individuals (SVL >47 mm class) moved more frequently than smaller individuals (SVL <37 mm class; χ^2 = 13.41, df = 2, p < 0.001). The greatest distance moved per day was 19 m (38 m in 2 days; SVL = 38 mm), but the maximum distance moved between capture and recapture was 116 m upstream (SVL = 40 mm, recapture interval = 15 days) and 133 m downstream (SVL = 41 mm, recapture interval = 26 days). One individual that was recaptured three times (SVL = 52 mm) moved 38 m upstream within 14 days, 71 m downstream within 27 days, and then 105 m upstream within 88 days. Another individual was recaptured

Fig. 1. Upstream-biased movement distribution of recaptured larval red salamanders (*Pseudotriton ruber*; $N = 253$, skew = 0.361, $p = 0.0190$). Note that this distribution is leptokurtic, suggesting that most individuals remain at their location of capture, but few individuals move great distances (kurtosis = 3.988, $p < 0.001$).

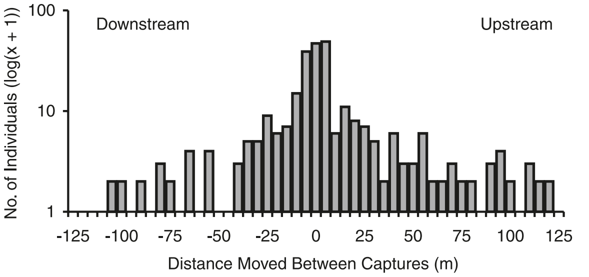


Table 1. Skew and kurtosis of movement distributions of each size cohort of larval red salamanders (*Pseudotriton ruber*).

Size cohort (mm)	Skew	*p*	Kurtosis	*p*
<37	0.358	0.109	3.789	<0.001
37–47	0.284	0.239	3.885	<0.001
>47	0.902	0.035	4.433	<0.001
All	0.361	0.019	3.988	<0.001

in the exact same metre 117 days after its first capture (SVL = 37 mm).

Overall, larvae exhibited upstream-biased movements (Fig. 1; skew = 0.361, $p = 0.019$); however, if we examine size cohorts separately, smaller larvae (<37 and 37–47 mm classes) did not exhibit directionally biased movement (Table 1), but larger larvae (>47 mm class) exhibited upstream-biased movement (Table 1). Movement distributions for all size cohorts yielded leptokurtic distributions (Fig. 1; kurtosis = 3.988, $p < 0.001$), indicating that more individuals moved long distances and remained at their point of capture than would be predicted by a normal movement distribution. Lastly, size cohorts were distributed differently throughout this stream, with greater proportions of large individuals found in downstream reaches and greater proportions of small individuals found in upstream reaches (Fig. 2; $N = 871$, $H = 16.29$, df = 2, $p < 0.001$). The net directionality of movement for all larval cohorts was unrelated to rainfall ($N = 14$, $R^2 = 0.059$, $p = 0.405$) but was positively correlated with higher daily stream-water temperature ($N = 14$, $R^2 = 0.337$, $p = 0.029$; Fig. 3). When stream-water temperatures were higher, net directionality of movement was upstream (Fig. 3). Vice versa, when stream-water temperatures were coolest, net movement was biased downstream (Fig. 3).

Fig. 2. Size distribution of larval red salamanders (*Pseudotriton ruber*) within this stream. Larger individuals (>47 mm) were found more frequently downstream (median = 65 m), whereas small individuals (<37 mm) were found more frequently upstream (median = 103; $N = 871$, $H = 16.29$, df = 2, $p < 0.001$). Each bar represents the proportion of the number of individuals of a size cohort captured in a 10 m region to the total number of that size cohort.

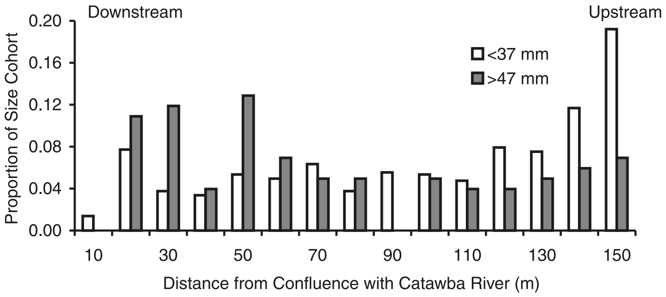
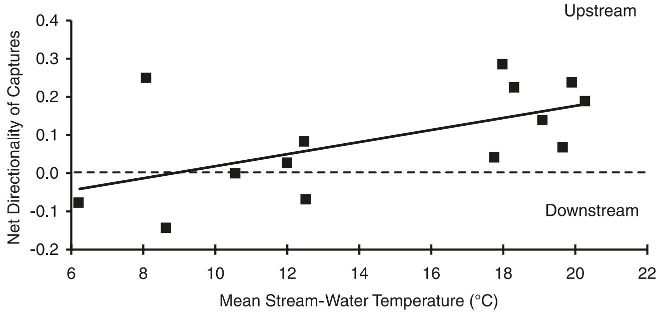


Fig. 3. Direction of movement by red salamanders (*Pseudotriton ruber*) is positively correlated with mean stream-water temperature ($y = 0.0158x - 0.1397$, $R^2 = 0.337$, $p = 0.029$). When temperatures were warmer, more larvae were captured moving upstream, but when temperatures were cooler, more larvae were captured moving downstream. Net direction of movement is the net frequency of captures moving upstream (+) or downstream (–) and the broken line represents no net direction of movement. Direction of movement was determined by the direction of the trap in which the individual was captured.



Discussion

We predicted that larvae of stream salamanders would exhibit movement consistent to the colonization hypothesis (Müller 1954; Bruce 1986; Lowe 2003). We predicted small larvae would exhibit downstream movement via drift because their small sizes reduce their capacity to avoid drift, and therefore small larvae would be most abundant in downstream reaches owing to drift. Likewise, we predicted that large larvae would exhibit upstream-biased movements to counteract downstream drift of smaller individuals, and therefore, large larvae would be most abundant in upstream reaches of a stream, consistent with the colonization hypothesis. We found that larval *P. ruber* exhibited considerable individual variation in movement behaviour, with approximately half of the individuals remaining within a few metres of their original capture location for long periods of time, and others moving over 70 m on several occasions. Our data suggest that larval *P. ruber* did not experience downstream drift, but that larger larvae were more likely to move upstream. Contrary to previous findings of Bruce (1986) and Lowe (2003) with other species of stream salamanders, we found that no size cohort exhibited downstream movement and only one size class showed upstream-biased movements. Contrary to our predictions under the colonization hypothesis, we also found that small larvae were found upstream more frequently than downstream and higher proportions of large larvae were found in downstream reaches.

Stream temperature appeared to influence the direction of larval movement. Increased water temperatures caused larvae to move upstream towards seeps containing cooler water and perhaps more permanent water. Likewise, when temperatures were cooler, relatively more larvae were captured moving downstream, which may be indicative of higher susceptibility to drift at lower temperatures (Marvin 2003). Rainfall did not appear to influence activity or direction of movement despite observations that many amphibians move more frequently during rain events (Todd and Winne 2006). Although our sampling did not encounter any heavy storm discharge, we did not detect significant downward displacement following heavy rain events between sampling occasions (K.K. Cecala, S.J. Price, and M.E. Dorcas, unpublished data). Following these heavy storm discharges, individuals may be displaced downstream and recovered to their initial position prior to our sampling, or these discharges did not affect the longitudinal position of larval *P. ruber*. Unfortunately, our sampling was unable to elucidate the relationship between heavy storm discharge and drift, but owing to our discovery of no downstream skewed movement, increased stream discharge was not likely an influential factor promoting downstream drift in this stream.

Our data did not support passive drift as an explanation of stream movement in stream salamanders. Although we observed upstream movement by large larvae consistent with the colonization hypothesis, no size cohort exhibited downstream movement as predicted by this hypothesis (Müller 1954). Typically, the colonization hypothesis has included at least two life stages (larva or adult) that may move along stream corridors in different manners. Although our study did not investigate the directional movement of adults, we found no net displacement of individuals downstream, which suggests that upstream movement was not necessary to counteract the movement of the population downstream. Therefore, because there is no net movement downstream by small larvae or all larvae, the basis of the colonization hypothesis for *P. ruber* is not supported by our results.

Our alternative hypothesis, the production hypothesis, had only limited support from our data as well (Waters 1965). Although drift under this hypothesis can be periodic and regulated by local resource availability, our only observations of net downstream movements occurred at low water temperatures found during the winter. Productivity may decline at lower temperatures (Rosemond 1994; Morin et al. 1999), but so does the metabolism of amphibians (Feder and Burggren 1992). Furthermore, during the fall and winter, allochthonous resources appear to concentrate in the upstream reaches of this stream. Therefore, drift during these periods is likely unrelated to seeking stream reaches with high resource availability. Furthermore, as temperatures cool, salamander swimming abilities decrease (Marvin 2003), which would also likely result in more downstream movement. Although we did not measure resource availability within this site, movement shifts upstream should have occurred when resources were concentrated upstream if the production hypothesis dictated these stream movements.

Overall, we found little support for the two primary movement hypotheses of stream animals, but we did find that high individual variation exists and that abiotic factors may influence the directionality of movement. Our results are contradictory to Bruce (1986) and demonstrate differences in stage-specific movements. Previous salamander movement studies have been conducted in streams greater in length than this model system (Bruce 1986; Lowe 2003). Although our results may differ owing to differences in stream length, our sampling design allowed us to survey the entire stream rather than small subsections, and we were able to examine small- and large-scale movements throughout the entire length of this stream. Although stream flow also contributes to the loss of resources to downstream reaches, our data suggests that concomitant movement downstream by larval stream salamanders is minimal. In the absence of drift, new movement hypotheses are necessary to understand why persistent upstream movement exists.

If individuals are not subject to drift by strong stream currents, they may actively move from their existing location. Reasons to move may include several the presence or absence of predators or competitors (Waser 1985; Fraser et al. 1995; Dahlgren and Eggleston 2000), habitat suitability (Winker et al. 1995; Bélanger and Rodríguez 2004), dispersal or recolonization (Fagan 2002; Lowe 2003; Macneale et al. 2004), genetic predisposition or boldness (Wilson et al. 1993; Fraser et al. 2001), or changes in life stages (Stamps 1983; Petranka 1998; Dahlgren and Eggleston 2000). Because each size cohort of larval *P. ruber* demonstrated persistent leptokurtic distributions, we conclude that larval movement was nonrandom (Gilliam and Fraser 2001). Furthermore, because some factors may have affected size cohorts differently, a single factor driving larval movements appears unlikely (Gilliam and Fraser 2001).

At our study stream, salamanders may have moved upstream to avoid predators or to find more suitable habitat (Fraser et al. 1995). One known predator of larval stream salamanders are juvenile northern water snakes (*Nerodia sipedon* (L., 1758)) found most frequently in downstream reaches of our study stream (K.K. Cecala, S.J. Price, and M.E. Dorcas, unpublished data). Therefore, if a larval salamander chose to leave its location because of the presence of a snake predator, the salamander would need to move upstream to avoid high densities of predators (Fraser et al. 1995). Likewise, suitable habitats for *P. ruber* in the North Carolina Piedmont likely have relatively permanent water at low to moderate temperatures (Petranka 1998). Changes in water condition may cause individuals to seek out areas with more favorable conditions. Seeps found in upstream reaches are often areas with access to permanent water at lower temperatures (Bilby 1984; White et al. 1987). We found high abundances of salamanders in areas surrounding the primary seeps, as well as additional side seeps (K.K. Cecala, S.J. Price, and M.E. Dorcas, unpublished data). Lastly, some researchers have suggested that reproduction at upstream reaches gives these offsprings an advantage over offsprings hatched in downstream reaches because young at upstream reaches have farther to move downstream before encountering unsuitable habitat (e.g., higher order streams; Anholt 1995). Similarly, *P. ruber* have been documented to nest underground in seeps (Petranka 1998), and small larvae (i.e., recent hatchlings) within this stream were found exclusively within upstream reaches (>100 m from confluence; K.K. Cecala, S.J. Price, and M.E. Dorcas, unpublished data). Rather than describing broad movement hypotheses in streams, we must consider the individualistic causes of movement regardless of whether they are specific to individuals (e.g., genetic predisposition; Fraser et al. 2001) or to populations (e.g., predators; Fraser et al. 1995).

Because salamanders can play a large role in regulating stream communities (Wyman 1998; Davic and Welsh 2004), more research describing the local and behavioural causes of movements may help explain patterns of productivity and community interactions in low-order streams. Lastly, understanding proximal causes of movement may assist in revising movement hypotheses to accurately reflect the variable interplay between the existing movement hypotheses or in developing new movement hypotheses.

Acknowledgements

The Davidson College Herpetology Laboratory, particularly Leigh Anne Harden, Michelle Kirlin, and Lauren McCullough, are thanked for assistance with data collection; Kim Coffey and Don Seriff of Mecklenburg Parks and Recreation are thanked for their assistance and support of our study; Gene Vaughan of Duke Power for providing rainfall data; and Winsor Lowe and the Maerz's Laboratory are thanked for many comments that improved the manuscript. Manuscript preparation was aided by the Environmental Remediation Sciences Division of the Office of Biological and Environmental Research, US Department of Energy through Financial Assistance Award number DE-FC09-96SR18546 to the University of Georgia Research Foundation. Funding was provided by the Davidson College Department of Biology; a Grant-in-Aid-of-Research administered by Sigma Xi; the Yarbrough Research Grant administered by the Collegiate Academy, North Carolina Academy of Science; Duke Power; and National Science Foundation grants (DEB-0347326 and DBI-1039153) to M.E.D.

References

Adams, S.B., and Frissell, C.A. 2001. Thermal habitat use and evidence of seasonal migration by Rocky Mountain tailed frogs, *Ascaphus montanus*, in Montana. Can. Field-Nat. **115**: 251–256.

Anholt, B.R. 1995. Density dependence resolves the stream drift paradox. Ecology, **76**: 2235–2239. doi:10.2307/1941697.

Bailey, L.L. 2004. Evaluating elastomer marking and photo identification methods for terrestrial salamanders: marking effects and observer bias. Herpetol. Rev. **35**: 38–41.

Bélanger, G., and Rodríguez, M.A. 2002. Local movement as a measure of habitat quality in stream salmonids. Environ. Biol. Fishes, **64**: 155–164. doi:10.1023/A:1016044725154.

Bilby, R.E. 1984. Characteriztics and frequency of cool-water areas in a western Washington stream. J. Freshwat. Ecol. **2**: 593–602.

Bruce, R.C. 1986. Upstream and downstream movements of *Eurycea bislineata* and other salamanders in a southern Appalachian stream. Herpetologica, **42**: 149–155.

Campbell Grant, E.H., Lowe, W.H., and Fagan, W.F. 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. Ecol. Lett. **10**: 165–175. doi:10.1111/j.1461-0248.2006.01007.x. PMID:17257104.

Cecala, K.K., Price, S.J., and Dorcas, M.E. 2007*a*. A comparison of the effectiveness of recommended doses of MS-222 (tricaine methanesulfonate) and Orajel® (benzocaine) for amphibian anesthesia. Herpetol. Rev. **38**: 63–66.

Cecala, K.K., Price, S.J., and Dorcas, M.E. 2007*b*. Diet of larval red salamanders (*Pseudotriton ruber*) examined using a nonlethal technique. J. Herpetol. **41**: 741–745. doi:10.1670/07-019.1.

Dahlgren, C.P., and Eggleston, D.B. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology, **81**: 2227–2240.

Davic, R.D., and Welsh, H.H. 2004. On the ecological roles of salamanders. Annu. Rev. Ecol. Evol. Syst. **35**: 405–434. doi:10.1146/annurev.ecolsys.35.112202.130116.

Elliott, J.M. 2002. The drift distances and time spent in the drift by freshwater shrimps, *Gammarus pulex*, in a small stony stream, and their implications for the interpretation of downstream dispersal. Freshw. Biol. **47**: 1403–1418. doi:10.1046/j.1365-2427.2002.00874.x.

Fagan, W.F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology, **83**: 3243–3249.

Feder, M.E., and Burggren, W.W. 1992. Environmental physiology of the amphibians. University of Chicago Press, Chicago.

Fong, D.W., and Culver, D.C. 1994. Fine-scale biogeography differences in the crustacean fauna of a cave system in West Virginia, USA. Hydrobiologia, **287**: 29–37. doi:10.1007/BF00006894.

Fraser, D.F., Gilliam, J.F., and Yip-Hoi, T. 1995. Predation threat as an agent of population fragmentation in a tropical watershed. Ecology, **76**: 1461–1472. doi:10.2307/1938148.

Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N., and Skalski, G.T. 2001. Explaining leptokurtic distributions: intrapopulation variation in boldness and exploration. Am. Nat. **158**: 124–135. doi:10.1086/321307. PMID:18707341.

Gilliam, J.F., and Fraser, D.F. 2001. Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. Ecology, **82**: 258–273.

Glozier, N.E., and Culp, J.M. 1989. Experimental investigations of diel vertical movements by lotic mayflies over substrate surfaces. Freshw. Biol. **21**: 253–260. doi:10.1111/j.1365-2427.1989.tb01363.x.

Hairston, N.G., Sr. 1986. Species packing in *Desmognathus* salamanders: experimental demonstration of predation and competition. Am. Nat. **127**: 266–291. doi:10.1086/284485.

Iversen, T.M., Thorup, J., and Skriver, J. 1982. Inputs and transformation of allochthonous particulate organic matter in a headwater stream. Holarct. Ecol. **5**: 10–19.

Kohler, S.L. 1985. Identification of stream drift mechanisms: an experimental and observational approach. Ecology, **66**: 1749–1761. doi:10.2307/2937371.

Kopp, M., Jeschke, J.M., and Gabriel, W. 2001. Exact compensation of stream drift as an evolutionary stable strategy. Oikos, **92**: 522–530. doi:10.1034/j.1600-0706.2001.920313.x.

Lancaster, J., Hildrew, A.G., and Gjerlov, C. 1996. Invertebrate drift and longitudinal transport processes in streams. Can. J. Fish. Aquat. Sci. **53**: 572–582. doi:10.1139/cjfas-53-3-572.

Lowe, W.H. 2002. Landscape-scale spatial population dynamics in human-impacted stream systems. Environ. Manage. **30**: 225–233. doi:10.1007/s00267-001-2687-y. PMID:12105763.

Lowe, W.H. 2003. Linking dispersal to local population dynamics: a case study using a headwater salamander system. Ecology, **84**: 2145–2154. doi:10.1890/0012-9658(2003)084[2145:LDTLPD]2.0.CO;2.

Lowe, W.H., Likens, G.E., and Cosentino, B.J. 2006*a*. Self-organisation in streams: the relationship between movement behaviour and body condition in a headwater salamander. Freshw. Biol. **51**: 2052–2062. doi:10.1111/j.1365-2427.2006.01635.x.

Lowe, W.H., Likens, G.E., McPeek, M.A., and Buso, D.C. 2006*b*. Linking direct and indirect data on dispersal: isolation by slope in a headwater stream salamander. Ecology, **87**: 334–339. doi:10.1890/05-0232. PMID:16637359.

Lowe, W.H., Likens, G.E., and Power, M.E. 2006*c*. Linking scales in stream ecology. Bioscience, **56**: 591–597. doi:10.1641/0006-3568(2006)56[591:LSISE]2.0.CO;2.

Macneale, K.H., Peckarsky, B.L., and Likens, G.E. 2004. Contradictory results from different methods for measuring direction of insect flight. Freshw. Biol. **49**: 1260–1268. doi:10.1111/j.1365-2427.2004.01266.x.

Marvin, G.A. 2003. Aquatic and terrestrial locomotor performance in a semiaquatic plethodontid salamander (*Pseudotriton ruber*): influence of acute temperature, thermal acclimation, and body size. Copeia, 2003: 704–713. doi:10.1643/HA02-108.1.

Morin, A., Lamoreux, W., and Busnarda, J. 1999. Empirical models predicting primary productivity from chlolophyll *a* and water temperatures for stream periphyton and lake and ocean phytoplankton. J. N. Am. Benthol. Soc. **18**: 299–307. doi:10.2307/1468446.

Müller, K. 1954. Investigations on the organic drift in north Swedish streams. Rep. Inst. Freshwat. Res. Drottningholm, **35**: 133–148.

Otto, C. 1971. Growth and population movements of *Potomophylax cingulatus* (Trichoptera) larvae in a south Swedish stream. Oikos, **22**: 292–301. doi:10.2307/3543853.

Petranka, J.W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C.

Rissler, L.J., Wilbur, H.M., and Taylor, D.R. 2004. The influence of ecology and genetics on behavioral variation in salamander populations across the Eastern Continental Divide. Am. Nat. **164**: 201–213. doi:10.1086/422200. PMID:15278844.

Robertson, J.M., Lips, K.R., and Heist, E.J. 2008. Fine scale gene flow and individual movements among subpopulations of *Centrolene prosoblepon* (Anura: Centrolenidae). Rev. Biol. Trop. **56**: 13–26. PMID:18624225.

Rosemond, A.D. 1994. Multiple factors limit seasonal variation in periphyton in a forest stream. J. N. Am. Benthol. Soc. **13**: 333–344. doi:10.2307/1467363.

Rosi-Marshall, E.J., and Wallace, J.B. 2002. Invertebrate food webs along a stream resource gradient. Freshw. Biol. **47**: 129–141. doi:10.1046/j.1365-2427.2002.00786.x.

Siler, E.R., Wallace, J.B., and Eggert, S.L. 2001. Long-term effects of resource limitation on stream invertebrate drift. Can. J. Fish. Aquat. Sci. **58**: 1624–1637. doi:10.1139/cjfas-58-8-1624.

Skalski, G.T., and Gilliam, J.F. 2000. Modeling diffusive spread in a heterogeneous population: a movement study with stream fish. Ecology, **81**: 1685–1700.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. W.H. Freeman and Company, San Francisco.

Stamps, J.A. 1983. The relationship between ontogenetic habitat shifts, competition, and predator avoidance in a juvenile lizard (*Anolis aeneus*). Behav. Ecol. Sociobiol. **12**: 19–33. doi:10.1007/BF00296929.

Tilley, S.G. 1968. Size–fecundity relationships and their evolutionary implications in five desmognathine salamanders. Evolution, **22**: 806–816. doi:10.2307/2406905.

Todd, B.L., and Raben, C.F. 1989. Movement and habitat use by stream-dwelling smallmouth bass. Trans. Am. Fish. Soc. **118**: 229–242. doi:10.1577/1548-8659(1989)118<0229:MAHUBS>2.3.CO;2.

Todd, B.D., and Winne, C.T. 2006. Ontogenetic and interspecific variation in timing of movement and responses to climatic factors during migrations by pond-breeding amphibians. Can. J. Zool. **84**: 715–722. doi:10.1139/Z06-054.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. **37**: 130–137. doi:10.1139/f80-017.

Waser, P.M. 1985. Does competition drive dispersal? Ecology, **66**: 1170–1175. doi:10.2307/1939169.

Waters, T.F. 1965. Interpretation of invertebrate drift in streams. Ecology, **46**: 327–334. doi:10.2307/1936336.

White, D.S., Elzinga, C.H., and Hendricks, C.P. 1987. Temperature patterns within the hyporheic zone of a northern Michigan river. J. N. Am. Benthol. Soc. **6**: 85–91. doi:10.2307/1467218.

Williams, D.D., and Levens, G.P. 1988. Evidence that hunger and limb loss can contribute to stream invertebrate drift. J. N. Am. Benthol. Soc. **7**: 180–187. doi:10.2307/1467417.

Williams, D.D., and Williams, N.E. 1993. The upstream/downstream movement paradox of lotic invertebrates: quantitative evidence from a Welsh mountain stream. Freshw. Biol. **30**: 199–218. doi:10.1111/j.1365-2427.1993.tb00802.x.

Willson, J.D., and Dorcas, M.E. 2003. Quantitative sampling of stream salamanders: a comparison of dipnetting and funnel trapping techniques. Herpetol. Rev. **34**: 128–130.

Wilson, D.S., Coleman, K., Clarke, A.B., and Biederman, L. 1993. Shy–bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. J. Comp. Psychol. **107**: 250–260. doi:10.1037/0735-7036.107.3.250.

Winker, K., Rappole, J.H., and Ramos, M.A. 1995. The use of movement data as an assay of habitat quality. Oecologia (Berl.), **101**: 211–216. doi:10.1007/BF00317286.

Wyman, A.H. 1998. Experimental assessment of salamanders as predators of detrital food webs: effects of invertebrates, decomposition and the carbon cycle. Biodivers. Conserv. **7**: 641–650. doi:10.1023/A:1008856402258.

Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, N.J.

Zhang, X., Johnson, S.N., Crawford, J.W., Gregory, P.J., and Young, I.M. 2007. A general random walk model for the leptokurtic distribution of organism movement: theory and application. Ecol. Model. **200**: 79–88. doi:10.1016/j.ecolmodel.2006.07.016.