

# Barriers to the recovery of aquatic insect communities in urban streams

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## SUMMARY

1. Worldwide, increasing numbers of stream restoration projects are being initiated to rehabilitate waterways modified by urbanisation. However, many of these projects have limited success in restoring stream communities. Prompted by this, we investigated previously unrecognised barriers to aquatic insect colonisation in urban streams.
2. To investigate whether the availability of suitable substrata for oviposition limited the longitudinal distribution of caddisflies, large boulders were added to the upstream reaches of one stream. Prior to the addition, more egg masses were observed downstream and this longitudinal pattern persisted subsequently.
3. Malaise trapping revealed that adult caddisfly diversity and abundance was greater downstream than upstream. Furthermore, in a previous study the authors found larval caddisflies reflected the longitudinal distribution of adults.
4. The only obvious potential obstructions between reaches were roads beneath which the stream flowed through culverted crossings. Malaise trapping was used to examine the effect of road culverts and bridges on caddisfly dispersal. Numbers of caddisflies caught declined upstream and about  $2.5 \times$  more individuals were taken in traps immediately below than above five culverts.
4. Bridges, which had a more open structure than culverts, had no significant effect on the size of catches made above and below them.
5. Road culverts could act as partial barriers to upstream flight, with consequences for larval recruitment in urban streams. We recommend that urban planners and designers of restoration projects consider possible synergistic effects of poor oviposition habitat and barriers to aquatic insect dispersal, which may be critical for the colonisation of urban headwater streams and for the maintenance of stream insect populations.

*Keywords:* dispersal barriers, oviposition, restoration, road culverts, Trichoptera

## Introduction

Worldwide, numerous streams have been modified by urbanisation, which has resulted in the impairment of physicochemical conditions and the degradation of benthic communities (Suren, 2000; Paul & Meyer, 2001). In many developed nations organisations and

community groups have sought to rehabilitate streams through restoration projects whose main focus often has been to improve physical habitat. Activities such as the replanting of riparian vegetation, the re-establishment of bed substrata and flow heterogeneity and the reinstatement of pool-riffle sequences have been undertaken (Riley, 1998). However, contrary to the 'field of dreams hypothesis' (i.e. build it and they will come, Palmer, Ambrose & Poff, 1997), many urban stream communities have failed to recover even after stream conditions have improved (Larson, Booth & Morely, 2001; Walsh & Breen, 2001;

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Blakely & Harding, 2005; Suren & McMurtrie, 2005). To facilitate their recovery, a much better understanding of limiting mechanisms is required.

Bond & Lake (2003) suggested that ecological processes such as dispersal and recruitment might limit biotic responses to physically restored streams; however, their importance for colonisation of urban streams by aquatic invertebrate taxa has received little attention. Aquatic insects can populate waterways in three main ways: downstream drift, upstream migration and oviposition via aerial dispersal (Williams & Hynes, 1976). Although all three ways can be important for repopulating stream reaches, aerial dispersal of winged adult stages, especially ovipositing females, is vital (Williams & Hynes, 1976; Bunn & Hughes, 1997). This is particularly clear of headwater tributaries, where an upstream source of colonists is lacking (Wallace, Vogel & Cuffney, 1986; Flory & Milner, 2000). Moreover, the dispersal ability of individual taxa may be critical when a local source of repopulating adults is not available, or is limited in size (Cushing & Gains, 1989; Milner *et al.*, 2000). In addition, suitable oviposition habitat must be available if colonisation is to succeed.

Many freshwater insects have specific oviposition requirements. In particular, numerous caddisfly species deposit egg masses on the undersides of boulders in stream channels (Anderson & Wallace, 1984). Some Australian hydrobiosid caddisflies select emergent rocks where water velocities are  $>40 \text{ m s}^{-1}$  as oviposition sites, whereas the size of the emergent rock is more important than water velocity for other hydrobiosid species (Reich & Downes, 2003a). Other caddisflies lay their eggs on overhanging vegetation, submerged organic matter, or emergent pieces of wood (Hoffmann & Resh, 2003). Because stream beds in urban areas are often dominated by fine substrata such as silt and sand and have a paucity of large cobbles, emergent boulders or wood (Paul & Meyer, 2001), the availability of suitable oviposition sites may limit caddisflies and other aquatic insects.

Successful recruitment also requires that egg-laying females have access to appropriate habitat. In relatively pristine systems adults can disperse along stream corridors (longitudinal dispersal) and/or overland between streams (e.g. Macneale, Peckarsky & Likens, 2005). In urban areas, however, longitudinal dispersal may be the dominant pathway used by most aquatic species as the highly modified landscape may impede

or prevent lateral dispersal. Unfortunately, dispersal along urban waterways may also be obstructed by structures such as road crossings, bridges and culverts. Thus, Resh (2005) found that culverted stream crossings had a major effect on the upstream migration of diadromous shrimps and other non-insect taxa in French Polynesia, and few individuals of some species were found above stream crossings. Longitudinal connectivity and an absence of in-stream barriers, such as dams, piped sections of streams, waterfalls and weirs, have also been identified as critical for the successful recolonisation of waterways by many freshwater fish species (Concepcion & Nelson, 1999; Wiens, 2002; Wheeler, Angermeier & Rosenberger, 2005). Thick riparian vegetation and road networks may also pose significant barriers to dispersing aquatic insects (Collier & Smith, 1998; Briars, Cariss & Gee, 2002), although few studies have investigated their effects in urban streams (but see Wheeler *et al.*, 2005).

In this study we investigated obstacles to insect colonisation of urban streams in Christchurch, New Zealand. Since the arrival of European settlers in the early 1840s, development of the city has resulted in dramatic changes to the extensive network of wetlands and meandering spring-fed streams that once covered the alluvial floodplains of the region (Dendy, 1900). During the establishment of Christchurch, wetlands were drained and streams were straightened to increase drainage efficiency during floods. As a consequence, the ecological health of streams was compromised, with many having low in-stream and riparian habitat heterogeneity, and being subject to inputs of pollutants in storm-water during heavy rainfall events. 'Clean-water taxa' that were once abundant (e.g. mayflies and caddisflies) have been replaced by more 'pollution tolerant' taxa such as oligochaete worms, chironomid larvae and snails (Robb, 1980, 1992). Despite the water quality of these primarily spring-fed streams generally being good during baseflow (Blakely & Harding, 2005), the biological communities are not responding well to restoration work by the Christchurch City Council (Blakely & Harding, 2005; Suren & McMurtrie, 2005). For example, in Okeover Stream, of where many reaches have been subjected to extensive riparian and in-stream restoration, the benthic macroinvertebrate community has shown little response to the changes with caddisfly numbers in particular remaining low over much of its length (Blakely & Harding, 2005).

To investigate obstacles to aquatic insect colonisation, we assessed the availability of oviposition substrata and considered potential barriers to adult dispersal in headwater reaches of four Christchurch urban streams. Specifically, we tested whether: (i) the availability of oviposition substrata suitable for caddisflies could be limiting their distribution and (ii) whether structures such as road culverts act as obstructions that impede upstream flight of adult caddisflies along stream channels.

## Methods

### Study sites

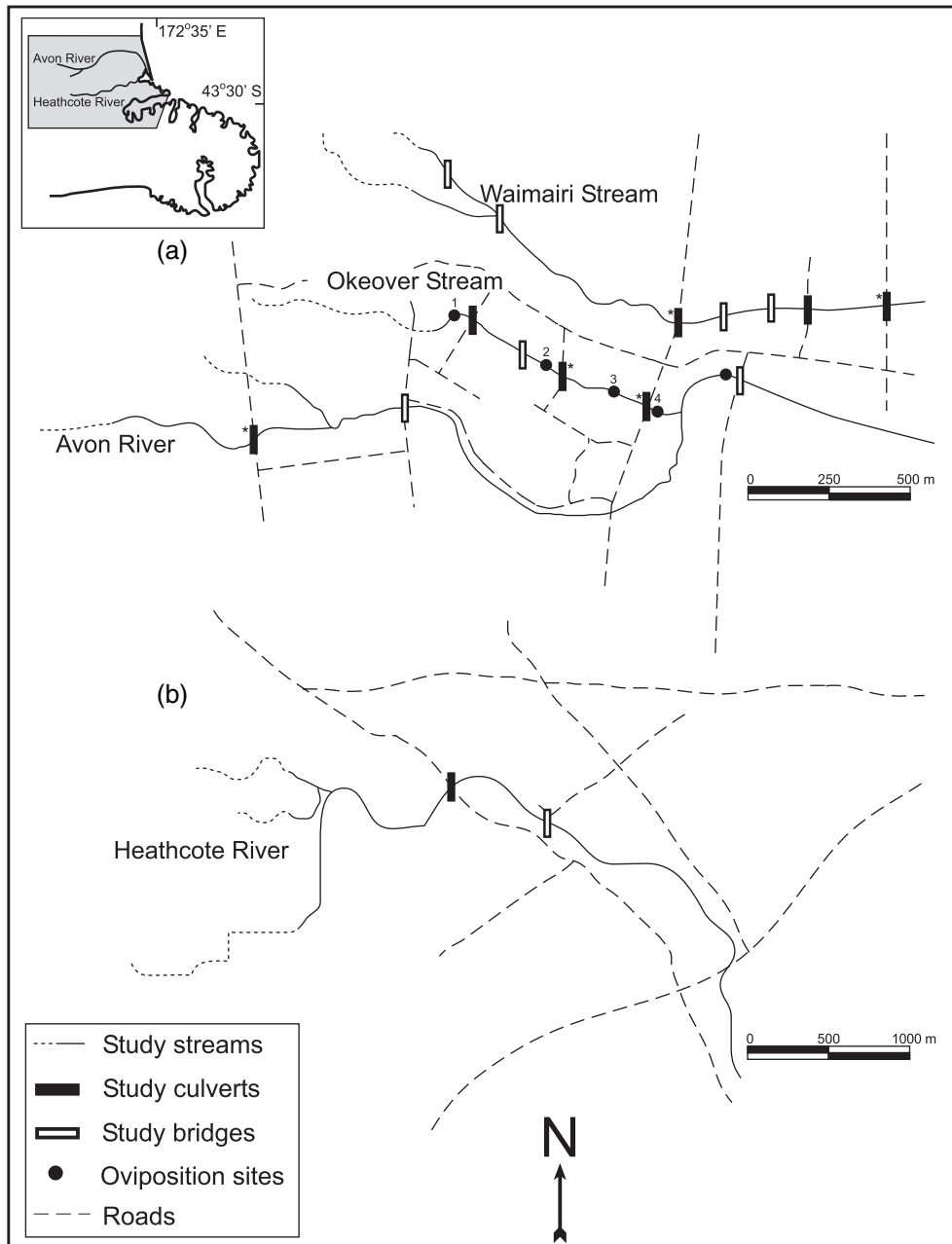
The study was undertaken in the upper reaches of four spring-fed, first and second order tributaries of the Avon and Heathcote rivers, which arise in the western suburbs of Christchurch (approximate population 345 000). An oviposition survey was carried out in Okeover Stream, and the effect of road culverts and bridges on adult caddisfly dispersal was examined in the Okeover and Waimairi streams and the Avon and Heathcote rivers (Fig. 1). All waterways were exposed to comparable levels of urbanisation: Okeover Stream and the Avon River headwaters flowed mainly through the University of Canterbury campus (established 1974), whereas Waimairi Stream and the Heathcote River were situated in long established residential areas. All waterways were shallow (0.05–0.15 m deep), narrow (<3.6 m wide wetted channels), with cobble and silt/sand-dominated riffles and pools with similar water velocities (0.15–0.3 m s<sup>-1</sup>) at base-flow. Grasses, planted native shrubs (*Hebe*, *Pseudopanax* and *Coprosma* species), and sedges (*Carex*) were the dominant bank vegetation, and numerous storm-water pipes guided runoff directly into the streams. Gastropod snails [*Potamopyrgus antipodarum* (Smith), *Physella acuta* (Draparnaud)], the amphipod *Paracalliope fluviatilis* (Thomson), chironomid larvae and several caddisflies including *Pycnocentroides aureola* (McLachlan), *Pycnocentria evecta* McLachlan (both Conoesucidae), the hydroptilid *Oxyethira albiceps* (McLachlan) and a hydrobiosid, *Hydrobiosis parumbripennis* McFarlane, dominated the benthic fauna. However, caddisfly richness and abundance was markedly greater in downstream reaches (Blakely & Harding, 2005). For example, at oviposition site 4 on Okeover Stream (Fig. 1) larvae of seven caddisfly

species were present with a mean total abundance of 309 ( $\pm 34.9$ ) m<sup>-2</sup>, whereas 250 m upstream only five species were found and a mean total abundance 69 ( $\pm 29.7$ ) m<sup>-2</sup>. Furthermore, *H. parumbripennis* and *O. albiceps* were more abundant downstream [59 ( $\pm 14$ ) and 5 ( $\pm 5$ ) m<sup>-2</sup>, respectively], than in the uppermost 400 m of the stream, where only *O. albiceps* was found at very low density [5 ( $\pm 5$ ) m<sup>-2</sup>; Blakely & Harding, 2005].

### Availability and use of oviposition substrata

We assessed oviposition of the hydrobiosid caddisfly *H. parumbripennis*, over the peak oviposition period, from 7 to 23 January 2003 (austral summer) in four, 10-m long reaches along 700 m of Okeover Stream (Fig. 1). *Hydrobiosis parumbripennis* was the only caddisfly to deposit eggs on the undersides of boulders in this stream. Of the other caddisflies present, the conoesucids release loose spherical egg masses directly into the water (Pendergrast & Cowley, 1966) and little is known about oviposition of the New Zealand hydroptilid *O. albiceps*. The amount of substratum potentially available for egg laying females was determined by counting all emergent and submerged boulders (i.e. >256 mm, longest dimension) in each 10 m reach. Other potential oviposition sites, such as overhanging vegetation, logjams, bricks, concrete, bottles and wood panels (all common in urban waterways) were noted but not used for egg mass counts. The number of *H. parumbripennis* egg masses on five of the largest boulders (or cobbles in reaches where boulders were absent or few) in each reach was counted on 7 January 2003. To determine whether substratum availability might be limiting oviposition by *H. parumbripennis* in reaches where boulders were rare, five large clean boulders (256–350 mm, longest axis) were placed randomly in the middle of the stream channel at each of the four reaches on 8 January 2003. Two weeks later the number of egg masses on each boulder was counted.

An estimate of the numbers of all caddisfly species potentially ovipositing in each reach was obtained using standard Malaise traps (1.9 m high, with 36.8 m<sup>3</sup> of trapping area), on three occasions during the peak flight period in January 2003: before, during and after the artificial substrata were added. Traps (one per reach) were set across the stream channel with their bottom edges touching the water surface



**Fig. 1** Map of the four study streams in Christchurch, New Zealand. The four oviposition study reaches along Okeover Stream are indicated by numbers 1–4, and the study culverts and bridges are shown along (a) the Avon, Waimairi and Okeover streams and (b) the Heathcote River (\*denotes the five culverts used in the first Malaise trapping survey). The location of the Avon and Heathcote rivers are shown in the inset, where grey shading indicates the Christchurch urban area.

and caught adults flying both up- and downstream, although they were not separated. Trapped insects accumulated in containers of 70% ethanol and were emptied after 48 h.

To determine whether the egg laying activity of *H. parumbripennis* differed when oviposition substrata

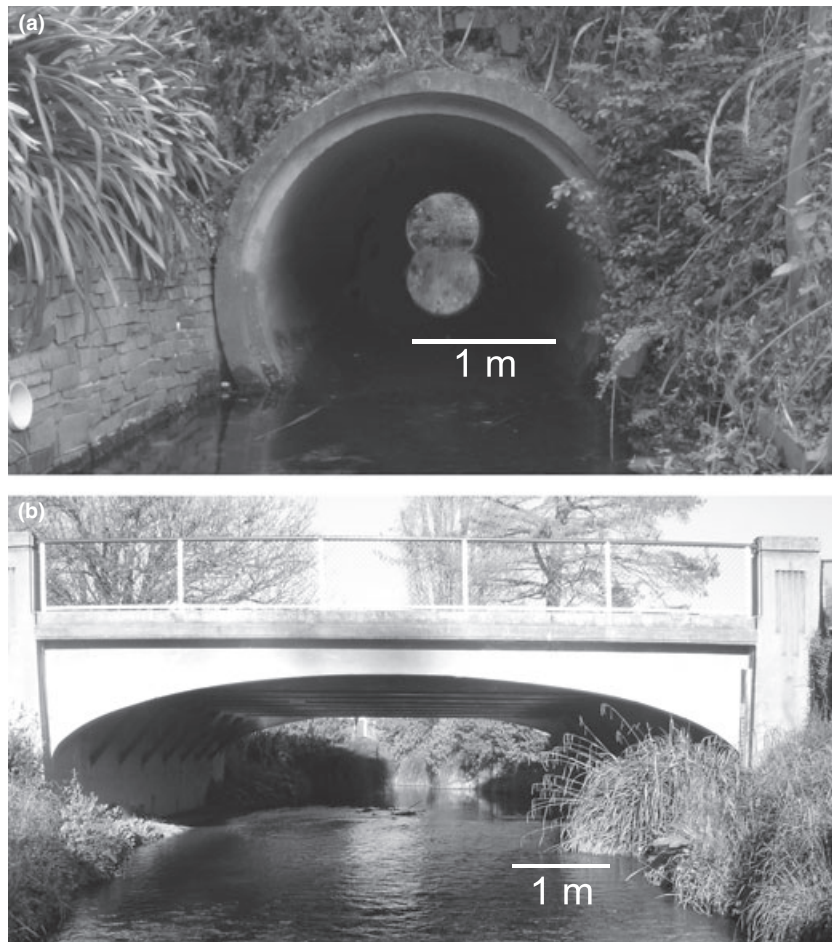
were more readily available, numbers of egg masses on substrata naturally occurring along Okeover Stream were compared with numbers found after two weeks on the added boulders, using two-way ANOVA. Boulders were used as replicates, whereas study reaches and boulder addition were fixed main effects.

Numbers of all caddis species and *H. parumbripennis* adults caught over 48 h in each study reach were converted into 24-h catch rates and compared, separately using one-way ANOVAs, with the three sampling periods as replicates. The total number of all caddis species and *H. parumbripennis* adults potentially ovipositing in each reach were compared before and after the boulder additions, separately using *t*-tests. Catches from Malaise traps set at each site before the additions were compared with the mean values of catches from Malaise traps over the two weeks following boulder addition.

*Road culverts as barriers to adult caddisfly dispersal*

Three Malaise trapping studies were conducted to assess the impacts of road culverts as potential obstructions to upstream flight of adult caddisflies.

First, we investigated the general effect of road culverts on caddisfly flight. This was carried out on three occasions at each of five replicate road culverts spanning the Okeover, Waimairi and Avon River headwater streams during the peak flight period (29 January to 4 February 2003). All culverts were approximately 22 m long, had similar internal dimensions (1.0–1.9 m high, 1.3–2.7 m wide) and external heights ranged from 1.3 to 4.5 m from the water surface to the road surface (Fig. 2a). A control trap was set 50 m downstream of each culvert in conjunction with a trap either directly upstream or downstream of the culvert. Because downstream traps may interfere with catches in traps upstream, if used simultaneously, the Malaise traps directly above and below culverts were used alternately over six consecutive days and nights; however, the control traps were always present. As most adult caddisflies



**Fig. 2** A typical (a) road culvert spanning the Avon River headwaters and (b) road bridge crossing the Heathcote River headwaters.

(66–74%) have been caught (and therefore appear to fly) within 30 cm of the stream surface in these urban waterways (J. S. Harding, unpublished data), traps were positioned as close as possible ( $\leq 1$  m) to the culvert opening to measure their effect on longitudinal dispersal. Malaise trap collecting jars were emptied every 24 h.

To assess the impact of road culverts as potential barriers to upstream flight, daily catches of caddisflies were expressed as average up- and downstream ratios at each culvert. Ratios were calculated by dividing up- and downstream catches by the control. The ratios were then ln-transformed and averaged for the three sampling periods at each culvert. MANOVA was used to test for differences in up- and downstream catch ratios of all caddis species, *O. albiceps* alone and all caddis species other than *O. albiceps*, using the five road culverts as replicates.

#### Cumulative effects of successive road culverts

The cumulative effect of successive road culverts on caddisfly catches was investigated in February 2004 using Malaise traps set across the stream channel directly upstream ( $\leq 1$  m) of three road culverts along each of Okeover and Waimairi streams. Each culvert was no more than 650 m upstream of the previous one. Collecting jars were emptied after five days and nights.

To determine whether multiple culverts were associated with a successive reduction in the number of potentially reproducing adults present upstream, the total number of all caddisfly species, *O. albiceps* and all species except *O. albiceps* caught over 120 h at each site were converted into 24-h catch rates. These were tested with chi-squared Goodness-of-Fit tests, where equal numbers of adults were expected upstream of each of the three culverts if they had no effect on caddis abundance. The two streams were tested separately, using road culverts as replicates. Because this trial lacked a control in the form of streams lacking culverts that could be trapped at similar longitudinal intervals, the results obtained must be considered preliminary as they could have been influenced by confounding local factors.

#### Road culverts versus bridges as barriers

The relative effectiveness of road bridges and culverts as barriers to caddisfly flight was investigated in

February 2004 by Malaise trapping directly upstream ( $\leq 1$  m) and 50 m downstream of eight culverts and eight bridges along the four urban streams (Fig. 1). All road bridges covered a similar length of stream as culverts (22 m) but the space beneath them was much more open (Fig. 2). Catches were collected after 96 h and expressed as bridge and culvert catch ratios as described above. MANOVA was used to test for differences in catch ratios of all caddis species and *O. albiceps* alone at bridges and culverts, with individual bridges and culverts as replicates.

Adult caddisflies were counted and identified to species under 10–60 $\times$  magnification using taxonomic guides and published descriptions (Mosely & Kimmins, 1953; Neboiss, 1986). All analyses were performed on Systat version 10 (Wilkinson, 1989). Residual plots were used to check for normality and response variables were  $\ln(x + 1)$  transformed where necessary to meet assumptions of normality and homogeneity of variances (Zar, 1999). Where appropriate, significant differences in site means were determined with Fisher's Least Significant Differences *post hoc* test.

## Results

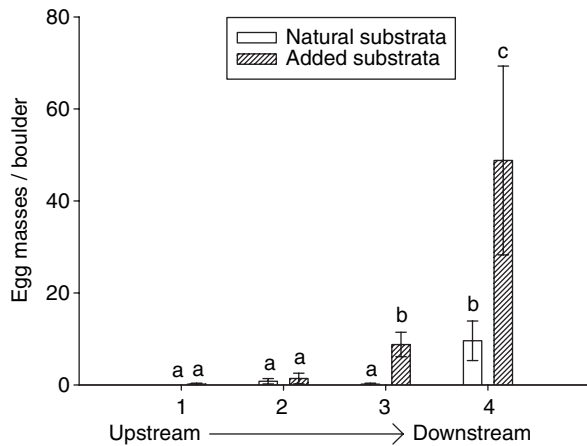
#### Availability and use of oviposition substrata

Boulders were naturally rare in Okeover Stream although more were present in the upstream than downstream reaches (Table 1). However, 91% of hydrobiosid egg masses were found on boulders in the furthest downstream reach (ANOVA reach effect:  $F_{3,32} = 21.05$ ,  $P < 0.001$ ) and none was found in the upper-most reach (Fig. 3). The average number of hydrobiosid egg masses found on emergent boulders added to the stream reaches was greater than on natural substrata but only in the two downstream

**Table 1** Numbers of boulders and other potential oviposition substrata recorded in four 10 m reaches, numbered longitudinally downstream, along Okeover Stream in January 2003

Reach	Emergent boulders/10 m	Submerged boulders/10 m	Other*/10 m
1 (upstream)	13	2	0
2	10	1	2
3	1	0	0
4 (downstream)	1	0	2

\*Other substrata included overhanging vegetation, logjams, bricks, concrete blocks, beer bottles and wood panels.



**Fig. 3** Mean ( $\pm$  SE) number of *Hydrobiosis parumbripennis* egg masses found on natural ( $n = 5$ ) substrata in four reaches and on boulders ( $n = 5$ ) added to the reaches for 2 weeks in January 2003. Significantly different site means are indicated by different letters.

reaches. Thus, the original longitudinal pattern of egg mass distribution became more marked two weeks after the boulders were added (ANOVA reach: boulder interaction:  $F_{3,32} = 3.64$ ,  $P = 0.023$ ). Furthermore, the number of potentially ovipositing caddisflies in the four study reaches did not differ significantly over the two week boulder manipulation period ( $t_{0.05,5} = 2.57$ , all caddis species:  $P = 0.705$ ; *H. parumbripennis*:  $P = 0.580$ ).

Although only *H. parumbripennis* laid egg masses on boulders, the hydroptilid *O. albiceps* dominated (>60%) adult catches in all study reaches along Okeover Stream. Nevertheless, *H. parumbripennis* was encountered in all study reaches, albeit in small numbers (Table 2). Significantly more adult caddisflies were caught in the reach furthest downstream, than in the three upstream reaches (ANOVA:  $F_{3,8} = 21.06$ ,  $P = 0.001$ ; Fig. 4a). The distribution of trapped

*H. parumbripennis* adults mirrored that of total caddis adults, with significantly more being caught downstream than upstream (ANOVA:  $F_{3,8} = 44.45$ ,  $P < 0.001$ ; Fig. 4b).

#### Road culverts as barriers to adult caddisfly dispersal

Upstream and downstream trapping resulted in many more adult caddis being caught below than above road culverts, although there was no difference in the number of adults captured in the downstream traps and their respective control traps (Fig. 5a). Downstream trap: control trap catch ratios were significantly greater than upstream trap: control trap ratios for all caddisfly species, *O. albiceps* and all caddis species except *O. albiceps* (Fig. 5b; Table 3). *Hydrobiosis parumbripennis* was captured in all traps, but in numbers too small to be tested statistically.

#### Cumulative effects of successive road culverts

Caddisfly abundance declined progressively above three successive culverts along Okeover Stream, with fewer adults being observed upstream of each road culvert than would be expected if adults were distributed equally (Fig. 6a; Table 4). This pattern was not found in Waimairi Stream where more adults were encountered upstream of the third culvert, than above the previous two (Fig. 6b; Table 4). However, when *O. albiceps* was excluded from the analysis a significant decline above successive road culverts was found in both Okeover and Waimairi streams (Fig. 6; Table 4).

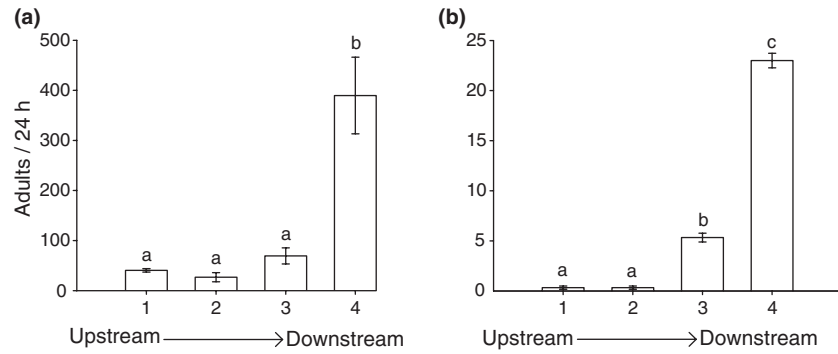
#### Road culverts versus bridges as barriers

Significantly fewer caddis adults were captured upstream of road culverts than bridges (Fig. 7a).

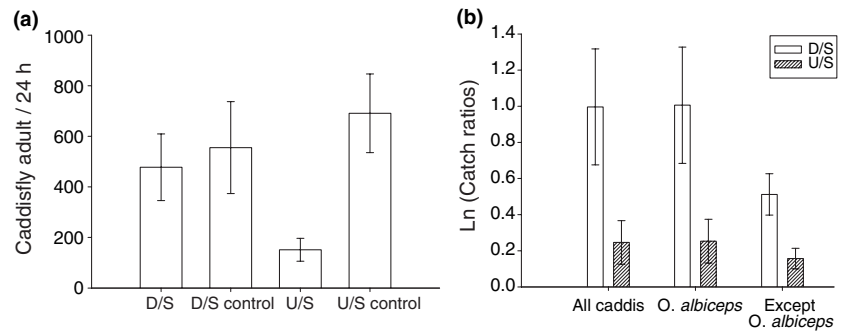
Family	Species	Reaches (upstream–downstream)			
		1 ( $n = 42$ )	2 ( $n = 28$ )	3 ( $n = 71$ )	4 ( $n = 390$ )
Hydrobiosidae	<i>Hydrobiosis parumbripennis</i>	1 (2.4)	1 (3.6)	5 (7.0)	23 (5.9)
	<i>Psilochorema tautoru</i>	0 (0.0)	0 (0.0)	2 (2.8)	0 (0.0)
Hydroptilidae	<i>Oxyethira albiceps</i>	40 (95.2)	27 (96.4)	43 (60.6)	326 (83.6)
Conoesucidae	<i>Pycnocentroides aureola</i>	0 (0.0)	0 (0.0)	6 (8.5)	13 (3.3)
	<i>Pycnocentria evecta</i>	0 (0.0)	0 (0.0)	12 (16.9)	24 (6.2)
Oeconesidae	<i>Oeconesus maori</i>	1 (2.4)	0 (0.0)	1 (1.4)	1 (0.3)
Leptoceridae	<i>Triplectides obsoletus</i>	0 (0.0)	0 (0.0)	1 (1.4)	1 (0.3)
Polycentropodidae	<i>Polyplectropus altera</i>	0 (0.0)	0 (0.0)	1 (1.4)	2 (0.5)

**Table 2** Mean number and relative abundances (%) of eight caddisfly species caught in Malaise traps on three sampling occasions, in four reaches along Okeover Stream, January 2003

**Fig. 4** Mean ( $\pm 1$  SE,  $n = 3$ ) number of (a) all caddisflies, and (b) *Hydrobiosis parumbripennis* adults captured in four reaches along Okeover Stream in January 2003. Significantly different site means are indicated by different letters.



**Fig. 5** Mean ( $\pm 1$  SE) (a) number of adult caddisflies captured downstream (D/S) and upstream (U/S) of five road culverts and in their respective control traps in three 24 h periods, in January and February 2004, and (b) ln-transformed catch ratios of all caddis adults, *Oxyethira albiceps* and all caddis except *O. albiceps*.



**Table 3** Multivariate and univariate ANOVAs examining the effects of road culverts on upstream flight of adult caddisflies along Okeover and Waimairi streams and the Avon River headwaters in January and February 2004. Catches were calculated as ln-transformed ratios and significant differences ( $P < 0.01$ ) were determined by Fisher's LSD *post hoc* tests, where D/S > U/S means catch ratios downstream of culverts were significantly greater than ratios upstream of culverts.

Response variable	Source	SS	d.f.	F-value	P-value	Differences
MANOVA	Model	0.23	3,6	6.89*	0.023	
All caddis	Model	1.14	1	6.08	0.039	D/S > U/S
	Error	1.50	8			
<i>O. albiceps</i>	Model	1.17	1	5.95	0.041	D/S > U/S
	Error	1.57	8			
Except <i>O. albiceps</i>	Model	0.39	1	5.66	0.045	D/S > U/S
	Error	0.56	8			

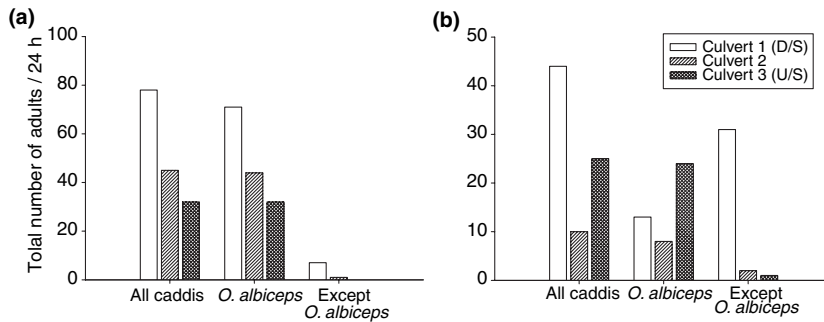
\*Wilks' lambda.

Furthermore, when catch ratios of all caddis species and *O. albiceps* were investigated, separately, all upstream trap: control trap ratios at bridges were significantly greater than those at culverts (Fig. 7b; Table 5), indicating that bridges had no effect on upstream caddisfly flight.

## Discussion

Our results suggest that the availability of oviposition substrata may be affecting recruitment of the caddisfly *H. parumbripennis*. When suitable oviposition sub-

strata were added to Okeover Stream, the number of egg masses deposited increased markedly. Although nothing has been reported on the oviposition requirements of hydrobiosid caddisflies in New Zealand, recent work in Australia has shown that females of several hydrobiosid species have very specific oviposition site requirements (Reich & Downes, 2003b). The cues that females use to determine suitable sites are likely to be diverse, but include water velocity around emergent boulders and 'landing pad' size (Reich & Downes, 2003a). The paucity or absence of boulders in New Zealand urban streams, which often have low in-



**Fig. 6** Numbers of adult caddisflies (all caddis, *Oxyethira albiceps*, and all caddis except *O. albiceps*) caught in 24 h in Malaise traps directly upstream of three successive culverts, on (a) Okeover and (b) Waimairi streams, February 2004.

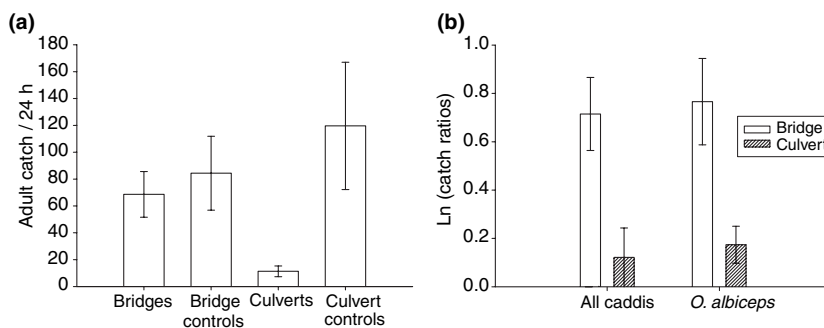
**Table 4** Chi-squared goodness of fit tests on the effects of three successive road culverts on upstream flight of all caddisfly adults, *Oxyethira albiceps*, and all caddis species except *O. albiceps*, along Okeover and Waimairi streams in February 2004. Significant differences ( $P < 0.01$ ) indicated, where 1 > 2 > 3 shows caddisfly catches were greatest at the first culvert (downstream) and decreased upstream being lowest above the third culvert.

	$\chi^2$ -value	d.f.	P-value	Differences
<b>Okeover Stream</b>				
All caddis	21.8	2	<0.001	1 > 2 > 3
<i>Oxyethira albiceps</i>	16.3	2	<0.001	1 > 2 > 3
Except <i>O. albiceps</i>	10.8	2	0.005	1 > 2 = 3
<b>Waimairi Stream</b>				
All caddis	22.1	2	<0.001	1 > 2 < 3
<i>Oxyethira albiceps</i>	8.9	2	0.011	1 = 2 < 3
Except <i>O. albiceps</i>	51.2	2	<0.001	1 > 2 > 3

stream habitat heterogeneity (Suren, 2000), may limit egg laying and translate into depauperate larval populations. Similarly, Purcell, Friedrich & Resh (2002) noted that the abundance and diversity of larval mayflies, stoneflies and caddis were only slightly higher in restored than unrestored reaches of an urban stream in California and concluded that this was because of a general lack of oviposition substrata throughout the stream.

The degree to which boulders are embedded in the streambed is also likely to limit oviposition by hydrobiosids as eggs are only laid on their under surfaces (Pendergrast & Cowley, 1966; J. G. Pendergrast & D. R. Cowley, personal observation) The larger numbers of egg masses laid on boulders placed on the streambed than on natural boulders (that were at least partially embedded) supports this view. Nevertheless, the availability of suitable oviposition substrata cannot be the only factor limiting the upstream distribution of caddisflies in our streams, as even when boulders were made more readily available along the stream many more egg masses of *H. parumbripennis* were still deposited in the furthest downstream reach.

Trapping of adults in the four reaches used to investigate oviposition revealed that adult caddisflies were also unevenly distributed along Okeover Stream, with about four times as many captured in the furthest downstream reach than in the three upstream reaches. *Oxyethira albiceps* was the most abundant caddis caught in all reaches and its longitudinal distribution mirrored that of the *H. parumbripennis* egg masses and (although taken in small numbers) the adults of that species. This consistent pattern suggests that the lack of *H. parumbripennis* egg masses upstream, even after adding boulders, was due not only to a paucity of oviposition substrata but



**Fig. 7** Mean ( $\pm 1$  SE) (a) number of adult caddisflies captured upstream of eight road bridges, eight road culverts and in their respective control traps over 4 days in February 2004, and (b) ln-transformed catch ratios of all caddis adults and *Oxyethira albiceps*.

**Table 5** Multivariate and univariate ANOVAs comparing the effects of road culverts with road bridges on upstream flight of adult caddisflies along Okeover and Waimairi streams and the Avon and Heathcote River headwaters in February 2004. Catches were calculated as ln-transformed ratios and significant differences ( $P < 0.01$ ) were determined by Fisher's LSD *post hoc* tests, where bridges > culverts means catch ratios above bridges were significantly greater than above culverts.

Response variable	Source	SS	d.f.	F-value	P-value	LSDs
MANOVA	Model	0.47	3,12	4.47*	0.025	
All caddis	Model	1.41	1	13.85	0.002	Bridges > culverts
	Error	1.42	14			
<i>O. albiceps</i>	Model	1.40	1	9.27	0.009	Bridges > culverts
	Error	2.12	14			

\*Wilks' lambda.

to few adults being present upstream. Of course, the lack of adults in upstream reaches could also reflect the scarcity of eggs, larvae or pupae of the previous generation at these sites. However, because many caddisflies including *H. parumbripennis* and *O. albiceps* are active flyers that were collected consistently at distances >50 m (and up to 200 m) from a stream by Collier & Smith (1998), they might be expected to disperse considerable distances along Okeover Stream if barriers to flight are absent. Larval distributions at the oviposition sites along Okeover Stream provide further evidence for this. Because Blakely & Harding (2005) found that larval caddisfly distributions mirrored the egg mass and adult abundances obtained in the present study, it is likely that barriers to dispersal limit the number of adults that reach the headwaters of the stream.

Roads were the only prominent physical features that divided our study reaches, and our Malaise trapping programme indicated that they and the culverts that ran beneath them, were impeding upstream flight. Thus, adult caddisfly abundance was greatly reduced above road culverts, with a 250% decline in adults encountered upstream, compared with downstream, of them. However, the number of adult caddisflies captured upstream of road culverts did not fall to zero, indicating that culverts were not absolute barriers to dispersal. Although steep mountainsides and dense vegetation are known to be barriers to insect flight (Jackson & Resh, 1989; Collier & Smith, 1998), very few studies have investigated the effects of anthropogenic barriers on aquatic insect dispersal. Smith & Collier (2001) suggested that the heavily urbanised Auckland isthmus could be a significant barrier to the caddisfly *Orthopsyche fimbriata* (McLachlan) and Purcell *et al.* (2002) speculated that underground piping and water

pollution were likely barriers to aquatic insect dispersal in California. The waterways in our study are not piped underground except at road culverts and water chemistry did not vary along the study streams (Blakely & Harding, 2005), therefore, a lack of surface flow or reaches of poor water quality would not have been significant barriers to adult caddisfly dispersal.

Road culverts probably impede aerially dispersing aquatic insects in several ways. First, because they are narrow and constrict the stream channels culverts potentially limit the likely flight paths of low-flying insects. Stream corridors are the main 'highways' for the dispersal of adult aquatic insects (Petersen *et al.*, 2004) and are likely to be particularly important in highly modified urban landscapes. By acting as physical barriers, culverts might inhibit further upstream flight and induce oviposition below them. Our finding that bridges, which have less constricted space beneath them, had less impact on the upstream flight of caddisflies supports this contention. Secondly, the flight behaviour of individuals that attempt to fly through a culvert or across a road may be disrupted, but because we lack an understanding of the cues aquatic insects use to disperse this remains conjectural. It is also possible that individuals attempting to fly through culverts suffer high mortality through predation. We observed many spider webs inside some culverts and they potentially trap caddisflies as well as other insects that enter them. Adult aquatic insects can be an important food resource for terrestrial predators, including riparian spiders (Nakano, Miyasaka & Kuhara, 1999; Kato, Iwata & Wada, 2004), which have the potential to reduce their numbers considerably.

A final important question that remains is how many females are needed to 'replenish' upstream reaches? Bunn & Hughes (1997) suggested that recruit-

ment of some species in small streams could result from oviposition by only a few females. However, although some adult caddis were found along the entire length of Okeover Stream, larval populations were minimal in upstream reaches. Thus, the small numbers of adults in these upstream reaches appeared to be insufficient to sustain populations of comparable size to those found downstream. This was despite only small differences in riparian vegetation, water quality and in-stream habitat heterogeneity that might otherwise explain the significant longitudinal differences in the abundances of adults and larvae. Our results suggest, therefore, that in urban streams where dispersing adults are faced with multiple barriers and oviposition habitat is poor, recruitment can be reduced to levels at which populations are difficult to sustain. We propose that while urban stream restoration projects should continue to target the primary factors that degrade urban catchments, such as altered stream hydrology and channel morphology, stormwater runoff, and reductions in riparian cover (e.g. Suren, 2000; Paul & Meyer, 2001; Walsh *et al.*, 2005), the introduction of in-stream substrata that can act as oviposition sites should be included in restoration programmes, and the constriction of streams by culverts and associated physical barriers should be minimised wherever possible in order to help sustain stream communities along the lengths of streams.

### Acknowledgments

Thanks to members of the Freshwater Ecology Research Group, University of Canterbury, Steve Ormerod and an anonymous referee for comments that improved the manuscript, John Ward for help with adult caddisfly species identifications and those who helped with fieldwork. Funding was provided by the Christchurch City Council via Rachel Barker and the University of Canterbury.

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(Manuscript accepted 8 June 2006)