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Dispersal of adult aquatic insects in catchments of differing land use

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Summary

1. There have been widespread changes in land use in the uplands of the UK but the implications for dispersal of adult stages of aquatic invertebrates are poorly known. We estimated the lateral dispersal of adult aquatic insects (Plecoptera, Trichoptera, Ephemeroptera) in seven small, upland streams draining catchments under three categories of land use (coniferous plantation forest, cleared forest, moorland).

2. Malaise traps were set out in transects perpendicular to each stream. More than 29 000 adult insects were taken, distributed among 15 species of stoneflies, 40 species of caddisflies and eight taxa of mayflies. Overall species diversity and equitability were highest in the moorland catchments, and few species were numerous in all catchments.

3. Nearly all the mayflies were taken in the moorland catchments, where caddisflies were also most abundant. Fewest stoneflies were taken in the forested catchments.

4. The vast majority of insects were taken either directly over, or very close to, the stream channel. Half the stoneflies were taken within 18 m of the channel, while 90% had travelled less than 60 m. Caddisflies and mayflies travelled even shorter distances. Although there were differences in lateral dispersal between some catchments, there was no overall effect of land use.

5. The overall sex ratio in stoneflies and mayflies in the riparian zone was close to 1 : 1 and lateral dispersal was similar between the sexes. Male mayflies outnumbered females in the riparian zone and males travelled further from the stream, on average, than females. In catches taken directly over the stream, female stoneflies outnumbered males.
6. Regardless of land use, the flight of mayflies and caddisflies was concentrated along the stream, rather than perpendicular to it. This was also true for two numerous stoneflies (*Amphinemura sulcilcollis* and *Protonemura meyeri*) and for female stoneflies overall.

7. Synthesis and applications. The stream corridor, including the riparian strip extending 10–20 m on either side of the channel, is the main habitat for adult aquatic insects, and its management may affect the biodiversity of aquatic communities. The stream corridor is also revealed as the main 'highway' for adult dispersal. While there is no evidence from this study of an effect on interstream dispersal of land use elsewhere in the catchment, such an effect cannot yet be refuted because rare long-distance dispersal events are difficult to record.

Key-words: aquatic insects, dispersal, forestry, land use

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Introduction

For many organisms and ecosystems, basic information is still lacking on the population consequences

Correspondence: I. Petersen, School of Biological Sciences, Queen Mary, University of London, London El 4NS, UK (email I.Petersen@pcps.ucl.ac.uk). of changes in land use and habitat fragmentation (McCullough 1996). Freshwaters are naturally occurring examples of fragmented habitats scattered through a landscape that is subject to anthropogenic changes. However, as a key component of the population dynamics of aquatic insects, dispersal through the landscape has often been ignored and thus its impact on local ecological processes has been underestimated (Palmer, Allan

© 2004 British Ecological Society & Butman 1996; Rundle *et al.* 2002). No ecosystem is 'closed' to its neighbours, however, and the dynamics of populations in catchments depend upon 'inputs' and 'outputs' as well as on intrinsic processes (Peckarsky, Taylor & Caudill 2000; Hanski 2001; Bohonak & Jenkins 2003; Caudill 2003a).

Aquatic insects often have a larval stage confined to the aquatic environment, while the adult is terrestrial. Thus, while dispersal of the larvae can theoretically occur between populations if their habitats are linked by water, dispersal between unconnected aquatic systems requires overland movement by the adults. Mechanisms of dispersal within streams, such as drift and upstream larval movement, have been studied extensively (Waters 1972; Söderström 1987; Brittain & Eikeland 1988; Mackay 1992; Allan 1995; Jackson, McElravy & Resh 1999; Elliott 2002a; Elliott 2002b). Except for some assessments of the direction of flight by adult insects along the stream corridor, however, our knowledge of the dispersal of adult aquatic insects is still in its infancy (Petersen et al. 1999b; Kopp, Jeschke & Gabriel 2001; Caudill 2003b).

Only recently has more attention been given to the lateral dispersal (i.e. that away from the stream channel) of adult aquatic insects (Jackson & Resh 1989a; Sode & Wiberg-Larsen 1993; Collier & Smith 1995; Kovats, Ciborowski & Corkum 1996; Kuusela & Huusko 1996; Collier & Smith 1998; Griffith, Barrows & Perry 1998; Petersen *et al.* 1999a; Briers, Cariss & Gee 2002; Miller, Blinn & Keim 2002). Further, little is known about the impact of dispersal on larval distribution, although a few examples suggest that adult flight and female oviposition can initiate marked patchiness in populations and communities in the water itself (Statzner 1978; Harrison & Hildrew 1998; Peckarsky, Taylor & Caudill 2000).

Features that might affect the movement of adult aquatic insects among river catchments are potentially important targets for river basin management. Although the recovery of rivers affected by past environmental impacts has long been an issue in lotic ecology, the role of recolonization via interbasin dispersal is poorly described (Malmqvist et al. 1991; Bohonak & Jenkins 2003). For instance, increased landscape fragmentation might affect the recovery of stream communities from changes in water quality, such as acidification, through an impact on dispersal between streams (Bradley & Ormerod 2002). In this example, dispersal is particularly important in recovery, as acidification has often affected the whole upper reaches of river systems, thereby removing upstream populations from which recolonization could occur. Moreover, the role of catchment afforestation in acidification means that affected streams are sometimes set in extensive blocks of non-native conifers (Ormerod, Donald & Brown 1989). In the UK, more than 10% of the land area is occupied by such non-native trees, but in upland areas the cover increases substantially and sometimes involves whole subcatchments (Ormerod et al. 1993). Although

© 2004 British Ecological Society, Journal of Applied Ecology, **41**, 934–950 environmentally sound forest management is increasingly being developed, such land-use patterns might have major ramifications for dispersal and connectivity among catchments (Taylor *et al.* 1993).

Some research suggests that the riparian vegetation might influence the distribution of adult aquatic insects (Sweeney 1993; Collier, Smith & Baillie 1997; Harrison et al. 1998; Harrison & Harris 2002) but there are few convincing tests of whether the distribution and dispersal of adult aquatic insects differ between different types of land use (Collier & Smith 1995, 1998; Petersen et al. 1999a; Delettre & Morvan 2000; Briers, Cariss & Gee 2002). In densely vegetated landscapes, adult chironomids appeared to be mainly confined to the stream from which they emerged, in contrast to open landscapes where the species assemblage remained similar at different distances from the waterbody (Delettre & Morvan 2000). Petersen et al. (1999a) found that some stonefly species were more numerous in deciduous woodland than on open heath land. Similarly, the abundance and species richness of adult aquatic insects differed among catchments running through different types of forest in New Zealand (Collier & Smith 1995; Collier, Smith & Baillie 1997) and Wales (Briers, Cariss & Gee 2002). However, little is known about what determines the overall distribution of adult aquatic insects, although different factors have been suggested, such as food availability (Harper 1973), predation risk and the likelihood of encountering mates (Stewart 1994). Equally, the complexity of riparian vegetation and variation in physical factors, such as temperature, humidity, wind and light or shade, could affect distribution (Collier & Smith 1995; Petersen et al. 1999a; Delettre & Morvan 2000; Briers, Cariss & Gee 2003).

The present study is the first in which lateral dispersal is compared in replicated catchments with contrasting land use (coniferous forest, cleared forest and open moorland). We investigated whether the dispersal of stoneflies, mayflies and caddisflies differed in catchments with different type of land use and whether the distribution of males and females was similar. Finally, we compared the magnitude of lateral dispersal with that along the stream channel. This information was then used to consider the implications of upland land use on dispersal and connectivity of populations of aquatic insects in streams.

Materials and methods

STUDY SITES

The study was carried out on seven tributaries, all draining into the Llyn Brianne reservoir in mid-Wales, UK (latitude $52^{\circ}8'$ N, longitude $3^{\circ}45'$ W; Fig. 1). In previous research these streams had been designated LI 1–7 (Weatherley, Rutt & Ormerod 1989; Weatherley & Ormerod 1990) and, for comparative purposes, this nomenclature was retained. The streams were all similar in size (mean stream width 1.5 - 1.8 m) but had catchments

936 *I. Petersen* et al.



Fig. 1. Map of Llyn Brianne, mid-Wales, UK. The numbers indicate the catchments (equivalent to LI 1–7) where transects of Malaise traps were placed.

of contrasting land use, consisting of coniferous forest (two streams, LI 1 and LI 4), cleared coniferous forest (two streams, LI 2 and LI 3) and open moorland (three streams, LI 5, LI 6 and LI 7). The water chemistry and valley slope also varied among catchments (Table 1). The vegetation at the open moorland sites was dominated by grasses and mosses early in the season (mid-March to mid-June). Thereafter, bracken Pteridium aquilinum (L.) Kuhn dominated, reaching a height of about 1.8 m by the end of the study. At the forested sites there were dense plantations of sitka spruce Picea sitchensis Carriere and lodgepole pine Pinus contorta Douglas ex Loudon and the ground was covered in pine needles and mosses. The cleared catchments were felled in 1996 (LI 2) and 1999 (LI 3) and the ground cover was a mixture of grass tussocks and woody debris. Measurements of stream pH and aluminium were obtained from the Environment Agency (UK).

SAMPLING DESIGN

Adult stoneflies (Plecoptera), mayflies (Ephemeroptera) and caddisflies (Trichoptera) were caught in Malaise (1937) traps that were placed along a transect, at distances of 0, 15, 30, 45, 60 and 75 m, perpendicular to the stream channel at each of the seven tributaries. The traps were staggered 5 m on each side from the transect in order to reduce interference between them. In addition, one trap was placed directly across each stream 15 m to one side of the transect. The traps were emptied every 8 days in the period 17 March-25 September 2000 and the samples, which contained insects killed in 70% industrial methylated spirit (IMS), brought back to the laboratory for sorting. The insects were identified to species using Hynes (1977) for stoneflies, Elliott & Humpesch (1983) and Harker (1989) for mayflies and Macan (1973) and Malicky (1983) for caddisflies. Males and females were counted separately and subsequently preserved in 70% IMS. Females of the mayflies, and of the caddisflies Wormaldia and Hydropsyche, could not be identified to species. If only one species within each genus was found it was assumed that the females belonged to the same species as the identified males. However, they were identified only to genus if more than one species had been found within that genus. Data on nymphal abundance were obtained by the Catchment Research Group, University of Cardiff (Cardiff, UK), using a standardized 3-min kick-sampling procedure (Weatherley & Ormerod 1987). Samples were taken annually in March-April from 1990 to 2000.

DATA ANALYSES AND STATISTICAL METHODS

Analyses of data on adult mayflies and caddisflies were based on records from 17 March to 25 September 2000. Analysis of data on adult stoneflies was based on results from 17 March to 16 August 2000, which covered the majority of the flight periods for all but a few species.

SPECIES DIVERSITY AND EQUITABILITY

A measurement of species diversity and equitability was estimated for each site using the Shannon index of

 Table 1. Seven tributaries draining into the Llyn Brianne reservoir, mid-Wales, UK. Measurements of pH and aluminium were obtained by the Environment Agency (unpublished, public access data)

				A 1 $(1, 1, 2, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3,$	pH			
	Catchments	Land use	Catchment slope	1998 annual mean	1998 annual mean	2001 July		
LI 1	Nant y Bustach	Forest	0.34	0.39	5.08	5.12		
LI 2	Nant y Nannog	Cleared forest	0.24	0.44	4.93	5.53		
LI 3	Nant y Craflwyn	Cleared forest	0.24	ND	ND	ND		
LI4	Nant Cwmbys	Forest	0.20	0.06	6.21	6.51		
LI 5	(Innominate)	Moorland	0.45	0.03	6.09	5.63		
LI6	Nant y Craflwyn	Moorland	0.35	0.05	6.93	6.97		
LI7	Mynydd Trwsnant	Moorland	0.56	ND	ND	6.88		

diversity (H) and equitability (J). H and J were calculated, respectively, as:

$$H = -\sum_{i=1}^{S} P_i \ln P_i$$
$$J = \frac{-\sum_{i=1}^{S} P_i \ln P_i}{\ln S}$$

where P_i is the proportion of total individuals in the *i*th species and *S* is species richness (Begon, Harper & Townsend 1990).

ABUNDANCE, LATERAL DISTRIBUTION AND LAND USE

Abundance and lateral dispersal were investigated by analysis of the distribution of insects caught in each of the seven transects of Malaise traps placed perpendicular to the stream channels. Data analyses were performed on the most common species, although few species occurred at all catchments. In order to compare the dispersal pattern between catchments of differing land use, it was therefore necessary to pool the data at the level of insect order, and stoneflies, mayflies and caddisflies were examined as separate groups. This might conceal differences in dispersal among the species within orders, and the data should therefore be interpreted with some caution. However, there was no analytical alternative to the strategy adopted and, where single common species were analysed separately, few deviations from the more general pattern were revealed. For caddisflies and mayflies, few individuals were caught at LI 1 and LI 1-4, respectively, and consequently statistical analyses could not be performed on data from these catchments. As the data consisted of counts of insects at increasing distance from the stream, two models for lateral distribution were fitted (the negative exponential, $y = ae^{-bx}$, and an inverse power function, $y = ax^{-b}$, where y = numbers caught at distance x from the stream channel) by maximum likelihood using generalized linear modelling (GLM) in GENSTAT for Windows (NAG 1997), assuming a Poisson distribution likelihood with a logarithmic link function but allowing for over-dispersion of counts (Bullock & Clarke 2000; McCullagh & Nelder 1989). By using this method we circumvented the problem of zero counts, which exists in fitting models by least square regression on log- or log-log-transformed data (Bullock & Clarke 2000). A comparison of the mean residual deviance between the models generated on the basis of the exponential and power functions showed that the latter gave a consistently better fit to the observed data, and this model was consequently used.

© 2004 British Ecological Society, Journal of Applied Ecology, **41**, 934–950 For each of the common species, and the three insect orders, one GLM was first fitted to all data (model a: constant + distance), the result of which indicated whether the catch declined with distance from the stream channel. The distance from the stream was then used as the covariate in further analysis. By adding terms to the GLM (model b: model a + catchment; model c: model b + distance × catchment), additional effects of differences in abundance between catchments and the interaction between distance and catchment were examined. A significant result of the latter indicated that dispersal differed between the individual catchments. The comparisons were made on the basis of the difference in residual deviance between the models. As the residual difference had a χ^2 distribution, it was possible to evaluate whether a more complex model should be preferred to a simpler one (McConway, Jones & Taylor 1999). Examination of the effect of land use was performed in a similar way: the catchment term in the models was replaced with land use and comparisons were made between the three types [model d: model a + land (use); model e: model $d + distance \times land (use)$]. Pairwise comparison was made between the estimated parameters by means of t-statistics (McConway, Jones & Taylor 1999) to find which differed from which. Adjustments for multiple comparisons were made by sequential Bonferroni procedure (Holm 1979), in which the P-values were ranked and the smallest value were tested at the 0.05/c significance level, the next at 0.05/c(c-1), etc., where c equals the number of tests carried out for each model. This procedure provides more power for the individual tests and is recommended in favour of the conventional Bonferroni procedure (Quinn & Keough 2002). The regression coefficients (b) of the fitted models were interpreted as 'dispersal potential' (i.e. the rate at which the catch declined with distance from the stream) and the relationship between this and the valley slope of the catchments was tested using Spearman's rank correlation.

Estimates of the distance not exceeded by 50% (i.e. median distance) and 90% of individuals in each taxon within the study area were obtained by integrating the model within the distance at which the traps were placed (*x*). Hence, the integrals obtained were an estimate of local distribution rather than an absolute estimate of dispersal range.

MALE AND FEMALE DISTRIBUTION

Comparison of the sex ratio was performed on the catch in the: (i) Malaise traps placed in the riparian zone (i.e. all traps excluding that placed directly across the stream channel); (ii) trap placed across the stream channel; and (iii) first Malaise trap placed on the stream bank (i.e. that nearest the stream). For the analysis of (i) a GLM was first fitted to all data for each taxonomic group (model a: constant + catchment + distance + catchment × distance). The data were then split according to sex and, by adding terms [model b: model a + (sex); model c: model b + distance \times sex], any additional effects of sex on abundance and lateral dispersal were examined. A significant result of the latter would then indicate that dispersal differed between the sexes. For the analyses of (ii) and (iii), the catches of males and

females were compared with a paired *t*-test. The analyses were performed at the level of insect order and for those individual species that occurred in at least three catchments (the minimum number of replicates required for a paired *t*-test). Only catchments in which the sum of the catches of males and females was more than 10 specimens were included in the analyses. This was done to increase the power of the tests (Sokal & Rohlf 1995). Adjustments for multiple comparisons were again made by sequential Bonferroni procedure (Holm 1979), where *c* equals number of tests carried out on species within each taxa. The paired *t*-tests were performed in MINITAB on logarithmically transformed data.

DISTRIBUTION CLOSE TO THE STREAM CHANNEL

In order to study the direction of movement of adult aquatic insects, catches in the Malaise traps placed directly across the stream channel were compared with the catches in the first trap along each transect, i.e. that positioned directly on the stream bank. The traps across the streams caught insects moving along the stream channel, whereas the traps on the stream bank caught insects moving perpendicularly to the stream. If the prevailing flight direction was along the stream channel, most insects would be caught in the trap placed over the stream. If flight was dominated by insects moving perpendicularly, however, more insects should be trapped on the stream bank. No difference between the catches would indicate a lack of differentiation between longitudinal and lateral flight direction close to the streams. The data were analysed using a paired ttest, with the catchments as replicates. The analyses were performed at both the order and species level and with the same criteria applied as above.

Results

SPECIES COMPOSITION, RICHNESS AND DIVERSITY

A total of more than 22 500 stoneflies, 4430 caddisflies and 2230 mayflies was caught, the total catch comprising 15 and 40 species of stoneflies and caddisflies, respectively, and eight taxa of mayflies (Table 2). Overall species diversity and equitability were highest in the moorland catchments, but varied between taxa and catchments (Table 3). Only a few species were numerous in all catchments and, in most cases, just a few species dominated the catch. Thus, Amphinemura sulcicollis, Leuctra hippopus and Leuctra nigra were among the five most common stoneflies taken at LI 1-4, where they accounted for 74-84% of all plecopterans. Leuctra inermis and Siphonoperla torrentium dominated the catches at LI 6-7, where they accounted for 52-57% of the stoneflies. At LI 5 the catches were dominated by Nemoura cinerea, although the nymphs of this species are not confined to running water (Hynes 1977) and it

© 2004 British Ecological Society, *Journal of Applied Ecology*, **41**, 934–950 is likely that many of the individuals caught in this catchment did not originate in the stream. Indeed, nymphs of *Nemoura cinerea* were not found in the stream (Table 2). If *Nemoura cinerea* was excluded from the analysis, the species composition at LI 5 resembled that at LI 6–7 (Table 2).

The caddisfly *Plectrocnemia conspersa* was among the five most common caddisflies species at LI 1–5, whereas *Philopotamus montanus* dominated the catches at LI 6 and LI 7. *Micropterna lateralis* was also numerous in several catchments, although larvae of this species are able to live in temporary streams and ditches (Wallace, Wallace & Philipson 1990) and, again, it is likely that many of the adults caught did not originate from the stream. The same is true of three species of the genus *Limnephilus*, as their larvae are inhabitants of temporary pools or ponds (Wallace, Wallace & Philipson 1990). Of the mayflies, *Baetis* sp. was most common and found primarily at LI 5–7.

ABUNDANCE, LATERAL DISTRIBUTION AND LAND USE

The majority of insects in this study were caught either over or close to the channel (Table 4) and, in general, the number of individuals caught declined with distance from the stream (model a: constant + distance; Table 5 and Fig. 2a), although there were occasional exceptions. For instance, a relatively high number of stoneflies was caught in the trap placed 30 m at LI 2 compared with traps placed at the same distance in the other catchments, suggesting an additional source of adults near this point (Fig. 2b). Similarly, species with larval stages not confined to running waters (Nemoura cinerea, Micropterna lateralis and Limnephilus sp.) had different distribution patterns (Table 4 and Fig. 2c). Further analyses on abundance and lateral dispersal were carried out excluding data from LI 2 and the species mentioned above from the remaining catchments.

ABUNDANCE

Abundance differed significantly between the catchments for both stoneflies and caddisflies (model b; Table 5). For stoneflies, abundance differed between all pairs of catchments except between LI 6 and LI 7, where no difference was found ($t_{(24)} = 0.08$, P = 0.935). The abundance of caddisflies also differed between most pairs of catchments, except LI 6 and LI 7 ($t_{(20)} = 1.27$, P = 0.217), LI 3 and LI 4 ($t_{(20)} = -0.72$, P = 0.477) and LI 3 and LI 5 ($t_{(20)} = 2.01$, P = 0.058). There was a clear difference in the abundance of mayflies, with very few caught in LI 1–4, leaving 97% of the total catch in LI 5–7 (Table 2). The abundance of male and female mayflies differed (see Male and female distribution) but the abundance did not differ among LI 5–7 within each sex (model b; Table 5).

When examined across land uses, a significant difference was found in the abundance of both stoneflies

939 Dispersal of adult aquatic insects

 Table 2.
 Total catch of adult stoneflies (Plecoptera), mayflies (Ephemeroptera) and caddisflies (Trichoptera). Bold figures denote species or taxa found in kick samples

	Foreste	ed	Clear fo	rested	Moorla	nd			
Land use Catchments	LI 1	LI 4	LI 2	LI 3	LI 5	LI 6	LI 7	Total	
Stoneflies									
Amphinemura sulcicollis	164	117	369	845	263	318	588	2 664	
Brachyptera risi	1	3	1	12	57	76	236	386	
Chloroperla tripunctata	0	0	0	0	20	56	197	273	
Isoperla grammatica	4	1	8	28	156	235	322	754	
Leuctra hippopus	41	119	598	227	128	400	286	1 799	
Leuctra inermis	4	8	68	130	557	1798	2365	4 930	
Leuctra moselyi	0	64	1	3	78	440	589	1 175	
Leuctra nigra	79	1042	2019	953	86	227	100	4 506	
Nemoura cambrica	0	0	1	0	0	1	0	2	
Nemoura cinerea	9	18	151	69	1239	63	83	1 632	
Nemoura erratica	0	55	0	4	8	13	17	97	
Nemurella pictetii	27	49	146	116	54	60	228	680	
Protonemura meveri	18	2	188	303	115	304	374	1 304	
Perlodes microcenhala	0	0	0	1	2	43	25	71	
Sinhonoperla torrentium	5	47	29	27	158	1145	894	2 305	
Sum	352	1525	3579	2718	2921	5179	6304	22 578	
	552	1525	5517	2710	2721	5175	0504	22 570	
Caddisflies	0	0		2	-		22		
Adicella reducta	0	0	2	2	5	44	22	75	
Beraea maurus	0	0	0	0	0	16	30	46	
Crunoecia irrorata	0	6	0	0	0	0	0	6	
Diplectrona felix	0	75	1	0	2	6	89	173	
Drusus annulatus	0	0	0	1	23	71	118	213	
Glossosoma conformis	0	0	1	0	0	0	96	97	
Halesus radiatus	1	0	10	12	14	2	2	41	
Hydropsyche siltalai	1	0	0	0	23	56	5	85	
Limnephilus centralis	1	1	3	0	20	1	1	27	
Limnephilus luridus	0	0	4	8	94	6	2	114	
Limnephilus sparsus	0	8	14	6	137	23	21	209	
Micropterna lateralis	4	82	23	21	399	22	31	582	
Micropterna sequax	1	5	0	0	0	0	0	6	
Odontocerum albicorne	0	1	0	0	0	47	13	61	
Philopotamus montanus	0	3	1	2	5	618	374	1 003	
Plectrocnemia conspersa	12	25	59	135	395	17	43	686	
Plectrocnemia geniculata	1	10	7	20	6	9	23	76	
Potamophylax cingulatus	1	27	2	38	8	5	5	86	
Rhyacophila dorsalis	1	0	4	0	3	102	78	188	
Rhyacophila obliterata	0	0	0	0	1	50	74	125	
Silo pallipes	0	0	0	2	13	96	158	269	
Stenophylax permistus	3	5	0	2	0	1	1	12	
Wormaldia occipitalis	0	45	0	0	2	72	82	201	
Others	1	7	4	7	13	15	11	58	
Sum	27	300	135	256	1163	1279	1279	4 4 3 9	
Mayflies									
Baetis sp.	0	38	10	5	306	428	729	1 516	
Ecdvonurus sp.	0	0	0	0	0	4	3	7	
Ephemerella ignita	Ő	Ő	Ő	1	Ő	99	166	266	
Hentagenja lateralis	Õ	Ň	Õ	Ô	Ň	167	159	326	
Leptophlehia marginata	0 0	0	0 0	0	0 0	1	1	520 2	
Paralentonhlehia submarginata	0 0	0	0	0	0	0	2	2	
Rhithrogena semicolorata	1	0	0	2	1	44	58	106	
Sinhlonurus lacustris	0	10	0	2 0	2	 0	0	100	
Sum	1	10	10	Q Q	200	7/3	1110	2 2 2 2 7	
	1	40	10	0	509	745	1110	2 231	
Total	380	1873	3724	2982	4393	7201	8701	29 254	

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and caddisflies (model d; Table 5). For stoneflies, significantly fewer individuals were caught in the forested catchments than in the cleared and moorland catchment (forested vs. cleared, $t_{(30)} = 3.47$, P = 0.002; for-

ested vs. moorland, $t_{(30)} = 4.75$, P = 0.001) but there was no difference between cleared forest and moorland $(t_{(30)} = 1.30, P = 0.203)$. For caddisflies, more individuals were caught in the moorland catchments than at

940

I. Petersen et al.

Table 3. Species richness, Shannon diversity and equitability index for stoneflies, mayflies and caddisflies and all three taxa pooled

Land use	Forested		Cleared	forest	Moorland			
Catchment	LI 1	LI 4	LI 2	LI 3	LI 5	LI 6	LI 7	
Species richness	Stoneflies	10	12	12	13	14	15	14
	Caddisflies	10	18	16	19	24	25	24
	Mayflies	1	2	1	3	3	6	7
	All three taxa	21	32	29	35	41	46	45
Diversity (H)	Stoneflies	1.56	1.23	1.41	1.69	1.88	2.00	2.06
• • •	Caddisflies	1.74	1.95	1.88	1.52	1.74	2.02	2.39
	Mayflies	0	0.51	0	0.90	0.04	1.12	0.99
	All three taxa	1.84	1.90	1.60	2.00	2.53	2.69	2.75
Equitability (J)	Stoneflies	0.68	0.50	0.57	0.66	0.71	0.74	0.78
1 2 ()	Caddisflies	0.76	0.67	0.68	0.51	0.55	0.63	0.75
	Mayflies	_	0.74	_	0.82	0.04	0.62	0.51
	All three taxa	0.60	0.56	0.47	0.55	0.68	0.70	0.72



Fig. 2. Lateral distribution of adult aquatic insects. In general, the numbers caught declined with distance from the stream, exemplified by (a) the distribution of *Amphinemura sulcicollis* at LI 6. Exceptions to this general pattern of lateral distribution were (b) *Amphinemura sulcicollis* at LI 2 and (c) *Nemoura cinerea* (circles) and *Micropterna lateralis* (triangles) at LI 5.

either of the other two categories (moorland vs. forested, $t_{(24)} = 3.81$, P = 0.001; moorland vs. cleared forest, $t_{(24)} = 3.36$, P = 0.003), while there was no difference between forested and cleared catchments ($t_{(24)} = 0.62$, P = 0.544). The abundance of mayflies was closely related to land use, and only a few individuals were caught outside the moorland catchments (Tables 2 and 4).

For the stoneflies, when examined at the level of species, the abundance resembled that of the whole order with a few exceptions, and differences in total numbers caught were found between many catchments (model b; Table 5). *Leuctra nigra* was most abundant in the cleared catchments (forested vs. cleared, $t_{(30)} = 4.21$, P = 0.001; cleared vs. moorland, $t_{(30)} = 5.83$, P = 0.001), whereas *Leuctra inermis* was most abundant in the moorland catchments (moorland vs. cleared, $t_{(20)} = 2.71$, P = 0.013). Only a few individuals of *Leuctra inermis* were caught in forested catchments. *Amphinemura sulcicollis, Leuctra hippopus* and *Protonemura meyeri* were also less abundant in the forested catchments than in the others. *Nemurella pictetii* was more numerous at LI 7 than at any other catchments and, hence, its abundance was not related simply to land use.

LATERAL DISTRIBUTION

Examined at the level of order, there was a significant interaction for stoneflies between catchment and distance (model c; Table 5), indicating that lateral distribution differed among catchments. Such differences were found between LI 3 and LI 6 ($t_{(24)} = 2.40$, P =0.024) and LI 6 and LI 7 ($t_{(24)} = 4.39$, P = 0.001), suggesting differences in lateral distribution among these catchments, with a steeper decline in the catches at LI 6 than at the other two (Fig. 3). There was no relationship between the lateral distribution of stoneflies (b in Table 6) and the valley slope of the catchments (Catchment slope in Table 1) (Spearman's rank correlation, stoneflies, n = 6, r = 0.371, P = 0.468). No difference was found between lateral distribution in the remaining catchments, and a common model could therefore be applied to the lateral distribution of stoneflies, excluding LI6 (Table 6 and Appendix b in Supplementary material).

The lateral distribution of stoneflies was not affected systematically by land use, as indicated by the lack of a significant interaction term between land use and distance from the channel (model e; Table 5). This was the case whether LI 6 was included in the data analysis or not (Appendix d in Supplementary material). When examined at the level of species, lateral distribution

	Forested				Cleared forest				Moorland												
	LI 1 LI 4				LI 2 LI 3			LI 5			LI 6			LI 7							
Land use Catchment Trap position	St	Ва	15-75	St	Ba	15-75	St	Ва	15-75	St	Ba	15-75	St	Ba	15-75	St	Ва	15-75	St	Ba	15-75
Stoneflies																					
Amphinemura sulcicollis	125	37	2	103	11	3	191	38	140	459	243	143	147	101	15	193	92	33	356	182	50
Brachyptera risi	1	0	0	2	0	1	1	0	0	3	9	0	20	26	11	21	47	8	119	84	33
Chloroperla tripunctata	0	0	0	0	0	0	0	0	0	0	0	0	6	12	2	35	20	1	137	38	22
Isoperla grammatica	4	0	0	1	0	0	2	3	3	14	14	0	70	78	8	132	96	7	119	105	98
Leuctra hippopus	27	9	5	93	22	4	284	178	136	93	104	30	40	25	63	107	201	92	28	100	158
Leuctra inermis	3	0	1	6	0	2	23	9	36	86	34	10	194	280	83	1079	627	92	1219	695	451
Leuctra moselyi	0	0	0	60	4	0	1	0	0	2	0	1	64	11	3	246	175	19	523	53	13
Leuctra nigra	44	32	3	746	230	66	1213	681	125	378	446	129	42	27	17	59	142	26	28	42	30
Nemoura cinerea	6	2	1	7	4	7	16	19	116	19	18	32	550	225	464	7	9	47	6	5	72
Nemurella pictetii	22	5	0	33	13	3	61	36	49	32	22	62	19	21	14	20	23	17	12	79	137
Protonemura meyeri	18	0	0	1	1	0	82	40	66	171	91	41	54	33	28	229	50	25	293	44	37
Siphonoperla torrentium	5	0	0	44	3	0	14	8	7	5	21	1	100	44	14	736	385	24	447	356	91
Caddisflies																					
Drusus annulatus	0	0	0	0	0	0	0	0	0	1	0	0	18	4	1	56	14	1	97	20	1
Limnephilus sparsus	0	0	0	0	2	6	1	0	13	0	1	5	35	35	67	0	3	20	0	0	21
Micropterna lateralis	2	1	1	13	9	60	11	6	6	12	6	3	199	134	66	6	6	10	9	7	15
Philopotamus montanus	0	0	0	3	0	0	1	0	0	2	0	0	3	0	2	547	71	0	336	36	2
Plectrocnemia conspersa	8	2	2	11	10	4	41	11	7	88	41	6	312	78	5	11	5	1	39	3	1
Rhyacophila dorsalis	1	0	0	0	0	0	4	0	0	0	0	0	3	0	0	69	33	0	63	14	1
Silo pallipes	0	0	0	0	0	0	0	0	0	2	0	0	8	4	1	59	35	2	104	45	9
Wormaldia occipitalis	0	0	0	32	9	4	0	0	0	0	0	0	2	0	0	66	6	0	73	7	2
Mayflies																					
Baetis sp.	0	0	0	38	0	0	10	0	0	5	0	0	229	68	9	388	30	10	683	21	25
Ephemerella ignita	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	95	4	0	159	5	2
Heptagenia lateralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	147	20	0	140	8	11

Table 4. Spatial distribution of the catch of adult stoneflies (Plecoptera), caddisflies (Trichoptera) and mayflies (Ephemeroptera). St, catch in the Malaise traps placed across the stream channel: Ba, catch in the first Malaise trap placed on the stream bank: 15–75, catch in five Malaise traps placed 15–75 m away from the stream channel. The table includes only species or taxa of which more than 200 specimens were caught

Table 5. Abundance, lateral distribution and land use. Results of accumulated analysis of deviance (approximate *P*-values);significant results in bold. Full summaries of analyses are given in Appendices a-d (see Supplementary material). Model a:constant + distance; model b: model a + catchment; model c: model b + distance × catchment; model d: model a + land use; model e:model d + distance × land use

	Dat	ta inclu	ided fro	om cate	hments	(LI)	Effect of a	catchment	Effect of land use		
	1	3	4	5	6	7	Model a	Model b	Model c	Model d	Model e
Stoneflies (Plecoptera)											
All stoneflies	+	+	+	+	+	+	< 0.001	< 0.001	0.004	< 0.001	0.912
Amphinemura sulcicollis	+	+	+	+	+	+	< 0.001	< 0.001	0.029	< 0.001	0.055
Leuctra hippopus	+	+	+	+	+	+	< 0.001	< 0.001	< 0.001	< 0.001	0.091
Leuctra inermis		+		+	+	+	< 0.001	< 0.001	0.001	< 0.001	0.921
Leuctra nigra	+	+	+	+	+	+	< 0.001	< 0.001	0.394	< 0.001	0.978
Nemurella pictetii		+	+	+	+	+	< 0.001	< 0.001	0.282	0.057	0.509
Protonemura meyeri		+		+	+	+	< 0.001	0.053	0.446	0.006	0.191
Siphonoperla torrentium				+	+	+	< 0.001	< 0.001	0.109	NA	NA
Caddisflies (Trichoptera) All caddisflies		+	+	+	+	+	< 0.001	< 0.001	0.068	< 0.001	0.334
Mayflies (Enhemeroptera)											
All females				+	+	+	< 0.001	0.213	0.143	NA	NA
All males				+	+	+	< 0.001	0.674	0.082	NA	NA

Table 6. Parameter estimates of inverse power functions ($y = ax^{-b}$) used as a model for the lateral distribution of adult stoneflies, caddisflies and mayflies. Models were fitted to each taxon based on an analysis of deviance (Appendix b in Supplementary material)

			Individual mo each catchmer	dels for 1ts	Common moo for each taxon	lels
Taxa		Catchment	a	b	a	b
Stoneflies		LI 1	84.690	1.084	64.264	0.663
		LI 3	1013.333	0.716	960.064	0.663
		LI 4	292.657	0.786	260.604	0.663
		LI 5	669.814	0.723	629.547	0.663
		LI 6	1864.970	0.932		
		LI 7	1846.413	0.600	1990.219	0.663
Caddisflies		LI 3			67.222	0.973
		LI 4			60.340	0.973
		LI 5			119.821	0.973
		LI 6			186.980	0.973
		LI 7			166.334	0.973
Mayflies	Males	LI 5			37.040	0.684
		LI 6			37.040	0.684
		LI 7			37.040	0.684
	Females	LI 5			17.939	1.123
		LI 6			17.939	1.123
		LI 7			17.939	1.123

differed among catchments for *Amphinemura sulcicollis*, *Leuctra hippopus* and *Leuctra inermis* (model c; Table 5) but this was not related systematically to land use (model e; Table 5). The lateral distribution of the remaining species examined did not differ (models c and e; Table 5).

The lateral distribution of caddisflies was not affected either by catchment (model c; Table 5) or by land use (model e; Table 5). For mayflies, a significant difference was found between the lateral distribution of males and females (see Male and female distribution), but there was no difference in the lateral distribution between LI 5–7 when the sexes were analysed separately (model c; Table 5). The mayflies were numerous only at the moorland catchments, and hence a statistical comparison between land uses was not possible although the difference was obvious.

It was estimated that half of the stoneflies went less than 18 m from the stream, while 90% travelled less than 60 m; the same distances were estimated for the mayfly males. The caddisflies and the mayfly females travelled shorter distances (Fig. 4). Half of the caddisflies, male mayflies and female mayflies travelled less than 9, 17 and 7 m from the stream, respectively. The equivalent distances for 90% of the populations were 50, 59 and 44 m, respectively.



Fig. 3. Lateral distribution of stoneflies at LI 6 and 7. Catches in Malaise traps at LI 6 (solid symbols) and LI 7 (open symbols). Models fitted for lateral distribution: the solid line and dashed line represent models for the catch at LI 6 and 7, respectively. See Table 6 for parameters of the models.

MALE AND FEMALE DISTRIBUTION

The overall sex ratio in stoneflies and caddisflies did not differ from 1 : 1 in the catches in the riparian zone (i.e. all traps excluding only that directly across the stream channel). Thus, there were no differences between the abundance of male and female stoneflies or caddisflies after the overall effects of catchment and distance had been taken into account (model b; Table 7). Neither was there any difference in the dispersal of the two sexes (model c; Table 7). Male mayflies were more abundant than females in the riparian zone (model b; Table 7) and a significant difference was found between the lateral distribution of males and females. While male mayflies were caught in relatively high numbers in the



Fig. 4. Lateral distribution at LI 5 of (a) stoneflies, (b) caddisflies and (c) mayfly males (solid line closed symbols) and females (dashed lines and open symbols). Symbols represent the total catch of insects taken in Malaise traps, and the lines are the models fitted (see Table 6 for parameters of the models). Distances not exceeded by 50% and 90% of the individuals are indicated by arrows.

traps at 15 m from the stream channel, only a few females were caught at any distance from the stream.

When analysed at the level of order, female stoneflies comprised the majority in the catches from traps placed

Table 7. Distribution of stoneflies, caddisflies and mayflies split up between genders in relation to catchments. Accumulatedanalysis of deviance: the numbers in the deviance column give the incremental variability (as 'deviance') attributable to the factorsin the model added sequentially. Approximate P indicates whether the model represents a significant improvement on the previousmodel (McConway, Jones & Taylor 1999)

Models	d.f.	Deviance	Mean deviance	Deviance ratio	Approx. P
Stoneflies					
Model a: constant + distance + catchment + distance × catchment	11	17823.390	1620.308	176.24	< 0.001
Model b: model a + gender	1	2.766	2.766	0.30	0.585
Model c: model b + distance \times gender	1	22.866	22.866	2.49	0.120
Residual	58	533·232	9.194		
Total	71	18382-260	258.905		
Caddisflies					
Model a: constant + distance + catchment + distance × catchment	9	1820.125	202.236	109.20	< 0.001
Model b: model a + gender	1	0.518	0.518	0.28	0.599
Model c: model b + distance \times gender	1	4.970	4.970	2.68	0.108
Residual	48	88.899	1.852		
Total	59	1914.512	32.449		
Mayflies					
Model a: constant + distance + catchment + distance \times catchment	5	405.935	81.187	28.65	< 0.001
Model b: model a + gender	1	47.633	47.633	16.81	< 0.001
Model c: model b + distance \times gender	1	12.438	12.438	4.39	0.045
Residual	28	79.358	2.834		
Total	35	545.364	15.582		

Table 8. Test of sex ratio in catches from Malaise traps placed across the stream channel (Stream) and those directly on the stream bank (Bank), results of paired *t*-tests; significant results in bold. An asterisk* indicates significance after a sequential Bonferroni procedure was performed on the tests of individual species of stoneflies, with the stream and bank tested separately (i.e. c = 10); n = sample size (number of catchments included in the analyses); - = test was not possible as too few individuals were caught. See also Fig. 5

	Stream			Bank				
Taxa	n	t	<i>P</i> -value	п	t	<i>P</i> -value		
Stoneflies								
All stoneflies	7	5.38	0.002	7	1.42	0.204		
Amphinemura sulcicollis	7	5.65	0.001*	7	2.54	0.044		
Brachyptera risi	3	1.21	0.350	3	0.69	0.562		
Isoperla grammatica	4	-0.54	0.825	4	-1.39	0.260		
Leuctra hippopus	7	2.95	0.026	6	0.54	0.615		
Leuctra inermis	5	2.59	0.061	4	-1.64	0.200		
Leuctra moselyi	4	0.50	0.649	3	-3.71	0.066		
Leuctra nigra	7	4.60	0.004*	7	2.66	0.038		
Nemurella pictetii	6	0.81	0.448	6	-0.32	0.760		
Protonemura meyeri	6	3.25	0.020	5	-3.02	0.039		
Siphonoperla torrentium	5	1.44	0.220	4	0.01	0.996		
Caddisflies								
All caddisflies	7	0.85	0.429	7	-0.58	0.788		
Plectrocnemia conspersa	6	0.78	0.472	4	-0.47	0.673		
Wormaldia occipitalis	3	2.20	0.159	_	_	_		
Mayflies								
All Mayflies	4	0.04	0.972	3	-1.64	0.242		
<i>Baetis</i> sp.	4	0.05	0.963	3	-1.35	0.309		

across the stream channel, whereas the equivalent catches of mayflies and caddisflies did not differ from a 1 : 1 sex ratio (Table 8 and Fig. 5). No difference in sex ratio was found in the catches in the traps placed on the stream bank for any of the three taxa (Table 8 and Fig. 5). When analysed at species level, a female bias remained in the catches over the stream for some of the most common stoneflies (*Amphinemura sulcicollis* and *Leuctra nigra*), even after adjustments for multiple comparisons had been made (Table 8). The sex ratio for the remaining species varied among catchments. Of the caddisflies and mayflies, data analysis was possible at the species level only for *Plectrocnemia conspersa*, *Wormaldia occipitalis* and *Baetis* sp., where no bias in sex ratio was found.

On the stream bank the pattern for single species resembled that of the whole order in that none of the species showed significant deviation from a 1 : 1 sex ratio after adjustment of multiple correction had been made for the species of stoneflies (Table 8).

DIRECTION OF MOVEMENT CLOSE TO THE STREAM CHANNEL

When analysed at the level of order, more caddisflies and mayflies of both sexes were caught in the Malaise traps placed across the stream channel than in the first trap on the stream bank (Table 9 and Fig. 5), indicating more flight activity along the channel than laterally. For the stoneflies, only the females were more likely to be taken in flight along the channel than on the stream bank, whereas the males were equally likely to be caught over the stream and on the stream bank (Table 9



Fig. 5. Sex ratio in the catches of aquatic insects taken in Malaise traps across the stream channel (Stream) or in the first trap on the bank (Bank). Black and hatched bars represent females and males, respectively, and vertical bars indicate standard errors: (a) stoneflies, (b) caddisflies and (c) mayflies. See also Table 8 for analyses of sex ratio.

and Fig. 5). Analysed at the species level the pattern resembled that of the whole order for mayflies and caddisflies. For the stoneflies only the catches of females of *Amphinemura sulcicollis* and *Protonemura meyeri* were

Table 9. A comparison of the catch in traps placed across the stream with that in traps placed on the stream bank. A significant result of a paired *t*-test indicates that more individuals were caught over the stream channel than on the stream bank, and thus were flying along the channel rather than perpendicular to it. An asterisk* indicates significance after a sequential Bonferroni procedure was performed. Female and male stoneflies were tested separately (i.e. c = 9); n = sample size (number of catchments included in the analyses)

Taxa		п	<i>t</i> -value	<i>P</i> -value
Stoneflies				
All stoneflies		7	3.84	0.009
All females		7	6.66	0.001
All males		7	1.71	0.138
Females of	Amphinemura sulcicollis	7	5.69	0.001*
	Brachyptera risi	3	-0.34	0.767
	Isoperla grammatica	3	8.97	0.012
	Leuctra hippopus	7	1.39	0.214
	Leuctra inermis	5	4.27	0.013
	Leuctra nigra	7	1.13	0.300
	Nemurella pictetii	6	0.72	0.502
	Protonemura meyeri	6	6.04	0.004*
	Siphonoperla torrentium	4	2.19	0.116
Males of	Amphinemura sulcicollis	7	2.02	0.089
	Brachyptera risi	3	-0.98	0.431
	Isoperla grammatica	4	-1.58	0.213
	Leuctra hippopus	7	-1.36	0.222
	Leuctra inermis	5	0.28	0.799
	Leuctra nigra	7	-0.32	0.763
	Nemurella pictetii	6	-0.02	0.950
	Protonemura meyeri	6	1.65	0.174
	Siphonoperla torrentium	6	0.61	0.569
Caddisflies		_		
All caddisflies		7	9.54	< 0.001
All females		7	9.85	< 0.001
All males		7	7.78	< 0.001
Females of	Plectrocnemia conspersa	5	4.60	0.010
	Wormaldia occipitalis	3	4.96	0.038
Males of	Plectrocnemia conspersa	4	3.38	0.043
	Wormaldia occipitalis	3	4.18	0.053
Mayflies			5.04	0.010
All mayflies		4	5.26	0.013
All females		4	4.67	0.019
All males	_	4	5.34	0.013
Females of	Baetis sp.	4	4.40	0.022
Males of	Baetis sp.	4	5.45	0.012

significant higher in the traps placed over the stream channel than in those on the bank, after the sequential Bonferroni procedure had been applied (Table 9). For the remaining species examined, no significant difference was found between the catches over the stream and in the first trap on the stream bank.

Discussion

ABUNDANCE AND SPECIES COMPOSITION

Variation in species composition and abundance among catchments was associated with land use, with the highest species diversity at the moorland sites together with the highest abundance of caddisflies and mayflies. The lowest abundance of stoneflies was in the forested catchments. Studies of larval abundance and taxon richness from catchments in the same area revealed a similar distribution pattern and coincided with the physicochemical environment in the streams, with the highest pH and lowest aluminium concentration measured in the moorland streams (Weatherley, Rutt & Ormerod 1989; Weatherley & Ormerod 1990; Bradley & Ormerod 2002). Perhaps not surprisingly, this strongly suggests that the total number of adults, as well as the species composition, is affected by factors that determine the benthic (larval) community. Little is known about how much the size of larval population and species composition is determined by the factors influencing the adults (Zwick 1990; Enders & Wagner 1996). Peckarsky, Taylor & Caudill (2000) and Caudill (2003b) demonstrated that recruitment of eggs was limited by regional rather than local supply of adult mayflies, suggesting a movement of adult females. Further investigations are required to establish the links between larval and adult numbers, and models including both adult and larval stages will be useful tools for the analysis of population dynamics (Wilbur 1980; Speirs et al. 2000; Bohonak & Jenkins 2003; Caudill 2003b).

LATERAL DISTRIBUTION

No difference was found between catchments in the lateral distribution of caddisflies and within the sexes of mayflies, although there was a difference in the lateral distribution of stoneflies between catchments, with a steeper decline in the catches with distance in LI 6 than in LI 3 and LI 7. The distribution did not correlate with the slope of the catchment nor with land use. Similar abundances were found in LI 6 and LI 7 and therefore the difference in lateral distribution between these sites cannot be explained simply by abundance.

Overall, most adult insects stayed close to the stream channel and half of the stoneflies travelled less than 18 m, while 90% travelled less than 60 m. The local dispersal range of the caddisflies and female mayflies was even shorter, with half the individuals caught within 7-11 m of the stream channel. It is possible that the dispersal range of caddisflies and mayflies in this study is underestimated compared with that of the stoneflies as their abundance was much lower, and the chance of catching caddisflies and mayflies further from the stream channel was therefore lower. The general trend is that most adult aquatic insects stay close to the stream channel from which they emerged (Svensson 1974; Sode & Wiberg-Larsen 1993; Kuusela & Huusko 1996; Collier & Smith 1998). Hence, our estimates of the dispersal range of stoneflies, mayflies and caddisflies are similar to those derived previously (Jackson & Resh 1989b; Griffith, Barrows & Perry 1998; Petersen et al. 1999a; Delettre & Morvan 2000; Briers, Cariss & Gee 2002). Note, however, that we followed Bullock & Clarke (2000) by building GLM assuming a Poisson distribution likelihood but allowing for overdispersion of counts (McCullagh & Nelder 1989, chapter 6), which in effect is assuming that the variance was not constant across the sites. This makes comparison among our models potentially difficult.

EFFECT OF LAND USE ON DISPERSAL

The fact that most adult aquatic insects stay close to the stream channel may also explain why there was little distinction between lateral dispersal in the different land uses. However, it is still too early to conclude that land use has no effect on lateral dispersal. For instance, adult abundance was much lower in the forested catchments than in the other catchments. Therefore, although there was no difference in the decline of the catch with distance (b in the models) between the land uses, the chances are that fewer individuals will reach substantial distances from the channel in the forested catchments than in the cleared or moorland ones (Fig. 6). Further, there could be an undetected effect of land use on long-distance dispersal, which may be important in the recovery of streams from acidification, pollution, physical changes and disturbance (Sode & Wiberg-Larsen 1993; Wilcock, Hildrew & Nichols 2001). Such rare dispersal events, although difficult to detect

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Fig. 6. Comparison of absolute dispersal distances between populations with low (dashed lines) and high (solid lines) population densities. Given that two populations have the same dispersal potential, i.e. equal slope of the lines (*b* in the models in Table 6), individuals from populations with a low abundance will have less chance of reaching suitable habitats at further distances than individuals from larger populations.

using conventional trapping techniques, could be sensitive to coniferous afforestation. Recent evidence based on genetic markers, for instance, suggests that populations of *Plectrocnemia conspersa* (the most abundant caddisflies at Llyn Brianne) are genetically homogeneous over distances of up to 20 km or more, inferring frequent dispersal over such distances (Wilcock, Nichols & Hildrew 2003).

MALE AND FEMALE DISTRIBUTION

The overall sex ratio in the riparian zone did not differ from 1:1 for caddisflies and stoneflies. While only a few female mayflies were caught at any distance from the stream, a relatively high number of males was caught in the traps placed 15 m from the stream channel. The adult life span of mayflies is relatively short (Brittain 1987). It is possible that females are time limited in finding suitable oviposition sites and are, therefore, more concentrated over the stream channel and less likely than males to be caught in the riparian zone. It should be emphasized that most mayflies were caught over the stream channel, however, and this was the case for both males and females. Only for the stoneflies was there a significant deviation from a 1:1 sex ratio over the stream channel, with more females than males. The same pattern was observed by Petersen et al. (1999a), where the females of several species were in the majority over the stream channel towards the end of the flight period. The search for egg-laying sites, combined with a longer female life span, may provide a plausible explanation for the female-biased catches over the stream channel (Sheldon & Jewett 1967; Hynes 1974; Petersen 2002). Thus, differences between the distributions of the sexes and of the taxa may be explained by differences in mating and reproductive behaviour.

947 *Dispersal of adult aquatic insects*

DIRECTION OF MOVEMENT CLOSE TO THE STREAM CHANNEL

More individual mayflies and caddisflies were caught in traps placed across the stream channels than in the trap on the banks, indicating that most flight activity of these taxa was concentrated over the stream channel itself. Of the stoneflies, some of the females were also more likely to be taken in flight along the channel than on the stream bank, whereas there was no difference for the males. The reason for this difference in distribution between the sexes in stoneflies may be found in their mating and oviposition behaviour. As mating for many species of stoneflies occurs on the ground shortly after emergence (Brinck 1949), it is possible that male stoneflies have an equal chance of encountering receptive females on the stream bank as on emergent substrata in the stream. Females, once they are mated and their eggs matured, may be governed by the search for oviposition sites, and hence may have a higher flight activity along the stream channel.

ROUTES OF DISPERSAL

The vast majority of the insects caught in this study was taken either over the stream channel or in the first trap on the stream bank (Table 4). This suggests that most flight activity is in the 'stream corridor' itself rather than laterally away from the stream channel. Many empirical and a few theoretical studies have dealt with migration along the stream channel, inspired by Müller's (1954) postulated 'colonization cycle'. Empirical studies have not been able to provide evidence for universal upstream flight (Allan 1995; Petersen et al. 1999b; Kopp, Jeschke & Gabriel 2001) and theoretical studies have raised questions about its 'necessity', in terms of population persistence (Anholt 1995; Kopp, Jeschke & Gabriel 2001; Speirs & Gurney 2001). Computer simulations suggest that the exact compensation of stream drift by upstream movement is an evolutionarily stable strategy (Kopp, Jeschke & Gabriel 2001). Exact compensation by upstream flight seems rather unlikely under natural conditions, however, and random dispersal by adults may be enough to maintain the population (Speirs & Gurney 2001). Some studies of genetic population structure suggest that movement of aquatic invertebrates within streams is limited, resulting in significant genetic differentiation at the reach scale, and that larvae at the reach scale are likely to be the offspring of only a few matings (Bunn & Hughes 1997). In contrast, Peckarsky, Taylor & Caudill (2000) explained local egg recruitment by inter-reach dispersal by females of Baetis, and Hershey et al. (1993) found that between one-third and one-half of an adult Baetis population flew 1.6-1.9 km upstream from where it emerged. Similarly, swarms of caddisflies marked with a radioisotope were found up to 16 km upstream of a reactor effluent (Coutant 1982) and dispersal among ponds by adult females of the mayfly Callibaetis ferrugineus hageni was

© 2004 British Ecological Society, Journal of Applied Ecology, **41**, 934–950 demonstrated by means of stable isotope techniques (Caudill 2003b). Apart from the studies by Coutant (1982) and Hershey *et al.* (1993), little is known about actual adult dispersal distances of aquatic insects along the stream channel and more information is required (Bohonak & Jenkins 2003). Future research should therefore be aimed at quantifying the extent and distance of dispersal within the stream corridor in both upstream and downstream directions. The research should relate dispersal within the stream corridor to land use, to clarify whether the various types of riparian vegetation act as a barrier or corridor for dispersal (Delettre & Morvan 2000). Focus should be brought on landscape connectivity within the stream corridor in relation to population dynamics (Taylor *et al.* 1993).

IMPLICATIONS FOR MANAGEMENT

Throughout much of the UK and Europe, the interaction between forest management, riparian zones and river ecosystems has been increasingly emphasized in forest policy (Forestry Commission 2000). Indeed, in many locations, active and sympathetic forest management offers one of the best mechanisms for enhancing upland stream and river quality. With much forest in the UK reaching the end of its first major rotation after initial planting during the 1950s and 1960s, there are now opportunities to re-examine forest design with particular emphasis on forest–water linkages. As in other areas of stream management and ecology, however, the requirements of adult insects have so far received little emphasis in such design issues.

These results confirm the importance of the riparian zone, i.e. the area close to the stream channel (e.g. 20 m on either side), as a buffer zone. Here, care is required over aspects of forest management such as habitat structure and the application of pesticides. This study extends previous work, by emphasizing the value of buffer zones intrinsically in the protection of aquatic insects, the adult stages of which are concentrated in this zone, but also for the riparian insectivores for which aquatic insects provide an important food source (Jackson & Fisher 1986; Collier, Bury & Gibbs 2002). Further, we recommend that attention should be paid to the role of landscape structure, catchment vegetation and interbasin connectivity in the life of aquatic insects, the dispersal of which may determine how aquatic habitats are linked. As most flight activity appears to occur along the stream corridors, the dispersal of adults could well be dependent on the vegetation structure of the stream and river network in facilitating linkage directly across headwaters.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/ journals/suppmat/JPE/JPE942/JPE942sm.htm

Appendix a. Lateral distribution of stoneflies in relation to *catchments*, examined at species level.

Appendix b. Lateral distribution of stoneflies, caddisflies amd mayflies in relation to *catchments*, examined at order level.

Appendix c. Lateral distribution of stoneflies in relation to *land use*, examined at species level.

Appendix d. Lateral distribution of stoneflies and caddisflies in relation to *land use*, examined at order level.

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