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Self-organisation in streams: the relationship between movement behaviour and body condition in a headwater salamander

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SUMMARY

1. When movement behaviour is correlated with traits affecting fitness, it may affect population performance directly, independent of extrinsic habitat conditions.
2. In a previous 3-year, capture–recapture study, upstream movement by the salamander *Gyrinophilus porphyriticus* compensated for low reproduction in the upper 500 m of Merrill Brook, a first-order stream in northern New Hampshire (U.S.A.). This immigrant subsidy resulted from excess reproduction in the downstream section (i.e. the lower 500 m of stream length) and from consistently upstream-biased movement by salamanders. Reproduction in the two stream sections was positively correlated with mean body condition. Using 6 years of capture–recapture data, this study examines whether the movement behaviour of *G. porphyriticus* is related to body condition and thereby directly influences mean body condition and reproduction in the two sections of Merrill Brook.
3. Upstream-biased movement and greater mean body condition in the downstream section were consistent across 6 years of data collection. In Merrill Brook and four other streams, however, individuals with high body condition were more likely to move upstream and low-condition individuals were more likely to move downstream. Movement direction was unrelated to the size, sex and initial location of individuals. Body condition was positively related to growth rate, further supporting its link to reproductive potential, and positively autocorrelated through time in individuals that moved.
4. Results of this 6-year study suggest that the movement behaviour of *G. porphyriticus* partially compensated for environmental factors differentiating mean body condition and reproduction along Merrill Brook and illustrate the potential for this form of self-organisation to occur in linear habitats such as streams and rivers.

Keywords: amphibian, dispersal, *Gyrinophilus porphyriticus*, headwater streams, population biology

Introduction

To evaluate the large body of theory on how population dynamics and evolution may be influenced by the movement of individuals (e.g. Wright, 1951; Hastings, 1993; Wilson, 2001), there is a need for direct, empirical examinations of the link between movement behaviour and its population-level consequences (Clobert *et al.*, 2001; Nathan, 2001). Many theoretical predictions addressing both the demographic and evolutionary consequences of movement are derived from spatial variation in population performance across the landscape (Pulliam, 1988; McPeek & Holt, 1992; Holt & McPeek, 1996). In this context, population performance may be quantified using local carrying capacities and rates of survival and

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reproduction. Combined with the movement behaviour of a focal species, these measures of population performance determine whether an area is a net source or recipient of dispersing individuals and can therefore be used to predict demographic interdependence and genetic differentiation among habitat patches in the broader landscape (Hanski & Gilpin, 1997).

In empirical studies, spatial variation in population performance is often attributed to extrinsic habitat conditions, both abiotic (e.g. Schlosser, 1998; Kreuzer & Huntly, 2003) and biotic (e.g. Caudill, 2003; Cronin, Haynes & Dillemuth, 2004). However, when movement is correlated with other phenotypic traits, it may affect population performance directly, independent of extrinsic conditions (Roff & Fairbairn, 2001; Tyutyunov, Senina & Arditi, 2004). For example, movement can reinforce extrinsic controls on population performance when individuals with traits reducing fitness are more likely to move into low-quality, 'sink' habitat than individuals with traits increasing fitness (Holt, 1985; Pulliam, 1988). Alternatively, movement can offset extrinsic controls on population performance when low-fitness individuals are more likely to move into high-quality, 'source' habitat than high-fitness individuals. Studies examining both large-scale patterns of animal movement in freshwater systems and the individual traits associated with movement behaviour are sparse (Fraser *et al.*, 2001; Ims & Hjermann, 2001).

In a previous study, Lowe (2003) used capture–recapture analyses to examine the relationship between movement and local population dynamics in the headwater stream salamander *Gyrinophilus porphyriticus* (Green) (Plethodontidae). With 3 years of data (1999–2001) from Merrill Brook, a first-order stream in northern New Hampshire, U.S.A., this study assessed the relative contributions of local demographic processes (i.e. survival and reproduction) and dispersal to population growth rates in two sections of the steam. The stream was divided into contiguous downstream and upstream sections, defined as the lower and upper 500 m of stream length, respectively. Because of low local reproduction in the upstream section, population persistence there (i.e. $\lambda \geq 1$) was dependent on immigration from the downstream section. This immigration resulted from the combination of (i) local reproduction in the downstream section in excess of that required for population persistence there and (ii) a consistent upstream bias in the movement of *G. porphyriticus*. Upstream-biased movement was also observed in 11 other streams located throughout New Hampshire. Local reproduction in the two sections of Merrill Brook was positively correlated with mean body condition of *G. porphyriticus*, measured as size-corrected mass. This relationship supports the validity of body condition indices as measures of fitness and reproductive potential (Jakob, Marshall & Uetz, 1996; Green, 2001; Schulte-Hostedde *et al.*, 2005).

The current study examines whether movement is related to body condition in *G. porphyriticus* and thereby directly affects spatial variation in population performance along Merrill Brook. Using 6 years of capture–recapture data (1999–2004), we tested the following predictions: (i) movement behaviour is related to body condition in *G. porphyriticus* such that low-condition animals are more likely to move into the upstream section of Merrill Brook than high-condition animals and (ii) relative body condition is retained through time, independent of where an individual moves. Confirmation of these predictions would support the hypothesis that the movement behaviour of *G. porphyriticus* reinforces spatial variation in population performance along Merrill Brook (i.e. local reproduction in the downstream section > local reproduction in the upstream section). Short-term capture–recapture studies were conducted in four additional New Hampshire streams to assess the generality of the predicted relationship between body condition and movement in *G. porphyriticus*. We also used the capture–recapture data from Merrill Brook to determine whether upstream-biased movement by *G. porphyriticus* and the relationship between mean body conditions of salamanders in the two stream sections were consistent throughout the 6-year sampling period.

Methods

Study species and sites

Gyrinophilus porphyriticus belongs to the family Plethodontidae, the lungless salamanders. This species is found in small, cool, well-oxygenated streams along the Appalachian uplift, from central Alabama to southern Quebec (Petranka, 1998). Females lay eggs deep in the streambed, oviposition occurs from May to

September in the north-eastern U.S.A. (Bishop, 1941), and egg production is positively related to female size (snout-vent length, SVL; Bruce, 1972, 1978). Larvae are strictly aquatic and the larval period has been estimated to be 3–5 years, with a modal period of 4 years (Bruce, 1980). Adults are highly aquatic, but forage terrestrially at night (DeGraaf & Rudis, 1990; Deban & Marks, 2002). During the day, larvae and adults are found in interstitial spaces among the larger substratum particles of the streambed (Bruce, 2003). In the northern Appalachians, larval size range is 26–80 mm SVL and adults can reach 120 mm SVL (Lowe, 2003). In this part of the species' range, both stages feed primarily on aquatic and terrestrial invertebrates (Lowe, Nislow & Likens, 2005).

The primary study site for this work was Merrill Brook, a fishless, first-order stream in Dartmouth College's Second College Grant, located in northern New Hampshire, U.S.A. Merrill Brook flows into the fourth-order Dead Diamond River. A wetland at the confluence serves as a barrier to brook trout (*Salvelinus fontinalis* Mitchill) that might enter Merrill Brook from the larger river. This study was designed 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 with the wetland.

The predominant tree species in the Merrill Brook drainage were *Acer saccharum* (Marsh), *Betula alleghaniensis* (Britton), *Fagus grandifolia* (Erhart), *Betula papyrifera* (Marsh), *Populus tremuloides* (Michx), *Picea rubens* (Sargeant), and *Abies balsamea* (Linnaeus). Undisturbed headwater streams in New Hampshire display low conductivity (12.0–15.0 μS cm^{-1}), slight acidity (pH of 5.0–6.0), high dissolved oxygen content (80–90% saturation) and moderate mid-day temperatures in the summer (13.0–17.0 °C) (Likens & Bormann, 1995). Results of sampling throughout Merrill Brook before and during this study matched these data. Other salamanders encountered in Merrill Brook included *Eurycea bislineata* (Green) and *Desmognathus fuscus* (Green) (both Plethodontidae).

To assess the generality of the movement behaviour of *G. porphyriticus* observed in Merrill Brook, we also examined movement within 125-m long study reaches of four fishless headwater streams in the Hubbard Brook Experimental Forest (HBEF), located in central New Hampshire, U.S.A. Vegetation surrounding these streams and aquatic conditions within the streams were similar to those of Merrill Brook (Likens & Bormann, 1995).

Field methods

Salamander surveys of each section of Merrill Brook were conducted during 3-day periods in mid-June, mid-July and mid-August of 1999–2004, resulting in a total of 18 surveys of each section. A cover-controlled, active search sampling method was used (Heyer *et al.*, 1994). Moving upstream, rocks located within the channel and along the edge, and measuring between 64 and 256 mm in diameter (cobble; Platts, Megahan & Minshall, 1983) were turned. Surveys continued until 600 rocks had been turned in each section. The even distribution of cobble within both study sections allowed for a constant effort of just over one rock per metre of stream length. An aquarium dip-net was used 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 Technologies, Shaw Island, WA, U.S.A.) and marked individuals were recorded. The longitudinal position (distance from the confluence, m), length (SVL, mm) and mass (mg) of all individuals encountered were recorded. All surveys of Merrill Brook were conducted by the senior author to eliminate among-observer sampling variation.

In the HBEF streams, eight capture–recapture surveys of the 125-m long study sections were conducted at standardised intervals between 26 June and 17 July 2003. The same methods used to survey Merrill Brook were used in the HBEF streams, but 125 rocks were turned per survey. All surveys of the HBEF streams were conducted by BJC.

Analysis of movement at the population level

Movement of *G. porphyriticus* in Merrill Brook was examined at the population level to determine if the upstream bias observed in data from 1999 to 2001 was maintained through 2004. The movement of recaptured individuals was measured as the distance along the stream (m) from the position of last capture. Population-level 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. We used Kolmogorov–Smirnov tests to assess differences in (i) the movement distributions of larvae and adults and (ii) the movement distributions of animals in the downstream and upstream sections of Merrill Brook. To assess directional bias, we tested for skewness of the movement distribution (Zar, 1984). To determine if directional bias was consistent through time, we divided movement data into three groups differentiated by recapture interval: 1–2 months (within-year recaptures), 10–14 months (between-year recaptures) and ≥22 months (>1 year between recaptures). We then tested for skewness of the movement distribution of each group.

Analysis of individual movement behaviour

To analyse individual movements, recaptured individuals were first categorised into three groups according to the distance and direction of movement. 'Upstream movers' were defined as animals that had moved more than 1 m upstream since the last capture. 'Downstream movers' were defined as animals that had moved more than 1 m downstream since the last capture. All other recaptured animals were categorised as 'stayers' (i.e. movement ≤1 m in either direction). The 1-m threshold for distinguishing movers from stayers was selected based on prior analyses of movements from 1999 to 2001 (Lowe, 2003) indicating that this criterion would divide the population of recaptured individuals into roughly equal groups of upstream movers, downstream movers and stayers.

Using logistic regression, we tested the hypothesis that the movement direction of *G. porphyriticus* individuals was related to body condition. With ordinary least squares (OLS) linear regression, log-transformed SVL and mass measurements from all individuals captured in each survey were used to calculate size-corrected mass (log mg), an index of body condition (Jakob *et al.*, 1996; Green, 2001; Schulte-Hostedde *et al.*, 2005). The use of OLS linear regression was justified by the lack of statistical support for more complex models of the functional relationship between log SVL and log mass (W.H. Lowe, unpubl. data) and by the lack of significant correlations between log SVL and the residuals from these regressions (Pearson product-moment correlations: absolute value of $r < 0.0001$, $n = 30–102$, $P = 1.0$; Green, 2001).

Condition data were standardised to the range of values in each survey, resulting in standardised values between 0 and 1, then pooled across surveys for logistic regression analysis. This approach reflected the expectation that movement would be most strongly related to the condition of an individual relative to the condition of other animals in the stream at the time of initial capture. To test the assumption that these standardised condition values reflected variation in individual fitness (Schulte-Hostedde *et al.*, 2005), we used Spearman rank correlation analysis (r_s) to examine the relationship between condition at the time of capture and growth during the subsequent recapture interval (mm month^{-1}) among all recaptured individuals.

To assess alternative predictors of movement, as advocated by Ims & Hjermann (2001), we tested the hypotheses that movement direction varied with individual size (log SVL) and with initial location (m from confluence). If movement behaviour was dependent on whether an individual was captured in the downstream or upstream section of Merrill Brook, we expected to find a significant relationship between movement direction and initial location. This analysis and the Kolmogorov–Smirnov test of movement distributions in the two sections also assessed potential bias in our data resulting from the distribution of salamanders in Merrill Brook. For example, if higher abundance of salamanders in the downstream section increased the likelihood of observing upstream movements, we expected (i) movement direction to be related to initial location and (ii) a significant difference between population-level movement distributions in the two sections. The sex of 57 recaptured individuals was identified in the field using the characteristics described in Noble (1954). With these data and using a chi-squared test, we were also able to determine if sex was a predictor of movement behaviour.

For movement behaviour to contribute to a consistent difference between stream sections in mean body condition, as was observed in the 1999–2001 data set (Lowe, 2003), the relative condition of individuals that move must be positively autocorrelated through time, independent of the distance moved. To determine if this was the case in Merrill Brook, the correlation between initial condition and recapture condition in movers was examined using Pearson product-moment correlation analysis and pooling data across recapture intervals and movement distances. To assess directly if change in body condition (recapture condition – initial condition) was independent of time and distance of movement, we examined its correlation with recapture interval (months) and distance moved (m) using Spearman rank correlation analysis.

The generality of a relationship between body condition and movement direction in *G. porphyriticus* was evaluated by examining movement in the four HBEF streams. Recaptured animals were categorised as upstream movers, downstream movers and stayers using the same criteria applied to the Merrill Brook animals and we used logistic regression to examine the relationship between movement direction and body condition, size and initial location. The sex of HBEF animals was not identified. Recaptured animals were pooled across streams and sampling dates for this analysis. Because all surveys occurred within a 3-week period, body condition data were standardised to the range of values across the eight surveys of each stream.

Analysis of spatial and temporal variation in mean body condition

We used analysis of variance (ANOVA) to assess temporal variation in the mean body condition of salamanders in the two sections of Merrill Brook. Mean body condition of all previously unmarked *G. porphyriticus* individuals captured in a section was the response variable in this analysis. To avoid pseudo-replication, recaptured animals were not included in this analysis. Stream section, survey year and the section × year interaction were initially entered as sources of variability. Only significant sources were included in the final ANOVA model ($P < 0.05$). To evaluate temporal variation in condition, it was necessary to pool individuals across all surveys and to use a single regression analysis to calculated 'global' estimates of size-corrected mass.

Results

Population-level movement

A total of 972 *G. porphyriticus* individuals were marked over the 6 years of surveys of Merrill Brook. All unmarked animals captured were marked. The total number of recaptured animals was 287. Based on results of Kolmogorov-Smirnov tests, there was no difference ($P > 0.05$) between the movement distributions of larvae and adults ($n = 101$ and 186, respectively) or between the movement distributions of individuals in the downstream and upstream sections of Merrill Brook ($n = 183$ and 104, respectively). Pooling individuals across all recapture intervals, the movement distribution showed upstream bias [skewness (±SE) = 2.10 ± 0.14, $n = 287$, P (skewness = 0) < 0.002; Fig. 1), indicated by a skewness value significantly >0. Movement distributions of the three recapture-interval groups also showed significant upstream bias (1–2 months: skewness = 7.04 ± 0.24, $n = 105$, $P < 0.002$; 10–14 months: skewness =2.08 ± 0.26, $n = 86$, $P < 0.002$; ≥22 months: skewness = 1.19 ± 0.25, $n = 96$, $P < 0.002$), indicating that the directional bias was consistent through time.

Individual movements

Of the recaptured individuals, 115 were upstream movers, 84 were downstream movers and 88 were stayers. Among individuals that were recaptured twice, there was no relationship between movement category in the first recapture interval and movement category in the second recapture interval (chi-squared test: $n = 46$, $P = 0.11$). Therefore, these data were included as separate observations in analyses.

There was a significant relationship between the body condition of *G. porphyriticus* individuals and movement direction in the subsequent recapture interval (logistic regression: $\chi^2 = 5.69$, d.f. = 1, $P = 0.02$; Fig. 2): individuals with high body condition were more likely to move upstream and individuals with low body condition were more likely to move downstream. Movement direction was unrelated to individual size (logistic regression: $\chi^2 = 2.21$, d.f. = 1, $P = 0.14$), unrelated to initial location along the stream (logistic regression: $\chi^2 = 1.74$, d.f. = 1, $P = 0.19$) and unrelated to the sex of the individual (chi-squared test: $P = 0.44$, $n = 57$). The findings that the direction of movement was unrelated to initial location and that movement distributions did not differ between the two sections of Merrill Brook (Kolmogorov–Smirnov test, $P > 0.05$) indicate that our results were not biased by the distribution of individuals within the stream. Using higher thresholds to

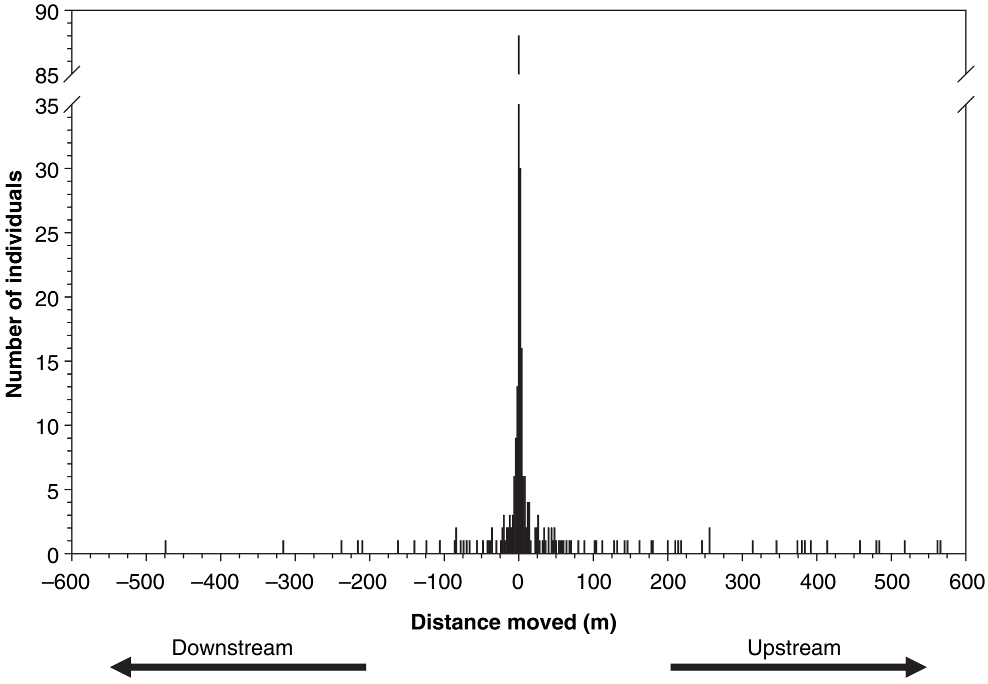

Fig. 1 Movement distribution of *Gyrinophilus porphyriticus* individuals recaptured in Merrill Brook ($n = 287$) between 1999 and 2004. Positive values represent upstream moves and negative values represent downstream moves. Data are from three surveys conducted each year in mid-June, mid-July and mid-August, and are pooled over all recapture intervals.

distinguish movers from stayers (e.g. 3 m or 5 m) had no qualitative effect on these results.

Initial condition was positively correlated with growth in the subsequent recapture interval ($r_s = 0.20$, $n = 287$, $P < 0.001$), reinforcing the validity of body condition as an index of individual fitness and reproductive potential (Bruce, 1972, 1978). Among movers, initial condition was positively correlated with recapture condition ($r = 0.35$, $n = 199$, $P < 0.001$). Eliminating from this analysis animals that were recaptured twice had little effect on the correlation ($r = 0.32$, $n = 153$, $P < 0.001$). Change in condition was unrelated to the duration of the recapture interval ($r_s = -0.14$, $n = 199$, $P = 0.06$) and unrelated to the distance moved in that interval ($r_s = -0.10$, $n = 199$, $P = 0.18$).

We observed the same relationship between body condition and movement direction in the four HBEF streams as was observed in Merrill Brook (logistic regression: $\chi^2 = 3.68$, d.f. $= 1$, $P = 0.05$). The marginal significance of this relationship in the HBEF stream may be related to sample sizes. The total number of movers in the HBEF streams, combining upstream and downstream movers, was 14. Numbers of recaptured individuals in each stream were 23, 22, 28 and 24. Movement direction was unrelated to size (logistic regression: $\chi^2 = 1.94$, d.f. $= 1$, $P = 0.16$) and initial location (logistic regression: $\chi^2 = 0.28$, d.f. $= 1$, $P = 0.6$) in the HBEF streams.

Spatial and temporal variation in mean body condition

Body condition of *G. porphyriticus* individuals was greater in the downstream section than in the upstream section of Merrill Brook across all 6 years that this study was conducted ($F = 58.83$, d.f. $= 1, 965$, $P < 0.0001$; Fig. 3). There was also a significant effect of survey year on body condition ($F = 66.0$, d.f. $= 5, 965$, $P < 0.001$), but no section × year interactive effect.

Discussion

Over 6 years of data collection, the population of *G. porphyriticus* in Merrill Brook exhibited an upstream bias in movement (Fig. 1). This bias was independent of life history stage, stream section and recapture interval. The movement of *G. porphyriticus* individuals was related to body condition but, contrary to our prediction, we found that animals with low body

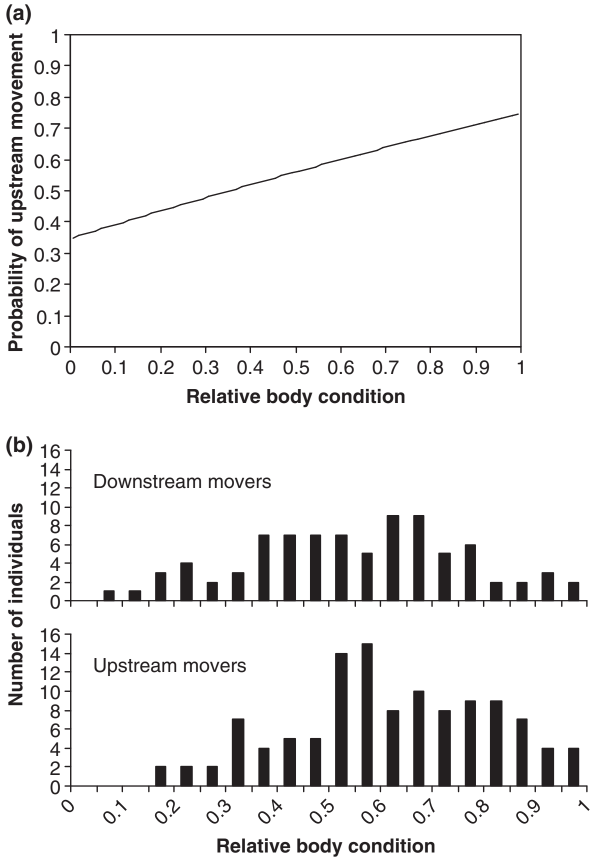

Fig. 2 (a) Line representing logistic regression predictions for the response of probability of upstream movement (1 – probability of downstream movement) to relative body condition of *Gyrinophilus porphyriticus* individuals that moved more than 1 m along Merrill Brook, New Hampshire, U.S.A., between captures. Capture–recapture surveys were conducted in mid-June, mid-July and mid-August of 1999–2004. (b) Distributions of the relative body condition of individuals that were observed moving downstream (n = 84; upper panel) and upstream (n = 115; lower panel).

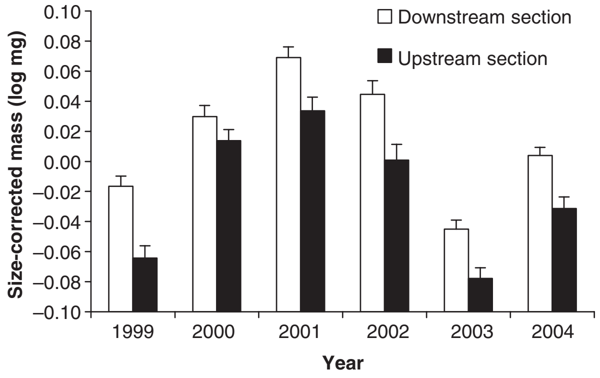

Fig. 3 Mean body condition (±SE) of *Gyrinophilus porphyriticus* individuals (size-corrected mass, log milligram) in downstream and upstream sections of Merrill Brook in 1999–2004. Data are from three surveys conducted each year in mid-June, mid-July and mid-August.

condition were more likely to move downstream and animals with high body condition were more likely to move upstream (Fig. 2). This relationship does not support the hypothesis that the movement behaviour of *G. porphyriticus* reinforces spatial variation in population performance along Merrill Brook – that is, lower mean body condition and reproduction in the upstream section relative to the downstream section (Fig. 3).

Through a mechanism of self-organisation (Kaitala, Ranta & Lundberg, 2001; Camazine *et al.*, 2003; Tyutyunov *et al.*, 2004), the movement behaviour of *G. porphyriticus* resulted in the sorting of animals with relatively high body condition into the upstream section of Merrill Brook and animals with relatively low body condition into the downstream section. The consistent difference between sections in mean body condition (Fig. 3), combined with estimates of section-scale demographic rates (Lowe, 2003), indicates that this process of self-sorting was not sufficient to compensate entirely for other factors producing variation in population performance along Merrill Brook (e.g. aquatic habitat conditions, prey availability and winter ice cover). However, the findings that relative body condition was positively related to growth rate in recaptured animals and that body condition was positively autocorrelated through time in individuals strongly suggest that the movement of *G. porphyriticus* acts to reduce – but not offset entirely – the difference between mean body condition in the two sections of Merrill Brook. We cannot yet directly assess the net effect of movers on mean body condition of *G. porphyriticus* in each section, but the strong and consistent upstream bias in population-level movement (Fig. 1) supports a model in which the compensatory effects of movement behaviour were primarily because of the transfer of high-condition individuals from the downstream section to the upstream section.

What is the cause of the relationship between body condition and movement direction in *G. porphyriticus*? This relationship was similar in Merrill Brook and the HBEF streams, which are approximately 130 km apart, suggesting that the underlying mechanism acts over a broad geographic area and may be related to consistent habitat characteristics of headwater streams. We know that direction of movement was independent of the size of the individual and its location along the stream, suggesting that this behaviour is unrelated to life history and unrelated to longitudinal trends in abiotic or biotic conditions within streams. Movement direction was also unrelated to the sex of the individual, suggesting that movement behaviour is not linked to sex-specific reproductive ecology in this species (e.g. the selection of egg-laying sites by females).

Upstream movement of high-condition animals would be expected if body condition was positively related to overall activity (e.g. Barbraud, Johnson & Bertault, 2003) and there was a genetically based directional bias in movement at the population level (Skalski & Gilliam, 2000; Roff & Fairbairn, 2001; Macneale, Peckarsky & Likens, 2005). One evolutionary hypothesis for this directional bias is that, within stream networks, the likelihood that a headwater specialist like *G. porphyriticus* will either remain in suitable habitat (e.g. when local density of competitors initiates movement) or encounter suitable habitat (e.g. during periods of range expansion) is dependably higher when movement is biased in the upstream direction rather than the downstream direction (Lowe, 2003). In an *a posteriori* analysis, we found no relationship between body condition and the distance moved by recaptured salamanders in Merrill Brook (Spearman rank correlation: $r_s = 0.003$, $n = 287$, $P = 0.96$), where distance was standardised by the length of the recapture interval in months. This result suggests that body condition is unrelated to overall activity, but there is a need for further investigation of the relationship between activity and body condition and of the evolutionary basis of upstream movement in this species.

If low-condition animals are less able to avoid in-stream conditions leading to downstream drift, such as high-discharge events (e.g. Kerby, Bunn & Hughes, 1995), this mechanism could act independently or in conjunction with the one described above to produce the observed relationship between body condition and movement direction. It is also possible that movement direction is primarily related to another trait of *G. porphyriticus* that is correlated with body condition, but was not measured in this study. Because this possibility still results in self-sorting by body condition, it does not affect our interpretation of the broader implications of the movement behaviour of *G. porphyriticus*.

Central to our conclusion that the movement of *G. porphyriticus* partially compensated for other controls on population performance along Merrill Brook is the finding that body condition was strongly and positively autocorrelated through time in individuals that moved along the stream, independent of the distance moved and the length of the recapture interval. Because physical and chemical habitat in headwater streams of the northern Appalachian Mountains is complex and heterogeneous (Likens & Bormann, 1995; DeWalle & Davies, 1997), even short-distance movements along the stream are likely to expose salamanders to new conditions affecting activity or physiology (e.g. substratum, water velocity and pH). Therefore, the autocorrelation of body condition through time may indicate that this trait has a significant genetic component, in addition to environmental controls (Merilä, 1996). Autocorrelation of body condition through time may also be related to legacy effects of developmental or ecological events occurring during the lifetime of the individual (Lindstrom, 1999).

Streams and rivers have a linear spatial structure and it is through the intersection of linear subunits that complex networks are formed (Benda *et al.*, 2004; Lowe, Likens & Power, 2006a). This study highlights an important but poorly understood consequence of this linear structure: the high potential for stream organisms to exhibit self-organisation dynamics. In species that are largely restricted to the channel or riparian corridor, including *G. porphyriticus* and other stream-associated amphibians (e.g. Storfer & Sih, 1998; Ferguson, 2000), fishes (e.g. Skalski & Gilliam, 2000; Peterson & Fausch, 2003) and many aquatic invertebrates (e.g. Hughes *et al.*, 1999; Macneale, Peckarsky & Likens, 2004), this linear structure limits large-scale movement to the downstream-upstream axis. Any correlation between individual traits and the direction of movement will lead to spatial sorting along this axis. These self-organisation dynamics may contribute to longitudinal trends in physiological activity (Taniguchi & Nakano, 2000), life history characteristics (Bruce, 1972) and genetic differentiation (Lowe *et al.*, 2006b).

The potential for self-organisation dynamics in streams and rivers also has important implications for the interpretation of dispersal rates (Pringle, 2001; Fagan, 2002; Lowe, 2002). To resolve what is known as the 'drift paradox', theory predicts that compensatory dispersal is critical to population persistence in stream organisms exposed to the advective force of the flowing water and associated loss of individuals to downstream dispersal, or drift (Müller, 1982; Anholt, 1995; Speirs & Gurney, 2001; Pachepsky *et al.*, 2005). However, several empirical studies have now documented asymmetrical rates of downstream and upstream movement in stream species (Skalski & Gilliam, 2000; Lowe, 2003; Macneale *et al.*, 2005). These data indicate that population persistence in streams and rivers is not always regulated by balanced movement in the downstream and upstream directions (Doncaster *et al.*, 1997; Kopp, Jeschke & Gabriel, 2001) and that other factors may be important in determining the demographic significance of drifting or actively dispersing individuals. If movement direction is correlated with attributes that affect individual fitness, as in the case of *G. porphyriticus*, then it is not possible to infer the demographic consequences of dispersal based on dispersal rates alone. For example, the demographic importance of downstream drift may be significantly reduced if drifting animals have low fitness. Similarly, the demographic contribution of upstream dispersers will increase as the fitness of dispersing individuals increases. These points underscore the broader value of empirical research on how individual-level attributes influence the large-scale demographic and evolutionary consequences of dispersal in streams and rivers.

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