

Flight activity of insects along a mountain stream: is directional flight adaptive?

MICHAEL J. WINTERBOURN* and ANNA L. M. CROWE†

*Department of Zoology, University of Canterbury, Christchurch, New Zealand

†Cawthron Institute, Nelson, New Zealand

SUMMARY

1. Flight activity of Trichoptera, Plecoptera and Ephemeroptera was studied by sticky trapping for 12 months at five sites along a New Zealand mountain stream. Over 19 000 insects were captured by the traps, which were located in forest and grassland reaches, including a reach with intermittent flow.
2. Most species occurred predominantly in forest or grassland, although some were trapped throughout the stream. Longitudinal distributions of adults and their larvae were strongly correlated.
3. Flight periods of 24 caddisflies, three mayflies and four stoneflies ranged from 2 to 12 months. Six species were trapped in all months and 17 (55%) in more than 5 months.
4. The most abundant forest-dwelling caddisfly species were over-represented on the downstream sides of sticky traps located in, and immediately below, forest indicating a majority was flying upstream. Upstream flight compensates for downstream drift of larvae and should maximize the likelihood that forest-dwelling species will locate preferred habitat for egg, larval and/or adult development. Unlike the caddisflies, the stonefly *Spaniocerca zelandica* was over-represented on the upstream sides of traps, suggesting that some adults may float or fly downstream following emergence.
5. In contrast to forest-dwelling species, only one common caddisfly (*Oxyethira albiceps*) was over-represented on the downstream sides of traps at grassland sites. Unlike the forest-dwelling species, most species taken at the downstream sites probably came from a variety of sources, including a nearby stream.

Keywords: aquatic insects, flight direction, flight periodicity, sticky trapping, Trichoptera

Introduction

Understanding how the spatial distributions of different life cycle stages of animals are linked, and how they affect the abundance of each other, are fundamental ecological issues. Populations of numerous marine invertebrates with benthic or littoral adults are maintained via pelagic dispersal of larvae (Palmer,

Allan & Butman, 1996), whereas the terrestrial adult is the primary colonizing stage in the life cycle of many aquatic insects. Larval drift can also play an important role in the dispersal of insects within streams, but cannot account for their initial occurrence within a river system.

On a very large scale, the presence of some major insect groups (e.g. families of Hemiptera) on oceanic islands has been attributed to the ability of adult insects to traverse huge expanses of water (Laird, 1956; Gressitt, 1961). The speed of recovery of insect faunas following large-scale disturbance has also been attributed to the arrival of flying and wind-blown insects (e.g. Anderson, 1992; Edwards & Sugg, 1993).

Correspondence: Michael J. Winterbourn, Department of Zoology, University of Canterbury, Private Bag 4800, Christchurch, New Zealand. E-mail: m.winterbourn@zool.canterbury.ac.nz

Thus, 69 species of Trichoptera (caddisflies) were collected at Clearwater Creek in the blast zone of Mount St Helens in 1985, less than 4 years after the eruption (Anderson, 1992). Similarly, colonization of newly formed streams in Glacier Bay, Alaska, was by rapidly dispersing adult insects, notably egg-laying chironomids (*Diamesa* spp.; Milner, 1987), whereas invertebrates without terrestrial or aerial life cycle stages (molluscs, oligochaetes) arrived much later (Flory & Milner, 2000).

On a more local scale, the oviposition behaviour of adult insects can have a strong influence on the between-stream and within-stream distributions of larvae. For example, the disjunct distributions of two *Simulium* species in shaded and open reaches of a stream were determined by the oviposition behaviour of females (Timm, 1994), whereas the absence of *Baetis* larvae from some British streams with pH < 6 reflected avoidance of these streams by egg-laying females (Sutcliffe & Carrick, 1973). Presence of the alderfly, *Sialis fuliginosa* Pictet in a stream depends in part on the occurrence of suitable overhanging foliage where females can lay their eggs (Kaiser, 1961).

Much of what is known about the ecology of adult aquatic insects has been obtained through intensive trapping programmes (e.g. Svensson, 1974; Kovats, Ciborowski & Corkum, 1996; Ward *et al.*, 1996 and references therein), or more incidentally, during life history studies of individual species or assemblages. Such studies have provided information on emergence periods, flight periodicity, reproductive capacity, means of oviposition and to a lesser extent, movement patterns and dispersal. An expectation that upstream flights of adults prior to oviposition might compensate for downstream drift by larvae (the colonization cycle of Müller, 1954, 1982) has provided the conceptual focus for some studies (e.g. Svensson, 1974; Bird & Hynes, 1981; Hershey *et al.*, 1993). Indeed, Anholt (1995) argued that upstream-biased dispersal should be favoured by natural selection when upstream populations have been reduced by drift, so that higher per capita resource availability would favour the survival and growth of offspring produced from eggs laid there. Similarly, Peckarsky, Taylor & Caudill (2000) concluded that the predominantly upstream flights of *Baetis* females could be maintained by direct selection on individual females caused by behavioural and hydrological constraints on oviposition. Suitable egg-laying sites occurred

earlier in small tributaries than in mainstream reaches of their study streams, so upstream flight was needed if short-lived mayflies emerging downstream were to oviposit successfully.

One might also expect that the recolonization of stream substrata by insects following bed or flow disturbance would be enhanced by the deposition of eggs. While drift is considered to be the primary way that benthic organisms disperse downstream (Minshall & Petersen, 1985), flight is known to be an important colonizing mechanism following periods of drought (Mackay, 1992) and scouring spates (Gray & Fisher, 1981).

The work described in this paper forms part of a broader study of colonization pathways and population dynamics of invertebrates in a small mountain stream (McLeod, 1998). We investigated the flight periods and longitudinal distributions of Ephemeroptera, Plecoptera and Trichoptera trapped above the stream, and assessed directional movements of common species along the stream with bilateral sticky traps.

Methods

Study area

Middle Bush Stream is a small first-order stream on the eastern side of the Southern Alps, South Island (43°19'S, 171°46'E). It arises from a spring at 820 m a.s.l. and drains a 28-ha catchment supporting a mixture of subalpine scrub, stands of mountain beech forest [*Nothofagus solandri* var. *cliffortioides* (Hook f.) Poole] and tussock grassland. Mean annual rainfall is about 1250 mm (Greenland, 1977), and during the study period shade air temperature measured continuously at the Cass field station (about 100 m from Site 4 on Middle Bush Stream; Fig. 1) ranged from -10 to 31 °C (Table 1). Norrie (1969) concluded that 9.5–10 °C was likely to be the lower limit for mayfly and caddisfly flight at a northern New Zealand stream; air temperature at Cass exceeded this threshold for flight on some days every month by up to 7 °C.

Insects were trapped at six sites during the course of the study (Fig. 1). Site 0 was in the headwaters of the stream about 10 m above the beech forest and was used only in a subsidiary study (see below). Site 1 was in the lower section of the beech forest, Sites

Trapping methods and data collection

Adult stoneflies, caddisflies and mayflies (and mayfly subimagos) were collected by sticky trapping, which like other trapping methods, may be affected by insect behaviour and trap avoidance. Thus, Bird & Hynes (1981) found that some caddisflies flew over or around sticky traps, whereas mayflies and stoneflies did not seem to avoid them. In a New Zealand study, Collier & Smith (1995) found that trap-height (0.5–5 m) had no significant effect on numbers of mayflies and caddisflies caught alongside a forest stream. Our main trapping programme at all sites encompassed the calendar months November 1996–October 1997. A subsidiary programme to compare numbers of common, forest-dwelling caddisflies flying upstream, above, within and immediately below forest was undertaken at Sites 0, 1 and 2 from November 1997 to February 1998.

Each sticky trap consisted of a clear plastic sheet (450 × 1200 mm) folded in half and hung from a rope across the stream channel so that its lower edges touched the water. The sheets were attached to the rope (and a second rope closer to the water) with plastic clothes pegs so they did not flap and remained vertical at all times. Each sheet was coated with Tanglefoot® (Tanglefoot, Grand Rapids, MI, U.S.A.) (a clear, odourless substance that remains sticky when wet), applied with a paintbrush, so that both the upstream and downstream-facing surfaces (each 0.27 m²) were sticky.

One sticky trap was deployed at each site, the sheets being removed and replaced each month. To remove the insects, sheets were cut into pieces and immersed in mineral turpentine for up to 2 days. This dissolved the Tanglefoot®, releasing the insects without damaging them. It should be noted, however, that the condition of insects on traps varied considerably, and mayflies, in particular, were often in poor condition. After being removed from the turpentine solution, insects were rinsed thoroughly in water and 95%

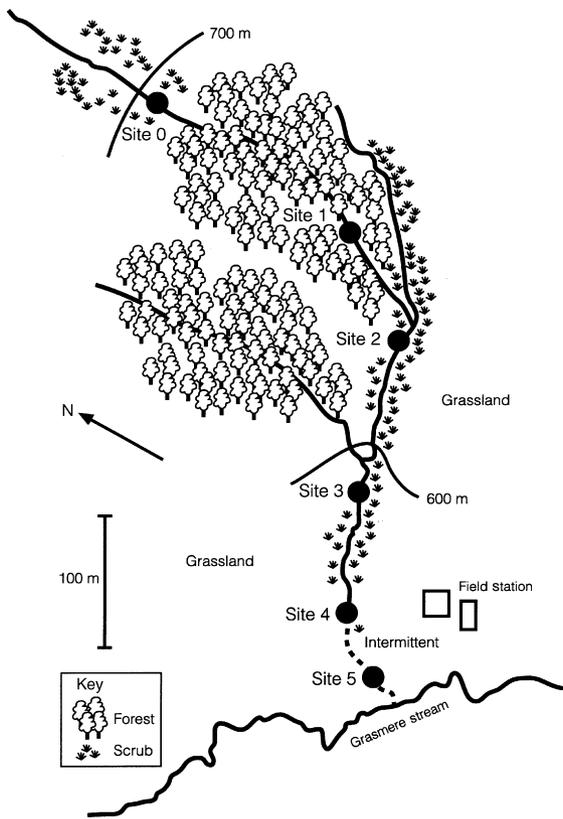


Fig. 1 Location of sticky trapping sites along Middle Bush Stream.

2–4 were below the forest in mixed scrub-tussock grassland, while Site 5 was in open grassland. The stony stream channel was about 1 m wide at all sites and cut through a shingle fan below Site 4. During the study, surface flow was permanent at Sites 0–4 but intermittent at Site 5. Thus, the bed at Site 5 was dry periodically in January and dry continuously from early February to late April when flow resumed.

The loss of surface flow downstream was caused by a combination of evaporation and downwelling into the gravels of the shingle fan when the water table fell in summer.

Table 1 Shade air temperatures (°C) recorded at the Cass Mountain Biological Station, November 1996–October 1997

	Month											
	N	D	J	F	M	A	M	J	J	A	S	O
Maximum	27	31	31	26	27	24	23	17	20	20	25	26
Minimum	1	2	4	-2	-5	-2	-6	-10	-9	-7	-6	4
Median	14	16.5	17.5	12	11	11	8.5	3.5	5.5	6.5	9.5	15

ethanol before being preserved in 95% ethanol. Insects were identified using published keys and descriptions, principally; Phillips (1930) and Towns & Peters (1996) (Ephemeroptera), McLellan (1991, 1993) (Plecoptera), and Neboiss (1986) (Trichoptera). Identities of a reference collection of caddisfly species were confirmed by Dr J. Ward (Canterbury Museum).

Benthic invertebrate populations at the five sites were sampled in 4 months (November 1996, February, June and September 1997). On each occasion, four samples were taken from riffles to a depth of about 10 mm with a Surber sampler (0.025 m², 0.5 mm mesh). All taxa were identified to the lowest possible taxonomic level and counted. In this paper, only mean densities of the common insect species taken on sticky traps are reported. Full details are given by McLeod (1998).

Data analysis

Similarity of assemblages of insects trapped at the five sites was examined by cluster analysis using the PC-ORD software program (McCune & Mefford, 1999). Presence-absence data for all months were pooled and site similarities assessed with Sorensen's similarity coefficient. Ward's method was used to cluster sites. To obtain an estimate of the average distance along the stream (Sites 1–5) at which common species occurred, we calculated 'mean site numbers' from abundance data. Our procedure was analogous to that used by Benke (1970) to determine 'mean instar numbers' of dragonfly larvae. Mean site numbers for adults and their larvae were plotted against each other, and the strength of the association between them tested by calculating Pearson's correlation coefficient. A chi-squared goodness-of-fit test was used to compare numbers of insects on the two sides of traps (and by inference, upstream and downstream movement) as carried out by Svensson (1974). Comparisons were made for individual sites where numbers of individuals were greatest, with monthly collections combined to increase sample size.

Results

The fauna

Over 19 000 adult mayflies, stoneflies and caddisflies were collected from the five sites over the course

Table 2 Numbers of families and species of Ephemeroptera, Plecoptera and Trichoptera caught on sticky traps at Middle Bush Stream, November 1996–October 1997

Taxa	> 100 individuals	< 100 individuals	Total species
Ephemeroptera			
Leptophlebiidae	1	0	1
Nesameletidae	0	1	1
Coloburiscidae	0	1	1
Plecoptera			
Notonemouridae	1	1	2
Gripopterygidae	1	1	2
Trichoptera			
Hydrobiosidae	5	12	17
Conoesucidae	1	4	5
Hydropsychidae	0	2	2
Leptoceridae	0	2	2
Oeconesidae	2	0	2
Philopotamidae	1	1	2
Philorheithridae	0	1	1
Polycentropodidae	0	1	1
Hydroptilidae	1	0	1

of the year (November 1996–October 1997). The Trichoptera was the most abundant and diverse order, containing 33 species in nine families and 95.8% of the individuals caught (Table 2). The Ephemeroptera and Plecoptera were represented by three and four species, respectively. In the following account, those species for which at least 100 individuals were taken are considered in most detail; i.e. 10 caddisfly, one mayfly and two stonefly species.

Longitudinal distribution of insects

The species composition of assemblages differed along the stream with the upstream (Sites 1 and 2) and downstream (Sites 3, 4 and 5) sites forming separate clusters (Fig. 2). Individual species therefore showed two general, longitudinal distribution patterns: predominantly in or adjacent to forest, and predominantly in grassland (Fig. 3).

Common caddisflies that exemplified the first pattern (most abundant in forest) were *Zelandopsycha ingens* Tillyard (Oeconesidae), *Hydrochorema tenuicaudatum* Tillyard (Hydrobiosidae) and *Hydrobiosella stenocerca* Tillyard (Philopotamidae). In contrast, *Oxyethira albiceps* McLachlan (Hydroptilidae) was the dominant species at the three downstream sites, but was rarely collected at Sites 1 and 2. Similarly,

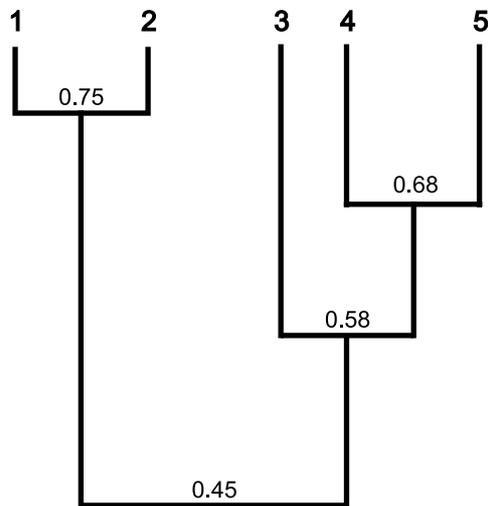


Fig. 2 Similarity of insect assemblages at the five sites based on 12-months presence-absence data. Sorensen's similarity coefficient and Ward's linkage method were used for clustering.

all or almost all *Pycnocentria evecta* McLachlan (Conoesucidae), *Neurochorema confusum* (McLachlan), *Psilochorema tautoru* McFarlane (both Hydrobiosidae) and *Oeconesus maori* McLachlan (Oeconesidae) were taken only at the three downstream sites. *Hydrobiosis parumbripennis* McFarlane and *Edpercivalia maxima* (McFarlane) (both Hydrobiosidae) had the most even longitudinal distributions of the caddisflies, although the former was principally a grassland species and the latter was most abundant in and close to the forest.

The most abundant stonefly, *Spaniocerca zelandica* Tillyard (Notonemouridae) occurred throughout the stream, whereas *Zelandobius furcillatus* Tillyard (Gripopterygidae) was taken only at Sites 4 and 5. The leptophlebiid *Deleatidium* was the only mayfly genus taken frequently on sticky traps. Most appeared to belong to a single species, which could not be identified positively using Towns & Peters (1996), the most recent revision of the genus. *Deleatidium* was common at Sites 2–5, but only two individuals were caught in the forest.

The longitudinal distributions of adults of the 12 most common species caught on sticky traps were also compared with the distributions of their larvae, as indicated by Surber sampling (Table 3). A very strong association was found between them as indicated by the highly significant correlation between their 'mean site numbers' ($r = 0.93$, $P < 0.001$, $n = 12$)

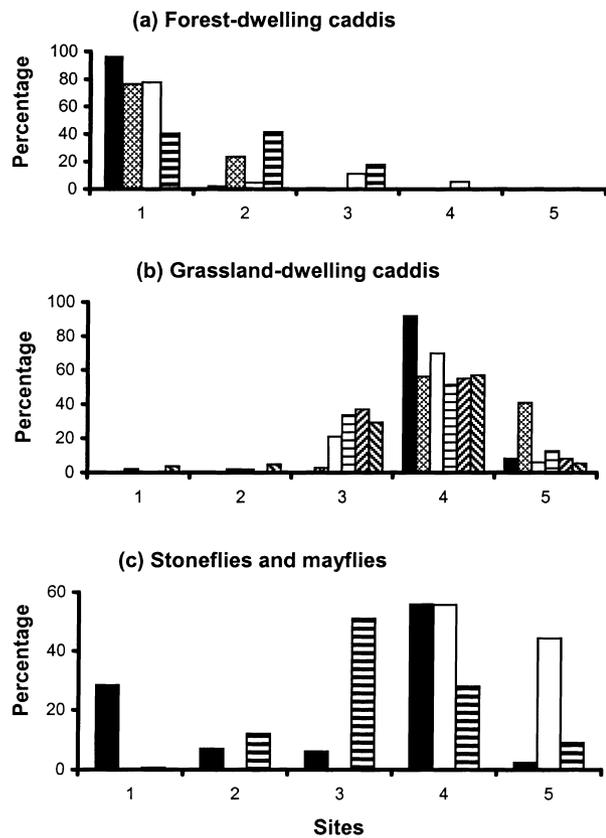


Fig. 3 Longitudinal distributions of common (a) predominantly forest-dwelling caddis, (b) predominantly grassland-dwelling caddis, and (c) stoneflies and a mayfly. Key to (a): *H. tenuicaudatum* (■), *Z. ingens* (▨), *H. stenocerca* (□), *E. maxima* (▤). Key to (b): *P. evecta* (■), *O. albiceps* (▨), *O. maori* (□), *P. tautoru* (▤), *N. confusum* (▧), *H. parumbripennis* (▩). Key to (c): *S. zelandica* (■), *Z. furcillatus* (□), *Deleatidium* sp. (▤).

(Fig. 4). Thus, species whose adults were captured predominantly in forest also had predominantly forest-dwelling larvae, while the opposite was true for species captured mainly in grassland.

Temporal flight activity

Flight periods of the 21 most abundant caddisflies taken in Middle Bush Stream (species represented by fewer than 10 individuals were not considered) ranged from 3 to 12 months, while those of mayflies and stoneflies ranged from 5 to 11 and 6 to 12 months, respectively (Table 4). Of the 13 most common species (Fig. 5), *S. zelandica*, *O. albiceps*, *H. parumbripennis* and *H. stenocerca* were taken every month, *Deleatidium* sp. and *P. tautoru* in 11 months, and *E. maxima* in 10.

	Sites				
	1	2	3	4	5
<i>Deleatidium</i> sp.	698	129	132	2555	1205
<i>Zelandobius furcillatus</i>	133	263	103	63	300
<i>Pycnocentria evecta</i>	8	5	53	258	35
<i>Spaniocerca zelandica</i>	133	263	103	63	300
<i>Psilochorema tautoru</i>	0	0	20	88	15
<i>Oeconesus maori</i>	0	10	0	65	5
<i>Hydrobiosis parumbripenis</i>	0	0	5	18	18
<i>Edpercivalia maxima</i>	8	13	5	5	3
<i>Zelandopsyche ingens</i>	8	10	0	0	0
<i>Hydrobiosella stenocerca</i>	5	0	3	0	0
<i>Oxyethira albiceps</i>	0	0	3	5	0
<i>Hydrochorema tenuicaudatum</i>	0	3	0	0	0
<i>Neurochorema confusum</i>	0	0	0	0	0

Table 3 Mean densities of larvae (numbers m^{-2}) of the 13 species most abundant on sticky traps at five sites along Middle Bush Stream over the trapping period. Species are listed in rank order of abundance, all sites combined

In contrast, *P. evecta* and *Z. ingens* had short flight periods of 4 and 3 months, respectively.

Flight direction

Inferences about flight direction (upstream versus downstream) were drawn, by comparing catches on the two sides of sticky traps (Table 5). At Site 1 the four predominantly forest-dwelling caddisflies

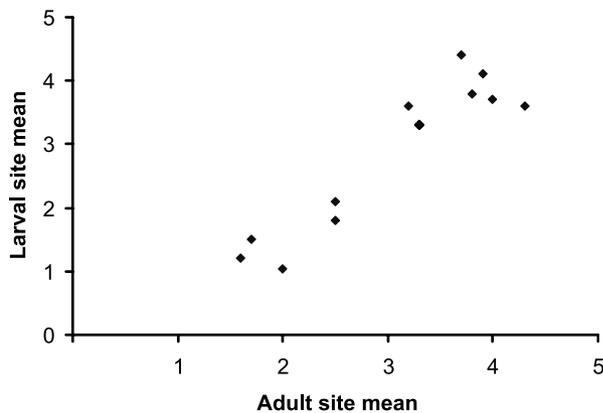


Fig. 4 Mean site numbers for adults (locations along the stream at which half the adults were found) plotted against mean site numbers for their larvae. $r = 0.93$, $P < 0.001$.

Z. ingens, *H. tenuicaudatum*, *H. stenocerca* and *E. maxima* were all significantly more abundant on the downstream sides of traps (62–79% of individuals) indicating more adults were flying upstream than downstream. Similarly, at Site 2 just below the forest *Z. ingens* and *E. maxima* were significantly over-represented (70 and 64%) on the downstream side of traps. However, only 26 *H. stenocerca* and 12 *H. tenuicaudatum* were captured at Site 2, as compared with 261 and 658 at Site 1, indicating few ventured outside the forest.

At Site 4, differences in numbers of caddisflies caught on the two sides of sticky traps were smaller than at the upstream sites (Table 5). Furthermore, the differences were statistically significant ($P < 0.05$) only for the very abundant *O. albiceps* and *P. evecta*, which were over- and under-represented on the downstream side, respectively.

Unlike the predominantly forest-dwelling caddisflies, the stonefly *S. zelandica* was most abundant on the up-stream side of traps at Site 1 and equal numbers were taken on the two sides of traps at Site 4 (Table 5). Mayfly numbers were too small at any one site to justify upstream–downstream analysis.

In a subsidiary trial run during the peak flight period (December–February 1997–98), caddisflies were

	Number of months											
	1	2	3	4	5	6	7	8	9	10	11	12
Ephemeroptera	–	–	–	–	1	–	1	–	–	–	1	–
Plecoptera	–	–	–	–	–	1	–	1	–	–	–	1
Trichoptera	–	–	2	5	2	3	1	2	0	1	2	3

Table 4 Numbers of Ephemeroptera, Plecoptera and Trichoptera species with flight periods of different lengths. Data for all sites combined. Species represented by fewer than 10 specimens omitted

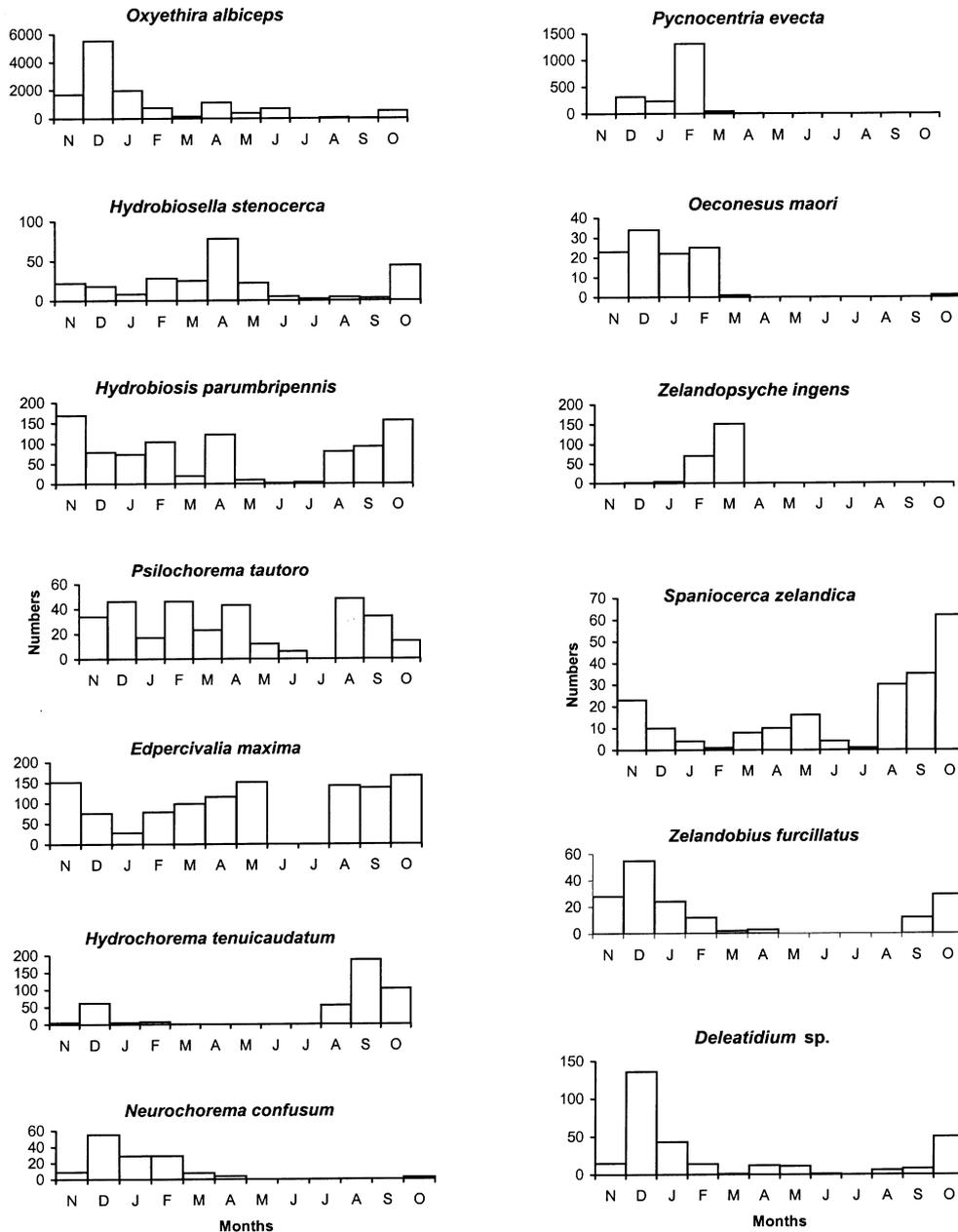


Fig. 5 Numbers of individuals of the 13 most abundant species captured each month from November 1996 to October 1997. Data for all sites combined.

trapped at a site above Middle Bush (Site 0) in addition to Sites 1 and 2. Seventy-three per cent of the three most abundant species (*E. maxima*, *H. tenuicaudatum*, *H. stenocerca*) were caught within the forest (Table 6). However, in contrast to 1996–97 (Table 5), only *H. stenocerca* was significantly more abundant on the downstream side of traps at Site 1. On the other hand, all three species were over-represented on the down-

stream side of the trap at Site 0, indicating most were flying upstream.

Discussion

Little is known about the quantitative processes that affect the adult stage of stream insects (Huryn & Wallace, 2000), although the potential effect of adult

Species	Site	n	Down side (%)	χ^2	P
<i>Z. ingens</i>	1	173	79	59.0	< 0.001
<i>Z. ingens</i>	2	53	70	8.3	< 0.01
<i>H. stenocerca</i>	1	261	70	40.6	< 0.001
<i>H. tenuicaudatum</i>	1	658	67	77.6	< 0.001
<i>E. maxima</i>	1	768	62	41.3	< 0.001
<i>E. maxima</i>	2	512	64	40.5	< 0.001
<i>O. albiceps</i>	4	10629	62	604.6	< 0.001
<i>H. parumbripennis</i>	4	670	53	1.93	> 0.05
<i>P. tautoru</i>	4	249	55	2.51	> 0.05
<i>N. confusum</i>	4	74	59	2.65	> 0.05
<i>O. maori</i>	4	73	47	0.34	> 0.05
<i>P. evecta</i>	4	1735	46	10.2	< 0.01*
<i>S. zelandica</i>	1	161	24	44.9	< 0.001*
<i>S. zelandica</i>	4	216	50	0	> 0.05

*Significantly more on the up-stream side of traps.

	Site 0			Site 1			Site 2		
	Up	Down	P	Up	Down	P	Up	Down	P
<i>H. tenuicaudatum</i>	5	14	< 0.05	28	29	n.s.	0	0	–
<i>E. maxima</i>	2	13	< 0.01	67	59	n.s.	11	12	n.s.
<i>H. stenocerca</i>	8	20	< 0.01	22	40	< 0.05	2	5	n.s.
Total	15	47		117	128		13	17	

dispersal and recruitment on gene flow among populations is receiving increasing attention (e.g. Schmidt, Hughes & Bunn, 1995; Bunn & Hughes, 1997). The colonization cycle hypothesis of Müller (1954, 1982), with its emphasis on upstream–downstream movements, has tended to dominate discussion on flight activity of stream insects, at the expense of other kinds of movements. However, movements of adult stream insects away from bodies of water have been the focus of some recent research (e.g. Kovats *et al.*, 1996; Collier & Smith, 1995, 1998; Petersen *et al.*, 1999).

In the present study, the flight activity of common species of Trichoptera, Plecoptera and Ephemeroptera was monitored along a small mountain stream over a period of 1 year. Flight periods of individual species ranged from 3 to 12 months, with most exceeding 6 months as reported for other New Zealand studies (Norrie, 1969; Ward *et al.*, 1996). However, as in those studies Conoesucidae were found to have short flight periods, a life history feature that has implications for the recolonization of intermittently dry streams (see below).

The distributions of larvae of common insect species differed along Middle Bush Stream, with several

Table 5 Proportions (%) of three forest-dwelling and five grassland-dwelling caddisflies, and one stonefly captured on the down-stream sides of sticky traps (i.e. moving upstream) at sites where they were most abundant. All collections combined. Site 1 in forest, Site 2 immediately below forest, Site 4 further downstream in grassland

Table 6 Numbers of three common caddisflies captured on the upstream (Up) and downstream (Down) sides of sticky traps, above (Site 0), within (Site 1) and below (Site 2) the forest in 3 months (December 1997–February 1998). *P*-values are for χ^2 -tests of Up versus Down comparisons (n.s. = > 0.05)

occurring mainly in either forest or grassland. The longitudinal distributions of adults caught on sticky traps at the five sites were strongly correlated with the distributions of their larvae, suggesting they had either recently emerged, or that dispersal of trapped individuals was limited. Research elsewhere (e.g. Svensson, 1974) indicates that the directions in which the adults of stream insects fly varies according to taxon, and in some species may be influenced by factors such as wind speed and wind direction (Madsen, Bengtson & Butz, 1973). Nevertheless, our bilateral trapping data indicated that a majority of individuals of several species, whose larvae are predominantly forest-dwelling, were flying upstream within the forest or just below it. An exception was the stonefly *S. zelandica*, which was taken in significantly greater numbers on the upstream side of traps within the forest. *Spaniocerca zelandica* is rarely seen flying and because many individuals were caught on traps close to the water they may have been floating passively downstream on the water surface following emergence on projecting stones. In contrast to the forest-dwelling caddisflies, flight directionality, as indicated by bilateral sticky trap catches, was weak or undetected in most grassland species. One likely

reason for this was that many trapped adults probably came from sources other than Middle Bush Stream.

Upstream flight by adults of forest-dwelling species was consistent with the colonization cycle of Müller, and may compensate for downstream drift of larvae. Results of the subsidiary trapping programme provide additional support for this proposal, as a majority of the three most common forest-dwelling insects captured in scrub above the forest had been flying upstream. However, the number of adults taken above the forest was much smaller than the number trapped within it. Directional flight into forest by a high proportion of caddisflies with predominantly forest-dwelling larvae, whether compensating for larval drift or not, can be seen as adaptive as eggs will then be laid in conditions most suitable for development of the immature stages. For example, a predictable supply of detrital food will be available for the obligate leaf and wood shredder *Z. ingens* (Winterbourn & Davis, 1976). Although nothing is known about the feeding requirements of adult caddisflies in New Zealand, it is possible that flight into forest may also enhance opportunities for feeding and hence reproductive development by adults of some species. Not only are such scenarios consistent with the natural selection-based explanations for directional flight of Anholt (1995) and Peckarsky *et al.* (2000), but also with the tenets of the colonization cycle.

Finally, what implications do our findings have for the recolonization of intermittently flowing reaches? Repeated observations by one of us (MJW) over the last 30 years indicate that variable lengths of the lower course of Middle Bush Stream dry up regularly, but for unpredictable periods of time. Unpublished experimental work by McLeod (1998) indicates that larvae in the permanently flowing upstream reaches, subsequently recolonize it by drift, while adults from undefined sources oviposit there when surface water returns. Because the stony bed of the intermittent reach dries rapidly to a depth of at least 30–40 cm, the hyporheic zone is of little importance as a refuge for epigeal invertebrates, many of which typically lack appropriate behaviour to avoid desiccation (Delucchi, 1989). Furthermore, colonization by upstream movement from Grasmere Stream (Fig. 1) is limited as tributary water enters it most of the time as sub-surface seepage. The opportunity to establish populations in the intermittent reach through oviposition

depends on adult females being present when water is present, and although some species found in this part of the stream have long flight periods, others, especially species of Conoesucidae, do not. Adults of *P. evecta*, for example, were trapped in very large numbers in the lower course of the stream during the dry period, but not when surface water returned. If recruitment from outside sources is necessary to maintain populations of species, as in some temporary streams (Dieterich & Anderson, 1995), one might expect to find considerable annual variation in larval population size depending on the degree of synchrony between flight periods and the occurrence of water. Furthermore, we would predict that such variation will be greater in species with short flight periods than in species with long ones. Long-term research will be needed to test these ideas.

Acknowledgments

Financial and logistic support for this study were provided by the Department of Zoology, University of Canterbury. We thank Dr Laurie Greenfield for permission to use the university field station at Cass as a base, and Pete Crowe, Loren Brown, Chris Glover, Rebecca McLeod and Helen Grant who acted as field assistants. Tracey Robinson and Kerry Winterbourn drafted Fig. 1, while constructive comments from three anonymous referees greatly improved the focus of the paper.

References

- Anderson N.H. (1992) Influence of disturbance on insect communities in Pacific Northwest streams. *Hydrobiologia*, **248**, 79–92.
- Anholt B.R. (1995) Density dependence resolves the stream drift paradox. *Ecology*, **76**, 2235–2239.
- Benke A.C. (1970) A method for comparing individual growth rates of aquatic insects with special reference to the Odonata. *Ecology*, **51**, 328–331.
- Bird G.A. & Hynes H.B.N. (1981) Movements of adult aquatic insects near streams in Southern Ontario. *Hydrobiologia*, **77**, 65–69.
- 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.
- Collier K.J. & Smith B.J. (1995) Sticky trapping of adult mayflies, stoneflies and caddisflies along three

- contrasting streams near Hamilton, New Zealand. *New Zealand Natural Sciences*, **22**, 1–9.
- Collier K.J. & Smith B.J. (1998) Dispersal of adult caddisflies (Trichoptera) into forests alongside three New Zealand streams. *Hydrobiologia*, **361**, 53–65.
- Delucchi C.M. (1989) Movement patterns of invertebrates in temporary and permanent streams. *Oecologia*, **78**, 199–207.
- Dieterich M. & Anderson N.H. (1995) Life cycles and food habits of mayflies and stoneflies from temporary streams in western Oregon. *Freshwater Biology*, **34**, 47–60.
- Edwards J.S. & Sugg P. (1993) Arthropod fallout as a resource in the recolonization of Mount St. Helens. *Ecology*, **74**, 954–958.
- Flory E.A. & Milner A.M. (2000) Macroinvertebrate community succession in Wolf Point Creek, Glacier Bay National Park, Alaska. *Freshwater Biology*, **44**, 465–480.
- Gray L.J. & Fisher S.G. (1981) Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran desert stream. *American Midland Naturalist*, **106**, 249–257.
- Greenland D.E. (1977) Weather and climate at Cass. In: *Cass: History and Science in the Cass District, Canterbury, New Zealand* (Ed. C.J. Burrows), pp. 93–116. Department of Botany Publication, University of Canterbury, Christchurch, New Zealand.
- Gressitt J.L. (1961) Problems in the zoogeography of Pacific and Antarctic insects. *Pacific Insects Monograph*, **2**, 1–94.
- 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.
- Huryn A.D. & Wallace J.B. (2000) Life history and production of stream insects. *Annual Review of Entomology*, **45**, 83–110.
- Kaiser E.W. (1961) On the biology of *Sialis fuliginosa* Pict. and *S. nigripes* Ed. Pict. *Flora Fauna, Silkeborg*, **67**, 74–96.
- Kovats Z.E., Ciborowski J.J.H. & Corkum L.D. (1996) Inland dispersal of adult aquatic insects. *Freshwater Biology*, **36**, 265–276.
- Laird M. (1956) Studies of mosquitoes and freshwater ecology in the South Pacific. *Royal Society of New Zealand Bulletin*, **6**, 1–213.
- Mackay R.J. (1992) Colonization by lotic macroinvertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 617–628.
- Madsen B.L., Bengtson J. & Butz I. (1973) Observations on upstream migration by imagines of some Plecoptera and Ephemeroptera. *Limnology and Oceanography*, **18**, 678–681.
- McCune B. & Mefford M.J. (1999) *PC-ORD. Multivariate Analysis of Ecological Data*, Version 4. MjM Software Design, Gleneden Beach, Oregon.
- McLellan I.D. (1991) Notonemouridae (Insecta: Plecoptera). *Fauna of New Zealand*, **22**, 1–62.
- McLellan I.D. (1993) Antartoperlinae (Insecta: Plecoptera). *Fauna of New Zealand*, **27**, 1–70.
- McLeod A.L. (1998) *Colonisation pathways of an intermittently flowing stream in relation to a changing flow regime and seasonality*. MSc Thesis, University of Canterbury, Christchurch, New Zealand.
- Milner A.M. (1987) Colonization and ecological development of new streams in Glacier Bay National Park, Alaska. *Freshwater Biology*, **18**, 53–70.
- Minshall G.W. & Petersen R.C. (1985) Towards a theory of macroinvertebrate community structure in stream ecosystems. *Archiv für Hydrobiologie*, **104**, 49–76.
- Müller K. (1954) Investigations on the organic drift in North Swedish streams. *Institute for Freshwater Research Drottningholm, Report*, **34**, 133–148.
- Müller K. (1982) The colonization cycle of freshwater insects. *Oecologia*, **52**, 202–207.
- Neboiss A. (1986) Atlas of Trichoptera of the SW Pacific-Australian region. *Series Entomologica*, **37**. W. Junk, Dordrecht.
- Norrie P.H. (1969) *The flight activity of Ephemeroptera and Trichoptera in a Waitakere stream*. MSc Thesis, University of Auckland, New Zealand.
- 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.
- 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., Winterbottom J.H., Orton S., Friberg N., Hildrew A.G., Speirs D.C. & Gurney W.S.C. (1999) Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, U.K. *Freshwater Biology*, **42**, 401–416.
- Phillips J.S. (1930) A revision of the New Zealand Ephemeroptera. *Transactions and Proceedings of the New Zealand Institute*, **61**, 271–390.
- 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.
- Sutcliffe D.W. & Carrick T.R. (1973) Studies on mountain streams in the English Lake District I. pH, calcium and the distribution of invertebrates in the River Duddon. *Freshwater Biology*, **3**, 437–462.

- Svensson B.W. (1974) Population movements of adult Trichoptera at a South Swedish stream. *Oikos*, **25**, 157–175.
- Timm T. (1994) Reasons for the shift in dominance between *Simulium* (N.) *vernum* and *Simulium* (S.) *ornatum* (Diptera: Simuliidae) along the continuum of an unpolluted lowland stream. *Archiv für Hydrobiologie*, **131**, 199–210.
- Towns D.R. & Peters W.L. (1996) Leptophlebiidae (Insecta: Ephemeroptera). *Fauna of New Zealand*, **36**, 1–143.
- Ward J.B., Henderson I.M., Patrick B.H. & Norrie P.H. (1996) Seasonality, sex ratios and arrival pattern of some New Zealand caddis (Trichoptera) to light traps. *Aquatic Insects*, **18**, 157–174.
- Winterbourn M.J. & Davis S.F. (1976) Ecological role of *Zelandopsyche ingens* (Trichoptera: Oeconesidae) in a beech forest ecosystem. *Australian Journal of Marine and Freshwater Research*, **27**, 197–215.

(Manuscript accepted 5 March 2001)