

# Stable isotopes identify dispersal patterns of stonefly populations living along stream corridors

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## SUMMARY

1. Populations in different locations can exchange individuals depending on the distribution and connectivity of suitable habitat, and the dispersal capabilities and behaviour of the organisms. We used an isotopic tracer,  $^{15}\text{N}$ , to label stoneflies (*Leuctra ferruginea*) to determine the extent of adult flight along stream corridors and between streams where their larvae live.

2. In four mass, mark-capture experiments we added  $^{15}\text{NH}_4\text{Cl}$  continuously for several weeks to label specific regions of streams within the Hubbard Brook Experimental Forest, NH, U.S.A. We collected adult stoneflies along the labelled streams (up to 1.5 km of stream length), on transects through the forest away from labelled sections (up to 500 m), and along an 800-m reach of adjacent tributary that flows into a labelled stream.

3. Of 966 individual adult stoneflies collected and analysed for  $^{15}\text{N}$ , 20% were labelled. Most labelled stoneflies were captured along stream corridors and had flown upstream a mean distance of 211 m; the net movement of the population (upstream + downstream) estimated from the midpoint of the labelled sections was 126 m upstream. The furthest male and female travelled approximately 730 m and approximately 663 m upstream, respectively. We also captured labelled mature females along an unlabelled tributary and along a forest transect 500 m from the labelled stream, thus demonstrating cross-watershed dispersal.

4. We conclude that the adjacent forest was not a barrier to dispersal between catchments, and adult dispersal linked stonefly populations among streams across a landscape within one generation. Our data on the extent of adult dispersal provide a basis for a conceptual model identifying the boundaries of these populations, whose larvae are restricted to stream channels, and whose females must return to streams to oviposit.

*Keywords:* Hubbard Brook Experimental Forest, insect flight, mark-recapture,  $^{15}\text{N}$ , Plecoptera

## Introduction

Dispersal of individuals away from their natal or breeding habitat can affect populations at many spatial and temporal scales (Gadgil, 1971; Pearman & Wilbur, 1990; Gaines & Bertness, 1993; Palmer, Allan & Butman, 1996; Hanski, 2001). Parameters

affected include the demographics of natal populations, population dynamics in neighbouring habitats (Hanski, 2001), colonisation patterns of novel or disturbed habitats (Palmer *et al.*, 1996), and the rates at which populations become genetically distinct (Schmidt, Hughes & Bunn, 1995; Bunn & Hughes, 1997; Hughes *et al.*, 1998; Peterson & Denno, 1998; Wilcock, Hildrew & Nichols, 2001). The temporal and spatial scales of these effects will depend on the traits of the organisms and the distribution of their habitats (e.g. Butman, 1987; Peckarsky, Taylor & Caudill, 2000; McLellan & Hovey, 2001), but some general patterns

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emerge. For example, dispersal that affects local population dynamics is more frequent and from a shorter distance than dispersal required for maintaining gene flow among distant populations (Bohonak, 1999). Thus, the frequency, distances and directions of dispersal need to be known to estimate the boundaries of populations and to predict the effects of dispersal on natal and surrounding populations.

When organisms are restricted to discrete habitat patches, population boundaries are often restricted by the habitat itself (e.g. ponds). In such cases, dispersal influences not only the growth rates of local populations, but also the dynamics of the entire metapopulation (Hanski, 2001). However, many populations exist in more continuous habitats that are physically connected but distributed linearly or in a branched pattern, such as along forest edges, streams, or roadsides. In these cases, it is more challenging to define discrete boundaries of local populations.

Population boundaries and the consequences of dispersal among connected habitats will depend on the pattern of the available habitat and the permeability or resistance of the surrounding areas (the matrix) to dispersal (Delettre & Morvan, 2000; Ricketts, 2001). While genetic isolation and distance among populations are often positively correlated (Bohonak, 1999), relationships may be more complex among interconnected habitats (Michels *et al.*, 2001). For example, when habitats are connected but highly branched, dispersal may be restricted to those pathways along connected habitats, or individuals may disperse through permeable surrounding areas (Fraser *et al.*, 1999; Sieving, Willson & De Santo, 2000; Bilton, Freeland & Okamura, 2001).

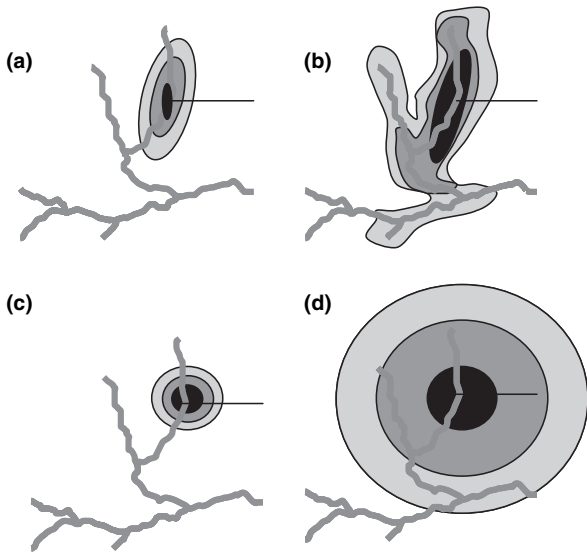
Streams are good examples of networks of connected aquatic habitats. Whether a network of stream habitats links or separates populations of aquatic organisms depends on the pattern of the network and on the dispersal behaviours of the organisms (Fisher, 1997; Hughes *et al.*, 1999, 2000; Wilcock *et al.*, 2001). The branching, hierarchical pattern along with the unidirectional flow of streams all may isolate populations in headwaters or integrate populations among different sections of streams connected by flow (Fisher, 1997; Speirs & Gurney, 2001). Certainly, for life stages or organisms restricted to stream channels, stream connectivity (distance along streams) is more relevant for predicting population boundaries than is the direct distance between streams. The degree to

which stream connectivity defines population boundaries is less clear for organisms with complex life cycles that include a terrestrial adult stage.

Despite indirect evidence from patterns of gene flow that dispersal of stream invertebrates across watersheds may be frequent (Jackson & Resh, 1992; Schmidt *et al.*, 1995; Bunn & Hughes, 1997; Hughes *et al.*, 1999; Bilton *et al.*, 2001; Kelly, Bilton & Rundle, 2001), most direct measurements of dispersal of stream invertebrates have been made within and along streams (Hershey *et al.*, 1993; Williams & Williams, 1993; Winterbourn & Crowe, 2001, but see Briers *et al.*, 2004). This linear perspective may be reasonable for taxa with aquatic stages restricted to the stream and/or with adults that stay nearby; and movement along streams and riparian areas may be most important for predicting population dynamics at the within-stream scale. Furthermore, the potentially high cost of dispersal across watersheds (Rankin & Burchsted, 1992; Bilton *et al.*, 2001) may select for dispersal along streams rather than random flight. Nonetheless, the extent of rare, cross-watershed flight by adults of aquatic insects (e.g. Griffith, Barrows & Perry, 1998; Petersen *et al.*, 1999a; Briers *et al.*, 2004) must be understood to ascertain larger-scale population boundaries and dispersal (see O'Neill, 2001).

We present two conceptual models as alternative hypotheses to predict how dispersal of terrestrial adults may affect boundaries of populations of organisms with aquatic larvae (e.g. some insects and amphibians). If the movement of adults was restricted to the stream channel or a narrow riparian zone, the distribution of adults would overlap with the stream or stream network, depending on the extent of dispersal (Fig. 1a,b). In contrast, if adult dispersal was random, the distribution of adults would not correspond with the structure of the stream or stream network (Fig. 1c,d).

We used direct measurements of adult dispersal to differentiate dispersal within and between local populations, thereby identifying population boundaries. We used distances travelled by the majority of individuals in any generation to define within-population movements, and distances travelled by a few long-distance dispersers to define movement among local populations. We also suggest that population boundaries of stream insects are not fixed, but instead may fluctuate depending on the sites from which individuals emerge as adults within the stream network.



**Fig. 1** Conceptual models as alternative hypotheses of population boundaries for stream insects with flying adults. The concentric shapes represent different probabilities that individuals emerging from a site (horizontal lines) will disperse within those areas. Darker shades indicate higher probability of dispersal (black = high, dark grey = medium and light grey = low numbers of individuals). Distributions may vary with the dispersal behaviour of adults: (a) flight distance is minimal and restricted to stream corridors; (b) flight distance is extensive and primarily along streams; (c) flight distance is minimal and random; or (d) flight distance is extensive and random, without regard to stream network.

In this study, we used  $^{15}\text{N}$  as a tracer to identify the dispersal patterns of individual adult *Leuctra ferruginea* (Walker), stoneflies whose larvae live in streams. This method enabled us to mark hundreds of thousands of dispersing individuals, thereby increasing the probability of capture and the precision of estimates of movement at a catchment scale (Macneale, Peckarsky & Likens, 2004). Our aim was to determine the distances and directions that individuals flew along streams and the frequency and potential pathways by which individuals colonised adjacent streams. We used our data to distinguish among the hypothetical patterns of population boundaries illustrated in Fig. 1.

## Methods

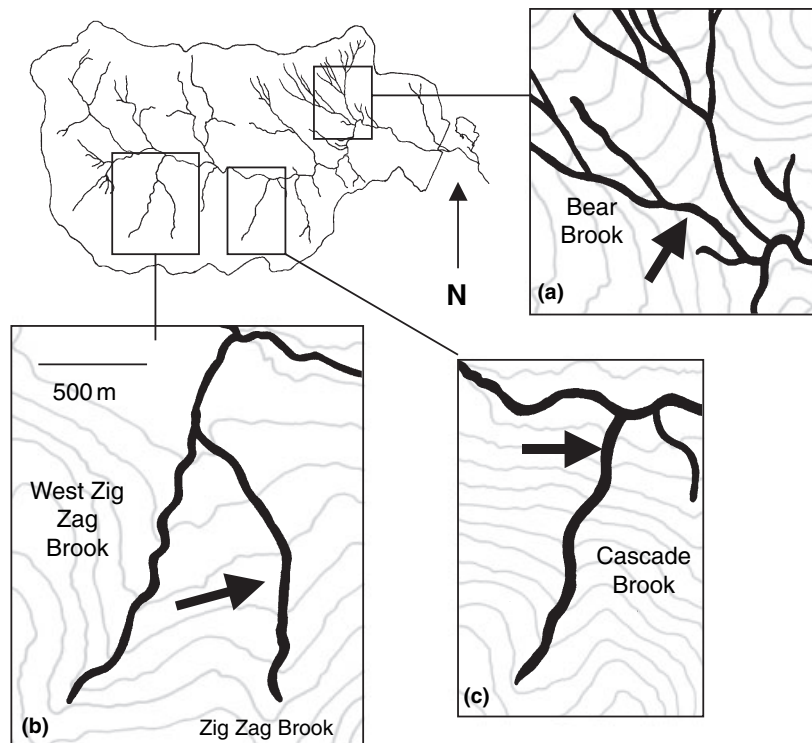
### Study system

We examined adult dispersal of *L. ferruginea* (Plecoptera; Leuctridae), within the Hubbard Brook Experi-

mental Forest (HBEF), NH, U.S.A. (latitude  $43^{\circ}56'\text{N}$ , longitude  $71^{\circ}45'\text{W}$ ; Fig. 2), a forest comprised of 30 to 40-m tall canopy trees (Likens & Bormann, 1995), and smaller streamside shrubs. Aquatic larvae live for about 10 months and feed on detritus in the HBEF streams. Larval density is highest in small headwater streams (Hall, Likens & Malcom, 2001), and dispersal via downstream drift is very low in the summer months (mean  $\pm$  SE =  $2.4 \pm 0.9$  individuals  $(100\text{ m})^{-3}$ , Macneale, 2003). Adults emerge in mid-July until late August in equal numbers, and live 4–8 weeks (Macneale, 2003). Females must feed on terrestrial vegetation to develop eggs and return to streams to oviposit; males feed as well but their increase in biomass as adults is less than that of females (Harper, 1973; Macneale, Likens & Peckarsky, 2002). Although these small stoneflies (female forewing length approximately 7 mm) have been described as 'clumsy' fliers (Hynes, 1976; Harper, 1989), they are often to be seen flying slowly many metres in one bout and are found very rarely crawling on the ground or stream bank after shedding their final larval exuviae (K.H. Macneale, personal observation).

### Marking stoneflies using $^{15}\text{N}$ additions

Marking the hundreds of thousands of stoneflies necessary to have a reasonable likelihood of capturing a representative group to measure dispersal directly was not trivial. To do so we added a  $^{15}\text{NH}_4\text{Cl}$  (10%  $^{15}\text{N}$ ) solution to three streams in HBEF (Fig. 2) over 4 years to isotopically enrich (label) the detrital food resources of stonefly larvae and ultimately the adults emerging from these streams. Details of the  $^{15}\text{N}$  additions are given in Macneale (2003) and Macneale *et al.* (2004) but are briefly summarised here. Although background concentrations of dissolved inorganic nitrogen (DIN) in these first and second order streams were low when experiments were conducted each summer ( $<5\ \mu\text{g L}^{-1}\ \text{NH}_4\text{-N}$ ,  $2\text{--}300\ \mu\text{g L}^{-1}\ \text{NO}_3\text{-N}$ ; Bernhardt, Hall & Likens, 2002), tracer-level additions resulted in no increase in nutrient concentrations (E.S. Bernhardt & K.H. Macneale, unpublished data). We used a peristaltic pump to drip the  $^{15}\text{NH}_4\text{Cl}$  solution continuously for 4–8 weeks at one point on each stream where mixing was thorough (Fig. 2). Additions were timed so that the microbial community colonising the detrital food resources was highly enriched during at least the last



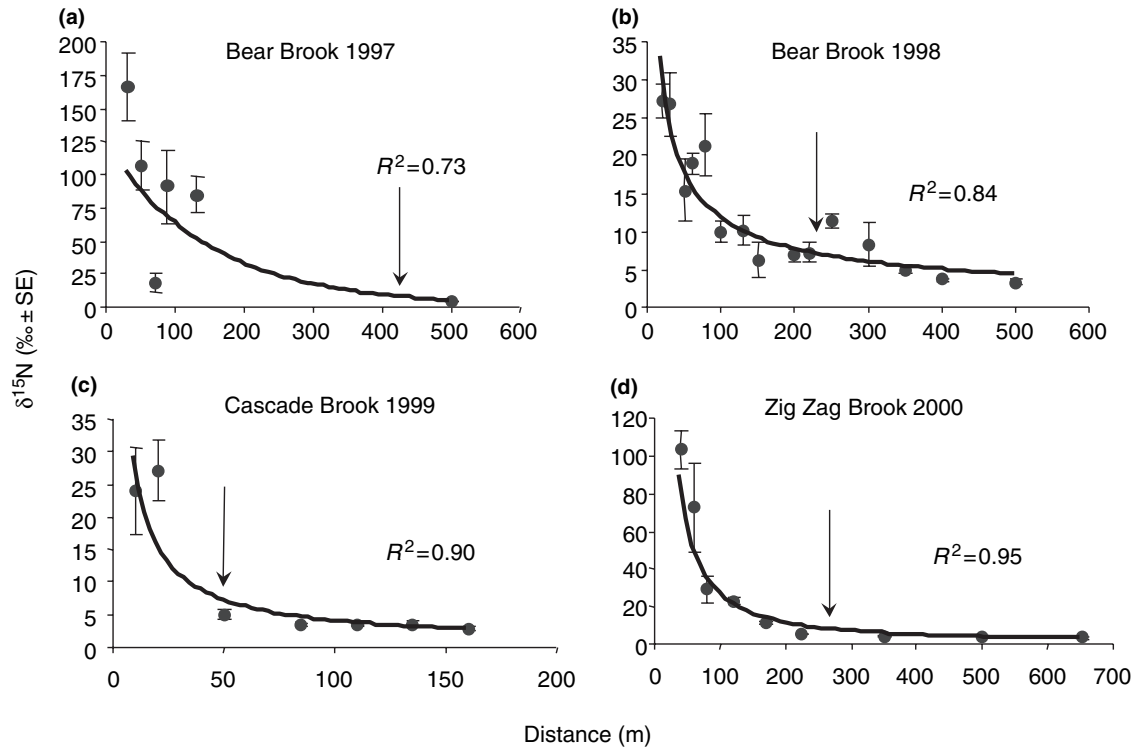
**Fig. 2** Map of the Hubbard Brook Experimental Forest, NH, U.S.A.  $^{15}\text{NH}_4\text{Cl}$  was added to each stream at sites indicated by arrows. (a) The lower reach of Bear Brook (Fisher & Likens, 1973; Meyer & Likens, 1979; Hall *et al.*, 2001), which was part of the nation-wide LINX project in 1997 (Peterson *et al.*, 2001), (b) Zig Zag Brook, and (c) Cascade Brook. Contour lines are 30.5 m, and the scale shown in (b) applies to all sites.

month of larval growth (i.e. spanning mid-June until late August). At Bear Brook in 1997 and 1998,  $^{15}\text{NH}_4\text{Cl}$  was dripped at a constant rate regardless of stream discharge. In Cascade Brook (1999) and Zig Zag Brook (2000), however, the rate of addition was adjusted daily according to discharge to standardise concentrations. The long duration and high target enrichment levels (500–1500‰ enrichment of stream water  $\text{NH}_4$ , see Macneale *et al.*, 2004) of these additions ensured sufficient labelling of the detrital microbial community and these detritus-feeding aquatic insects.

To assess the degree ( $\delta^{15}\text{N}$  of individual stoneflies) and spatial extent (metre of stream) of the enrichment, we analysed individual *L. ferruginea* emerging from up to 11 sites downstream of each addition throughout the entire *L. ferruginea* flight period (Fig. 3). The base of emergence traps rested on the stream substratum (but did not restrict movement of benthic larvae), and provided substratum on which emerging individuals crawled out and emerged (each sampled approximately  $0.12 \text{ m}^{-2}$ ). Live, freshly emerged adults were collected every 1–3 days from traps. We compared the  $\delta^{15}\text{N}$  values of potentially labelled individuals to reference (non-labelled) *L. ferruginea* emerging at least 25 m upstream of the  $^{15}\text{N}$  addition point. Reference individuals included both males and

females, because  $\delta^{15}\text{N}$  values did not differ by sex ( $\chi^2 = 0.91$ , d.f. = 1,  $P = 0.34$ ). A stonefly was considered labelled when its  $\delta^{15}\text{N}$  value was greater than a conservative threshold defined as 2 SD above the mean reference value (Macneale, 2003). For example, the mean  $\delta^{15}\text{N}$  value for reference individuals from Zig Zag Brook and West Zig Zag Brook was  $3.02\text{‰}$ , and the conservative threshold ( $\pm 2\text{SD}$ ) was  $4.25\text{‰}$ , above which we considered individuals from those streams to be labelled (Macneale, 2003; Macneale *et al.*, 2004).

However, although a female emerging with a  $\delta^{15}\text{N}$  value of  $4.5\text{‰}$  may have been enriched relative to non-labelled individuals, she did not retain a sufficient amount of that  $^{15}\text{N}$  after feeding as an adult to be detected as labelled. Because of feeding extensively on terrestrial foods, unlabelled females depleted their  $\delta^{15}\text{N}$  values by approximately  $2\text{‰}$  by the time oviposition began (Macneale, 2003). Using a mixing model to determine the depletion of  $\delta^{15}\text{N}$  in labelled females (McCutchan & Lewis, 2002, their equation 4 used for  $^{15}\text{N}$ ), we estimated that females emerging with  $\delta^{15}\text{N} < 7\text{‰}$  would effectively 'lose' their label before returning to the stream (Macneale, 2003). Accordingly, we adjusted the threshold for determining whether mature females were labelled to account for



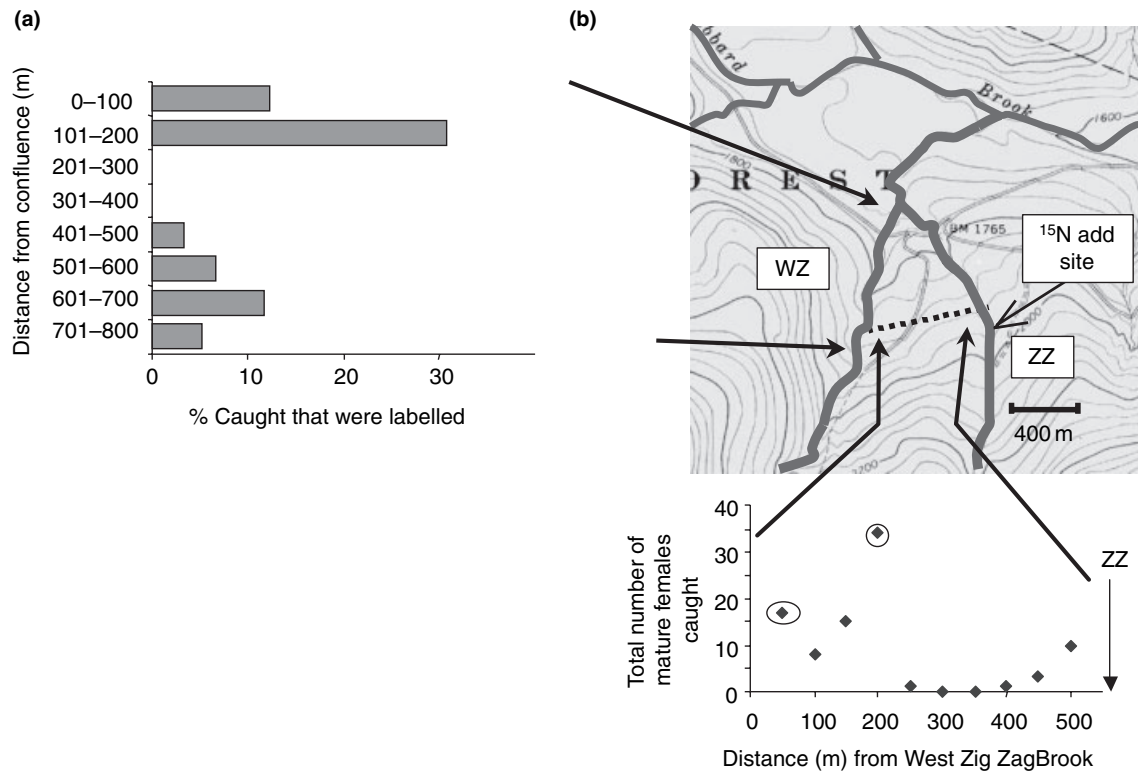
**Fig. 3** Mean ( $\pm$ SE)  $\delta^{15}\text{N}$  values (‰) of stoneflies at the sites where they emerged (distance downstream) for each  $^{15}\text{N}$  addition. Arrows indicate the effective endpoints of the labelled sections (see Macneale, 2003 for details). (a) Bear Brook 1997,  $n_{\text{total}} = 71$ . (b) Bear Brook 1998,  $n_{\text{total}} = 87$ . (c) Cascade Brook 1999,  $n_{\text{total}} = 66$ . (d) Zig Zag Brook 2000,  $n_{\text{total}} = 95$ .

adult feeding (included only those that had emerged with  $\delta^{15}\text{N} > 7\text{‰}$ , Macneale, 2003). This approach insured that the threshold for determining whether individuals were labelled was highly conservative for all streams. Individual stoneflies were frozen, degutted if guts contained food (appeared dark through the body wall), dried (oven dried for 24 h at 55 °C, or freeze dried for 24 h), pulverised, packed in aluminium tins, and weighed. Individuals were analysed using a Europa Scientific Geo 20/20 at the Cornell Laboratory for Stable Isotope Analysis, or a Europa Scientific Hydra 20/20 at the Stable Isotope Facility at the University of California, Davis, CA, U.S.A.; blind standards analysed with each set of samples at each lab showed that  $\delta^{15}\text{N}$  precision was consistently within  $\pm 0.2\text{‰}$ .

#### Capturing marked stoneflies

In all years and streams we collected dispersing adults from 500–600 m upstream to 1000 m downstream of each addition site to assess within catchment dispersal, and in 1998 and 2000 along transects

through the forest perpendicular to the labelled sections of Bear Brook and Zig Zag Brook to assess potential cross-watershed dispersal. Also in 2000, adults were caught along West Zig Zag Brook starting at the confluence of West Zig Zag and Zig Zag Brooks and extending 800 m upstream (see Fig. 4) to assess if individuals travelled into adjacent catchments. Adults were collected throughout the flight periods by hand while they were resting on vegetation and non-sticky traps, with a sweep net while they were flying, or on hanging or floating sticky traps (Macneale, 2003; Macneale *et al.*, 2004). We recorded the capture point along the stream (metre from label-addition point) for each individual collected by hand and sweep net, and in traps of all types that were spaced every 50 m along the streams. Resting stoneflies were collected by hand from non-sticky fibreglass screens (1 × 1 m), suspended approximately 1.5 m above the stream channel, one to three times per day along Bear Brook in 1997 (see Macneale *et al.*, 2004). On Zig Zag Brook, West Zig Zag Brook and Cascade Brook, we collected individuals every 2–3 days from hanging sticky traps made of 35 × 35 cm fibreglass screen, thinly coated



**Fig. 4** Dispersal of mature females from Zig Zag Brook. (a) Percentage of mature females that were caught labelled along West Zig Zag Brook (WZ). (b) Total number of mature females caught along the transect between Zig Zag (ZZ) and West Zig Zag Brooks. The circles around values indicate sites where a total of three labelled females was caught (one at 200 m, and two at 50 m from West Zig Zag Brook).

with Tangle-trap<sup>TM</sup> (The Tanglefoot Company, Grand Rapids, MI, U.S.A.) and suspended approximately 1.5 m above the stream channel or ground. Floating traps were 22 × 28 × 0.6 cm plexiglass sheets with bubble wrap or foam affixed to the bottom, and sheets of acetate on top. Tangle-trap<sup>TM</sup> was applied to each sheet, and every 2 days we removed a sheet for collection and exposed a clean sticky sheet. In the laboratory, we applied small drops of a citrus-based solvent (GooGone<sup>TM</sup>, Magic American Corporation, Cleveland, OH, U.S.A.) to the acetate sheets to help remove insects. All individuals used for isotope analyses were stored frozen until processed. Head capsule width and forewing length were measured for all individuals using an ocular micrometer (precision: head capsule width: ±0.02 mm; forewing length: ±0.08 mm).

#### *Analysis of dispersal patterns*

We collected and analysed males, immature females (those without fully developed eggs), and mature

females (those with fully developed eggs); but we focused our analyses on mature females returning to the stream to oviposit, because their movement is most relevant to the recruitment of the next generation. Mature females were often captured with extruded egg masses still attached to their abdomens, indicating they were within minutes of ovipositing.

For each labelled individual collected, we estimated the minimum linear distance it had travelled to the location where it was caught (known precisely) from its estimated site of emergence. We assumed conservatively that labelled stoneflies emerged from the midpoint of the labelled section of stream, which was halfway between the upper-most site where labelled reference individuals had emerged (upstream endpoint) and the downstream endpoint where the mean  $\delta^{15}\text{N}$  value of emerging reference stoneflies was above the threshold (approximately 7‰, vertical arrows in Fig. 3). While the use of the midpoint to estimate flight distances has the potential to introduce error in estimates of flight distance, it does not systematically bias our estimates of relative flight direction, because

the same error would presumably apply to movements upstream or downstream. From these data we estimated minimum distances flown by individuals, but did not make assumptions about flight paths or actual distances flown (see Discussion for possibilities). Finally, we estimated the total number of labelled individuals that emerged during each experiment by multiplying the estimated area of labelled stream ( $\text{m}^2$ ) by the average number of stoneflies caught in emergence traps ( $\text{m}^{-2}$ ).

## Results

### *Extent of $^{15}\text{N}$ label in stream sections as indicated by emerging stoneflies*

Addition of  $^{15}\text{N}$  effectively labelled from about 20 000 (Cascade Brook 1999) to 250 000 (Bear Brook 1998) stoneflies emerging from sections of each stream ranging in length from 40 m (Cascade Brook 1999) to 400 m (Bear Brook 1997) (Fig. 3). The  $\delta^{15}\text{N}$  values of the stoneflies emerging from the same distance downstream of  $^{15}\text{N}$ -additions also varied among streams and within the same stream (Bear Brook) between years (compare *y*-axes in Fig. 3). Much of this variation among streams and years could be attributed to the variation in stream discharge (Bear 1997 > Bear 1998 > Zig Zag 2000 > Cascade 1999; mean daily discharge of Bear 1997 during enrichment was four times that of Cascade 1999), and discharge was the best predictor of uptake lengths of DIN in streams throughout the HBEF and elsewhere in the United States (Peterson *et al.*, 2001; Bernhardt *et al.*, 2002). Variation in  $\delta^{15}\text{N}$  values of individuals emerging from the same location in any one stream (error bars in Fig. 3) was probably a function of variation in the extent of individual feeding and local variation in the extent of labelling (Macneale *et al.*, 2004). The observed range of decay distances of  $\delta^{15}\text{N}$  values was consistent with estimates of DIN uptake in streams within the HBEF (Bernhardt *et al.*, 2002), and the pattern of decay of  $\delta^{15}\text{N}$  values with distance from the addition sites was broadly consistent over years and streams (Fig. 3).

### *Distance and direction of adult dispersal along streams*

Capture rate of labelled stoneflies was quite high: of all stoneflies caught flying and analysed from sites

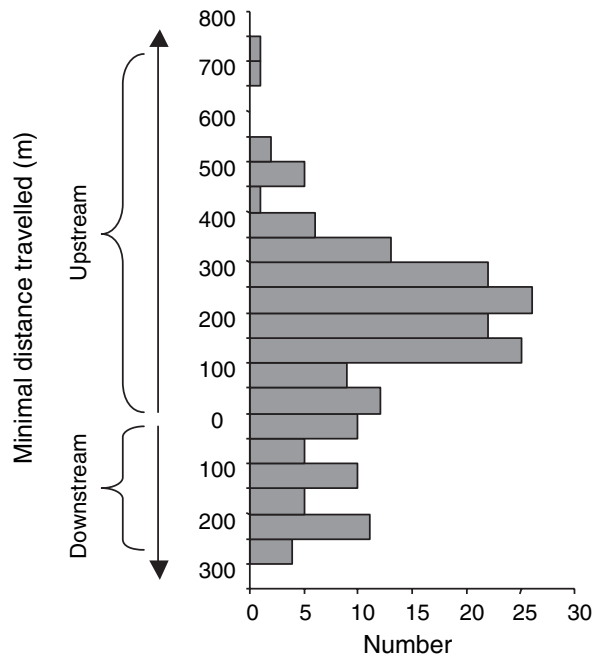


Fig. 5 Minimum distances travelled by *L. ferruginea* from the estimated sites of emergence to sites of capture, for all individuals from all streams. No net movement is represented at 0 m; 145 individuals moved upstream; 45 moved downstream.

along streams during the four experiments, 20% were labelled ( $n_{\text{total analysed}} = 966$ ,  $n_{\text{total labelled}} = 190$ ). The percentages of individuals that were caught and were labelled upstream, within, and downstream of labelled reaches were 21, 35, and 9%, respectively ( $n_{\text{total analysed}} = 446$ , 190, and 330, respectively). Strikingly, 76% of those labelled individuals had travelled upstream from their estimated sites of emergence (Fig. 5). This pattern was observed in all streams and all years (Macneale, 2003; Macneale *et al.*, 2004). The estimated mean absolute distances travelled by adult stoneflies ranged from 157 m (mature females – Cascade 1999) to 355 m (mature females – Bear 1997), but were remarkably similar among streams (Macneale *et al.*, 2004), and did not differ significantly by sex or state of maturation ( $F = 0.59$ , d.f. = 2, 187,  $P = 0.55$ ). There was no correlation between body size (head capsule width or forewing length) and distance dispersed.

### *Lateral and cross-watershed dispersal*

Analysis of 205 mature females captured along West Zig Zag Brook showed that 15 were labelled, and

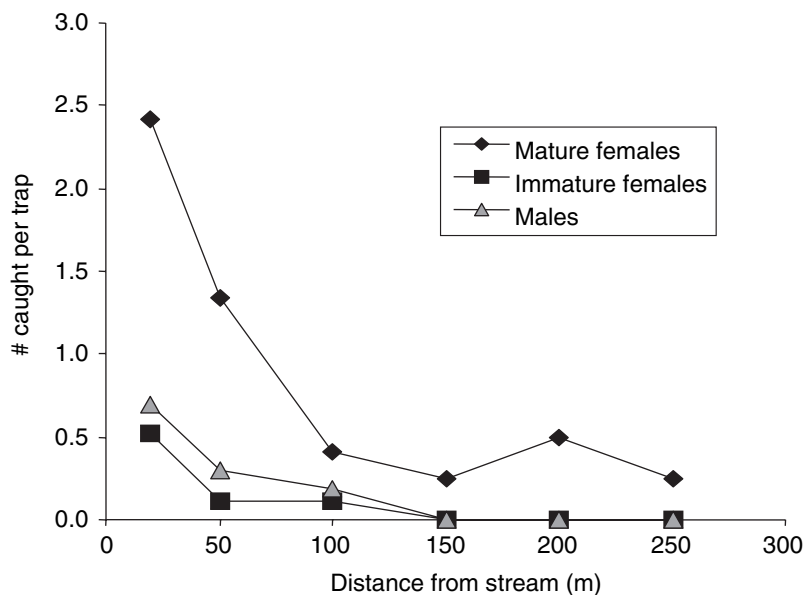
therefore had dispersed at least 500 m west from Zig Zag Brook (Fig. 4a). Those labelled individuals were caught between 50- and 800-m upstream of the confluence of the two tributaries (Fig. 2); but surprisingly, no labelled individuals were caught between 250- and 400-m upstream of the confluence, despite equal sampling effort throughout the reach (Fig. 4a). Three labelled mature females were also captured along the transect through the forest between the two tributaries; and interestingly, two of those were caught closer to West Zig Zag Brook than to the stream from which they had emerged (Fig. 4b).

For each of the 15 labelled individuals captured along West Zig Zag Brook, we used estimated emergence sites and the sites of capture to estimate dispersal distances via two potential pathways: along the stream channel or directly through the forest. In all cases the distances that females would have dispersed along the stream corridor (637–1387 m, down Zig Zag and up West Zig Zag Brooks) were greater than distances between Zig Zag and West Zig Zag Brooks through the forest (560–640 m). Also, all estimated distances through the forest were within the range of those measured for upstream movement (Fig. 5). Furthermore, if females were to have moved along the stream corridor from Zig Zag to West Zig Zag Brook, distances for 13 of the 15 females would have exceeded the maximum distance (663 m) estimated for any female moving upstream. These data, combined with our observation that few females flew

more than 200 m downstream, suggest that females flew from one branch of Zig Zag Brook to the other through the forest (Fig. 4).

Nevertheless, in the 2 years we sampled along lateral transects between streams as well as stream corridors, most adult stoneflies were caught near the streams. While catches along the entire Zig Zag transect indicate that the distribution of females may be patchy within the forest (Fig. 4b), most mature females were caught <50 m from the stream channel. In 1998, the numbers of males, immature females, and mature females caught on lateral transects west of Bear Brook dropped dramatically >50 m from the stream channel (Fig. 6). Similarly in 2000, for every mature female caught on traps hanging 50 m west of Zig Zag Brook, there were 33 females caught directly above the stream with the same trap effort. Interestingly, the greatest number of stoneflies caught in the forest (35 mature females) was at the approximate midpoint of the transect, 200 m from West Zig Zag Brook (Fig. 4b), in a flat, wet region that may attract adult stoneflies.

However, most stoneflies caught on lateral transects were not labelled, and thus had not emerged from nearby labelled stream sections (Figs 4a & 6). For all adults caught at least 20 m from the stream channel during all years, more than 75% had flown to those traps from some unlabelled stream reach, either up- or downstream, or from an adjacent stream. Furthermore, very few males or immature



**Fig. 6** Number of individuals caught per trap along transects perpendicular to the  $^{15}\text{N}$ -labelled section of Bear Brook in 1998. Individuals caught between 20 and 100 m from Bear were taken on transects east and west of Bear Brook; individuals caught over 100 m away were captured only west of Bear Brook.

adult females were caught on lateral traps during either year (e.g. Fig. 6). No males were caught on the lateral transect at Zig Zag Brook (2000), and no males were caught >100 m from Bear Brook in 1998 (Fig. 6). Therefore, most of the adult stoneflies captured in the forest were mature females that had emerged >100 m from the traps. Furthermore, the low percentage of labelled males and immature females caught far from the stream channel indicates that they also had dispersed significant distances before being captured.

## Discussion

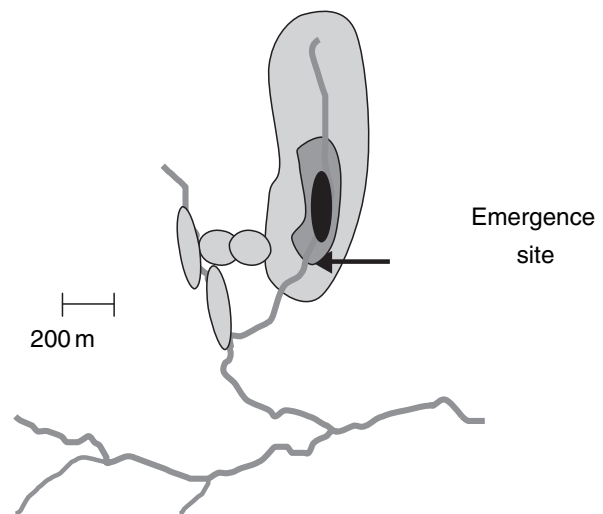
Data from four separate  $^{15}\text{N}$  additions in three different streams in the HBEF demonstrated convincingly that adult *L. ferruginea* with relatively immobile aquatic larvae dispersed predominantly upstream from where they emerged as adults. As has been observed for European *Leuctra* spp. (Kuusela & Huusko, 1996; Griffith *et al.*, 1998; Petersen *et al.*, 1999a, 2004), most adult stoneflies were captured along streams, with few travelling farther than 50 m inland from the stream edge. Surprisingly, some mature females dispersed from their natal stream and were captured along an adjacent stream. The directions and distances travelled were sufficient to enable dispersal across watersheds. Although individuals could have dispersed to the other watershed by flying downstream and then upstream along the stream corridor, that alternative route would cover distances and directions inconsistent with the known flight patterns of this species. These findings provide valuable insights about the dispersal, distribution and persistence of populations of stream insects on a landscape scale.

### *Distributions of individuals: implications for population boundaries*

The stable isotope additions enabled us to distinguish among the hypothetical models of population boundaries presented in Fig. 1. First, the predominance and distribution of individuals captured along stream channels suggest that mature females use the stream channel as a corridor (as in Fig. 1a,b), but do not disperse equally in both up- and downstream directions. Second, the capture of a few labelled mature females on the forest transect between the two

branches of Zig Zag Brook suggests that individuals can fly up to 600 m between streams through the forest. Third, the distribution of labelled females caught on the unlabelled branch of Zig Zag Brook also suggests that stoneflies had flown the shorter distance through the forest rather than the longer distances along a stream corridor (i.e. downstream along Zig Zag Brook and then back upstream West Zig Zag Brook). Therefore, we propose a conceptual model including: (i) upstream flight along the natal stream, (ii) minimal downstream flight along the natal stream, and (iii) cross-watershed dispersal to an adjacent stream (Fig. 7).

The pattern of the stream network and the distances among streams may, therefore, be as important as the connectivity of the network in predicting the degree to which *L. ferruginea* populations are isolated from one another in headwater streams. If streams in adjacent catchments were within the limits of the dispersal distances of mature females, then flying through the forest rather than along streams would be more direct, thereby reducing the potential energetic cost and risk of predation during dispersal. Therefore, the boundaries of the relatively narrow stream corridor and its position within a catchment, rather than the boundaries of the catchment itself, may influence the



**Fig. 7** A proposed model of population boundaries for *L. ferruginea* from streams in the HBEF based on data from mark-capture studies. The concentric shapes represent different probabilities that individuals emerging from a site (arrow) will disperse within those areas. Darker shades indicate higher probability of dispersal (black = high, dark grey = medium, and light grey = low numbers of individuals).

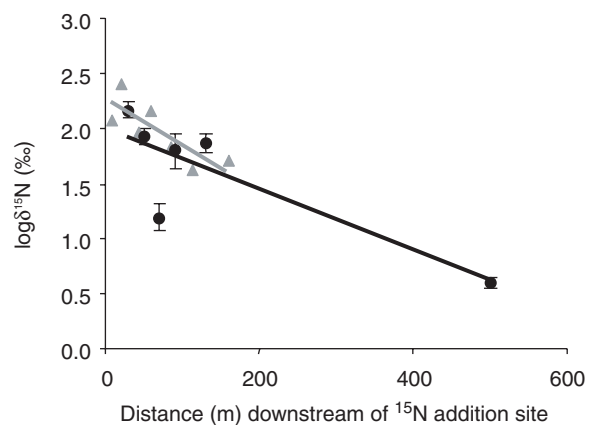
population boundaries of these stoneflies (see O'Neill, 2001).

The observed exchange of individuals between streams at a landscape scale in our study indicates that populations of stoneflies in different catchments were not isolated from one another. The maximum dispersal distances and high proportions of unlabelled stoneflies caught near the labelled stream sections indicate that significant dispersal by males or females away from their sites of emergence could occur before or after mating. Also, a small percentage of males and immature females could fly far enough to mate with individuals that emerged from other streams, and potentially populations in the uppermost reaches could exchange individuals with populations across ridges. The mean distance between the uppermost reach of Zig Zag Brook and the three nearest streams outside the Hubbard Brook Valley is 1.8 km, which is more than double the farthest dispersal distance measured in this study. Given the low probability of capturing the farthest flying individuals, we speculate that individuals could travel that far at a rate sufficient to maintain gene flow within and among populations of stoneflies in adjacent valleys. Similarly, estimates by Briers *et al.* (2004) suggest that cross-watershed dispersal of another *Leuctra* species was probably sufficient to maintain gene flow among groups across catchments, although they were not able to quantify actual dispersal rates.

Other studies have provided indirect data supporting the potential for dispersal across watersheds by aquatic insects. Wilcock *et al.* (2001) and Wilcock, Nichols & Hildrew (2003) proposed that, despite a highly fragmented larval habitat, the dispersal of a caddisfly [*Plectrocnemia conspersa* (Curtis)] over tens of kilometres was frequent, because there was little genetic differentiation along, within or among populations separated by <20 km. Smith & Collier (2001) describe similar results for another caddisfly [*Orthopsyche fimbriata* (McLachlan)] in New Zealand streams. In contrast, evidence of genetic isolation among streams in separate watersheds has been found for populations of a stonefly [*Yoraperla brevis* (Banks)] in Montana, U.S.A. (Hughes *et al.*, 1999), and a net-winged midge [*Elporia barnardi* (Edwards)] in South Africa (Wishart & Hughes, 2001), suggesting that steep mountains separating streams may be effective barriers to dispersal of aerial adult stages of some taxa.

#### Indirect evidence of low drift and upstream crawling rates

The predictable decline of individual  $\delta^{15}\text{N}$  values with distance from the addition points (Fig. 3) is attributed to the uptake dynamics of DIN but also reflects the relative sedentary behaviour of the larvae. First, no individual emerging >25 m upstream of any of the addition sites was enriched relative to individuals emerging from unlabelled streams. While this observation does not preclude the possibility that individuals crawl upstream, it suggests that few if any crawl that far. Regarding potential drift during summer, the similarity in shapes of the decay curves of  $^{15}\text{N}$ -uptake by detritus (Fig. 8) and of attached (sedentary) periphyton (J. Merriam, unpublished data) suggests that detritus transport downstream was minimal in Bear Brook (1997), despite one spate during which stream flows were as high as approximately  $450 \text{ L s}^{-1}$ . The relatively smooth decay of  $^{15}\text{N}$ -label with distance for most streams (Fig. 3), and similar slopes in the decay of  $^{15}\text{N}$  in detritus and emerging *L. ferruginea* (Fig. 8) are consistent with the hypothesis that larvae did not drift at high frequencies or over great distances during their last 2 months of development. High frequencies of *L. ferruginea* drifting into or out of the labelled section would have resulted in more



**Fig. 8** Log-transformed  $\delta^{15}\text{N}$  values of organic detritus (triangles) and mean ( $\pm$ SE)  $\delta^{15}\text{N}$  values of emerging *L. ferruginea* (circles) from Bear Brook in 1997. Detritus was collected on 29 July 1997, the last day of the  $^{15}\text{N}$ -addition, and a single, composite sample from each site was analysed (short line,  $R^2 = 0.68$ ; J. Merriam, unpublished data printed with permission). Stoneflies included in analyses emerged from 28 July to 18 August 1997 (long line fit through means,  $R^2 = 0.71$ ).

variation in the  $\delta^{15}\text{N}$  values at each site and throughout the length of the stream. These patterns corroborate measured drift densities in these streams (Macneale, 2003).

#### *Why do adults disperse upstream?*

The consistent pattern of upstream flight across streams and years indicates that individuals were either passively transported or actively flew upstream. It is unlikely that prevailing wind determined the flight direction, because we observed upstream flight in three catchments that varied in their orientation by  $180^\circ$  (Fig. 2). In addition, individuals were observed flying with and against slight breezes ( $<5 \text{ km h}^{-1}$ ) throughout the day (from 07:00 to 19:00 hours). Therefore, diurnal patterns of airflow would not explain observed dispersal patterns. From our direct observations and the data presented here, we argue that individuals actively flew upstream. In more disturbed areas with fragmented forest canopies, wind may be more important in determining dispersal distances and directions (see Briers *et al.*, 2004).

Interestingly, upstream flight and oviposition by fecund females of species with little downstream drift as larvae (Saltveit, Haug & Brittain, 2001; Siler, Wallace & Eggert, 2001) could result in individuals accumulating in the upstream reaches, suggesting that our relatively stable headwater stream populations (Macneale, 2003) may be regulated by density dependent factors (Anholt, 1995; Travis, Murrell & Dytham, 1999; Kerans, Chesson & Stein, 2000; Kopp, Jeschke & Gabriel, 2001; Hildrew *et al.*, 2004; but see Humphries, 2002). We speculate that upstream oviposition is adaptive, because those reaches are predictably of higher quality (e.g. lower interspecific competition, lower predation risk, or better abiotic conditions), as has been suggested for other taxa (Pearson & Kramer, 1972; Waters, 1972; Muller, 1982; Anholt, 1995; Peckarsky *et al.*, 2000).

Other evidence is consistent with the hypothesis that conditions in headwater streams favour better larval performance of these stoneflies. In HBEF streams the production to biomass ratio of *Leuctra* spp. in the second order Bear Brook was  $10.3 \text{ year}^{-1}$  compared with  $7.6 \text{ year}^{-1}$  in the fifth order Hubbard Brook (Hall *et al.*, 2001), indicating that upstream reaches are more productive. Both shredder density and detritus biomass were greater in the headwater

stream than in Hubbard Brook (Hall *et al.*, 2001), and the ratio of shredders to available leaf litter was lower in the headwater stream (Hall *et al.*, 2001). The predator-prey ratio was also lower in Bear Brook than in Hubbard Brook (Hall *et al.*, 2001; D. Warren, personal communication), suggesting the potential that per capita predation risk may be lower in the headwater stream. In addition, higher spring temperatures in headwater streams may increase growth rates of *L. ferruginea* (Macneale, 2003). Although the pH of HBEF streams increases with stream order (G.E. Likens & D.C. Buso, unpublished data), acidity does not appear to limit the distribution of *Leuctra* spp., which are abundant in HBEF streams with pH as low as 4.5 (Macneale, 2003). Thus, both biotic and abiotic conditions in the headwaters may favour better larval performance of these acid-tolerant stoneflies.

Our finding of a consistent pattern of upstream flight contrasts with the results of previous studies using interception traps (i.e. sticky traps, Malaise traps and window traps), which have suggested that downstream flight is as common as upstream flight in some related stonefly species (Jones & Resh, 1988; Williams & Williams, 1993; Petersen *et al.*, 1999b; but see Zwick, 1990). By using a  $^{15}\text{N}$ -label, we demonstrated definitively that the ultimate direction of dispersal was independent of the side of an interception trap on which stoneflies were captured, suggesting that conclusions about flight directions based on interception trap data without knowledge of the origin of individuals should be re-evaluated (Macneale *et al.*, 2004).

In conclusion, we propose that the dispersal patterns of adult *L. ferruginea* in the HBEF result in population boundaries that are not discrete, but instead are continuous among emergence sites and therefore along stream corridors (Fig. 7). Thus, boundaries of these populations may be influenced not only by environmental constraints affecting the distribution and quality of the aquatic habitat, but also by behavioural constraints of dispersing adults (the tendency of gravid females to fly upstream). Finally, although populations of taxa with at least one life stage restricted to a specific habitat may be concentrated within that habitat, local populations may also span the matrix between habitats (Fig. 7).

We assert that the distance and direction of adult stonefly dispersal is relevant to local population dynamics at the scale of single streams, and to persistence of populations at the landscape scale.

Most individuals at HBEF did not disperse away from their natal stream, but oviposited in stream sections upstream from their emergence sites. Cross-watershed dispersal on the scale of hundreds of metres may not be sufficiently frequent to affect population dynamics in adjacent streams, but could maintain gene flow among nearby streams. More studies, especially genetic studies paired with direct estimates of dispersal, are needed at the landscape scale to define the extent and nature of dispersal of populations of stream insects whose larvae live only within streams, but whose adults move throughout the adjacent landscape.

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### References

- Anholt B.R. (1995) Density-dependence resolves the stream drift paradox. *Ecology*, **76**, 2235–2239.
- Bernhardt E.S., Hall R.O. & Likens G.E. (2002) Whole-system estimates of nitrification and nitrate uptake in streams of the Hubbard Brook Experimental Forest. *Ecosystems*, **5**, 419–430.
- Bilton D.T., Freeland J.R. & Okamura B. (2001) Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics*, **32**, 159–181.
- Bohonak A.J. (1999) Dispersal, gene flow, and population structure. *Quarterly Review of Biology*, **74**, 21–45.
- Briers R.A., Gee J.H.R., Cariss H.M. & Geoghegan R. (2004) Inter-population dispersal by adult stoneflies detected by stable isotope enrichment. *Freshwater Biology*, **49**, 425–431.
- Bunn S.E. & Hughes J.M. (1997) Dispersal and recruitment in streams: evidence from genetic studies. *Journal of the North American Benthological Society*, **16**, 338–346.
- Butman C.A. (1987) Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanography and Marine Biology*, **25**, 113–165.
- Deletre Y.R. & Morvan N. (2000) Dispersal of adult aquatic Chironomidae (Diptera) in agricultural landscapes. *Freshwater Biology*, **44**, 399–411.
- Fisher S.G. (1997) Creativity, idea generation, and the functional morphology of streams. *Journal of the North American Benthological Society*, **16**, 305–318.
- Fisher S.G. & Likens G.E. (1973) Energy flow in Bear Brook, New Hampshire – integrative approach to stream ecosystem metabolism. *Ecological Monographs*, **43**, 421–439.
- Fraser D.F., Gilliam J.F., MacGowan M.P., Arcaro C.M. & Guillozet P.H. (1999) Habitat quality in a hostile river corridor. *Ecology*, **80**, 597–607.
- Gadgil M. (1971) Dispersal – population consequences and evolution. *Ecology*, **52**, 253–261.
- Gaines S.D. & Bertness M. (1993) The dynamics of juvenile dispersal – why field ecologists must integrate. *Ecology*, **74**, 2430–2435.
- Griffith M.B., Barrows E.M. & Perry S.A. (1998) Lateral dispersal of adult aquatic insects (Plecoptera, Trichoptera) following emergence from head-water streams in forested Appalachian catchments. *Annals of the Entomological Society of America*, **91**, 195–201.
- Hall R.O., Likens G.E. & Malcom H.M. (2001) Trophic basis of invertebrate production in 2 streams at the Hubbard Brook Experimental Forest. *Journal of the North American Benthological Society*, **20**, 432–447.
- Hanski I.A. (2001) Population dynamic consequences of dispersal in local populations and in metapopulations. In: *Dispersal* (Eds J. Colbert, E. Danchin, A.A. Dhondt & J.D. Nichols), pp. 283–298. Oxford University Press Inc., New York, USA.
- Harper P.P. (1973) Life histories of Nemouridae and Leuctridae in southern Ontario (Plecoptera). *Hydrobiologia*, **41**, 309–356.
- Harper P.P. (1989) Zoogeographical relationships of aquatic insects (Ephemeroptera, Plecoptera, and Trichoptera) from the Eastern James Bay drainage. *Canadian Field-Naturalist*, **103**, 535–546.

- Hershey A.E., Pastor J., Peterson B.J. & Kling G.W. (1993) Stable isotopes resolve the drift paradox for Baetis mayflies in an Arctic river. *Ecology*, **74**, 2315–2325.
- Hildrew A.G., Woodward G., Winterbottom J.H. & Orton S. (2004) Strong density dependence in a predatory insect: large-scale experiments in a stream. *Journal of Animal Ecology*, **73**, 448–458.
- Hughes J.M., Bunn S.E., Cleary C. & Hurwood D.A. (2000) A hierarchical analysis of the genetic structure of an aquatic insect *Bungona* (Baetidae: Ephemeroptera). *Heredity*, **85**, 561–570.
- Hughes J.M., Bunn S.E., Hurwood D.A. & Cleary C. (1998) Dispersal and recruitment of *Tasiagma ciliata* (Trichoptera: Tasiimiidae) in rainforest streams, south-eastern Australia. *Freshwater Biology*, **39**, 117–127.
- Hughes J.M., Mather P.B., Sheldon A.L. & Allendorf F.W. (1999) Genetic structure of the stonefly, *Yoraperla brevis*, populations: the extent of gene flow among adjacent montane streams. *Freshwater Biology*, **41**, 63–72.
- Humphries S. (2002) Dispersal in drift-prone macroinvertebrates: a case for density-independence. *Freshwater Biology*, **47**, 921–929.
- Hynes H.B.N. (1976) Biology of Plecoptera. *Annual Review of Entomology*, **21**, 135–153.
- Jackson J.K. & Resh V.H. (1992) Variation in genetic structure among populations of the caddisfly *Helicopsyche borealis* from three streams in northern California, U.S.A. *Freshwater Biology*, **27**, 29–42.
- Jones T.S. & Resh V.H. (1988) Movements of adult aquatic insects along a Montana (USA) springbrook. *Aquatic Insects*, **10**, 99–104.
- Kelly L.C., Bilton D.T. & Rundle S.D. (2001) Population structure and dispersal in the Canary Island caddisfly *Mesophylax aspersus* (Trichoptera, Limnephilidae). *Heredity*, **86**, 370–377.
- Kerans B.L., Chesson P.L. & Stein R.A. (2000) Assessing density-dependent establishment and dispersal: an example using caddisfly larvae. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 1190–1199.
- Kopp M., Jeschke J.M. & Gabriel W. (2001) Exact compensation of stream drift as an evolutionarily stable strategy. *Oikos*, **92**, 522–530.
- Kuusela K. & Huusko A. (1996) Post-emergence migration of stoneflies (Plecoptera) into the nearby forest. *Ecological Entomology*, **21**, 171–177.
- Likens G.E. & Bormann F.H. (1995) *Biogeochemistry of a Forested Ecosystem*. 2nd edn. Springer-Verlag, New York, USA.
- Macneale K.H. (2003) Life history and dispersal of a stonefly *Leuctra ferruginea* (Plecoptera: Leuctridae), in the Hubbard Brook Experimental Forest, New Hampshire. PhD thesis, Cornell University, Ithaca, NY, USA.
- Macneale K.H., Likens G.E. & Peckarsky B.L. (2002) Feeding strategy of an adult stonefly (Plecoptera): implications for egg production and dispersal. *Verhandlungen der Internationale Vereinigung für theoretische und angewandte Limnologie*, **28**, 1140–1146.
- Macneale K.H., Peckarsky B.L. & Likens G.E. (2004) Contradictory results from different methods for measuring direction of insect flight. *Freshwater Biology*, **49**, 1260–1268.
- McCutchan J.H. Jr & Lewis W.M. (2002) Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. *Limnology and Oceanography*, **47**, 742–752.
- McLellan B.N. & Hovey F.W. (2001) Natal dispersal of grizzly bears. *Canadian Journal of Zoology*, **79**, 838–844.
- Meyer J.L. & Likens G.E. (1979) Transport and transformation of phosphorus in a forest stream ecosystem. *Ecology*, **60**, 1255–1269.
- Michels E., Cottenie K., Neys L., De Gelas K., Coppin P. & De Meester L. (2001) Geographical and genetic distances among zooplankton populations in a set of interconnected ponds: a plea for using GIS modelling of the effective geographical distance. *Molecular Ecology*, **10**, 1929–1938.
- Muller K. (1982) The colonization cycle of freshwater insects. *Oecologia*, **52**, 202–207.
- O'Neill R.V. (2001) Is it time to bury the ecosystem concept? (with full military honors, of course!). *Ecology*, **82**, 3275–3284.
- Palmer M.A., Allan J.D. & Butman C.A. (1996) Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends in Ecology and Evolution*, **11**, 322–326.
- Pearman P.B. & Wilbur H.M. (1990) Changes in population-dynamics resulting from oviposition in a subdivided habitat. *American Naturalist*, **135**, 708–723.
- Pearson W.D. & Kramer R.H. (1972) Drift and production of two aquatic insects in a mountain stream. *Ecological Monographs*, **42**, 365–385.
- Peckarsky B.L., Taylor B.W. & Caudill C.C. (2000) Hydrologic and behavioral constraints on oviposition of stream insects: implications for adult dispersal. *Oecologia*, **125**, 186–200.
- Petersen I., Masters Z., Hildrew A.G. & Ormerod S.J. (2004) Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology*, **41**, 934–950.
- Petersen I., Winterbottom J. H., Orton S. & Hildrew A.G. (1999b) Does the colonization cycle exist? In: *Nordic Benthological Meeting, Silkeborg, Denmark, National Environmental Research Institute* (eds N. Friberg & J.D. Carl), pp. 123–126. NERI Technical Report No. 266.

- Petersen I., Winterbottom J.H., Orton S., Friberg N., Hildrew A.G., Spiers D.C. & Gurney W.S.C. (1999a) Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, U.K. *Freshwater Biology*, **42**, 401–416.
- Peterson M.A. & Denno R.F. (1998) The influence of dispersal and diet breadth on patterns of genetic isolation by distance in phytophagous insects. *American Naturalist*, **152**, 428–446.
- Peterson B.J., Wollheim W.M., Mulholland P.J. et al. (2001) Control of nitrogen export from watersheds by headwater streams. *Science*, **292**, 86–90.
- Rankin M.A. & Burchsted J.C.A. (1992) The cost of migration in insects. *Annual Review of Entomology*, **37**, 533–559.
- Ricketts T.H. (2001) The matrix matters: effective isolation in fragmented landscapes. *American Naturalist*, **158**, 87–99.
- Saltveit S.J., Haug L. & Brittain J.E. (2001) Invertebrate drift in a glacial river and its non-glacial tributary. *Freshwater Biology*, **46**, 1777–1789.
- Schmidt S.K., Hughes J.M. & Bunn S.E. (1995) Gene flow among conspecific populations of *Baetis* sp. (Ephemeroptera): adult flight and larval drift. *Journal of the North American Benthological Society*, **14**, 147–157.
- Sieving K.E., Willson M.F. & De Santo T.L. (2000) Defining corridor functions for endemic birds in fragmented south-temperate rainforest. *Conservation Biology*, **14**, 1120–1132.
- Siler E.R., Wallace J.B. & Eggert S.L. (2001) Long-term effects of resource limitation on stream invertebrate drift. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 1624–1637.
- Smith B.J. & Collier K.J. (2001) Allozyme diversity and population genetic structure of the caddisfly *Orthopsyche fimbriata* and the mayfly *Acanthophlebia cruentata* in New Zealand streams. *Freshwater Biology*, **46**, 795–805.
- Speirs D.C. & Gurney W.S.C. (2001) Population persistence in rivers and estuaries. *Ecology*, **82**, 1219–1237.
- Travis J.M.J., Murrell D.J. & Dytham C. (1999) The evolution of density-dependent dispersal. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 1837–1842.
- Waters T.F. (1972) Drift of stream insects. *Annual Review of Entomology*, **17**, 253–272.
- Wilcock H.R., Hildrew A.G. & Nichols R.A. (2001) Genetic differentiation of a European caddisfly: past and present gene flow among fragmented larval habitats. *Molecular Ecology*, **10**, 1821–1834.
- Wilcock H.R., Nichols R.A. & Hildrew A.G. (2003) Genetic population structure and neighbourhood population size estimates of the caddisfly *Plectrocnemia conspersa*. *Freshwater Biology*, **48**, 1813–1824.
- Williams D.D. & Williams N.E. (1993) The upstream/downstream movement paradox of lotic invertebrates: quantitative evidence from a Welsh mountain stream. *Freshwater Biology*, **30**, 199–218.
- Winterbourn M.J. & Crowe A.L.M. (2001) Flight activity of insects along a mountain stream: is directional flight adaptive? *Freshwater Biology*, **46**, 1479–1489.
- Wishart M.J. & Hughes J.M. (2001) Exploring patterns of population subdivision in the net-winged midge, *Elporia barnardi* (Diptera: Blephariceridae), in mountain streams of the south-western Cape, South Africa. *Freshwater Biology*, **46**, 479–490.
- Zwick P. (1990) Emergence, maturation and upstream oviposition flights of Plecoptera from the Breitenbach, with notes on the adult phase as a possible control of stream insect populations. *Hydrobiologia*, **194**, 207–223.

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