

## Relative importance of surface and subsurface movement on benthic community recovery in the Makaretu River, North Island, New Zealand

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**Abstract** Colonisation of macroinvertebrates following changes to the stream environment occurs rapidly through drift, oviposition, lateral movement, and vertical migration. To assess the influence of different sources of colonists on benthic macroinvertebrate community composition, a colonisation experiment using artificial substrate baskets was conducted in the braided Makaretu River in the southern Hawke's Bay (North Island, New Zealand). Both the numbers of taxa and individuals rapidly increased through time in baskets only allowing drifting and surface crawling invertebrates (surface), baskets only allowing invertebrates migrating from the hyporheic zone (hyporheic), and baskets that allowed both (controls). The numbers of taxa and density of individuals indicated that the artificial substrate baskets were similar to the benthos after 14 and 28 days, respectively. However, overall benthic community composition was not similar to the surrounding benthos until Day 42 in all three basket treatments. The colonisation rates identified from artificial baskets in the Makaretu River are consistent with other colonisation experiments undertaken in New Zealand and overseas. Elmidae (Coleoptera) was most abundant within surface treatments until Day 28 after which *Deleatidium* spp.

(Ephemeroptera) became dominant. The abundance of Elmidae and *Deleatidium* in the control treatments was consistent with colonisation patterns in the surface baskets. *Deleatidium* dominated baskets allowing access from the hyporheic zone throughout the experiment. It appears that Elmidae colonise quickly in greater numbers by drifting and/or crawling and *Deleatidium* colonises more slowly from the hyporheic zone, eventually replacing Elmidae as the most common animal. This indicates that the hyporheic zone provides a source of invertebrate colonists later during community recovery, whereas drifting and/or crawling provides colonists early during recovery.

**Keywords** artificial substrates; benthic invertebrates; colonisation; community recovery; drift; hyporheic zone; New Zealand; rivers; subsurface colonisation

### INTRODUCTION

Colonisation of macroinvertebrates in streams occurs rapidly through drift, oviposition, lateral movement, and vertical migration (Williams & Hynes 1976). The ability of invertebrates to recolonise denuded habitats is influenced by disturbance type (Lake 2000), variance, and intensity (Lake & Barmuta 1986; Resh et al. 1988). Invertebrate community recovery is also influenced by the abundance (Marchant et al. 1991) and type of taxa present (Death 1996) before disturbance. Benthic community composition is affected by the source of colonists, with community composition during recovery changing through species specific colonisation patterns (Williams 1977; Sagar 1983). However, in systems where frequent disturbance events affect the benthos, the stream biota may undergo different recovery patterns and community composition from those where disturbance is less common (Townsend et al. 1997). For example, biotic interactions may play a significant role in recovery patterns and community composition during stable conditions or at

stable sites, whereas disturbance may be more important at physically unstable sites in determining community composition (Resh et al. 1988). Therefore, community structure may not only be affected by the physical and chemical nature of the stream, but by the type and source of possible colonists for the benthos (Sagar 1983; Death 1995).

The recovery of benthic macroinvertebrate communities following disturbance is rapid, especially when only considering the intrinsic growth rates of stream invertebrates (Palmer et al. 1992). Such rapid recovery has led to the proposition that the rate of recovery is increased by animals colonising from refugia such as low shear stress zones (Lancaster & Hildrew 1993a,b), stream margins and banks, in-stream woody debris (Palmer et al. 1995), and the hyporheic zone (Sedell et al. 1990). Although disturbance has long been considered a major structuring force in stream communities (Power et al. 1988; Resh et al. 1988), attention has only recently increased on the hyporheic zone as a source of colonists for denuded benthic substrates (Gore & Milner 1990; Sedell et al. 1990; Palmer et al. 1992). The hyporheic refuge hypothesis predicts benthic taxa migrate into the hyporheic zone during increased disturbance intensity (e.g., discharge or dewatering), then later move back to the benthos after flows have stabilised (Williams & Hynes 1974). A few studies have identified large numbers of epigeic taxa within the hyporheos of New Zealand river systems (e.g., Boulton et al. 1997; Adkins & Winterbourn 1999; Fowler & Death 2001). However, the potential of taxa colonising the benthic region by drifting or crawling is yet to be fully quantified for all streams (Williams & Hynes 1974; Gore & Milner 1990; Sedell et al. 1990).

A number of experimental studies have explored the length of time for community recovery after disturbance (e.g., Cairns et al. 1971; Doeg et al. 1989; Death 1996) and a few have assessed the significance of different sources of colonists to this recovery (e.g., Townsend & Hildrew 1976; Williams & Hynes 1976; Williams 1977). However, none has investigated benthic colonisation patterns in North Island, New Zealand gravel bed rivers. Benthic communities of New Zealand provide favourable systems to assess recolonisation patterns because of the unstable (Winterbourn et al. 1981; Winterbourn 1987) and rapidly changing flow regime (Scrimgeour et al. 1988; Death 1995). The Makaretu River, like other southern Hawke's Bay braided rivers (Fowler & Death 2000) undergoes highly variable flow conditions, which increase the

likelihood of disturbance to benthic communities in the stream channel. This study assesses the relative contribution of invertebrates from below (i.e., the hyporheic zone) and those from above the streambed (i.e., drift and crawling) to colonisation of artificial substrates in the braided Makaretu River. This study assesses whether individual taxa use different colonisation pathways during benthic community recovery.

## STUDY SITE

The Makaretu River is a third-order braided river in the southern Hawke's Bay, North Island, New Zealand (NZMS 260; U23 957 270), within fluvial deposits 20–25 m wide and a wetted channel width between 3 and 5 m. The Makaretu River is a tributary of the Tukituki River and originates in the foothills of the Ruahine Ranges before flowing through predominantly agricultural land. The region is characterised by mild winters and warm summers, with mean annual rainfall of  $928 \pm 260$  mm (Site 969402, Ongaonga, Hawke's Bay Regional Council (HBRC)). The Makaretu River has greywacke fluvial geology and substrates at the study site comprise 5% boulders (>26 cm), 10% large cobbles (12.1–26 cm), 30% small cobbles (6.1–12 cm), 40% gravel (0.2–6 cm), and 15% sand/silt (<0.2 cm) greywacke particles. Overhead cover is minimal, although willow (*Salix* sp.) is present along the true left bank of the sampled riffle, while willow weed (*Polygonum* sp.) and mixed exotic grasses are present along the true right bank. The catchment (18 km<sup>2</sup>) is predominantly pastoral farming, although native bush comprises c. 6 km<sup>2</sup> of the upper catchment within the Ruahine Ranges to an altitude of 1000 m a.s.l. Freshes are common in the Makaretu River throughout the year, although midsummer generally produces the lowest flows (HBRC unpubl. data).

The Makaretu River had slightly acidic pH (mean 6.76; range 6.75–6.79), with water temperatures measured in the sampled riffle at days 7, 14, 28, and 42 between 12.9 and 16.3°C (mean 14.5°C). Mean velocity sampled midstream in the study riffle was 0.87 m s<sup>-1</sup> (range 0.7–1.01), conductivity was between 84 and 96  $\mu\text{S cm}^{-1}$  (mean 92  $\mu\text{S cm}^{-1}$ ). Dissolved oxygen concentration was between 9.3 and 12.1 mg litre<sup>-1</sup> (85–110% saturation) (mean 10.2 mg litre<sup>-1</sup>; 99.5%). The sample riffle had a mean depth of 18 cm (range 14–24 cm) and mean width of 3.3 m (range 3.2–3.4 m).

## METHODS

### Artificial substrate baskets

On 23 March 1997, 36 plastic baskets (34 cm long, 28 cm wide, and 6 cm deep), with 150 holes (0.5 cm diam.) in the base (but absent from the sides), were placed into the river channel (along a single riffle section) level with the surrounding bed surface. Each basket contained seven small cobbles (mean diam. 8 cm) and gravels between 2 and 4 cm diam., with the composition similar to the natural river sediments in the study reach. Baskets were placed in 12 rows of three baskets each separated by at least 30 cm. The baskets were placed randomly within the rows and were later removed from the stream channel by collecting the appropriate furthest downstream basket first. One third of the baskets allowed colonisation only via the hyporheic zone (hyporheic) by sealing the top of each basket with clear plastic sheets. One third of the baskets allowed colonisation by drift or crawling only (surface) by sealing the bottom of the basket with clear plastic sheets; whereas the final third had no restrictions (control). Additional Surber samples were collected at the end of the experiment to provide a reference assessment of the benthic community in the natural streambed substrates. The collection of two hyporheic treatment baskets on Day 42 was the result of the loss of one hyporheic basket from the sample riffle.

The placement of artificial substrates may alter hydrological exchange between the river and underlying substrates. However, the influence of this potential change was not regarded to be significant because baskets were placed mid-way along a sampled riffle in a section of the river that undergoes groundwater exfiltration into the surface water (HBRC 1999). The alteration of the hydraulic regime by the artificial baskets was not suggested to be significant considering the reference controls (Surber samples) were comparable to the artificial substrate communities after 42 days.

### Sampling protocol

Randomly selected baskets were removed from the riverbed between 30 March and 2 May 1997 at 7-, 14-, 28-, and 42-day intervals. On each sampling occasion, three replicates for each treatment (hyporheic, surface, and control) were removed into a large collecting net (300  $\mu$ m mesh) down stream of the sampled basket. Each sample was then sieved through 15 mm wire mesh on site to remove the gravel portion and stored in 70% ethanol for later sorting and identification. Individuals were classified

to the lowest possible taxon using the keys of Winterbourn & Gregson (1989) and Chapman & Lewis (1976). At the conclusion of the experiment, four Surber samples (30 cm wide and 30 cm long) were collected to a depth of 6 cm from the riffle immediately upstream of the artificial substrate baskets as reference samples for the benthos.

Depth and velocity (measured with a velocity head rod) were sampled at four random locations within the sampled riffle. Conductivity and temperature (measured with an Orion 122 conductivity meter), pH (measured with an Orion 250A pH meter), and dissolved oxygen (measured with a YSI 59 dissolved oxygen meter) were recorded at the head of the sampled riffle on each sampling occasion (refer to Study Site section).

### Data analysis

To assess whether sampling occasion and colonisation treatment differed with respect to community characteristics (i.e., number of taxa, number of individuals, Margalef's scores, Berger/Parker scores, and % of taxa belonging to Ephemeroptera, Plecoptera, and Trichoptera (% EPT), all variables were analysed with a 2-way analysis of variance using SYSTAT (1996). Before analysis, the total number of individuals and abundance of the seven most common taxa were log transformed to increase normality and homogeneity of variance of data. A visual assessment of probability plots confirmed the assumption of homogeneity of variance in the data. Tukey's HSD test was used *post hoc* to assess differences between sampling occasion and treatment.

To assess variation in community composition among treatments and between sampling occasions, a Detrended Correspondence Analysis (DCA) and a Multi Response Permutation Procedure (MRPP) (using Sorensen's distance measure) were performed using the PCORD statistical package (McCune & Mefford 1995). MRPP is similar to a multivariate analysis of variance without the requirement of multivariate normality and homogeneity of variance (Berry et al. 1983; Mielke 1984; Biondini et al. 1985). It tests the hypothesis of no difference between two or more predetermined groups of entities, with significance inferred at  $P < 0.05$ . The Berger/Parker dominance index (Berger & Parker 1970) and Margalef's index of species diversity (Clifford & Stephenson 1975) were used to assess two components of species diversity in stream systems. Assessment of the proportion of % EPT followed the approach of Lenat (1988) by dividing the sum of the number of individuals belonging to

EPT by the total number of all individuals in a sample.

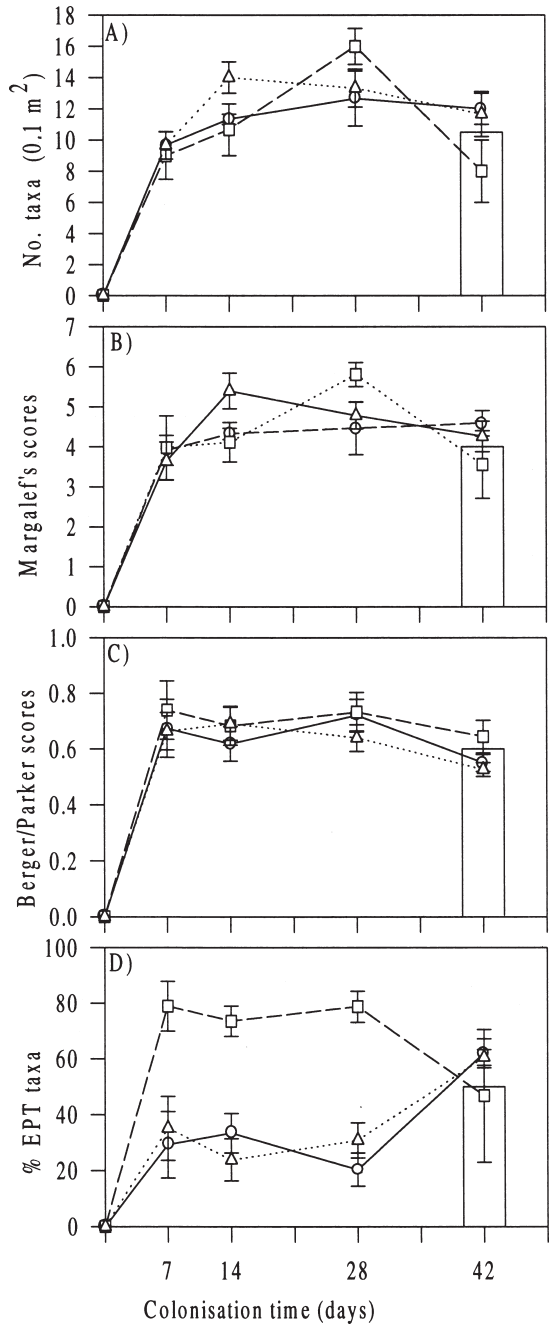
## RESULTS

### Diversity patterns

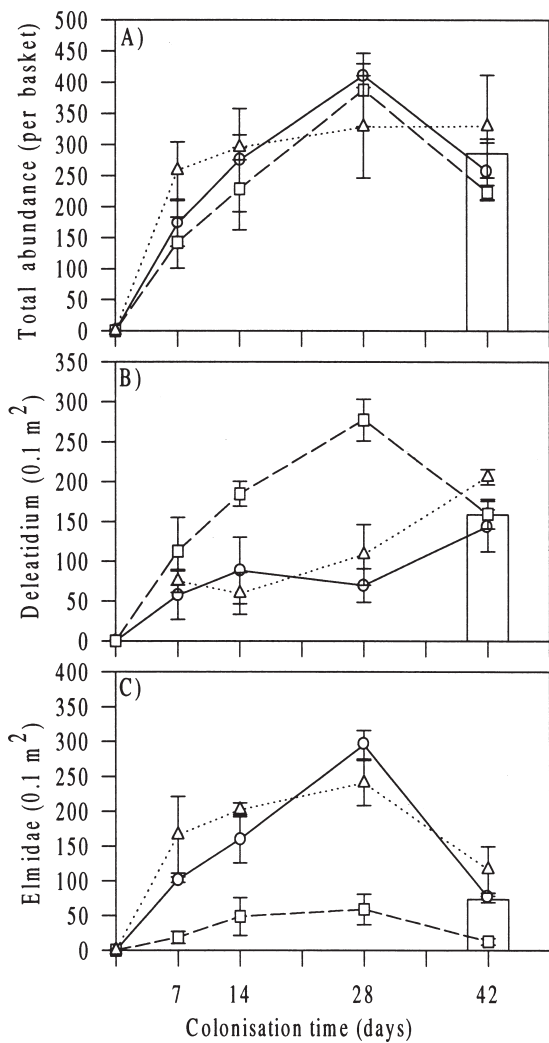
The number of taxa rapidly increased in all treatments within the first 7 days, before increasing steadily thereafter, peaking at Day 28 in control and hyporheic treatments, and at Day 14 in surface treatments ( $F_{3,29} = 5.95, P < 0.01$ ) (Fig. 1A). Number of taxa present was not significantly different among colonisation treatments overall ( $F_{2,29} = 0.61, P = 0.55$ ). Margalef's index of species diversity increased sharply within the first 7 days, and then remained constant in the controls, but increased to peak at Days 14 and 28 in the surface and hyporheic treatments, respectively ( $F_{3,29} = 2.96, P = 0.04$ ) (Fig. 1B). Margalef's scores were not significantly different between treatments ( $F_{2,29} = 0.15, P = 0.86$ ). The Berger/Parker index of species dominance was similar over time ( $F_{3,18} = 1.31, P = 0.29$ ) and between treatments ( $F_{2,29} = 1.26, P = 0.30$ ) (Fig. 1C). The % EPT increased rapidly in hyporheic treatments for the first 7 days then remained relatively stable over time. The control and surface treatments increased initially at Day 7 and remained constant until the end of the study when % EPT rapidly increased between Days 28 and 42 ( $F_{3,29} = 4.81, P < 0.01$ ) (Fig. 1D). The EPT scores were highest after 42 days of colonisation in the control and surface treatments, and highest in the hyporheic treatments in the first 7 days ( $F_{2,29} = 28.78, P < 0.01$ ). There was no significant interaction between time of sampling or treatment for number of taxa, Margalef's scores, Berger/Parker scores, or % EPT taxa.

### Invertebrate abundance

Density of invertebrates increased in all treatments over time overall, but remained relatively constant between Days 14 and 42 ( $F_{3,29} = 6.41, P < 0.01$ ). Hyporheic baskets had significantly fewer individuals than surface and control baskets overall ( $F_{2,29} = 4.58, P = 0.02$ ), but were similar to the other treatments at Day 42 (Fig. 2A). There was no significant interaction between time of sampling and treatment for a number of individuals. Numerically, *Deleatidium* was most abundant within the hyporheic treatment (Table 1; Fig. 2B), whereas Elmidae was most abundant in the control and surface treatments (Table 1; Fig. 2C). The numerical abundance of *Deleatidium* increased in all treatments



**Fig. 1** A, Mean ( $\pm 1$  SE) number of taxa; B, Margalef's scores; C, Berger/Parker scores; and D, % Ephemeroptera, Plecoptera, and Trichoptera (% EPT) scores within hyporheic (squares), surface (triangles), and control (circles) treatments from the Makaretu River (North Island, New Zealand) collected between 30 March and 2 May 1997. Bars in each graph represent Surber samples collected at Day 42.



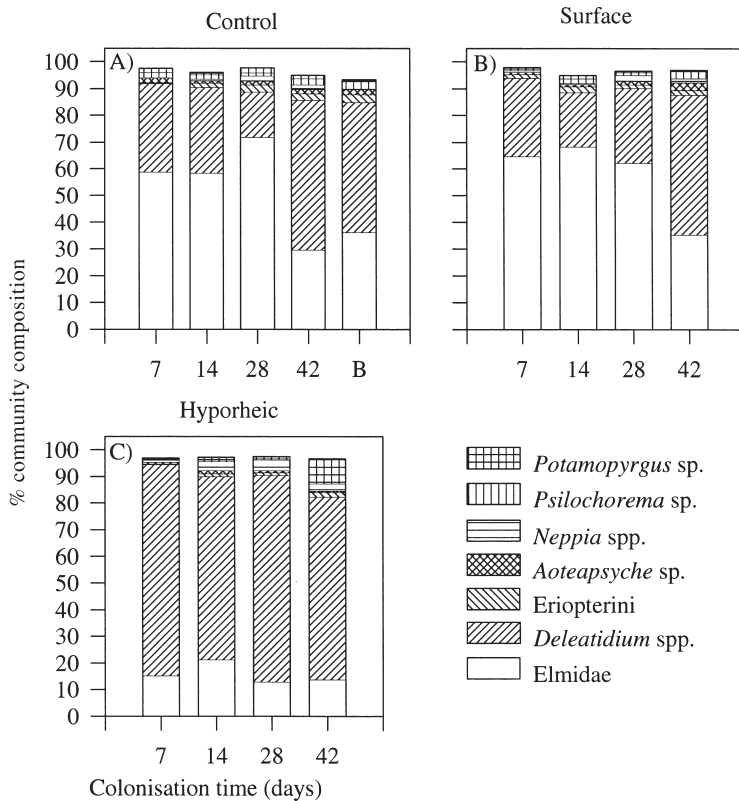
**Fig. 2** Mean ( $\pm 1$  SE) **A**, total number of individuals; **B**, *Deleatidium*; and **C**, Elmidae larvae within hyporheic (squares), surface (triangles), and control (circles) treatments from the Makaretu River (North Island, New Zealand) collected between 30 March and 2 May 1997. Bars in each graph represent Surber samples collected at Day 42.

through time, peaking at Day 28 in the hyporheic treatment, and at Day 42 in the control and surface treatments. All treatments had similar numerical abundance of *Deleatidium* on Days 7 and 42, but *Deleatidium* was at least 2 times more abundant during Days 14 and 28 in the hyporheic treatment compared with the control and surface treatments.

The density of Elmidae steadily increased through time in the control and surface treatments, peaking

**Table 1** *F* values testing differences between sampling occasion and treatment for the seven most common taxa from three artificial substrate treatments. Samples were collected on four occasions between 30 March and 2 May 1997 in the Makaretu River (North Island, New Zealand). Data are presented as means, with ranges in parentheses. (NS = not significant.)

Invertebrate:	Elmidae	<i>Deleatidium</i> spp.	<i>Neppia</i> sp.	<i>Aoteapsyche</i> sp.	Eriopterini	<i>Potamopyrgus</i> sp.	<i>Psilochorena</i> sp.
Mean count (0.1 m <sup>2</sup> )							
Control	156 (63–334)	90 (12–188)	3.4 (0–9)	3.9 (0–17)	5.5 (0–13)	3.8 (0–11)	5.3 (2–8)
Hyporheic	35 (4–103)	150 (35–330)	6.6 (0–23)	1.9 (0–9)	2.3 (0–6)	3.5 (0–10)	1.0 (0–4)
Surface	181 (74–264)	112 (29–223)	4.3 (0–9)	2.4 (0–13)	5.3 (2–10)	1.8 (0–5)	4.9 (0–13)
Sampling occasion d.f. = 2, 23							
<i>F</i> value	8.26	–	13.69	–	7.61	–	–
<i>P</i> value	<0.01	NS	<0.01	NS	<0.01	NS	NS
Treatment d.f. = 2, 23							
<i>F</i> value	45.72	–	–	–	5.99	–	11.25
<i>P</i> value	<0.01	NS	NS	NS	0.01	NS	<0.01
Time $\times$ treatment d.f. = 6, 23							
<i>F</i> value	–	2.51	–	–	–	–	–
<i>P</i> value	NS	0.05	0.02	NS	NS	NS	NS



**Fig. 3** Percent community composition for the seven most abundant taxa within **A**, control; **B**, surface; and **C**, hyporheic treatments collected between 30 March and 2 May 1997 in the Makaretu River (North Island, New Zealand). Percent composition bar "B" in the control graph represents Surber samples collected at Day 42.

at Day 28, before declining by Day 42 (Fig. 3B). By comparison, the abundance of Elmidae remained relatively constant in the hyporheic treatments between Days 7 and 28, before declining in abundance by Day 42. Overall, the numerical abundance of Elmidae was low in the hyporheic treatment throughout the 42-day experiment, but was significantly higher in the surface and the control treatments, especially at Day 28. Elmidae was least abundant in the surface and control treatments at Days 7 and 42.

The density of taxa such as Eriopterini, *Neppia* sp., *Aoteapsyche* sp., *Psilochorema* sp., and *Potamopyrgus antipodarum* was low in all treatments (Table 1). The abundance of *Neppia* was significantly highest in all treatments at Day 42 and lowest at Day 7. The abundance of *Psilochorema* was similar over time, but was significantly less abundant in the hyporheic treatments compared with the control and surface treatments. The abundance of Eriopterini was significantly highest at Days 28 and 42 and lowest at Day 7, and was highest in the control and surface treatments overall (Table 1). All other rare taxa were not significantly different among

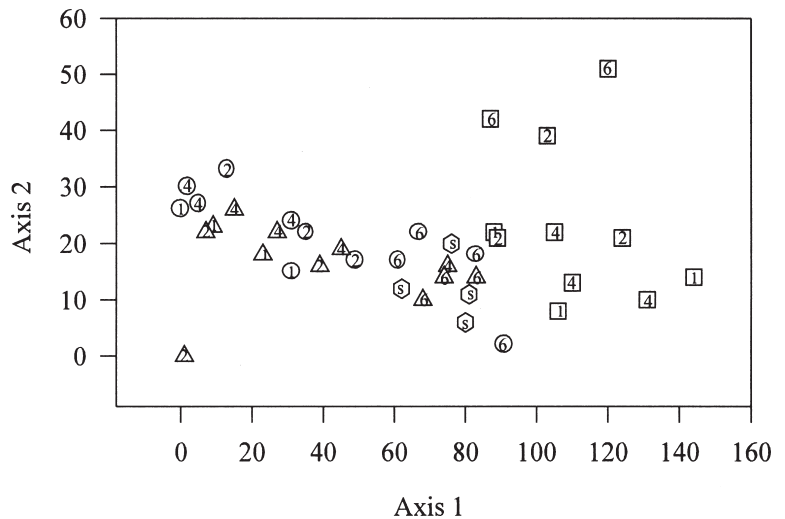
sampling treatments or over time. Refer to Table 1 for significant interactions for individual taxa.

### Community composition

Control (Fig. 3A) and surface treatments (Fig. 3B) had different community composition over the 42-day experiment, although with the exception of rare taxa (increased in % abundance over time) community composition was similar between Days 7 and 42 in the hyporheic treatment (Fig. 3C). The change in community composition over time in the control and surface treatments was because of the different relative abundance of *Deleatidium* and Elmidae, with Elmidae dominating samples within the first 28 days and *Deleatidium* dominating samples thereafter. The abundance of rare taxa such as Eriopterini, *Neppia*, *Aoteapsyche*, *Psilochorema*, and *P. antipodarum* constituted <12% of the community in all treatments overall.

Ordination of assemblage structure separated treatments along Axis 1 (Fig. 4), with the control (and additional Surber controls) plus surface treatments to the middle and left, while hyporheic samples grouped to the middle and top right. Sites were

**Fig. 4** DECORANA analysis of samples collected from hyporheic (squares), surface (triangles), and control (circles) treatments in the Makaretu River (North Island, New Zealand) between 30 March and 2 May 1997. Colonisation time is represented at Days 7 (1), 14 (2), 28 (4), and 42 (6). Hexagons (s) represent Surber samples collected on Day 42.



separated according to taxon abundance, with taxa such as Elmidae, Eriopterini, *Archicauliodes diversus*, *Coloburiscus humeralis*, Tabanidae (negatively correlated with Axis 1), and *Costachorema xanthopterum* (positively correlated with Axis 1) associated with control and surface treatments (Table 2). In contrast, *Deleatidium* (positively correlated with Axis 1) and *Pycnocentrella eruensis* (negatively correlated with Axis 2) were associated with the hyporheic treatments. Axis 1 accounted for 55.1% of the variation in the data while Axis 2 accounted for 15.2%.

MRPP showed community composition was significantly different among treatments overall ( $r = 0.06$ ,  $P = 0.03$ ) and between treatments at Days 7 ( $r = 0.20$ ,  $P = 0.01$ ), 14 ( $r = 0.26$ ,  $P = 0.02$ ), and 28 ( $r = 0.48$ ,  $P < 0.01$ ), but not at Day 42 ( $r = 0.24$ ,  $P = 0.06$ ). In addition, community composition differed within the control treatment in the first 14 days ( $r = 0.31$ ,  $P < 0.01$ ), but did not change thereafter. Community composition in the surface ( $r = 0.18$ ,  $P = 0.06$ ), and hyporheic treatments ( $r = 0.11$ ,  $P = 0.11$ ) was similar throughout the experiment. Moreover, benthic samples collected at Day 42 using a Surber were not significantly different in composition from the control treatment sampled at Day 42 ( $r = 0.23$ ,  $P = 0.12$ ).

## DISCUSSION

Stream macroinvertebrate communities in New Zealand are primarily structured by physical and physico-chemical disturbance, where fluctuations in

**Table 2** Significant Pearson's  $r^2$  values (after Bonferroni correction) for individual taxa along Axis 1 and Axis 2 of a Detrended Correspondence Analysis (DCA). Significance at  $P < 0.05$  is inferred at  $r^2 = \pm 0.532$ . (NS = not significant.)

Taxa	Axis 1	Axis 2
<i>Archicauliodes diversus</i>	-0.698	NS
<i>Costachorema xanthopterum</i>	NS	0.835
<i>Coloburiscus humeralis</i>	-0.618	NS
<i>Deleatidium</i> spp.	0.580	-0.720
Elmidae	-0.901	NS
Eriopterini sp.	-0.552	NS
<i>Pycnocentrella eruensis</i>	NS	-0.568
Tabanidae	-0.562	NS

flow strongly influences the distribution of species (Townsend et al. 1997; Winterbourn 1997). Such unpredictable and highly variable environmental conditions may offset the importance of biotic interactions in stream communities; however, factors such as competition for food resources or habitat can still significantly influence benthic community composition (McIntosh 2000), especially in stable sites or during stable conditions. The current study investigated the influence of surface and subsurface colonisation sources for a braided section of the Makaretu River during stable summer low flows to investigate whether individual taxon use different colonisation pathways during benthic community recovery.

Colonisation was rapid in all treatments, with species diversity comparable to the surrounding benthos within the first 7 days of colonisation. However, it was only after 28 and 42 days, respectively, that density and community composition were comparable to the benthos. These results are comparable with other studies in New Zealand, indicating that although all taxa colonise rapidly, pre-existing community composition may not be achieved for over 1 month (Sagar 1986; Scrimgeour et al. 1988). This duration of species recovery is also consistent with a number of international studies showing that a number of taxa recover within a few weeks (Boulton et al. 1991; Mathooko & Mavuti 1992) to periods exceeding 1 month (Williams & Hynes 1976; Meier et al. 1979).

The abundance of invertebrates colonising the benthos is known to vary with the source of invertebrates (Townsend & Hildrew 1976; Williams & Hynes 1976; Boulton et al. 1991). The type of taxa colonising and the subsequent community composition differed among treatments, with surface and control communities distinct from baskets colonised solely from within the stream bed. Community composition at Day 42 was no different between treatments (and Surber control samples) when *Deleatidium* was the most abundant taxon. *Deleatidium* also dominated the hyporheic treatments throughout the experiment, while Elmidae dominated the surface (and control) baskets until Day 28. This pattern of community recovery between surface and hyporheic treatments suggests *Deleatidium* colonised by vertical movement from within the bed and Elmidae colonised by drifting or crawling. Previous studies in New Zealand (e.g., Sagar 1986; Scrimgeour et al. 1988; Sagar & Glova 1992) have shown that *Deleatidium* represents a significant proportion of drifting invertebrates, so it was surprising that it was most common in the hyporheic baskets. Perhaps the flattened streamlined body shape of *Deleatidium* may explain the lower abundance of this taxon colonising by drifting or crawling in this study (see also Gayraud et al. 2000) compared with the more tubular shaped Elmidae.

By comparison, habitat preferences by Elmidae may have affected the preference of this taxon to colonise by drifting and/or crawling. Overall, the movement of bed substrates declines with increasing particle size (Carling 1983; Carson & Griffiths 1987). Elmidae, which may prefer finer sediments (Death 2000), may be more likely to colonise through surface movement because smaller substrates are more likely to move with changes in

flow. Thus, *Deleatidium* may passively enter the drift less often compared with Elmidae because this taxon is more abundant on larger substrates (Jowett & Richardson 1990; Quinn & Hickey 1990). Elmidae larvae may also be more prone to removal from bed substrates because these animals are less streamlined compared with *Deleatidium*.

Species diversity is known to be highly variable in streams in response to disturbance, resource availability, and the presence of suitable habitat (Minshall 1988; Resh et al. 1988). The type of disturbance (Lake 2000), the type of resources, and the availability of suitable physical habitat also influence colonisation of denuded habitats. Sagar (1986) found that colonisation of benthic communities occurred over periods between 15 days (summer) and 33 days (winter) after floods, whereas Scrimgeour et al. (1988) found that communities had reached pre-disturbed composition within 132 days after an extremely high flood event. The present study indicated that species diversity (richness, dominance, and number of taxa) was comparable to the benthos after 7 days of colonisation, but total abundance and overall community composition was not similar to the benthos until between 28 and 42 days of colonisation. By comparison, species dominance was similar between treatments and over time in this study, because braided river sections are often dominated by a single taxon (Sagar 1986; Scrimgeour et al. 1988; Fowler & Death 2000).

In the absence of disturbance, community composition may be strongly influenced by biotic interactions such as competition and predation (McIntosh 2000). In this situation, community structure has been suggested as essentially dependent on the original colonisation episode (i.e., founder controlled) (Yodzis 1986; see also Townsend 1989). However, considering Elmidae provided a greater density of colonisers early then declined later, while *Deleatidium* density was low initially but increased later, suggests Elmidae is an efficient early colonist, and *Deleatidium* colonises substrates later. This mayfly is frequently the most abundant insect in New Zealand streams (Boothroyd 2000; Winterbourn 2000). The dominance of the treatments by *Deleatidium* in this study may also reflect the habitat preference of *Deleatidium* for the cobble and gravel sized substrates (Jowett & Richardson 1990; Quinn & Hickey 1990) and the preference of finer substrates by Elmidae. By comparison, the proportion of *Deleatidium* and Elmidae may have remained constant in the hyporheic treatment because the hyporheic zone may provide a greater

source of colonising *Deleatidium* taxa in this river. Restricting colonisation to the hyporheic zone only may have allowed more of this taxon to colonise because of the inability of Elmidae to colonise by drifting and crawling. Therefore, removing the influence of a colonisation source (i.e., crawling and drift) may alter community composition in the short term by restricting the type of colonists (Williams 1977; Sagar 1983). However, restricting some colonising taxa (e.g., *Deleatidium*) may also be comparable to removing a keystone species from a population (see Paine 1969; Stone 1995) and might temporarily increase the abundance of earlier successional taxa (see Bond 1993).

In summary, both the number and density of taxa increased with time, with diversity patterns resembling the reference benthic samples after 7 days. However, community composition was not consistent with the surrounding benthos until between 28 and 42 days of colonisation, suggesting species diversity recovers rapidly, but abundance and community composition may not recover for some time. Both surface and subsurface movement provided significant sources of colonists for benthic community recovery in the Makaretu River. Elmidae dominated communities unrestricted by colonisation source until Day 28 when *Deleatidium* became the dominant taxon, in line with the composition of the surrounding benthos. By comparison, *Deleatidium* dominated substrates colonised by subsurface movement throughout the experiment. Communities colonised only from the hyporheic zone were distinct from the surface and control treatments until Day 42 when *Deleatidium* became the most abundant taxon in all treatments. In contrast, Elmidae dominated samples colonised by surface movement until Day 42 when *Deleatidium* became dominant. Therefore, Elmidae colonised in greater numbers through drifting and/or crawling, while *Deleatidium* colonised in greater numbers from the hyporheic zone.

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