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LINKAGES BETWEEN HYPORHEIC AND BENTHIC INVERTEBRATE COMMUNITIES IN NEW ZEALAND GRAVEL BED RIVERS



A thesis presented in fulfilment of the
requirements for the degree of
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ABSTRACT

Surber samples from the benthos and T-bar samples (14 mm PVC pipe diameter) from the hyporheos were collected from 8 Southern Hawkes Bay rivers, differing in environmental conditions and geological age, and 8 rivers of the Cass/Craigieburn region of Canterbury that had differing physical stability and hyporheic physicochemical characteristics. Gravel bedded rivers of the Southern Hawkes Bay (North Island) and Cass/Craigieburn region (South Island) were sampled to examine the spatial distribution of the hyporheos in relation to physicochemical factors, bed stability and the significance of the hyporheic zone as a refuge and/or source of invertebrate colonists to the benthos. Physical bed movement, the duration of channel dewatering and flow variance were used to measure disturbance to the hyporheos and benthos, respectively. Benthic invertebrate communities of many streams are subject to constant disturbance from fluctuations in flow, temperature, and bed movement. In contrast, the hyporheos residing in the hyporheic zone may not experience the same disturbance regimes because bed movement occurs less often in the hyporheic zone and there is less diel temperature, dissolved oxygen and flow fluctuations.

In the rivers investigated, broad (between river) and finer (within river) scale environmental factors influenced the composition of the hyporheos. Local geomorphology appeared to have a significant effect on the hyporheos by markedly increasing the proportion of epigeal animals (benthic animals resident in the hyporheos) at sites of young geomorphology (less than 0.05 mya). In contrast, hypogean animals (animals seldom encountered from the benthos) dominated geologically older sites (greater than 0.4 mya). Species diversity in the hyporheic zone was highest with intermediate levels of bed movement where both hypogean and epigeal animals were present. The greater abundance of epigeal fauna with increasing bed movement may reflect differences in disturbance regime between sites and in turn interstitial flow rates. However, it is unlikely that the geological age and stability of bed substrates determined community composition alone. Water chemistry was also an important factor determining community composition; epigeal animals were more abundant in the hyporheic zone when hyporheic water chemistry was similar to the surface river water (e.g., higher dissolved oxygen and lower conductivity). In contrast, hypogean animals dominated the hyporheos when water chemistry was least like the surface water (e.g., lower dissolved oxygen and higher conductivity).

Dewatering and bed movement may disturb the hyporheos by desiccating or physically disturbing the hyporheic zone, respectively. If the potential colonists of the hyporheic zone are removed by desiccation or physical abrasion, the types of invertebrate taxa colonising will change because some invertebrates may be less capable of colonising from this region. The proportion of epigeal animals may increase in the hyporheic zone with greater bed movement, but decline during stable conditions or at stable sites because the interstitial environment becomes less like the surface. Thus, the hyporheic zone may harbour benthic invertebrates during disturbance events and may be an important source of colonists for the benthos in frequently disturbed sites. In contrast, during stable conditions, or at stable sites, factors other than disturbance (e.g., substrate compactness, organic matter supply, competition or surface/groundwater interactions) may be more important in determining community composition. The diverse hyporheos identified in New Zealand rivers may be influenced by substrate composition, which may in turn alter interstitial flow patterns, discharge variance and the probability of bed movement.

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CHAPTER 1

GENERAL INTRODUCTION



Makaretu River, February 1997. Site 2 (refer chapter 2).

The hyporheic zone is defined as the active ecotone bounded by the stream channel above and true groundwater below (Schwoerbel 1961; White 1993; Boulton et al. 1998). This physical region contains the hyporheos; an interstitial community where taxa derived from subterranean (i.e., hypogean) and benthic (i.e., epigean) habitats, along with some forms peculiar to the hyporheic zone, may persist (Boulton et al. 1991; Palmer et al. 1992; Stanford & Ward 1993). The hyporheic zone is considered a patchy environment (Dole-Oliver et al. 1997) because physicochemical factors (e.g., temperature, dissolved oxygen and conductivity) vary spatially because of differences in surface and groundwater mixing (Triska et al. 1989; Williams 1993; Fraser et al. et al. 1996; Brunke & Gonser 1997; Valett et al. 1997; Fraser et al. & Williams 1998).

The biological composition of the hyporheos is strongly influenced by the physical and chemical nature of the hyporheic zone (Cooling & Boulton 1993) and the exchange of surface water with the groundwater (Stanford & Ward 1993; Jones & Holmes 1996; Downes et al. 1998). Hydrological differences in fast and slow moving water produce active and dead zones of resource availability (see Fischer et al. 1979; Jackman et al. 1984; Harvey & Bencala 1993). This in turn increases the types of microhabitats where surface and subterranean invertebrates can persist (Boulton et al. 1998). Surface water enters the hyporheic zone in areas of down welling (i.e., where surface water pressure is greater than the groundwater), while water exits the hyporheic zone where groundwater pressure is greater than the river channel (i.e., up welling) (Cooling & Boulton 1993; White 1993; Jones & Holmes 1996). Water exchange between the surface and interstitial region alters the extent of the hyporheic zone by changing the physicochemical characteristics of the mixing between surface and groundwaters (Williams 1993; Fraser et al. et al. 1996; Brunke & Gonser 1997). Substrate size, porosity and composition will influence these water exchange patterns, with more stable and compact substrates reducing water flow between the surface and groundwater (Downes et al. 1998).

Studies in New Zealand have identified a diverse assemblage of hypogean (e.g., Crustacea, Annelida and Acarina) and epigean animals (e.g., Ephemeroptera, Trichoptera, Coleoptera and Diptera) from the hyporheic zone. The effect of land use on the hyporheos was investigated by Boulton et al. (1997) and Montgomerie (1997); channel geomorphology by Olsen (1998); human perturbation (i.e., acid mine drainage) by Anthony

(1999). Spatial distributions of the hyporheos in a number of South Island rivers have also been examined by Adkins (1997) and Adkins & Winterbourn (1999), and colonisation pathways by Scarsbrook (1995) and McLeod (1998). However, despite these studies of hyporheic communities in New Zealand rivers only one has investigated the hyporheos in the North Island (Boulton et al. 1997), and little is known of hyporheic processes and the determinants of community composition for these New Zealand rivers.

In contrast, extensive studies on New Zealand benthic communities have investigated the effects of disturbance (Death & Winterbourn 1995; Townsend et al. 1997b), spatial and temporal variability (Cowie 1985; Scarsbrook & Townsend 1993; Death 1995; Townsend et al. 1997), land-use (Quinn & Hickey 1990a; Scott et al. 1994; Harding & Winterbourn 1995; Fahey & Jackson 1997; Quinn et al. 1997), discharge (Sagar, 1986; Scrimgeour et al. 1988; Scrimgeour & Winterbourn 1989), sediment (Ryan 1990), water chemistry (Graesser 1988; Close & Davies-Colley 1990a, b) and biotic interactions (Winterbourn 1990) on benthic community structure. However, with the exception of a few studies (e.g., Quinn & Hickey 1990a, b; Collier 1995, Collier et al. 1997), research has again been mainly focused in South Island catchments.

Benthic communities in New Zealand and elsewhere (Hildrew & Giller 1994) are discretely arranged into patches of differing resource availability. The abundance and type of these resources may be determined by the physical and chemical characteristics of the system, disturbance regime (see Frissell et al. 1986; Menge & Sutherland 1987) and/or biological processes (Greig-Smith 1979; Woodward 1987; Hildrew & Giller 1994). Resources for the biota may also be influenced by the interaction between surface and groundwater (Boulton 1993). Therefore, physical characteristics (Frissell et al. 1986; Resh et al. 1988; Scarsbrook & Townsend 1993; Townsend et al. 1997a; Kronvang et al. 1998), biotic interactions (McAuliffe 1984; Menge & Sutherland 1987; Hart 1992) and colonization processes (refer Williams 1976; Gore 1982; Mackay 1992) are very important in determining the benthic component of river systems.

A river's geomorphology markedly affects the streams nature by altering flow patterns, discharge magnitude and substrate characteristics (Quinn & Hickey 1990b; Scarsbrook & Townsend 1993; Kronvang et al. 1998). In contrast, the geology of lotic systems outside of the stream channel may influence the severity, intensity and frequency of disturbance (see Lake & Barmuta 1986; Robinson & Minshall 1986; Resh et al. 1988; Death & Winterbourn 1995; Death 1996). Thus, geomorphology ultimately influences stream invertebrate communities at larger scales by altering substrate stability (Death & Winterbourn 1995; Townsend et al. 1997), substrate size (Minshall 1984; Death 2000) and physicochemical conditions (e.g., dissolved oxygen, pH and temperature) (Statzner 1981; Quinn & Hickey 1990a). At finer scales and/or during stable conditions the interaction between different instream biotic components may also influence community dynamics (see Greig-Smith 1979; Peckarsky 1983; Menge & Sutherland 1987; Woodward 1987; Hart 1992). In fact, stable systems might be structured by competition or predation because organisms less resilient to physical or chemical disturbances are able to persist (Menge & Sutherland 1987).

The effect of disturbance from floods, droughts and temperature extremes on benthic communities has been an area of interest in stream ecology for a number of decades (e.g., Sagar 1986; Scrimgeour et al. 1988; Resh et al. 1988; Poff 1992; Death 1995; Death & Winterbourn 1995; Lancaster 1999). Disturbance intensity and variance (Lake & Barmuta 1986; Robinson & Minshall 1986; Resh et al. 1988), animal abundance (Marchant et al. 1991) and the type of invertebrates present before disturbance (Death 1996) influence the ability of lotic invertebrates to colonise denuded habitats. The proximity of disturbed regions to a source of colonists will also influence community composition (Gore 1982). Thus, while the type of taxa present before disturbance will influence community composition post disturbance, sources of colonists might play a role in regulating community composition. Benthic community composition and persistence may therefore be determined by the provision of invertebrate refugia and sources of invertebrate colonists (see Stanford & Ward 1993; Boulton et al. 1998).

A number of refugia and colonisation sources have been suggested for lotic systems (Williams & Hynes 1976; Townsend & Hildrew 1976; Sedell et al. 1990; Boulton et al. 1991; Mackay 1992; Williams & Smith 1996; Lancaster 1999). The hyporheic zone is one

such source. With the exception of the buildup of sediment in the interstices, the hyporheos is relatively well insulated from physical disturbance through bed movement and sediment transport (i.e., from increased discharge) that commonly disturbs the benthic region, because only rare and extreme bed movement will physically alter the hyporheic zone (Kochel 1988; Komar 1988; Haschenburger & Church 1998; Matthaei et al. 1999). Moreover, diel changes in water chemistry are buffered by slower interstitial flows and the interaction between hyporheic water and the physico-chemically stable groundwater region (Fraser et al. 1996; Jones & Holmes 1996; Valett et al. 1997). The hyporheic zone may therefore provide a suitable region where benthic invertebrates may seek refuge or persist despite environmental instability in the river channel above.

Differences in the hyporheos occur across large (i.e., between rivers and/or between ecoregions) and finer scale axes (i.e., between riffles within a river or between samples within one riffle) (Marchant 1988; Dole-Oliver & Marmonier 1992; Cooling & Boulton 1993). However, little is known about what physical (e.g., geomorphology, bed movement and substrate characteristics) or physicochemical (e.g., dissolved oxygen, pH, discharge and temperature) factors are most important in influencing hyporheic invertebrate distributions (see Williams 1993; Boulton et al. 1998). A number of authors regard the presence of benthic invertebrates in the hyporheos (i.e., epigeal animals) as a source of colonists after disturbance in the river channel (e.g., Williams & Hynes 1974, 1976; Townsend & Hildrew 1977; Williams & Smith 1996). The hyporheic refuge hypothesis predicts benthic taxa migrate into the hyporheic zone as disturbance intensity in the river channel increases, moving back to the benthos after flows have stabilised (Williams & Hynes 1974). However, changing physicochemical conditions can shift the boundaries of the hyporheic zone through space (e.g., between rivers) and time (e.g., seasonal fluctuations in the water table), perhaps altering refuge availability (Williams 1993). Nonetheless, the hyporheic zone may be a favoured refugium during disturbance of the river channel, and a subsequent source of colonists back to the denuded benthos post disturbance (see Williams & Hynes 1976; Townsend & Hildrew 1976; Boulton et al. 1991; Mackay 1992; Williams & Smith 1996).

Invertebrate samples from the hyporheic zone are relatively difficult to obtain (Fraser et al. & Williams 1996), thus effective sampling remains one of the major challenges for further hyporheic research (Palmer 1993). Several techniques exist for sampling of the hyporheos; however, comparisons of these sampling methods are far from conclusive because most have been undertaken at a single site and or during one sampling occasion (e.g., Fraser et al. & Williams 1997). Pump sampling (the technique used throughout this thesis) is an effective means of sampling the hyporheos at a large number of sites because of the relative ease and speed of sample collection, portability and the ability to collect water samples concurrently with the invertebrate samples. However, because the suction pressure in the hyporheic zone is unclear, the volume of sediment sampled is also unknown (Palmer & Strayer 1996). Pump sampling has been criticised for being taxon selective depending on substrate porosity (Collier & Scarsbrook 2000) through the straining effect of the interstices (Fraser et al. & Williams 1996). In contrast, freeze coring is relatively expensive (both in terms of equipment and labour), and the act of hammering the standpipe into the streambed can elicit an escape response in certain taxa (Breschko 1990). Cores may also take longer to freeze at sites of differing porosity because faster interstitial flow increases the duration of freezing. This variable water freezing onto the standpipe may also elicit escape reactions for invertebrate taxa. Colonisation pots are also labour intensive and have been criticised for physically disturbing the natural streambed characteristics by implanting plastic pipes (with perforated sides) and artificial substrates (Collier & Scarsbrook 2000). Colonisation pots also require at least 8 weeks before samples can be collected.

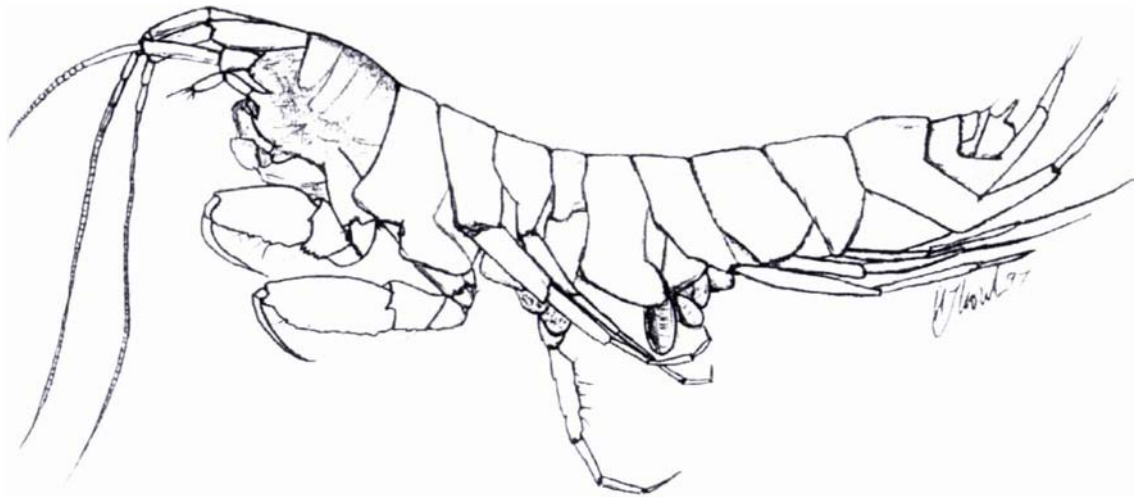
Overall, pump, colonization pot and freeze core hyporheic samplers provide an effective collection of qualitative hyporheic data (Fraser et al. 1996), although there may be bias associated with substrates of differing porosity and/or landuse (Scarsbrook unpubl. data). Palmer (1993) suggested that all sampling techniques meet some criteria, but not all, for collecting quantitative and unbiased hyporheic samples. However, it was noted that any one of the four samples tested by Fraser et al. (1996) would be suitable to provide an acceptable level of precision for hyporheic studies. Thus, the pump sampler described by Boulton et al. (1992) was used in this thesis because it disturbed the hyporheic zone the least, collects samples rapidly and provides samples for water chemistry where invertebrates are collected.

Bed movement, temperature and dewatering can be a disturbance for hyporheic and benthic communities. By using these three disturbances to lotic communities, the significance of the hyporheic zone as a refuge and/or source of invertebrate colonists to the benthos will be assessed. This thesis aims to identify whether hyporheic communities differ at two spatial scales (between and within rivers) and whether the hyporheic zone is influenced by disturbance in the river channel by increasing the proportion of benthic animals residing in the hyporheos by:

- Investigating whether the hyporheos of 8 North Island rivers differs, both between and within rivers, and if so what environmental factors are associated with these differences.
- Investigating 8 rivers in the South Island, where substrate stability has been shown to affect the benthos, whether this stability has a similar effect on the hyporheos.
- Examining whether the extent of channel dewatering affects the ability of the hyporheic zone to act as colonisation source for benthic recovery.
- Investigating the role of the hyporheos as a colonization source for benthic community recovery.
- Examining whether spatial patterns in the hyporheos can be attributed to differences in environmental characteristics of up- and down-wellings.

CHAPTER 2

SPATIAL PATTERNS IN HYPORHEIC COMMUNITIES OF GRAVEL BED RIVERS



ABSTRACT: Pump samples from the hyporheic zone were collected during autumn, winter and summer 1996/97 in eight Southern Hawkes Bay, New Zealand Rivers at 30, 60 and 90 cm well depths. Crustaceans such as Amphipoda, Ostracoda and Isopoda were numerically abundant in all rivers, while Acarina, Copepoda, Oligochaeta and Nematoda were rare. Epigeal invertebrates (25 taxa) comprised one quarter of the invertebrates collected from the shallow hyporheos (depth = 30 cm), but declined in abundance to comprise only 10 % of the hyporheos from the deepest wells. The difference among hyporheic communities at the level of rivers (among rivers) appeared to be associated with the geological age of the underlying deposits, with deposits greater than 0.4 million years old dominated by Crustacea, while epigeal taxa were more abundant within deposits less than 0.05 million years old. Physicochemical characteristics such as dissolved oxygen, temperature, conductivity and discharge variance were highly variable between sites, but there was no clear connection between the invertebrate communities and environmental characteristics from each site. Hyporheic communities differed between rivers predominantly in the abundance of their hypogean taxa, while smaller scale (i.e., depth) differences were the result of differences in the abundance of the epigeal animals. Because of the highly variable physicochemical environment, the hyporheic community did not appear to be related to the physicochemical characteristics at sites with young and old geology. Other site characteristics (i.e., substrate compactness and organic matter) may also be important in determining composition at some sites where the physicochemical characteristics may be less important in influencing community composition.

INTRODUCTION

The organisation of the biological component in river systems depends on the physical and chemical nature of those rivers (Townsend et al. 1983; Moss et al. 1987; Corkum 1989; Dole-Oliver et al. 1997). The physicochemical nature of these rivers is in turn highly variable both spatially and temporally (Hildrew & Giller 1994), and as such, the biological component may also be highly variable (Pringle et al. 1988; Townsend 1989). Substrate stability (Death & Winterbourn 1995; Townsend et al. 1997), substrate size (Minshall 1984; Death 2000) and chemical conditions (e.g., pH and dissolved oxygen) (Statzner 1981; Quinn & Hickey 1990a) are all known to influence benthic community structure. Stream benthic communities like many communities (Pickett & White 1985) are therefore arranged into patches along gradients of physical characteristics (Hildrew & Giller 1994).

Studies of the hyporheic zone have shown extensive distributions of invertebrates deep within river substrata (e.g., Hendricks 1993; Richards & Bacon 1994; Boulton & Stanley 1995). The hyporheic zone contains the hyporheos; an interstitial community where taxa derived from subterranean (hypogean) and benthic (epigean) habitats, along with some forms peculiar to the hyporheic zone may persist (Boulton et al. 1991; Palmer et al. 1992; Stanford & Ward 1993). The boundaries of the hyporheic zone can shift through space and time (Williams 1993) through changes in physicochemical conditions (e.g. temperature, dissolved oxygen, conductivity, pH and discharge). Therefore, the distribution of the hyporheos will be determined by the physical and chemical characteristics of the hyporheic zone (Dole-Oliver & Marmonier 1992; Boulton et al. 1998). Little is known about differences in the distribution of hyporheic communities between rivers, although studies have shown that geomorphology and water chemistry influence the boundaries of the hyporheic zone (see Williams 1993; Boulton et al. 1998).

Despite the growing number of studies investigating the hyporheic zone and its fauna (e.g., Stanford & Gaufin 1974; Stanford & Ward 1993; Wondzell & Swanson 1996), few have assessed spatial variation in the composition of the hyporheos within and between gravel bed rivers (Marchant 1988; Dole-Oliver & Marmonier 1992; Cooling & Boulton 1993). This chapter assesses whether hyporheic communities differ at two spatial scales (between and within rivers) in eight gravel bed rivers, and whether these differences change with depth and/or season.

STUDY SITES

All eight sites are in the Southern Hawkes Bay, New Zealand ($40^{\circ}00'S$, $176^{\circ}20'E$) (Fig. 1) and flow through predominantly agricultural land towards the East Coast of the North Island. The Tukituki and Waipawa are large braided rivers, meandering freely within fluvial deposits up to 150 m wide. The Makaretu is a small braided river, and although physically similar to the Tukituki and Waipawa, gravel deposits are only 20 to 25 metres wide. The Mangatewai, Mangatewainui, Ongaonga, Tangarewai and Tukipo River channels are constricted within banks between 3 and 9 m high. Fluvial deposits are smaller at these sites, with lateral channel movement restricted to gravel deposits between 10 and 20 m wide. In addition, the Tangarewai stream flows through a remnant of podocarp forest once characteristic of the whole area.

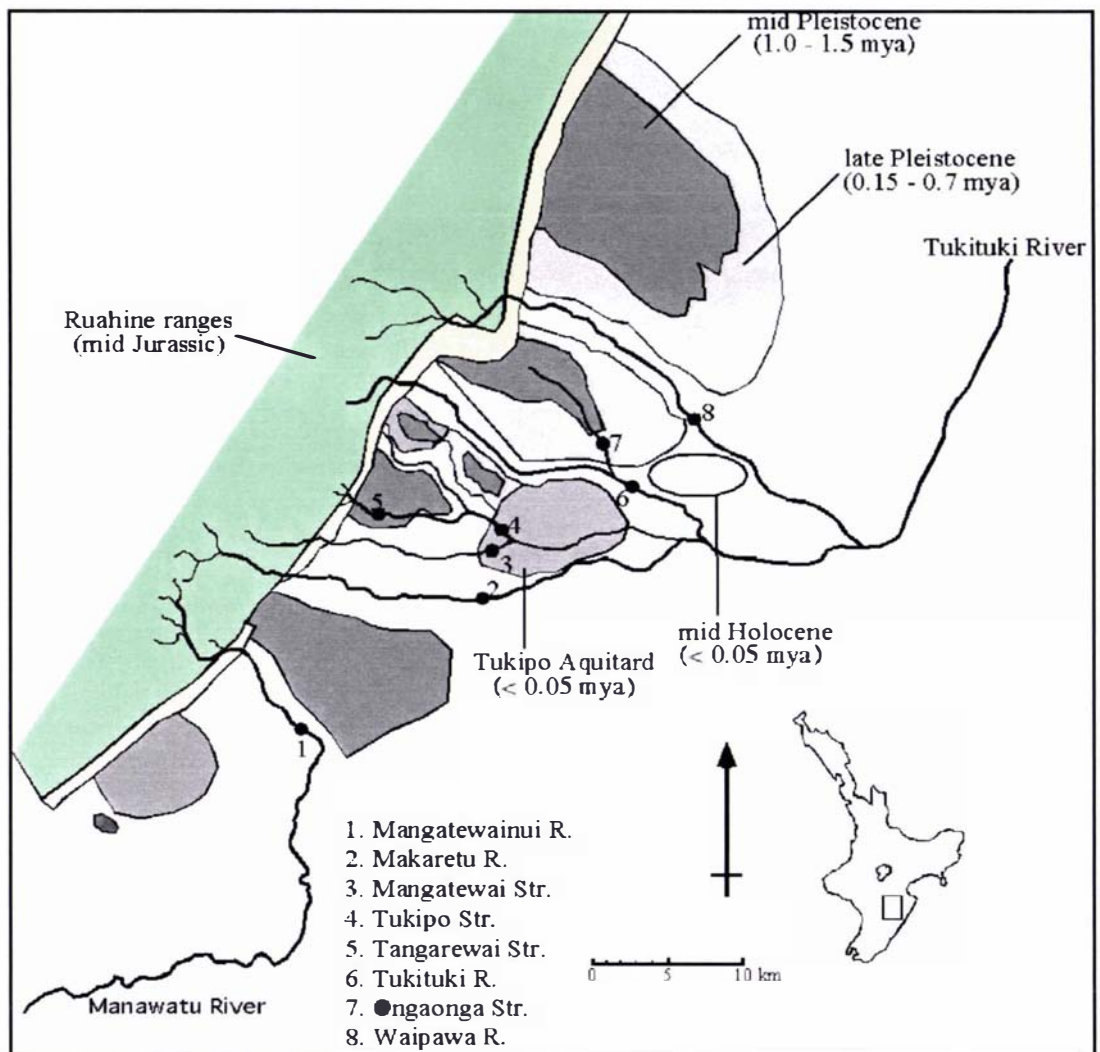


Fig. 1 Location of the study sites in the Southern Hawkes Bay, New Zealand sampled between April 20, 1996 and February 13, 1997.

METHODS

At each study site, samples were collected (20 April, 20 September 1996 and 13 February 1997) from 6 wells in the hyporheic zone using a pump sampler similar to that described by Boulton et al. (1992). A 1.5 metre long metal rod (13 mm diameter) with a 14 mm PVC tube sleeve was forced into the substrate at the downstream end of each sampled riffle, to three set depths, shallow (30 cm), medium (40-60 cm) and deep (50-130 cm) (refer to Table 1). All wells were taken from random locations at the downstream end of a riffle (up-wellings) at least 1 metre apart. Wells were reinserted on each sampling occasion. The ability to drive wells into the river substrate was dependent on substrate composition, with more heterogeneous (and compact) substrates reducing the maximum depth of wells. From each replicate well the metal rod was removed and 2 litres of water extracted from the PVC pipe using a hand operated bilge pump. The water samples were then sieved through 300 μm mesh and stored in 70 % ethanol for later sorting and identification using the keys of Chapman & Lewis (1976) and Winterbourn & Gregson (1989). The 300 μm mesh size was chosen to provide samples comparable to those collected from the benthos.

Conductivity, temperature and pH were measured on each occasion in the river channel and the deepest hyporheic well using an Orion 122 conductivity meter and an Orion model 250A pH meter, respectively. Dissolved oxygen was measured in the river channel and water extracted from each hyporheic depth prior to sieving using a YSI 59 dissolved oxygen meter. Current velocity and depth were measured using a velocity head rod mid stream along each sampled riffle. Substrate composition for each site was assessed visually to provide a percent substrate composition at each site. Periphyton biomass (total pigment concentration) was estimated by extracting pigments (using 90 % acetone at 5 °C for 24 h) from five gravels (mean diameter = 5 cm) collected on each sampling occasion. Total pigment concentration was calculated using the equations of Moss (1967a, b) and corrected for stone surface area using the approach of Graham et al. (1988). Channel stability was assessed using the Pfankuch assessment protocol (Pfankuch 1975; Rounick & Winterbourn 1982), which assigns index scores based on 15 physical characters of each site according to the observers evaluation of pre-determined criteria.

The smaller sample volumes (2 litres compared to 6 - 10 litres) (e.g., Marmonier & Cru  ze des Ch  tellers 1991; Dole-Oliver 1998) and larger sampling mesh (300 μm

compared to 63-150 μm) (e.g., Boulton et al. 1997; Hunt & Stanley 2000) compared to some other studies may be less suited to quantitative invertebrate samples. These factors may reduce animal abundance and diversity, but was not regarded as significant in this study because previous authors have noted that there does not appear to be a linear relationship between volume withdrawn and invertebrate density (cf. Cooling & Boulton 1993; Boulton et al. 1997). Animal density may also decline with increasing water extraction after 0.5 litres (Hunt & Stanley 2000).

Data analysis

To assess whether univariate community characteristics differed between site, depth and season, hyporheic samples were analysed with a 3-way (site $\times$ depth $\times$ season) analysis of variance (ANOVA), while environmental characteristics were assessed with a 2-way (site $\times$ season) analysis of variance (ANOVA) using SYSTAT (SYSTAT 1996). Visual inspection of plotted means was used post hoc to assess differences between site, depth and season. Pearson's correlation between environmental characteristics (using Bonferroni correction) was also performed with SYSTAT (1996).

Detrended correspondence analysis (DECORANA) and Multi Response Permutation Procedure (MRPP), with Sorensen's distance measure, were performed using the PC ORD statistical package (McCune & Mefford 1995) to assess variation in community composition and environmental characteristics among sites, depths and seasons. 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. DECORANA places communities within an ordination space according to faunal similarity and allows correlation with environmental characteristics to be explored along each ordination axis.

RESULTS

Physicochemical Characteristics

At all sites, greywacke gravels interspersed with large and small cobbles dominated the substrates (Table 1; Fig. 2). The Tukituki, Waipawa and Tangarewai sites had the highest hyporheic dissolved oxygen concentrations overall ($F_{7, 14} = 11.67$, $P < 0.01$), while the Mangatewainui, Ongaonga and Tukipo sites had the lowest. Dissolved

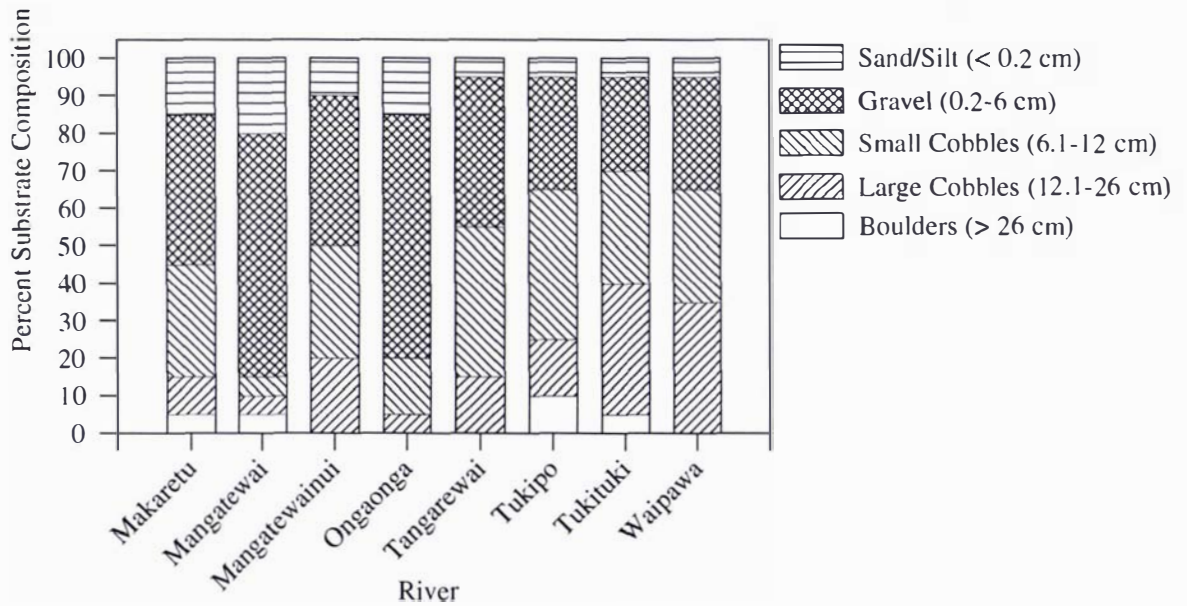


Fig. 2 Substrate composition of the eight study sites in the Southern Hawkes Bay assessed visually at the start of the sampling programme (April 13 1996).

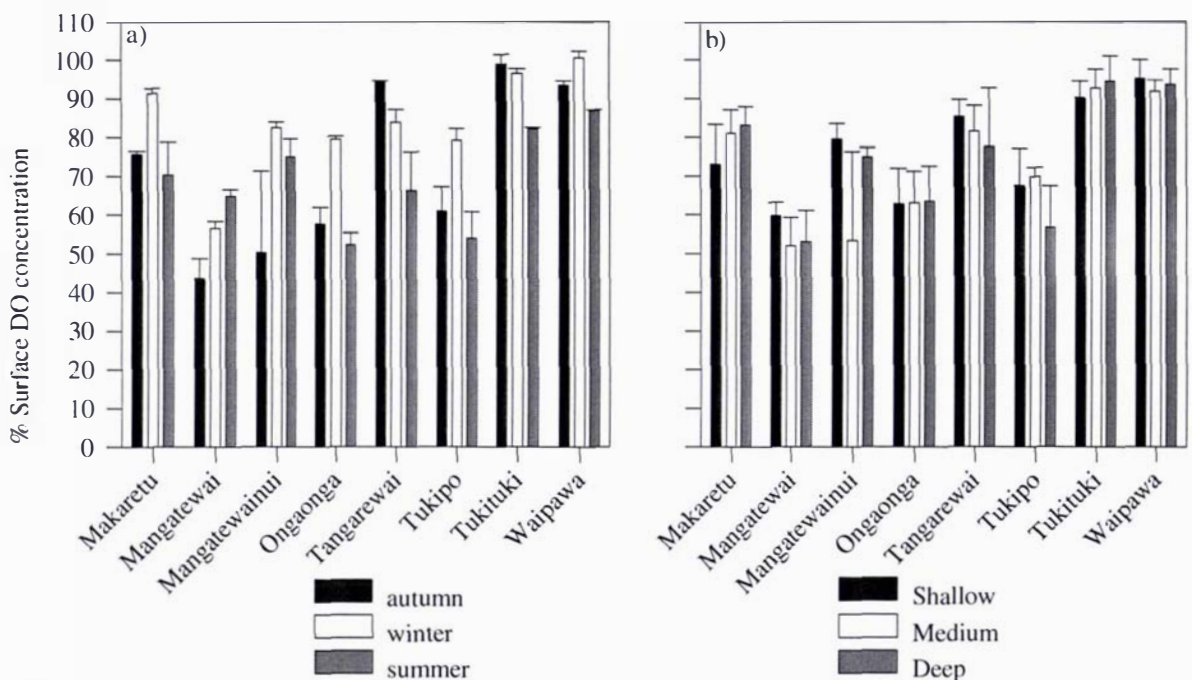


Fig. 3 Percent of surface dissolved oxygen concentrations for hyporheic water collected (a) on three occasions and (b) across three depths from the hyporheic zone ($n=72$), in eight rivers of the Southern Hawkes Bay between 20 April 1996 and 13 February 1997.

oxygen was highest during winter, lowest during summer ($F_{2, 14} = 26.11$, $P < 0.01$) (Fig. 3a) and consistently different among sites ($F_{7, 14} = 11.67$, $P < 0.01$). However, dissolved oxygen did not change between well depths within each site ($F_{2, 14} = 0.21$, $P = 0.81$) (Fig. 3b). Hyporheic water temperatures were highest at the Ongaonga (max = 17.5 °C), Tukipo (max = 21.9 °C) and Tangarewai (max = 18.5 °C) sites ($F_{7, 14} = 6.21$, $P < 0.01$), especially during summer (max = 21.9 °C), and lowest during winter (min = 10.2 °C) ($F_{2, 14} = 10.82$, $P < 0.01$) with temperatures 33 to 87 % lower than the river channel (refer Table 1). Hyporheic conductivity was highest in the Mangatewai (max =

163.5 μScm^{-1}) and Tukipo (max = 324 μScm^{-1}) ($F_{7, 14} = 30.80$, $P < 0.01$), but similar between seasons ($F_{2, 14} = 2.04$, $P = 0.17$). In contrast, pH was similar between rivers ($F_{2, 14} = 2.50$, $P = 0.07$), but highest during summer (max = 7.85) and lowest during winter (min = 7.06) ($F_{7, 14} = 4.35$, $P = 0.03$). No significant interactions were found between site and season for environmental factors.

Invertebrate Communities

A total of 65 taxa were identified from three depths in the eight rivers. The most abundant included 2 Amphipoda (*Phreatogammarus* sp. and an undetermined Amphipoda), Acarina (9 morphospecies); 7 Collembola, 8 Ostracoda, including one morph from the genus *Gomphocythere*; 3 Copepoda, a Stygocarida Crustacea

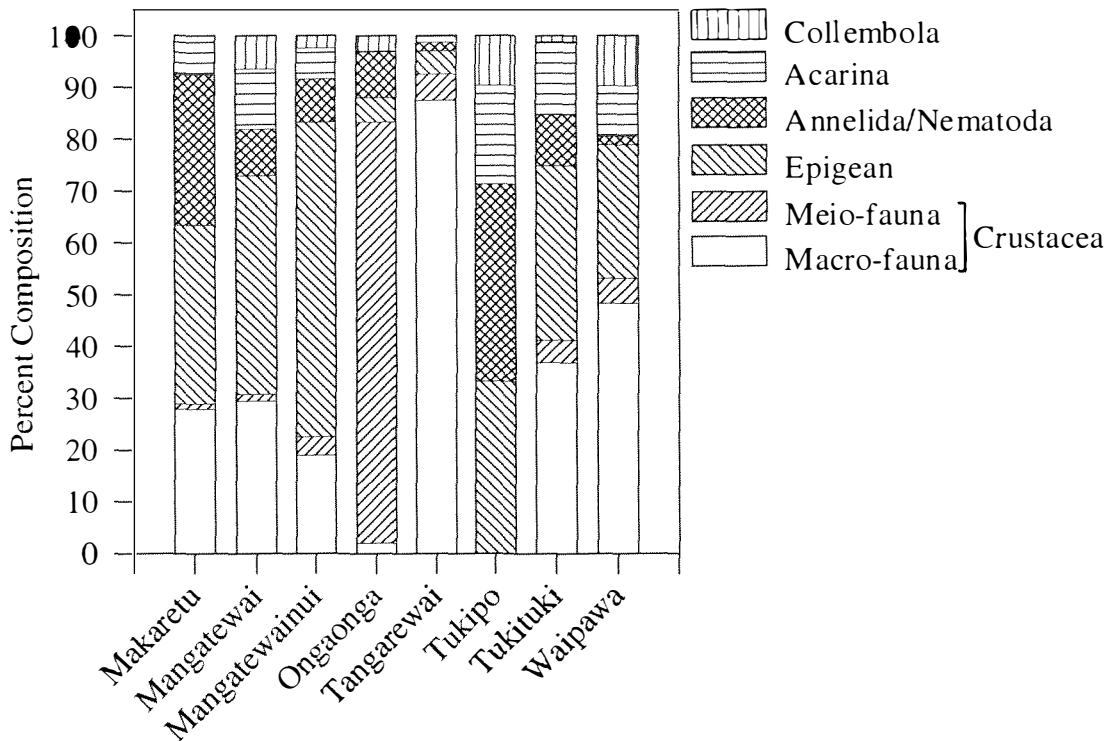


Fig. 4 Relative abundance (sum of depths & seasons) of invertebrates within the hyporheic zone in eight rivers of the Southern Hawkes Bay sampled between April 1996 and February 1997. Crustacea are separated into macro-fauna (i.e., Amphipoda and Isopoda) and meio-fauna (i.e., Ostracoda, Copepoda and Stygocarida).

Table 1. Environmental variables and site characteristics for the hyporheic zone and river channel sampled between April 20, 1996 and February 13, 1997 in the Southern Hawkes Bay, New Zealand. (S) Represents samples collected from the river channel, while (H) represents samples collected from the hyporheic zone. Values are presented as a range of seasons and with sample depth.

Variables	Makaretu	Mangatewai	Mangatewainui	Ongaonga	Tangarewai	Tukipo	Tukituki	Waipawa
Stream Order	3	4	3	3	3	4	4	4
Site a.s.l (m)	240	260	320	210	300	185	185	190
River origin a.s.l (m)	1000	850	1000	500	620	700	1680	1725
Distance inland (km)	83	81	122	77	88	80	74	71
Pfankuch scores (total)	101	76	78	73	82	72	98	105
(bottom component)	46	32	24	27	36	25	52	48
Conductivity (S) (μScm^{-1}) (n=3)	67 - 99.3	103.4 - 105	67 - 84	111.5 - 122.5	91.6 - 98.4	61.8 - 103.0	119.8 - 178.1	88 - 109.8
Conductivity (H) (μScm^{-1}) (n=3)	85.7 - 121.3	124 - 263.5	81.4 - 163.5	115 - 120.5	99.2 - 145	240 - 327	72.6 - 103.2	80.2 - 96.5
River depth (cm) (n=12)	12 - 40	16 - 23	17 - 18	4 - 16	26 - 28	21 - 63	16 - 25	15 - 43
Shallow wells (cm)	30	30	30	30	30	30	30	30
Medium wells (cm)	60	60	50	40	60	50	60	60
Deep wells (cm)	90	90	70	50	130	70	90	90
pH (S) (n=3)	7.59 - 7.85	7.47 - 7.55	7.72 - 7.82	7.71 - 8.1	7.5 - 7.58	7.44 - 8.79	7.47 - 7.52	7.14 - 8.3
pH (H) (n=3)	7.3 - 7.85	7.4 - 7.5	7.33 - 7.85	7.3 - 7.5	7.41 - 7.58	7.06 - 7.58	7.52 - 7.82	7.14 - 7.5
Total pigment ($\mu\text{g}/\text{cm}^2$) (n=15)	0.02 - 1.59	0.49 - 6.08	0.01 - 4.48	0.42 - 1.26	0.01 - 1.59	0.01 - 5.02	0.14 - 1.41	0.28 - 1.01
Temperature ($^{\circ}\text{C}$) (S) (n=12)	10.2 - 15.7	11.3 - 13.2	10.3 - 14.8	13.4 - 15.8	13.1 - 18.5	12.9 - 21.9	11.1 - 17.2	7.4 - 24
Temperature ($^{\circ}\text{C}$) (H) (n=12)	5.1 - 14.2	5.5 - 11.9	4.9 - 10.3	10.6 - 17.5	9.8 - 14.6	9.2 - 16.5	5.1 - 11.0	8.8 - 14.2
Width (m) (n=6)	9.4 - 14.1	4.4 - 9.4	11.5 - 13.9	5.1 - 8.0	3.2 - 3.6	13.8 - 14.3	4.2 - 25	9.1 - 19.3
Velocity (m/s^{-1}) (n=12)	0.94 - 0.99	0.77 - 1.13	0.89 - 0.99	0.59 - 0.8	0.46 - 1.4	0.86 - 1.02	0.99 - 1.13	0.7 - 1.13

(Syncarida) and 2 Isopoda (*Cruregens fontanus* and one Isopoda from the Family Phreatoicidae, refer Table 2). On rare occasions, the freshwater polychaete *Namanereis tiriteae* was collected from the Mangatewainui River and Ongaonga Stream. Crustacea (e.g., Amphipoda, Ostracoda and Isopoda) dominated hyporheic wells at all depths, while Acarina, Collembola and other hypogean taxa (e.g. Oligochaeta and Nematoda) were rare at all well depths (Fig. 4). Epigean taxa comprised 20 % of the hyporheos by abundance overall.

The total number of taxa collected was not different between well depths ($F_{2, 60} = 2.96$, $P = 0.06$), but was highest in the Ongaonga (mean = 7 taxa per 2 litre sample) and Tangarewai Streams (mean = 6) (Fig. 5a), and lowest in the Mangatewai (mean = 2 taxa per 2 litre sample) and Tukipo Streams (mean = 1) overall ($F_{7, 60} = 5.32$, $P < 0.01$). Numbers of taxa did not change markedly between seasons ($F_{2, 60} = 0.03$, $P = 0.76$). The total number of individuals collected was highest in the Ongaonga and Tangarewai sites ($F_{7, 60} = 3.19$, $P < 0.01$) (Fig. 5b), with Ostracoda and Amphipoda numerically most abundant in the Ongaonga and Tangarewai sites, respectively. Invertebrate density did not differ between seasons ($F_{2, 60} = 2.16$, $P = 0.12$) or between well depths ($F_{2, 60} = 0.45$, $P = 0.64$).

Table 2. Rank abundance for the 5 most common taxa in the hyporheic zone sampled between April 20, 1996 and February 13, 1997 in the Southern Hawkes Bay, New Zealand.

	Makaretu	Mangatewai	Mangatewainui	Ongaonga
1	<i>Phreatogammarus</i>	<i>Phreatogammarus</i>	Elmidae	Ostracoda sp4
2	Oligochaeta	Elmidae	<i>Phreatogammarus</i>	Ostracoda sp7
3	<i>Austroclima</i>	Acarina sp1	<i>Austroclima</i> spp.	Oligochaeta
4	Chironomid C	Oligochaeta	Chironomid C	Ostracoda sp5
5	Acarina sp12	Collembola sp9	<i>Hydrobiosis</i> spp.	Copepoda sp1

	Tangarewai	Tukipo	Tukituki	Waipawa
1	<i>Phreatogammarus</i>	Nematoda	<i>Phreatogammarus</i>	<i>Phreatogammarus</i>
2	Copepoda sp1	Chironomid A	<i>Deleatidium</i> spp.	<i>Deleatidium</i> spp.
3	Phreatoicidae	Acarina sp2	Acarina sp9	Acarina sp4
4	Oligochaeta	Acarina sp9	Oligochaeta	Chironomid A
5	<i>C. fontanus</i>	Chironomid E	<i>Austroclima</i> spp.	Elmidae

Twenty-five epigeal taxa were collected from the hyporheic zone of the 8 rivers. These included 8 Trichoptera, 9 Diptera, 5 Ephemeroptera, 2 Mollusca, 2 Plecoptera, 1 Coleoptera and 1 Megaloptera. Epigeal taxa (e.g., *Deleatidium* spp., Elmidae, Chironomidae, *Oxyethira albiceps*, *Potamopyrgus antipodarum*) were most abundant within the shallow wells (where they comprised 25% of individuals) ($F_{2, 60} = 4.85$, $P = 0.01$). Epigeal taxa were most abundant during summer ($F_{2, 60} = 4.95$, $P = 0.01$).

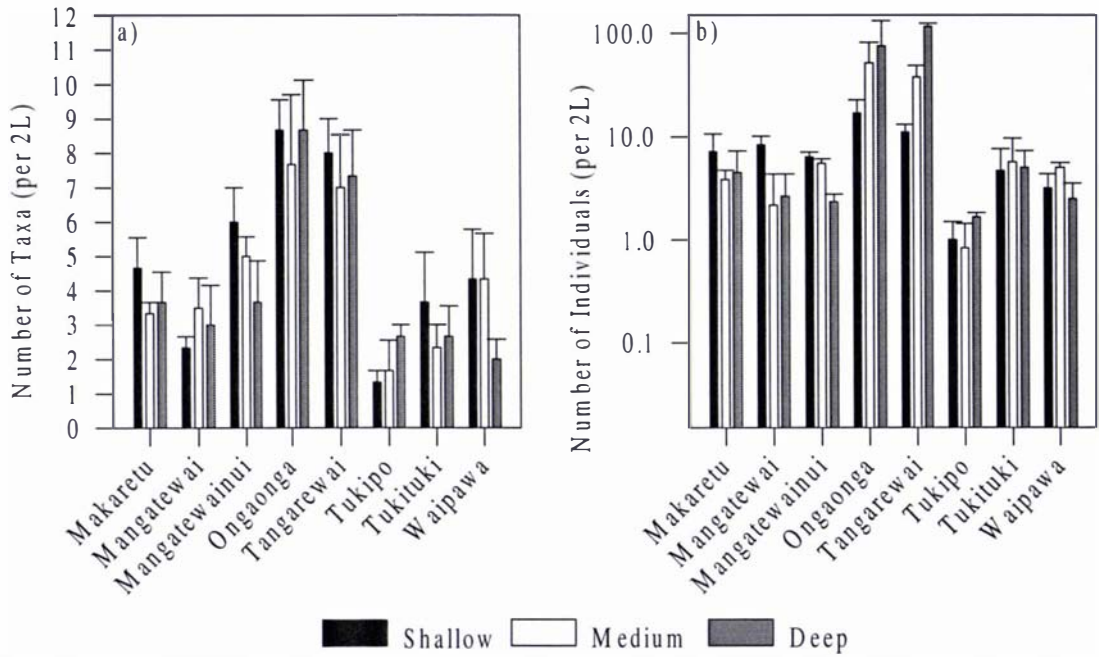


Fig. 5 Mean (± 1 S. E.) number of taxa (a) and number of individuals (b) for hyporheic samples collected in 8 rivers of the Southern Hawkes Bay between 20 April, 1996 and 13 February, 1997.

However, numbers of epigeal taxa did not differ between sites ($F_{7, 60} = 1.44$, $P = 0.21$). The density of epigeal animals was also similar among sites ($F_{7, 60} = 2.12$, $P = 0.06$) and between seasons ($F_{2, 60} = 0.87$, $P = 0.42$), but declined with increasing well depths ($F_{2, 60} = 4.12$, $P = 0.02$).

In contrast, numbers of hypogean taxa were similar between depths ($F_{2, 60} = 0.40$, $P = 0.68$) and seasons ($F_{2, 60} = 0.02$, $P = 0.98$), but higher in the Ongaonga and Tangarewai Streams than the other six sites ($F_{7, 60} = 4.61$, $P < 0.01$). Density of hypogean taxa was also higher in the Ongaonga and Tangarewai Streams ($F_{7, 60} = 3.11$, $P = 0.01$), but the numbers of hypogean taxa were similar between well depths ($F_{2, 60} = 0.64$, $P = 0.53$) and between seasons ($F_{2, 60} = 1.74$, $P = 0.18$).

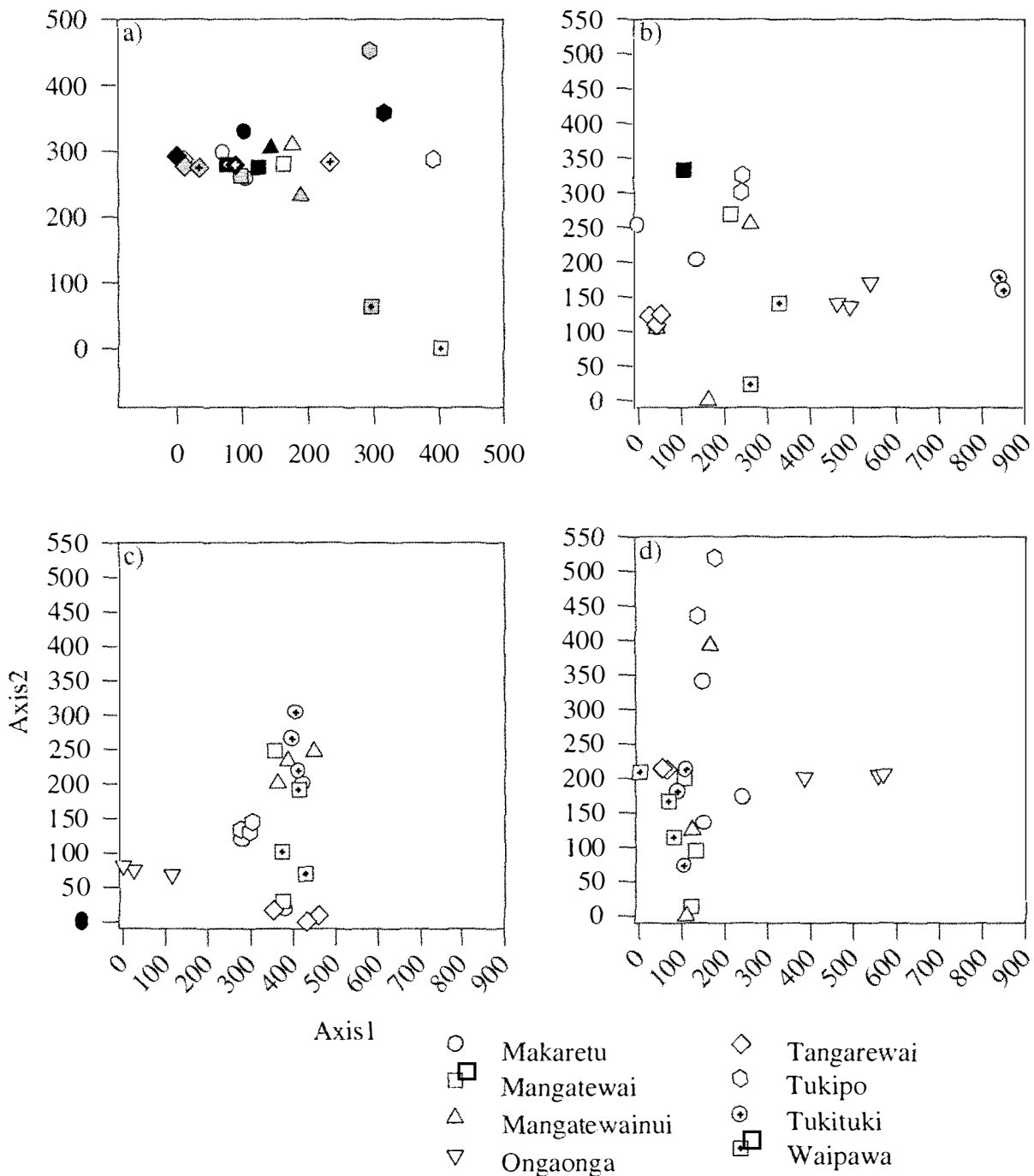


Fig. 6 DECORANA analyses of communities from 3 well depths (sum of seasons) (a), and from two litre pump samples collected in autumn (b), winter (c) and summer (d) from eight rivers in the Southern Hawkes Bay between April 1996 and February 1997. The Ongaonga site was removed from (a) (see text for explanation). Shallow, medium and deep wells in (a) are represented by 's', 'm', and 'd' respectively.

Ostracoda dominated the Ongaonga samples and were separated from all the other sites in an ordination; they were therefore removed from subsequent ordinations assessing spatial patterns. Ordination of assemblage structure separated hyporheic samples into three broad groups with respect to the most abundant taxa overall (Fig. 6a). Samples to the upper

right (Tukipo) were associated with greater proportions of Acarina sp2. In contrast, samples to the lower right (Waipawa) were associated with Acarina sp8., Stygocarida, *Zelandobius confusus*, and Chironomid F. All other samples (from Makaretu, Mangatewai, Mangatewainui, Tangarewai and Tukituki) were grouped to the upper left because *Phreatogammarus*, *C. fontanus* (left of group); Copepoda sp2., Nematoda, Chironomid E and *O. albiceps* (associated to the centre and right) were more abundant. The sites to the upper right were associated with the highest conductivity, while sites to the left were associated with higher water temperatures. Axis 1 accounted for 17 % of the variance of the data while axis 2 accounted for 1 % of the variance of the data.

The ordination of assemblage structure for seasonal samples (including the Ongaonga) during autumn (Fig. 6b), winter (Fig. 6c) and summer (Fig. 6d) separated the samples into two broad groups. The Ongaonga community was distinct in all seasons, and with the exception of the Tukituki River during autumn (3 animals), it was the only site with Ostracoda. Tangarewai samples were also grouped closely together in all seasons because macrofauna (e.g., *Paraleptamphopus*) dominated the community. All other sites were associated together to the left (autumn and summer) or right (winter) along axis 1. Community patterns along axis 1 were associated with increasing surface flow conditions and a decline in dissolved oxygen from left to right, while pH and conductivity increased from the bottom to the top of axis 2. Hyporheic samples did not differ in community composition between seasons (MRPP, $r = 0.02$, $P = 0.06$).

With the exception of the Ongaonga samples, differences between samples were low within each river, but there were significant differences in community structure among sites (MRPP, $r = 0.58$, $P < 0.01$). The composition of hypogean (MRPP, $r = 0.59$, $P < 0.01$) and epigean (MRPP, $r = 0.13$, $P = 0.01$) taxa also differed among sites. Overall, community composition of the hyporheos changed with well depth (MRPP, $r = 0.01$, $P = 0.02$) through the declining density of epigean animals. However, the hypogean (MRPP, $r = -0.01$, $P = 0.99$) and epigean (MRPP, $r = 0.01$, $P = 0.32$) component of the hyporheos did not change significantly between sites.

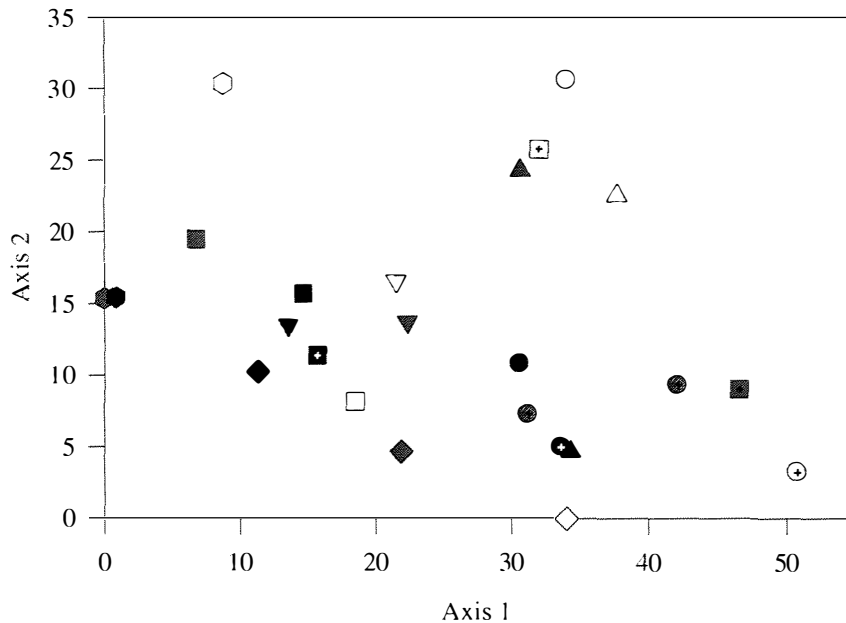


Fig 7. A DECORANA using environmental characteristics measured in autumn (clear shapes), winter (grey shapes) and summer (black shapes). Plotted points represent the Makaretu (circle), Mangatewai (square), Mangatewainui (right way up triangle), Ongaonga (upside down triangle), Tangarewai (diamond), Tukipo (hexagon), Tukituki (circle with cross) and Waipawa (square with cross).

A DECORANA analysis of environmental characteristics from the hyporheic zone of the 8 sites spread sites along axis 1 (Fig. 7). The Tukipo (all seasons) was grouped to the left of axis 1, while samples from the Mangatewai (all seasons), Ongaonga (all seasons), Tangarewai (autumn and winter) and Waipawa (summer) were found to the centre left of axis 1. Autumn samples from the Tangarewai and Waipawa, summer samples from the Tukituki and samples from the Makaretu (all seasons) and Mangatewainui (all seasons) were associated to the centre right of axis 1. In contrast, the Tukituki (autumn and winter), winter samples from the Waipawa were grouped to the right of axis 1. Hyporheic dissolved oxygen and pH increased towards the right of axis 1, while hyporheic and surface conductivity increased towards the left of axis 1. Stream temperature and conductivity, and hyporheic temperature increased towards the bottom of axis 2, while stream width, depth and velocity increased towards the top of axis 2. Axis 1 accounted for 67.8 % in the variance of the data, while axis 2 accounted for 1.5 % of the variance in the data. Environmental characteristics were significantly different between the 8 sites surveyed (MRPP, $A = 0.34$, $P < 0.01$), but the Ongaonga and Tangarewai sites were not significantly different to the Makaretu, Mangatewai, Mangatewainui, Tukipo, Tukituki and Waipawa sites (MRPP, $A = 0.03$, $P = 0.09$).

DISCUSSION

Taxonomic richness was lowest, but abundance was highest when Crustacea (e.g. Amphipoda, Isopoda and Ostracoda) numerically dominated the hyporheos. In contrast, higher taxonomic richness was associated with a greater abundance of epigean taxa (i.e., when epigean taxa comprised greater than one quarter of the hyporheos in the upper 30 cm of substrates). Hyporheic community composition changed with well depth only because the abundance of epigean animals declined with increasing depth, but the hypogean proportion of the community did not change. However, hyporheic density and taxa number did not differ between well depths overall because variation in the number of individuals between replicate wells was so high. The number of taxa and individuals was higher in the Ongaonga and Tangarewai sites with old (> 0.4 mya) substrates. This reflects the increased taxa number and abundance of the hypogean proportion of the community. However, none of the measured physicochemical characteristics at a site was associated with the geological age of the substrates; geological age was associated only with the resident biota. Sites with young geology (< 0.05 mya) may have had a greater proportion of epigean taxa because of less stable bed substrates (chapter 3), or some other unmeasured physicochemical characteristic at each site.

The abundance of Ostracoda in old substrates (~ 0.4 mya) in the Ongaonga was probably related to the finer and more compact substrates at this site yielding low interstitial flows essential for Ostracoda survival (Chapman & Lewis 1976). The Tukipo aquitard (deposits that restrict water movement) probably led to increased conductivity and lower dissolved oxygen in the hyporheic zone of the Tukipo and Mangatewai Streams as there would be greater water retention associated with the presence of an aquitard (Domineco & Schwartz 1990). The low dissolved oxygen and high conductivity may have significantly reduced the density of other invertebrates in the hyporheic zone. Community composition may also be changed by resource availability (Dole-Oliver & Marmonier 1992; Boulton et al. 1998); thus, the dominance of Amphipoda in the Tangarewai hyporheos was linked with high particulate organic matter supplied from the surrounding forest remnant.

Geologically, the Tangarewai (mid Pleistocene) and Ongaonga (late Pleistocene) sites are within old terrace deposits of strongly weathered gravels, sands and silts between

1.25 and 0.4 million years old. In contrast, the Tukipo and Mangatewai Streams are within clay bound gravels (Tukipo aquitard) (mid Holocene) and the remaining sites are within Ruataniwha alluvium (mid Holocene), all less than 50 000 years old (Recent terrace aquifer group) (HBRC 1999). The substrates in geological age are therefore oldest at the Tangarewai and Ongaonga sites and youngest at the Makaretu, Mangatewai, Mangatewainui, Tukipo, Tukituki and Waipawa sites (see Fig. 1). Older substrates were associated with significantly higher invertebrate densities of hypogean animals (especially Ostracoda and Amphipoda) compared to sites with young substrates, which had greater abundance of epigean animals. Geological age may alter the size and compactness of substrates and extent of alluvial deposition, which in turn may alter the interaction between solutes and sediments (White 1993; Richards & Bacon 1994; Wondzell & Swanson 1996). For example, finer substrates increase the residence time of advected surface water, allow longer contact time for solutes to interact with sediments and increase the change in water chemistry so that it becomes less like the river channel.

In contrast, the six sites with younger alluvial sediments have a less diverse hypogean fauna because the physicochemical characteristics at these sites were less suited to these taxa. The physicochemical characteristics may have increased the proportion of epigean animals at these sites because the environment was suited to these taxa. Benthic taxa may also move into the hyporheic zone in response to increased substrate movement in the river channel (Matthei et al. 1999; Chapter 3). Therefore, geomorphology may be the primary influence on community composition at the younger sites because bed substrates are in constant flux. At older sites however, the substrate may be more stable and other factors such as reduced interstitial flows (Marmonier & Cruezé des Châtelliers 1991; chapter 3) or higher resource availability (e.g., organic detritus) (Dole-Oliver & Marmonier 1992; Boulton et al. 1998) may be more important in influencing community composition.

Geologically the age of underlying sediments may also explain differences in hyporheic communities between other regions of New Zealand. In the hyporheic zone of young geomorphology in the river systems of the Taieri (Otago, South Island) (Scarsbrook 1995, Huryn 1996; Montgomerie 1997; Olsen 1998), the Waimakariri (Canterbury, South Island) (Adkins 1997; Mcleod 1998; Adkins & Winterbourn 1999) and Waipa (Waikato, North Island) (Boulton et al. 1997), epigean animals were the most abundant taxa, whereas densities of hypogean animals (i.e., Crustacea) were low. These sites all have substrates of

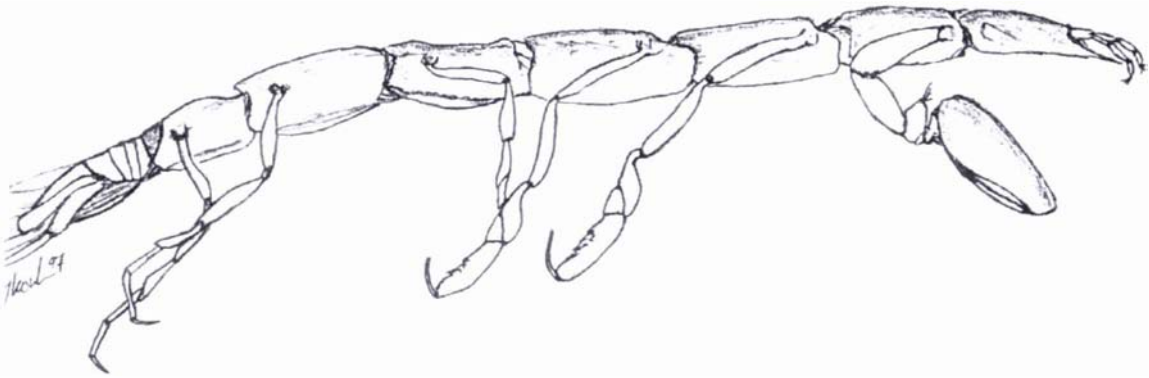
young geological age (Waimakariri < 0.1 mya, Taieri < 0.05 mya and Waipa < 0.1 mya), which may explain the abundance of epigean animals and paucity of Crustacea, similar to that found in the six sites with young deposits in the Southern Hawkes Bay (< 0.05 mya). In contrast, older substrates (cf. 1 mya) near Reefton have a diverse crustacean dominated hyporheos (Anthony 1999) similar in composition to the two older Southern Hawkes Bay sites (cf. 1.25 - 0.4 mya).

Within the substrates of all 8 sites, reducing the extent of the hyporheic zone and its connectivity to the groundwater may influence invertebrate abundance. For example, the presence of clay (aquiclude) layers within sediments in the Waipa catchment (Boulton et al. 1997) and the Tukipo aquitard (50 m deep) (i.e., Tukipo and Mangatawai Streams) in this study (HBRC 1999) may prevent the exchange of subsurface water layers with the river channel (Boulton et al. 1997) thereby reducing hyporheic invertebrate density. Community composition may also be influenced by elevated water temperature. The increase in the density and number of epigean animals during summer in this study suggests disturbance by elevated water temperature may influence community composition (Boulton et al. 1998).

This study suggests geomorphology may influence hyporheic community composition, with hypogean taxa more abundant at sites with older substrates, while epigean taxa were more abundant with younger substrates. This finding was supported in other New Zealand studies where greater density and abundance of Crustacea were collected from sites with older bed deposits (cf 1 mya) and epigean animals were more numerous within sites with young deposits (cf < 0.1 mya). The proportion of epigean taxa may also increase in the hyporheic zone in response to disturbance events in the river channel. For example, disturbances such as bed movement (chapter 3), dewatering (chapter 4) or elevated surface water temperatures (Boulton et al. 1998) may change the density of benthic taxa in the hyporheos. Geomorphology may change the flow regime and this in turn influences hyporheic community composition at sites with young deposits. Whereas, other environmental factors such as organic matter supply or substrate compactness may determine composition at sites with older deposits, where disturbance is a less influential determinant of community structure.

CHAPTER 3

THE EFFECT OF ENVIRONMENTAL STABILITY ON HYPORHEIC COMMUNITY STRUCTURE



ABSTRACT: Thirty-six hyporheic water samples were collected in up-wellings from two well depths (30 and 60 cm) from 8 rivers of differing stability in the Cass-Craigieburn region, South Island during January 1998. Stability at these sites was assessed by measuring the movement of five marked stones from 3 size classes, which was converted to a stone movement index by multiplying the distance traveled by the mean weight of stones in each size class. Hyporheic water chemistry was more similar to surface water chemistry at unstable sites than at stable sites. The greatest diversity of both epigeal and hypogean animals occurred in streams at intermediate levels of disturbance, probably because less compact substrates allowed increased interstitial flow from the surface channel. Interstitial physicochemistry may equally play a role in determining the communities present because stable sites were spring fed and groundwater had a greater influence on the water chemistry. The density of the hyporheos declined linearly and the abundance of epigeal animals increased with greater bed movement. Epigeal taxa may be less abundant at stable sites because the chemical nature of the water is least like the river channel (e.g., low dissolved oxygen, high temperature and high conductivity), while the abundance of hypogean animals is greater, as these taxa are more tolerant of this water chemistry.

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INTRODUCTION

Disturbance has been a topical issue in stream ecology over the past few decades (e.g., Resh et al. 1988; Hildrew & Giller 1994), especially with regard to the response of benthic community composition to physical and chemical change. One of the most commonly investigated disturbances is the rapid increase in discharge and associated bed movement (e.g., Scrimgeour et al. 1988; Mackay 1992; Matthaei et al. 1997). However, extended periods of low or intermittent flow (Williams 1977; Sagar 1983), or elevated surface water temperatures (Stanford & Ward 1983) may constitute equally severe disturbances to lotic communities. In contrast, physical disturbance to the hyporheic zone will only occur via large scale bed movement during high discharge events (Haschenburger & Church 1998; Matthaei et al. 1999), via temporal fluctuations in the water table (Williams 1993) or through siltation of interstices. Community persistence within the hyporheic zone must depend on the ability of organisms to resist disturbance events in a similar manner to benthic communities (Hildrew & Giller 1994).

A number of physical regions within river systems have been suggested as sources of colonists to the benthos following disturbance (e.g., Williams & Hynes 1976; Sedell et al. 1990; Lancaster 1999). The hyporheic zone, an active ecotone bounded by the stream channel above and true groundwater below (Schwoerbal 1961; White 1993; Boulton et al. 1998) is one such postulated refugium. However, the relative importance of the hyporheic zone as a refugium may strongly depend on the physical nature of the river environment (Palmer et al. 1996; Matthaei et al. 1999), because the hyporheic zone is only likely to be physically altered by rare, intense disturbance events (e.g., floods) (Williams, 1977; Kochel 1988, Komar 1988).

The hyporheic refuge hypothesis, popularised by Williams & Hynes (1974), suggests benthic invertebrates migrate into the hyporheic zone to survive floods, providing a source of colonists to the denuded benthos post-disturbance. The hyporheic zone may also provide a refuge for the benthos against elevated surface water temperatures (Boulton et al. 1998) and channel dewatering (Williams & Hynes 1976; Boulton 1989). However, despite a number of studies (e.g., Williams & Hynes 1974; Palmer et al. 1992), the importance of the hyporheic zone as a refuge has yet to be tested under a wide range of

environmental conditions (Dole-Oliver et al. 1997). Many physical and chemical factors interact with the biota to alter hyporheic community composition spatially and temporally (Dole-Oliver et al. 1992; Boulton et al. 1998; Brunke & Gonser 1999); however, how these differ in frequently disturbed systems is unclear (Marmonier & Châtelliers 1991; Dole-Oliver et al. 1997; Brunke & Gonser 1999).

There is a paucity of studies comparing the hyporheic zone in rivers of contrasting substrate stability. Using bed movement as a measure of substrate stability, this study predicts that with increasing bed movement hyporheic community composition will change from a hypogean dominated community to one where benthic taxa become proportionately more abundant. Vertical distribution of the hyporheos will also be examined between stable and unstable sites to assess the potential for vertical migration of refuging animals.

STUDY SITES

The eight study sites are first to third order tributaries of the Waimakariri River located in the Cass-Craigieburn region of the Southern Alps. The four stable sites arise from springs producing relatively stable flows and temperatures, while the four unstable sites have more variable flow and temperature regimes (Death & Winterbourn 1994). The streams are small to moderate in size, having similar substrate composition (mean stable sites = 7.18 cm; unstable sites = 7.67 cm, refer Death & Winterbourn 1995), moderately hard water and low nutrient concentrations. Overall, physical and chemical characteristics of the surface channel do not differ between the 'stable' and 'unstable' site groups (Death & Winterbourn 1995; Table 1).

Table 1. Mean environmental characteristics from 30 and 60 cm wells in the hyporheic zone and from surface water (R) for 8 sites (4 stable and 4 unstable) in the Cass-Craigieburn region of the Southern Alps. Sites were sampled between January 10 and 14 1998. Measures of bed movement are taken from Death & Winterbourn (1994).

	Width (m)	Depth (cm)	Velocity (m/sec)	DO (mg/L)			pH			Conductivity (μScm^{-1})			Temperature ($^{\circ}\text{C}$)			Bed movement measure
Depth (cm)				R	30	60	R	30	60	R	30	60	R	30	60	
Stable Sites																
Slip Spring	4.1	9.3	0.22	9.8	7.4	3.8	8.6	7.7	7.7	59.9	61.9	69.2	9.4	16.4	15.4	0.0
Porter River	3.2	17.3	1.08	10.7	8.3	7.6	8.3	7.7	8.0	56.4	55.7	64.5	10.2	13.2	15.9	0.7
Middle Bush Stream	1.0	4.4	0.54	11.6	9.2	7.9	8.4	8.5	8.6	104	106	107	8.3	9.3	11.4	1.4
Cora Lynn Stream	1.1	8.3	0.63	11.1	2.5	4.7	8.1	7.4	8.1	132	135	134	8.7	14.4	15.7	6.3
Unstable Sites																
Craigieburn Cutting	1.4	5.2	0.66	11.6	8.8	8.5	8.1	8.1	7.9	48.1	51.8	52.8	10.9	10.4	11.7	18.6
Whitewater Stream	4.9	17.6	1.01	9.5	7.0	6.7	8.3	8.0	8.1	50.4	52.2	54.3	15.2	17.7	19.9	17.2
Kowai River	3.2	18.0	0.91	9.7	8.2	7.6	8.1	8.2	8.3	54.5	55.3	57.2	15.3	14.5	17.7	63.8
Bruce Stream	6.3	27.8	1.29	9.8	8.4	8.0	8.3	8.4	8.7	96.6	102	102	11.8	14.9	16.5	96.9

METHODS

Sample Collection

Thirty-two hyporheic water samples were collected using a pump sampler similar to that described by Boulton et al. (1992) from the 8 study sites between 10 and 14 January 1998. A 1.5 m long metal rod (13 mm diameter) with a 14 mm PVC tube sleeve was forced into the substrate at the downstream end of each sampled riffle (up-welling), to 2 set depths (30 and 60 cm). Four 2 litre water samples from 4 separate wells, 2 from each depth, were then extracted from each study site using a hand operated bilge pump, sieved through 300 μ m mesh and stored in 70% ethanol for later sorting and identification using the keys of Winterbourn & Gregson (1989) for epigeal taxa and Chapman & Lewis (1976) for Crustacea. Taxa that could not be identified using the available keys were assigned to morphospecies.

Substrate stability at each study site was assessed once per month by Death & Winterbourn (1994) between December 1987 and May 1989, and was similar in January 1998 to that quantified by Death and Winterbourn (1995) (McIntosh pers. Comm.). At each site the movement of five marked stones in each of three size classes (91-180, 60-90, and < 60 mm) was measured and converted into an index of stone movement by multiplying the distance travelled by the mean weight of stones in that size class and summed for all stones at each site. Thus, a score of zero means no stones moved, while a score of 100 indicates all stones were lost from the study site (Death & Winterbourn 1994).

Conductivity and temperature were measured at each site mid stream along the sampled reach and from 1 well for each depth within each river using an Orion 122 portable conductivity meter. Water samples were collected from the river channel and hyporheic zone in a similar manner for measurement of pH and dissolved oxygen using an Orion (model 250A pH) meter and a YSI (model 59) dissolved oxygen meter respectively. Current velocity ($n = 4$) and depth ($n = 4$) were recorded mid stream along each sampled reach using a velocity head rod.

Data analysis

Diversity measures and chemical parameters were analysed with an analysis of covariance (ANCOVA) using SYSTAT (1996). Bed movement as defined in Death & Winterbourn (1995) was used as a covariate and depth as treatment. Data were also analysed with a Spearman rank correlation (with Bonferroni correction) using SYSTAT (1996). The number of individuals was log transformed prior to univariate analysis to improve homogeneity of variance. Visual inspection of plotted means was used post hoc to assess differences between rivers and depths. In addition to species number, two measures of species diversity were used, Simpson's index of equability or evenness (Simpson 1949) and Margalef's index of species richness (Clifford & Stevenson 1975).

Multi Response Permutation Procedure (MRPP) (using Euclidean distance measure) and Detrended Correspondence Analysis (DECORANA) were performed using the PCORD statistical package (McCune & Mefford 1995). Beal smoothing was performed on community composition data to reduce the influence of zeros in the data set. MRPP is a non-parametric procedure for testing the hypothesis of no difference between two or more groups of entities. It 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). DECORANA orientates samples in ordination space in relation to community similarity.

RESULTS

Physicochemical Parameters

Physicochemical characteristics measured in the surface channel between January 10 and 14, 1998 are presented in Table 1 (and see Death & Winterbourn 1995). Bed movement ($n=16$) (Table 1) was positively correlated with dissolved oxygen ($r = 0.54$, $P < 0.05$) and pH ($r = 0.69$, $P < 0.01$) and negatively correlated with temperature ($r = -0.64$, $P < 0.01$). Conductivity did not differ with stability ($r = -0.07$, $P > 0.05$). Hyporheic dissolved oxygen was similar to surface concentrations at 30 cm (mean = 5.38 mg/L), but distinct from the surface at 60 cm (mean = 4.45 mg/L) ($F_{1, 13} = 5.07$, $P = 0.04$). pH ($F_{1, 13} = 7.43$, P

= 0.02) and temperature ($F_{1,13} = 11.99$, $P < 0.01$) were higher at 60 cm than at 30 cm or the surface.

Diversity Patterns

A total of 25 taxa were collected from the hyporheic wells (30 and 60 cm) (Fig. 1a) Oligochaeta, Copepoda and Amphipoda were the most common hypogean taxa, while *Potamopyrgus antipodarum*, *Stictocladus* spp. and *Deleatidium* spp. were the most

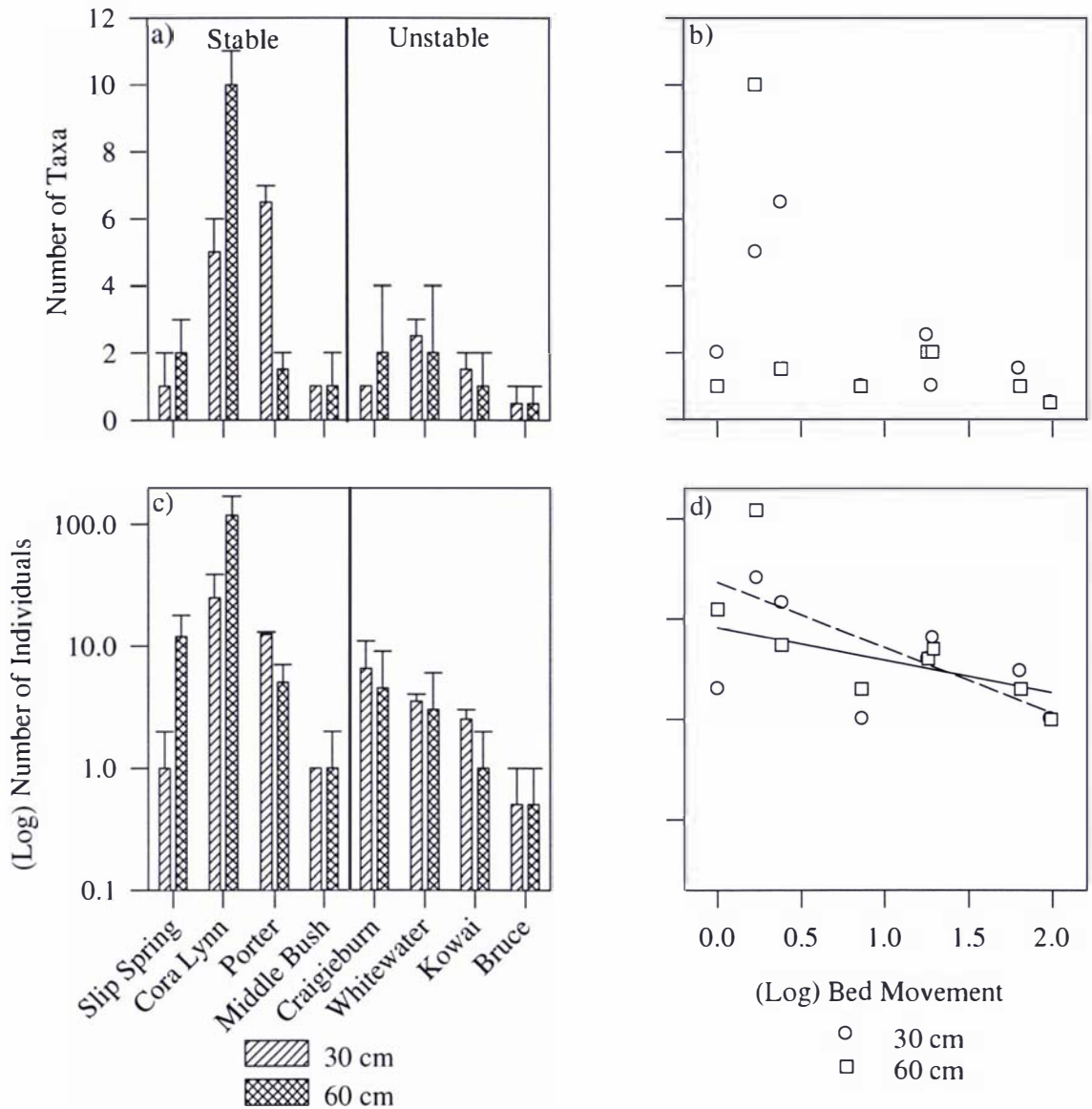


Figure 1. Mean (± 1 S.E.) number of taxa (a) and total individuals (c) between sites, and (b) number of taxa and (d) log number of individuals as a function of bed movement collected from two well depths from 8 streams in the Cass-Craigieburn region, Southern Alps between January 10 and 14, 1998. Sites and bed movement measures are ordered from most to least stable.

abundant epigeal taxa. The number of species did not change linearly with bed movement ($F_{1, 13} = 1.85, P = 0.20$) (Fig. 1b). A quadratic relationship did not describe the relationship between bed movement and the number of taxa ($F_{1, 13} = 2.46, P = 0.47$) or individual counts ($F_{1, 13} = 3.95, P = 0.84$). Number of species was similar between well depths across all streams ($F_{1, 13} = 0.02, P = 0.90$). Of the 28 taxa collected, *Oligochaeta*, *Olinga feredayi*, *Paraleptamphopus subterraneus*, *Stictocladus*, *Deleatidium*, chironomid G and Eriopterini were common to stable and unstable sites and overlapped between well depths within each site. Twenty three taxa were only identified from stable sites and 12 taxa were exclusive to unstable sites. Total invertebrate density ranged between 1 and 117 invertebrates per 2 litre water sample overall (Fig. 1c). Replicated individual counts were similar between well depths ($F_{1, 13} = 0.26, P = 0.62$), but densities were 7 times greater at stable sites ($F_{1, 13} = 1.85, P = 0.04$) (Fig. 1d). This difference between stable and unstable sites could be attributed to the high abundance of animals in the stable Porter River.

Simpson's ($F_{1, 13} = 1.98, P = 0.18$) (mean stable = 0.25, range = 0 – 0.75; unstable = 0.10, range = 0 – 0.69) and Margalef's index scores (mean stable = 1.45, range = 0 – 2.99; unstable = 1.25, range = 0 – 2.16) ($F_{1, 13} = 1.66, P = 0.22$) were both similar at all sites. Simpson's ($F_{1, 13} = 0.39, P = 0.54$) (mean stable = 0.13, range = 0 – 0.69; unstable = 0.22, range = 0 – 2.99) and Margalef's scores (mean stable = 1.35, range = 0 – 2.3; unstable = 1.35, range = 0 – 2.5) ($F_{1, 13} = 0.02, P = 0.90$) were also similar between well depths. In contrast, the relative proportions of higher order taxonomic groups differed with respect to stability (Fig. 2). Epigeal animals were 5 times more abundant at unstable sites than stable sites, while hypogean taxa were 3 times more abundant at stable sites. In all streams, the epigeal portion of the hyporheos comprised the caddisflies *O. feredayi*, *Aoteapsyche* spp. and *Hydrobiosis* spp., 4 species of Chironomidae (*Stictocladus* and chironomid F, G and H), *Neppia* spp., *P. antipodarum* and *Deleatidium* (Table 2).

Benthic taxa were present in the hyporheos (as the epigeal portion) at all sites and well depths. The percentage of benthic taxa in the hyporheos was significantly higher at unstable sites compared to stable sites ($F_{1, 13} = 48.01, P < 0.01$) (Fig 3a). Overall, the density of invertebrates was lower, but not the number of epigeal animals (Fig 3c), at unstable sites (see Table 3). Benthic taxa present in the hyporheos of stable sites included

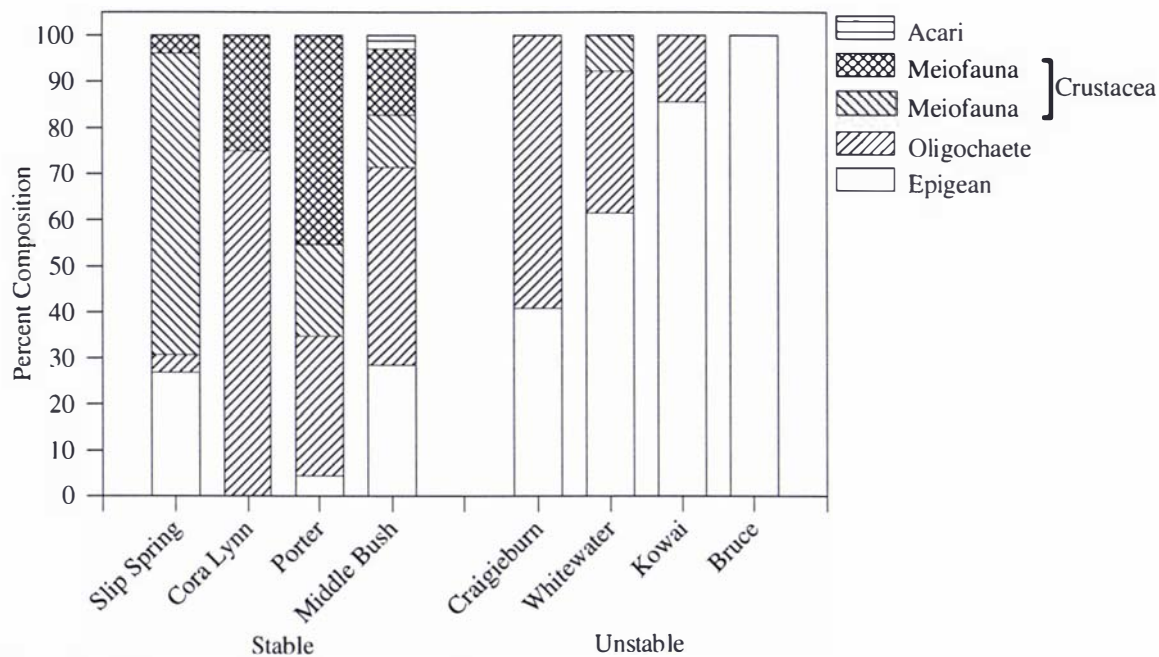


Figure 2. Higher order taxonomic composition of hyporheic samples collected from 8 streams in the Cass-Craigieburn region, Southern Alps between January 10 and 14, 1998. Composition bars are presented as a mean of replicates and depths.

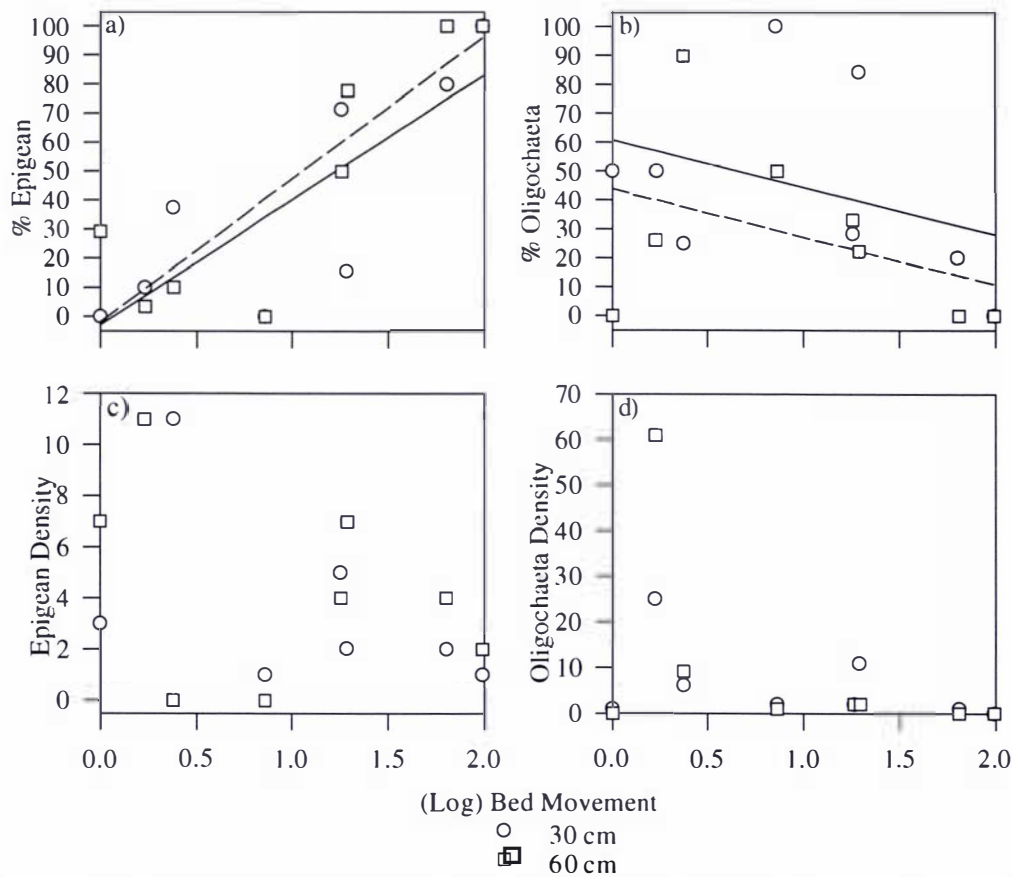


Figure 3. Percent composition (a) and density (c) of epigean animals and percent composition (b) and density (d) of Oligochaeta from the hyporheos of 8 streams in the Cass-Craigieburn region, Southern Alps between January 10 and 14, 1998.

the Plecoptera *Cristaperla fimbria*, *Neppia* and two Chironomidae (*Stictocladus* and morph G), but these were absent from the unstable sites. In contrast, Elmidae, *Aoteapsyche* and *Hydrobiosis* were present in unstable sites but absent from stable sites. With the exception of one *C. fimbria* specimen (a stonefly generally found in small forested streams) collected from Middle Bush Stream, only taxa identified from each rivers' benthos were collected from the epigeal proportion of the corresponding hyporheos (see Death 1991).

Oligochaeta exhibited a contrasting trend to epigeal animals, with the greatest percent abundance found in stable sites ($F_{1, 13} = 6.37, P = 0.03$) (Fig. 3b). However, the density of Oligochaeta was not correlated with bed movement (Fig. 3d), but was correlated with declining dissolved oxygen concentrations and flow rate (Table 3). In contrast, the number of macrofauna (i.e., Amphipoda) ($F_{1, 13} = 2.45, P = 0.14$) and meiofauna (i.e., Ostracoda, Copepoda and Stygocarida) ($F_{1, 13} = 4.06, P = 0.07$) were similar among sites. The percent abundance of Oligochaeta ($F_{1, 13} = 1.53, P = 0.24$), macrofauna ($F_{1, 13} = 0.93, P = 0.35$) and meiofauna ($F_{1, 13} = 0.03, P = 0.87$) were similar between well depth for each site, but macro and meiofauna declined with increasing bed movement (see Table 3). The macrofauna included 3 Amphipoda; *Phreatogammarus* sp., *P. subterraneus* and an unnamed Amphipoda. In contrast, meiofauna comprised a cyclopoid Copepoda, three Ostracoda (morphs 1, 10 and 11), an unidentified stygocarid (Syncarida) and one Acarina.

Community Composition

Ordination of assemblage structure graded samples along axis 1 based on environmental stability (Fig. 4) and generally grouped samples from each river together along axis 1. Axis 1 accounted for 71 % of the variance of the data while axis 2 accounted for 15.6 % of the variance. In addition, MRPP showed community composition was significantly different between the stable and unstable sites ($P = 0.01$), but composition was not different between well depths ($P = 0.95$). Of the taxa identified from the hyporheic zone, greater numbers of Elmidae and *Neppia* (epigeal taxa), and lower numbers of Ostracoda sp1 (meiofauna), *Phreatogammarus* (macrofauna) and *P. antipodarum* (epigeal) were associated with declining environmental stability. The separation of a shallow (30 cm) well from the stable Slip Spring to the upper left was the result of the presence of Stygocarida (Syncarida).

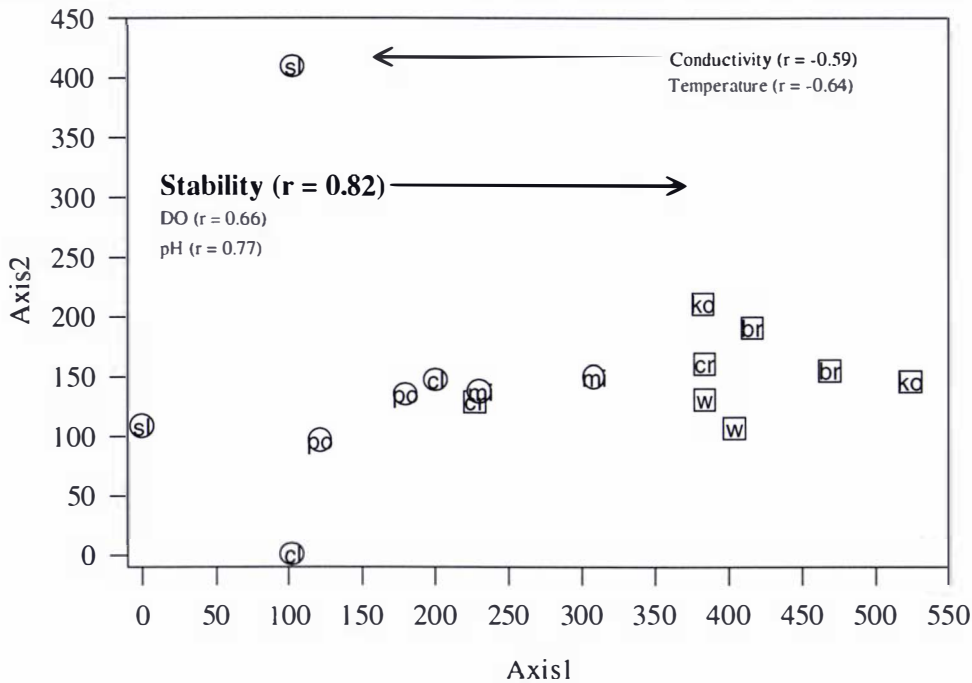


Figure 4. DECORANA analysis for mean community composition collected from 2 well depths pump samples from each of 2 depths between January 10 and 14 1998. Samples were collected in 4 stable (circles, mean of replicates) and 4 unstable (squares, mean of replicates) sites in the Cass-Craigieburn region, Southern Alps. Sites are: Slip Spring (sl), Cora Lynn Stream (cl), Porter River (po), Middle Bush Stream (mi), Craigieburn Cutting (cr), Whitewater Stream (w), Kowai River (ko) and Bruce Stream (br).

DISCUSSION

The distribution of invertebrates in the hyporheos from the 8 sites is consistent with the prediction that proportionally more benthic macroinvertebrates are found in the hyporheic zone of unstable sites. The reverse trend was shown for hypogean taxa, with greater density and diversity in stable sites. This is consistent with the idea that the hyporheic zone may comprise more benthic invertebrates in frequently disturbed sites compared to stable sites. The higher abundance of hypogean animals in stable sites may be a response to habitat suitability because these taxa prefer physicochemical conditions least like the surface, which are only found at stable sites. The greater abundance of hypogean animals in stable sites may also be influenced by the spring fed hydrology at these sites. Thus, a combination of refugium from bed movement and similar physicochemical conditions to the river channel lead to the dominance of benthic animals at unstable sites. Whereas, chemical characteristics that were similar to the surface and a lack of spring fed hydrology led to the paucity of hypogean animals at these same sites.

Table 2. The most abundant taxa collected from 8 sites and two depths during January 1998 in the Cass-Craigieburn region, South Island. Taxa that have benthic origins are represented by an asterisk (*), while all other taxa are hypogean in origin.

Slip Spring		Cora Lynn		Porter		Middle Bush	
30cm	60cm	30cm	60cm	30cm	60cm	30cm	60cm
Oligochaeta	<i>P. subterraneus</i>	Oligochaeta	Oligochaeta	<i>P. subterraneus</i>	Copepoda 1	Oligochaeta	Oligochaeta
Stygocarida	* <i>P. antipodarum</i>		Copepoda 1	Copepoda 1	Oligochaeta	Ostracoda 1	Coleoptera A
	*Chironomid H			* <i>Deleatidium</i> spp.	<i>P. subterraneus</i>	<i>P. subterraneus</i>	
				* <i>Neppia</i> spp.	Amphipoda 7	* <i>Stictocladius</i> spp.	
				<i>Phreatogammarus</i> sp.	Ostracoda 1	* <i>O. feredayi</i>	

Craigieburn		Whitewater		Kowai		Bruce	
30	60	30	60	30	60	30	60
Oligochaeta	*Chironomid F	*Elmidae	*Elmidae	* <i>Stictocladius</i> spp.	* <i>Deleatidium</i> spp.	* <i>Deleatidium</i> spp.	* <i>Deleatidium</i> spp.
* <i>O. feredayi</i>	Oligochaeta	Oligochaeta	Oligochaeta	Oligochaeta	* <i>Hydrobiosis</i> spp.		
	* <i>Stictocladius</i> spp.	*Chironomid G	<i>P. subterraneus</i>				
	*Eriopterini	* <i>Aoteapsyche</i> spp.	*Eriopterini				

Table 3. Correlation (r_s) of seven physicochemical (at 30 and 60 cm wells) and stability parameters (from the surface channel) (n=36) with diversity measures from the study streams. Mean velocity and stability parameters were derived from mean monthly measurements collected by Death & Winterbourn (1994), while temperature, flow (sample) and the chemical parameters were measured at the time of invertebrate sampling from the hyporheic zone. The post-hoc test was using Bonferroni correction, which was significant at $r = \pm 0.513$ ($P = 0.000446$). Significant correlations are marked with an asterisk (*) in bold.

	Conductivity	DO	pH	Velocity (mean)	Flow (sample)	Temperature	Bed Movement
Margalef's	-0.27	0.01	-0.14	-0.02	0.09	-0.21	-0.27
Simpson's	0.01	-0.30	-0.05	-0.40	-0.17	-0.07	-0.45
Taxa:							
Epigeal	-0.31	0.20	0.10	0.17	0.36	-0.50*	-0.09
Macrofauna	-0.17	0.01	-0.12	0.02	0.33	0.04	-0.39
Meiofauna	0.04	-0.48*	-0.47	0.02	-0.02	0.60*	-0.56*
Oligochaeta	-0.13	-0.31	-0.39	-0.50*	-0.25	-0.09	-0.30
Total	-0.25	-0.06	-0.22	-0.04	0.11	-0.21	-0.39
Individuals:							
Epigeal	-0.24	0.13	-0.02	0.13	0.27	-0.39	-0.20
Macrofauna	-0.18	0.03	-0.10	-0.01	0.30	0.02	-0.39
Meiofauna	-0.17	0.03	-0.37	-0.14	-0.03	0.34	-0.62*
Oligochaeta	-0.14	-0.25	-0.22	-0.41	0.06	-0.16	-0.39
Total	0.18	-0.21	-0.04	-0.24	-0.14	-0.15	-0.54*
Composition:							
% Epigeal	-0.27	0.66*	0.74*	0.62*	0.58*	-0.61*	0.77*
% Macrofauna	-0.01	-0.2	-0.35	0.01	0.05	0.22	-0.61*
% Meiofauna	-0.05	-0.05	-0.40	-0.19	-0.16	0.46	-0.61*
% Oligochaeta	0.07	-0.53*	-0.45	-0.63*	-0.38	0.22	-0.41

At intermediate levels of bed movement both hypogean and epigean animals were abundant in the hyporheic community because the physicochemistry would allow both hypogean and epigean animals to survive. Thus the greatest hyporheic species diversity was identified at intermediate levels of bed movement because the environmental conditions suited both epigean and hypogean taxa. Residence time of interstitial water will increase with lower substrate porosity, increase the contact time for solutes to interact with sediments and magnify the change in water chemistry between surface and hyporheic zones (Grimm & Fischer 1984; Triska et al. 1989). The greater residence time of interstitial water may also increase the use of oxygen during respiration by organisms.

Lower dissolved oxygen and higher conductivity in the groundwater can be an example of this. The increasing abundance of Crustacea with declining bed movement at these sites may indicate that hypogean taxa are tolerant of conditions unsuited to benthic taxa such as low dissolved oxygen and/or elevated water temperature (Danielopol 1989; Cooling & Boulton 1993). An increase in hypogean abundance in stable sites may be related to factors other than disturbance (see Chapter 2) such as the greater influence of groundwater in the spring fed stable sites (refer Chapter 6). Epigean animals are more common in the hyporheos when surface water has just entered the hyporheic zone (e.g., downwelling) because benthic taxa are passively transported into the hyporheic zone (refer chapter 6; Cooling & Boulton 1993).

Community composition did not change with increasing depth to 60 cm in these sites as has been found in studies elsewhere (e.g., White 1993; Richards & Bacon 1994). The source of stream flow may thus alter community composition between sites by changing substrate composition (i.e., flow variance and the probability of bed movement), but not between depths because interstitial flow and subsequent water chemistry is similar within each site. This may in turn influence the chemical parameters between rivers more-so than within rivers because the source of flow would be similar within a single up-welling at a site. Abundance of individuals also changed between sites, with both Ostracoda and Copepoda common at stable sites but absent from sites of intermediate and low stability probably because the physiochemical conditions became unsuitable for them. *Stictocladius* became abundant with intermediate levels of bed movement, while *Deleatidium* was the

only taxon tolerant of the least stable conditions. In comparison, Oligochaeta and *P. subterraneus* were common in all but the two least stable sites, suggesting these taxa may be tolerant of the widest environmental conditions.

In summary, hyporheic community composition and diversity is controlled to some degree by bed stability and/or flow source (e.g., surface or spring fed), with a greater percentage of epigeal animals present in the hyporheos with increasing bed movement. Substrates in these stable sites may have more interstitial water contributed from the groundwater. This would alter water chemistry because of greater interstitial water residence time and the opportunity for solutes to interact with sediments (Grimm & Fischer 1984; Triska et al. 1989). Water chemistry (e.g., dissolved oxygen, pH and temperature) at unstable sites was more similar to the river channel than at stable sites. Conditions at unstable sites are thus more favourable for epigeal invertebrates as they most closely resemble conditions in the river channel. Interstitial flow may alter water chemistry in stable sites because of spring fed conditions (e.g., lower dissolved oxygen and higher conductivity) and thus reduce epigeal abundance. Hypogean taxa may be tolerant of these conditions and become more abundant. At intermediate levels of disturbance the environments are suitable for both epigeal and hypogean taxa.

CHAPTER 4

THE EFFECT OF CHANNEL DEWATERING ON BENTHIC INVERTEBRATE COMMUNITY RECOVERY



ABSTRACT: This chapter provides investigates benthic community recovery in sites following channel dewatering of varying length. The recovery of benthic invertebrates was investigated in the Tukituki and Waipawa Rivers following extended channel dewatering of sites for 6, 10 or 14 week periods during the summer of 1997/98. After rewatering, benthic invertebrates rapidly colonised each defaunated site and although some invertebrates were numerically dominant at different times, 95 % of species were present within the first 7 days of rewatering. The number of taxa and individuals differed between sampling dates but not between dewatering treatments. Community composition changed over time; with *Tanytarsus*, *Maoriidamesa* and Elmidae being abundant early, while *Deleatidium* dominated communities later. Although colonisation was rapid in all sites, the control regions that remained wet and sites dry for only 6 weeks had a greater abundance of mayflies compared with those dewatered for 10 and 14 weeks, where Elmidae was most abundant. The greater abundance of *Deleatidium* in sites dewatered for a short time may be because this taxon is more likely to colonise from the hyporheic zone. In contrast, Elmidae may have dominated communities at sites dewatered for longer because drift provided the main source of colonists or simply because it is more resilient to desiccation than *Deleatidium*. These data suggest that with increasing duration of dewatering (e.g., by drought conditions or water extraction for irrigation) the hyporheic zone may decrease as a potential source of colonists to the disturbed benthos.

INTRODUCTION

Studies of the colonisation of denuded habitats by benthic invertebrates have been an active area of stream ecology research over the last two decades (Williams 1977; Sagar 1983; Mackay 1992; Williams & Smith 1996). Experimental studies investigating colonisation dynamics in benthic communities have shown invertebrates are present immediately after disturbance (Williams & Hynes 1976; Sagar 1983), although pre-existing community composition may not be achieved for months (Cairns et al. 1971). The ability of invertebrates to colonise benthic habitats is influenced by the type of disturbance (Lake & Barmuta 1986; Resh et al. 1988), frequency of disturbance (Lake et al. 1989), and the number (Marchant et al. 1991) and type (Death 1995) of taxa present pre-disturbance. The availability (Cairns et al. 1971) and proximity (Gore 1982) of undisturbed regions that provide a source of benthic colonists will also play a role in determining the duration of community recovery.

A number of habitats have been suggested as sources of colonists in river systems following disturbance (e.g., Williams & Hynes 1976; Townsend 1989; Cooling & Boulton 1993; Lancaster & Hildrew 1993). However, recovery of benthic communities following channel rewatering has received little attention (Larimore et al. 1959; Sagar 1983; Doeg et al. 1989). Migration of benthic animals into the hyporheic zone may play a major role in the survival of invertebrates during droughts (Williams 1977). The benthos may therefore migrate into the hyporheic zone where wetted interstitial substrates provide refugia while the surface channel runs dry (Williams 1977; Malicky 1982; Boulton 1989). The benthos may then be repopulated by immature stages moving from the hyporheos (Williams & Hynes 1977, Cooling & Boulton 1993) or emerging from eggs present in interstices once channel flow resumes (Abell 1984). Streams that maintain interstitial flow may therefore provide suitable refugia for benthic invertebrates, allowing them to colonise the benthos post disturbance (Godermakers & Pinkster 1981; Boulton et al 1992; Cooling & Boulton 1993). However, the hyporheic zone may not be a suitable refugium in all river systems, as interstitial flow can cease after extended dry periods (e.g., in intermittent streams), causing the hyporheos to desiccate (Boulton & Stanley 1995) and remove the hyporheic zone as a source of colonists to the benthos.

Dewatering is considered a major structuring force in stream invertebrate communities (Power et al. 1988; Resh et al. 1988). However, most rivers do not regularly run dry in New Zealand for extended periods despite a rapidly changing (Scrimgeour et al. 1988) and unpredictable (Winterbourn et al. 1981, Winterbourn 1987) flow regime. Rather, river sections dewater during extended periods of low rainfall where the lowering of the water table causes the loss of surface water to underlying aquifers. The objective of this study is to examine whether channel dewatering changes the rate of benthic community recovery and composition. Increasing the duration of dewatering may increase the likelihood of desiccation in the hyporheic zone and thus eliminate the hyporheos as a possible source of invertebrate colonists.

STUDY SITES

The Tukituki and Waipawa Rivers (40°00'S, 176°20'E), originate in the Ruahine Ranges from 1700 m a.s.l, have a greywacke fluvial geomorphology (Ruataniwha alluvium) and meander freely through predominantly agricultural land within fluvial deposits up to 150 m wide and 60 m deep (HBRC 1999). Riparian cover at each site was minimal because of the braided channel, although willow trees (*Salix* sp.) were common beside both rivers. Substrate composition was similar in both rivers, comprising 5% boulders (> 26 cm), 30% large cobbles (13-26 cm), 30% small cobbles (6-12 cm), 30% gravels (0.2-6 cm) and 5% sand/silt (< 0.2 cm). The Hawkes Bay Regional Council 1997 assessed substrate composition during an Instream Flow Incremental Methodology (IFIM) survey at both sites. Warm summers and mild winters characterize the region, with a mean annual rainfall of 928 ± 260 mm (site 969402, Ongaonga, Hawkes Bay Regional Council); summer produces the lowest annual flows and water table levels (HBRC 1999).

Four Tukituki (U22 027 351) and four Waipawa (U22 064 444) sites were located at 100 m intervals along a 300 m reach of stream, with a control site farthest upstream, followed by sites estimated to dewater for "6 weeks", "10 weeks" and "14 weeks", respectively. The duration of dewatering was estimated from aerial photographs taken monthly by the Hawkes Bay Regional Council during the 1997/1998 summer. Sites labelled 14 weeks went dry on 9 January 1998, with all other sites dewatering at 4 or 8

weeks thereafter. Sites were dewatered for 6, 10 and 14 weeks before flows resumed following rain on 3 April 1998. Groundwater data showed the water table during the drought of 1997/98 (reference BH 1376, site 894001) was the lowest since 1992 (152 mRL) (HBRC 1999). One section from each river that remained wetted throughout the summer period was considered a control, although flows at these sites were reduced during the summer period.

METHODS

Sampling Protocol

On four sampling occasions at 7, 14, 28 and 42 days after flows resumed (3 April 1998), three randomly placed 0.1 m² Surber samples (300 µm mesh) were collected from the control site and from each dewatered region (dry for 6, 10 and 14 weeks). Samples were stored in 70% ethanol for later sorting and identification using the keys of Winterbourn & Gregson (1989). Conductivity and temperature were measured using an Orion 122 portable conductivity meter; pH was analysed using an Orion 250A pH meter; river depth and velocity were assessed from four points randomly selected along each sampled riffle using a velocity head rod, while width was measured half way along each sampled riffle. Environmental characteristics for the Tukituki and Waipawa Rivers are presented in Table 1.

Algal biomass was assessed by extracting photosynthetic pigments (chlorophyll *a* and phaeophytin) with 90% acetone at 5 °C for 24 hours from five gravels (mean diameter = 5 cm). Gravels were collected at each site (C, 6, 10 and 14 weeks) and on each sampling occasion. Total pigment concentration was calculated using the formulae outlined in Moss (1967 a, b) and corrected for stone surface area using the approach described by Graham et al. (1988).

Table. 1 Environmental variables measured on four occasions between 10 April and 15 May 1998 in the Tukituki and Waipawa Rivers of the Southern Hawkes Bay. Values are represented as averages from the four sites on each sampling occasion.

Sampling Occasion	Tukituki				Waipawa			
	7	14	28	42	7	14	28	42
Conductivity ($\mu\text{S}/\text{cm}$)	107.6	108.9	100.9	101.4	123.9	125.7	121.2	122.0
Depth (cm)	16	14	15	18	20	12	18	20
Oxygen (mg/L)	9.0	8.9	10.2	12.5	9.0	9.6	10.5	11.5
pH	6.8	7.3	7.4	7.4	6.8	7.3	7.4	7.4
Temperature ($^{\circ}\text{C}$)	19	19	16	11	19	19	20	12
Width (m)	6.9	7.0	7.8	9.1	7.4	7.5	9.1	9.4
Velocity (m/sec)	0.99	0.94	0.94	0.92	0.87	0.70	0.87	1.01

Data analysis

To assess whether sampling occasion, duration of dewatering and differences between rivers affected community characteristics, Univariate Repeated Measures Analysis of variance was performed using SYSTAT (SYSTAT 1998). Tukeys HSD test was used post hoc to assess differences between sampling occasion, dewatering and rivers. Mean numbers of taxa and numbers of individuals for each site and sampling occasion were used for the analysis because only one dewatered treatment (dry for 6, 10, 14 weeks) was sampled within each river. Individual counts; total pigment concentration and abundance of the seven most common taxa was log transformed to improve normality and homogeneity of variance prior to this analysis. Diversity measured as species number.

Detrended correspondence analysis (DECORANA) and a Multi Response Permutation Procedure (MRPP) (using Euclidean distance measure) were performed using the PCORD statistical package (McCune & Mefford 1995) to assess the variation in community composition between dewatered treatments and each sampling occasion. DECORANA arranges sampled communities within ordination space in relation to how similar they are in composition to each other. Thus, more closely related communities (communities) are arranged more closely in ordination space. In contrast, MRPP is similar to a multivariate analysis of variance without the requirement of multivariate normality and homogeneity of variance.

RESULTS

Diversity patterns

The number of taxa present in both rivers (Fig. 1 a, b) recovered rapidly within the first 7 days of rewatering and did not change over the 42 day sampling period overall ($F_{3,9} = 0.31$, $P = 0.82$) or between dewatering treatments within each river ($F_{3,3} = 1.32$, $P = 0.41$). A total of 25 taxa were collected from the Tukituki River (Fig. 1a). The leptophlebid mayfly *Deleatidium* spp. was numerically most abundant, while the riffle beetle Elmidae and the caddisflies *Aoteapsyche* spp., *Oxyethira albiceps* and *Pycnocentropus* spp. were collected in moderate numbers from all Tukituki sites.

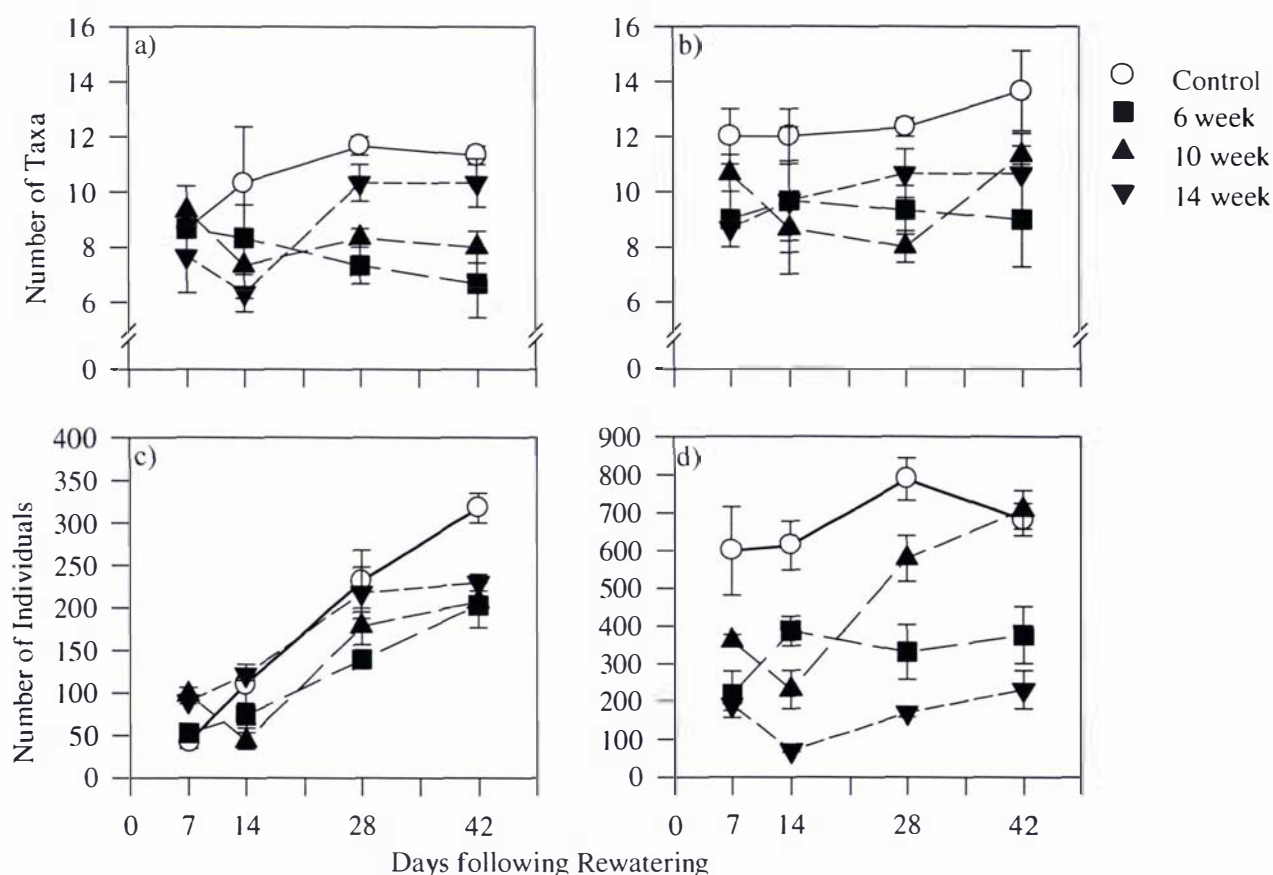


Fig. 1 Average (± 1 SE) number of taxa (a and b) and individuals (c and d) collected in three 0.1 m² Surber samples at four sites within the Tukituki (a and c) and Waipawa Rivers (b and d) after flow resumed on 3 April 1998.

Twenty six taxa were collected from the Waipawa River (Fig. 1b), and although *Deleatidium* was numerically most abundant, Elmidae, *Pycnocentroides* and the Chironomidae *Tanytarsus* spp. and *Maoridiamesa* spp. were numerous. Overall, similar numbers of taxa were identified in both the Tukituki and Waipawa Rivers ($F_{1,3} = 3.23$, $P = 0.17$). There was low species evenness at both rivers throughout the sampling period ($F_{3,3} = 3.48$, $P = 0.07$). Number of taxa was not significantly different among the dewatered treatments ($F_{3,3} = 0.37$, $P = 0.78$) or rivers ($F_{1,3} = 0.93$, $P = 0.41$).

The total number of individuals (Fig. 1 c, d) was similar between rivers ($F_{1,3} = 6.28$, $P = 0.09$), with the lowest mean number of individuals in the first 7 days and the highest after 42 days ($F_{3,9} = 11.53$, $P < 0.01$). Dewatered treatments had similar invertebrate densities overall ($F_{3,3} = 0.40$, $P = 0.78$). However, an interaction between the time of sampling and the river sampled ($F_{3,9} = 1.17$, $P = 0.03$) suggests invertebrate density

increased at different rates between rivers during the sampling period. This interaction may be related to increasing abundance through time in the Tukituki control samples, but not in the Waipawa controls.

Community Composition

With the exception of *Deleatidium*, Elmidae and *Tanytarsus*, the density of the most common taxa did not change with time, nor was there a difference between dewatering treatment or river (Table 2). The greatest numbers of *Deleatidium* were collected on day 42 and the lowest on day 7, whereas *Tanytarsus* and Elmidae showed the reverse trend. Percent abundance of higher order benthic invertebrate groups in the Tukituki (Fig. 2a-d) and Waipawa (Fig. 3a-d) were similar over time between controls (2a) and sites dry for 6 weeks (2b) in the Tukituki; and for controls (3a) and sites dry for 6 (3b) and 10 (3c) weeks in the Waipawa. By comparison, Ephemeroptera (i.e., *Deleatidium*) recovered more slowly in sites dry for longer periods (i.e., dry for 10 and 14 weeks in the Tukituki and 14 weeks in the Waipawa) and Chironomidae (i.e., *Maoridiamesa*) were more numerous early on in sites with longer dewatering duration.

Table. 2 *F* values testing the null hypothesis that individual taxon are significantly different between rivers, treatments and sampling occasions for the seven most common taxa collected in three Surber samples in the Tukituki and Waipawa Rivers between 10 April and May 15, 1998.

	River d.f., = 1, 3		Dewatered Treatment d.f., = 3, 3		Sampling Occasion d.f., = 3, 9	
	<i>F</i> value	<i>P</i>	<i>F</i> value	<i>P</i>	<i>F</i> value	<i>P</i>
<i>Deleatidium</i> spp.	6.32	0.09	0.88	0.54	8.66	< 0.01
Elmidae	1.42	0.32	0.52	0.70	3.21	0.04
<i>Aoteapsyche</i> spp.	1.33	0.33	0.08	0.97	1.67	0.24
<i>Pycnocentroides</i> spp.	0.53	0.52	0.73	0.60	1.66	0.25
<i>Tanytarsus</i> spp.	6.39	0.09	0.86	0.55	8.01	< 0.01
Eriopterini	0.57	0.51	0.72	0.61	0.85	0.50
<i>Maoridiamesa</i> spp.	6.65	0.08	1.04	0.49	5.94	0.06

Sites were grouped during an ordination of assemblage structure in the Tukituki (Fig. 3a) and Waipawa (Fig. 3b) Rivers according to the duration after rewatering. This pattern was generally consistent between the controls and dewatered treatments for both

rivers. Overall, samples collected 7 and 14 days after rewatering showed a greater spread along axis 1 (to the right), while sites collected 28 and 42 days after rewatering were

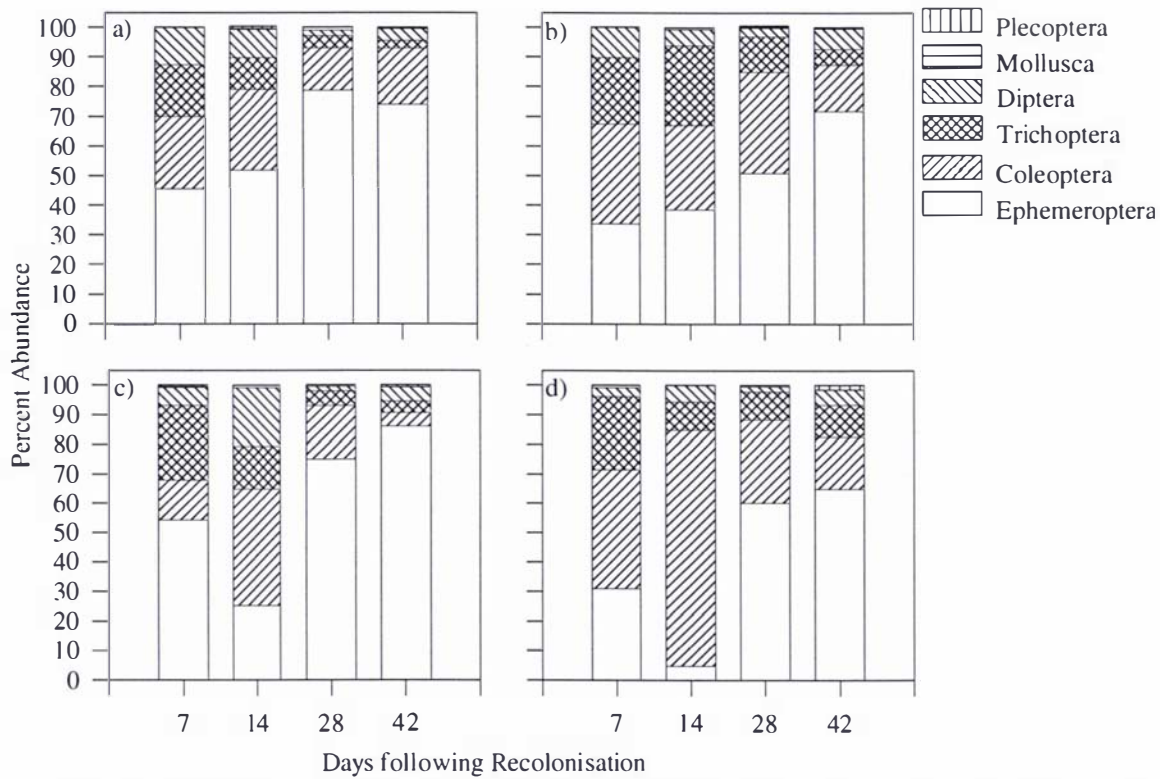


Fig. 2 Percent composition of benthic invertebrates in the Tukituki River at a control site (a) and sites dewatered for 6 (b), 10 (c) and 14 weeks (d) during summer 1997/98.

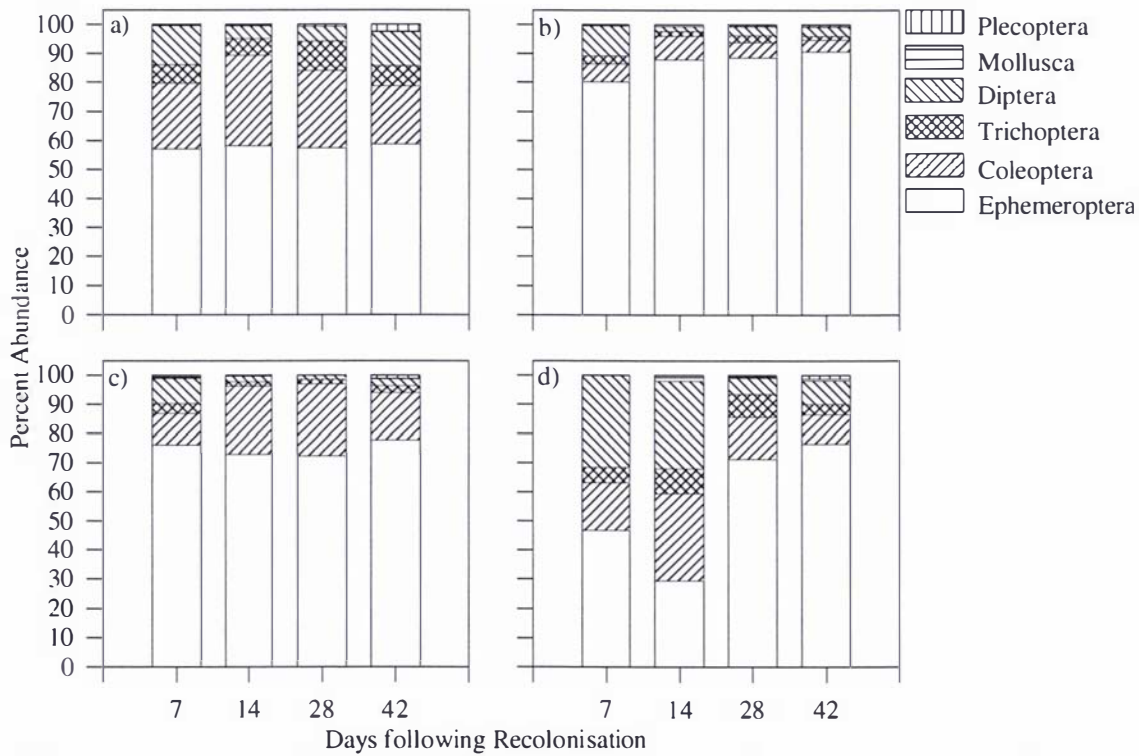


Fig. 3 Percent composition of benthic invertebrates in the Waipawa River at a control site (a) and sites dewatered for 6 (b), 10 (c) and 14 weeks (d) during summer 1997/98.

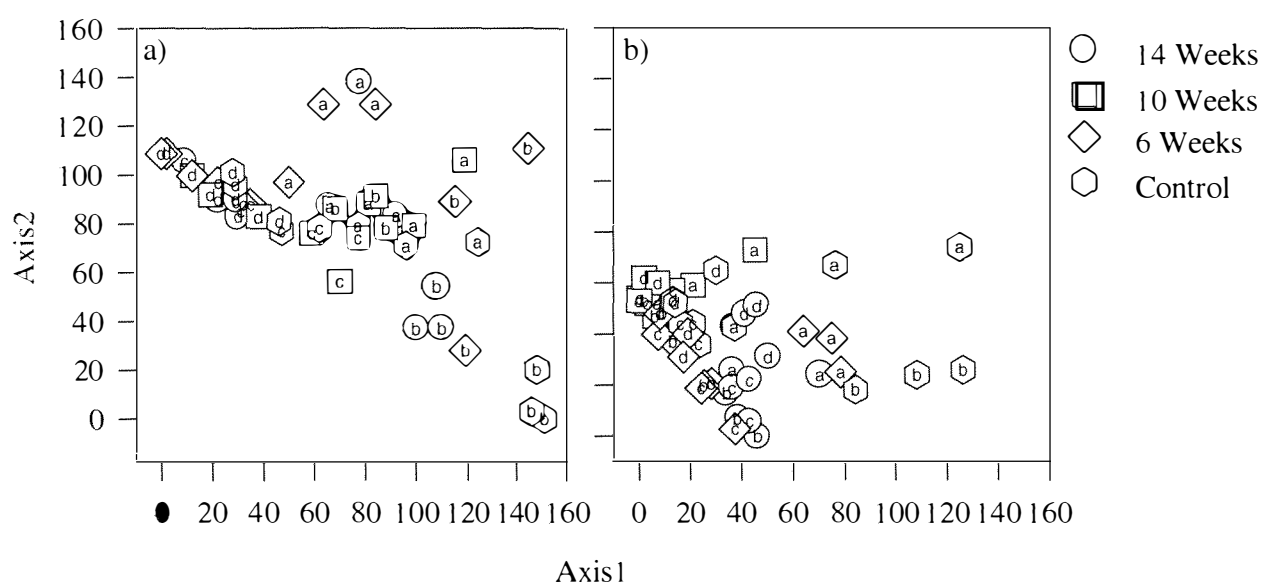


Fig. 4 DECORANA of benthic community structure between sites in the Tukituki (a) and Waipawa (b) Rivers. Shapes represent the duration each site remained dry. Samples collected 7, 14, 28 and 42 days after rewetting are represented by 'a, b, c and d' respectively.

grouped to the left of axis 1. Samples in the Tukituki to the right of axis 1 were associated with greater numbers of *Aoteapsyche*, chironomid 1, Elmidae and Eriopterini. In contrast, chironomid 3, *Deleatidium* and *Psilochorema* were more abundant in samples to the left of axis 1. Elmidae was positively correlated with axis 2. Samples to the right of axis 1 in the Waipawa River were associated with greater numbers of chironomid 1 and 3 and *Oxyethira albiceps*, while *Deleatidium* and *Psilochorema* were more abundant to the left of axis 1. Elmidae and Eriopterini were more abundant to the bottom (positive) of axis 2. Conductivity and water temperature were positively correlated with axis 1 in both rivers, while dissolved oxygen was negatively correlated with axis 1 in only the Waipawa River.

Communities from the Tukituki (MRPP, $r = 0.04$, $P = 0.04$) and the Waipawa (MRPP, $r = 0.34$, $P < 0.01$) were significantly different between dewatering treatments. Community composition was also different between each sampling occasion in the Tukituki (MRPP, $r = 0.34$, $P < 0.01$), but similar in the Waipawa with time (MRPP, $r = 0.02$, $P = 0.14$). Axis 1 accounted for 48.2 (Tukituki) and 32.8 (Waipawa) percent of the variance in the data. In contrast, axis 2 accounted for 1.7 (Tukituki) and 4.8 (Waipawa) percent of the variance in the data 2.

Periphyton

Total pigment concentration (chlorophyll *a* and phaeophytin) increased through time in both rivers ($F_{3,9} = 19.01$, $P > 0.01$), but was similar between rivers ($F_{3,3} = 0.41$, $P = 0.57$) and dewatering treatment (including control samples) within each river ($F_{3,3} = 1.10$, $P = 0.47$) (Fig 5).

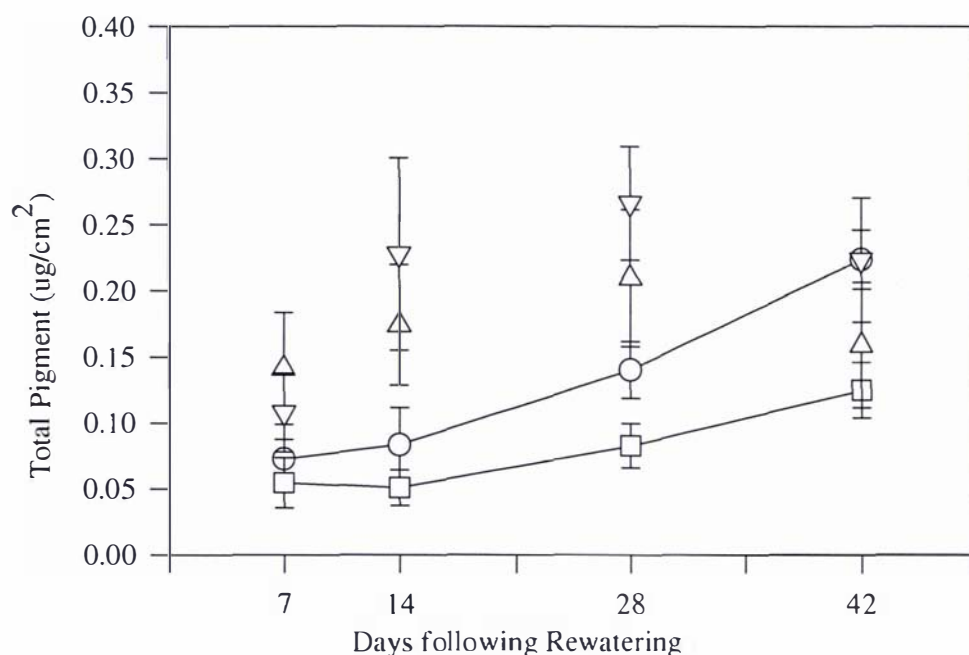


Fig. 5 Mean ($\pm$ S.E) Total pigment concentration (mean of sites within each river) for samples collected in the Tukituki (circles) and Waipawa (squares) Rivers. Triangles represent control sites from the Tukituki (right way up) and Waipawa (upside down) Rivers.

DISCUSSION

This study investigated recolonisation patterns of the benthos following rewating in two braided rivers where channel dewatering occurred for between 6 and 14 weeks. Benthic recovery was predicted to differ between sites of different dewatering duration from areas that were not dewatered. This prediction was based on the premise that the colonisation and refuge potential of the hyporheic zone would decline with increasing dewatering over time and with distance downstream (Cooling & Boulton 1993). The significance of wetted upstream regions as a source of colonists was also expected to decline with increasing distance downstream (Gore 1982). The length of time dewatered did not significantly alter the number or density of taxa recolonising the dewatered sites after the return of the surface water compared to the controls. However, recovery of individual taxa did change with

dewatering duration. Doeg et al. (1989) investigating substrate disturbance also found that intensity of disturbance did not affect the rate of benthic recovery as much as disturbance duration.

Periodic drought conditions may be an important factor affecting diversity patterns in stream systems (Everard 1996). The lack of groundwater discharge in the sites surveyed (HBRC 1999) compared to those in other systems (e.g., Wood & Petts 1999; Wright & Symes 1999) may increase the importance of dewatering in influencing benthic community composition at these sites. However, species diversity and abundance recovered over a similar period of time compared to a system where dewatering occurred for approximately 4 months (refer Wright & Symes 1999; Extence 1981). In contrast, Brooker et al. (1977) and Cowx et al. (1984) showed that species diversity and abundance declined in response to dewatering in other river systems. The differing responses of the benthic fauna in different river systems suggest invertebrate recovery may be influenced by the presence of refugia in some sites and the absence of refugia in others (Sedell et al. 1990).

Benthic invertebrates rapidly colonised each defaunated site, with diversity patterns from the dewatered treatments resembling those in the controls within 7 days of rewatering in both braided rivers. However, density was only comparable to the controls after 28 days of rewatering. Recovery patterns suggest animals such as *Tanytarsus* and Elmidæ larvae were the most abundant benthic colonists early before declining in abundance after 14 days. In contrast, *Deleatidium* became numerically dominant towards the end of the study (Sagar 1986), but was rare early. *Deleatidium* was consistently most abundant in the control sites and those dry for 6 weeks, but was slower to recover in sites that were dry for 10 and 14 weeks. This was in contrast to the findings of McLeod (1998) and Sagar (1983), where *Deleatidium* rapidly colonised the denuded benthos in South Island streams. However, in the alluvial gravels of the southern Hawkes Bay, longer dewatering periods and lowering of the water table may eliminate the hyporheic zone as a source of colonists, especially for *Deleatidium*, which may colonise predominantly from the hyporheic zone (chapter 5).

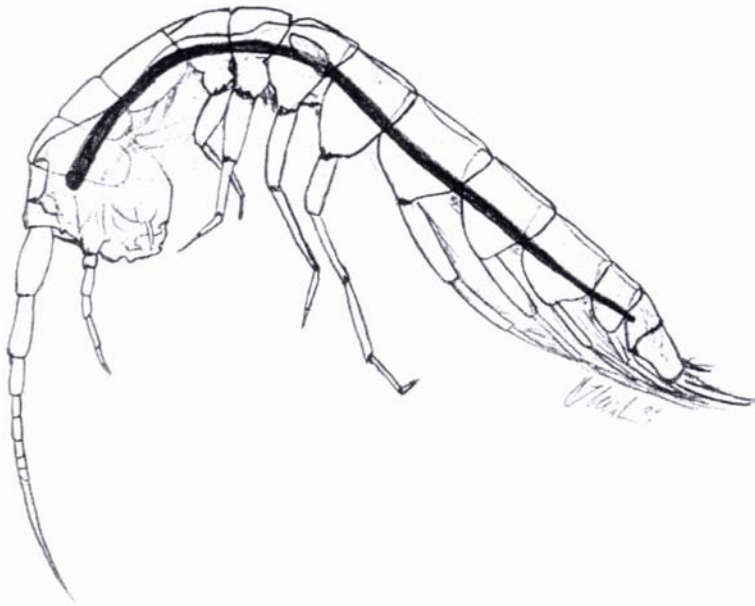
The increase in abundance of *Deleatidium* with time was consistent in both rivers and the artificial substrate experiment documented in chapter 5. Elmidæ larvae appeared rapidly in all sites, suggesting this taxon may colonise primarily by drift and crawling

(chapter 5), or that Elmidae was more resistant to desiccation than *Deleatidium*. In contrast, the slower recovery of *Deleatidium* in sites dry for 10 and 14 weeks may be due to its reliance on the hyporheic zone as a source of colonists. Previous authors have noted that mayflies (i.e., *Baetis* spp.) and certain other invertebrates may seek refuge (i.e., from discharge increase) within bed substrates (Lehmkuhl & Andersen 1972; Goedermakers & Pinkster 1981). This may explain why many invertebrates can rapidly recolonise the benthos after floods (e.g., Williams & Hynes 1976; Sagar 1983; Scrimgeour et al. 1988; chapter 5). Benthic animals may also colonise from eggs left in the dewatered substrates as long as these are not desiccated in the dry riverbed. However, recovery would be slower when the hyporheic zone is removed as a colonisation source because invertebrates may then only colonise from wetted upstream regions (i.e., drift), aerial oviposition or crawling. Nonetheless, benthic community recovery was rapid in both rivers presumably because drifting invertebrates are often the dominant colonists in the benthos (Williams & Hynes 1976; Brittain & Eikeland 1988).

In summary, the number of taxa and individuals recovered rapidly in all dewatered sites, with taxa counts and animal density similar to the controls within 7 and 28 days, respectively. Both numbers of taxa and individuals increased at a similar rate between dewatered treatments and were similar to the controls within 28 days. Dewatering duration did not influence the rate of recovery, but did alter the composition of benthic taxa because disturbance intensity may not be the primary controller of colonisation patterns. Chironomidae (e.g., *Tanytarsus*) and Coleoptera (e.g., Elmidae) colonised early, while Ephemeroptera (e.g., *Deleatidium*) colonised later. Moreover, colonisation by *Deleatidium* may have been slower at sites dry for 10 and 14 weeks due to desiccation of the hyporheic zone, compared to controls and sites dry for 6 weeks where the hyporheic zone may not have been as greatly affected. In contrast, Elmidae was abundant shortly after rewatering in all sites, but was more abundant in sites dry for 10 and 14 weeks. This beetle may colonise primarily through drift and crawling or be more resistant to desiccation.

CHAPTER 5

THE RELATIVE IMPORTANCE OF DRIFT AND SUBSURFACE MOVEMENT ON BENTHIC COMMUNITY RECOVERY



ABSTRACT: 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 Hawkes Bay between March 30 and May 2, 1997. Both the number of taxa and individuals rapidly increased through time in baskets only allowing surface drifting and crawling invertebrates (drift), only allowing invertebrates migrating from the hyporheic zone (hyporheic) and controls which allow both (controls), with the number of taxa and density 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 3 basket types. The colonisation rates identified from artificial baskets in the Makaretu are consistent with colonisation experiments undertaken overseas. Elmidae was most abundant within drift treatments until day 28 after which *Deleatidium* spp. became dominant. The abundance of Elmidae and *Deleatidium* in the control treatments was consistent with colonisation patterns in the drift baskets. In contrast, baskets with access from the hyporheic zone were dominated by *Deleatidium* throughout the experiment. It appears that Elmidae colonise quickly in greater numbers by drift and/or crawling and *Deleatidium* colonises more slowly from the hyporheic zone, eventually replacing Elmidae as the most common animal.

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 frequency and intensity (Lake & Barmuta 1986; Resh et al. 1988), animal abundance (Marchant et al. 1991) and the type of taxa present (Death 1996) before disturbance. Benthic community composition may also be affected by the source of colonists, with community recovery changing through species specific colonisation patterns (Sagar 1983; Williams 1977). Systems where frequent disturbance events affect the benthos may therefore have different recovery patterns from those where disturbance is less common (see Townsend et al. 1997). 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 (see Williams 1977; Sagar 1983; Death 1995).

Although disturbance has long been considered a major structuring force in stream communities (Williams & Hynes 1974; Power et al. 1988; Resh et al. 1988), attention has only recently focused 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). Many studies have identified large numbers of epigeal taxa within the hyporheos (e.g., Richards & Bacon 1994; Williams & Smith 1996; see chapter 2 and 4). However, few have identified the potential of these taxa as colonists to the benthos (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 have investigated benthic colonisation patterns in North Island braided 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). This study assesses the relative contribution of invertebrates from below (i.e., hyporheic zone) and those from above (i.e., drift and crawling) to colonisation of artificial substrates in the braided Makaretu River.

STUDY SITES

The Makaretu River is a third order braided river in Southern Hawkes Bay, New Zealand within fluvial deposits 20 to 25 m wide and a wetted channel width between 3 and 5 m. Substrate characteristics comprised 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 was minimal, although willows (*Salix* sp.) were present along one bank of the sampled riffle. The catchment (18 km²) is predominantly pastoral farming, although native bush comprises approximately 6 km² of the upper catchment within the Ruahine Ranges to an altitude of 1000 m a.s.l.

METHODS

Artificial Substrate Baskets

On 23 March 1997, 36 plastic baskets (34 × 28 × 6 cm), with 150 holes (0.5 cm diameter) in the base (but absent from the sides), were placed into the river channel (riffle section) level with the surrounding bed surface. Each basket contained 7 small cobbles (mean diameter 8 cm) and gravels between 2 and 4 cm diameter. Baskets were placed in 12 rows of 3 baskets (each separated by at least 30 cm). 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 allowed colonisation by drift or crawling only (Drift) by sealing the bottom of the basket with clear plastic sheets, and the final third had no restrictions (Control). Additional Surber sample controls were collected at the end of the experiment to provide an assessment of the benthic community in the natural stream bed substrates. 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, where vertical exchange between the river channel and hyporheic zone is least likely.

Sampling Protocol

Samples were collected after 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, Drift and Control) were removed into a large collecting net (300 μm mesh) downstream of the sampled basket. Replicates were 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 0.1 m^2 Surber samples were collected from the riffle immediately upstream of the artificial substrate baskets as an additional control.

Depth and velocity (measured with a velocity head rod), conductivity and temperature (measured with an Orion 122 conductivity meter), and pH (measured with an Orion 250A pH meter) were recorded on each sampling occasion. The Makaretu River was slightly acidic ($\text{pH} = 6.7 - 6.8$), with water temperatures between 13 and 16 $^{\circ}\text{C}$. Mean velocity was 0.87 m/sec (range = 0.7 - 1.13), conductivity was between 84 and 96 $\mu\text{S}/\text{cm}$, while dissolved oxygen concentration was between 9 and 12 mg/L.

Data Analysis

To assess whether sampling occasion and recolonisation treatment differed with respect to univariate community characteristics, all variables were analysed with a Repeated Measures Analysis of Variance using SYSTAT (SYSTAT 1996). Prior to analysis, the total number of individuals and abundance of the seven most common taxa was log transformed to increase normality and homogeneity of data. Visual inspection of plotted means 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 (DECORANA) and a Multi Response Permutation Procedure (MRPP) (using Sorensen's distance measure) were all performed

using the PCORD statistical package (McCune & Mefford 1995). To assess diversity the Berger/Parker dominance index (Berger & Parker 1970) and Margalef's index of species richness (Clifford & Stevenson 1975) were used. Assessment of the proportion of Ephemeroptera, Trichoptera and Plecoptera (EPT) followed the approach of Lenat (1988).

RESULTS

Diversity Patterns

The number of taxa ($F_{3, 18} = 7.85$, $P < 0.01$) (Fig. 1a) and density of invertebrates ($F_{3, 18} = 9.14$, $P < 0.01$) increased steadily in all treatments (Fig. 1b), peaking at day 28. The total density of invertebrates ($F_{2, 6} = 2.83$, $P = 0.14$) and number of taxa present ($F_{2, 6} = 1.99$, $P = 0.22$) was not different between colonisation treatments overall. Margalef's index of species richness (Table 1) was low early, but increased to peak at days 14 and 28 ($F_{3, 18} = 3.41$, $P = 0.04$) in all treatments ($F_{2, 6} = 0.36$, $P = 0.71$). The Berger/Parker index of species dominance reacted in a similar manner, showing community dominance was similar between treatments ($F_{2, 6} = 1.03$, $P = 0.41$), but highest at day 24 and lowest within the first 7 days ($F_{3, 18} = 31.90$, $P < 0.01$). The EPT (Table 1) also increased through time ($F_{3, 18} = 5.10$, $P = 0.01$), with the highest EPT scores after 42 days in the control and drift treatments. The EPT scores within hyporheic baskets declined over time, producing high EPT values in the first 7 days and the lowest after 42 days ($F_{2, 6} = 45.03$, $P < 0.01$).

Table 1. Mean (± 1 SE) biotic indices for samples collected using artificial substrate baskets (0.1 m^2) on four occasions between 30 March and 2 May 1997 in the Makaretu River, Southern Hawkes Bay. Treatments are represented by Control (C), Hyporheic (H) and Drift (D) baskets.

Treatment	EPT (%)			Berger/Parker			Margalef's		
	C	H	D	C	H	D	C	H	D
Day 7	38	83	32	0.64	0.74	0.66	3.90	3.97	3.64
Day 14	36	72	25	0.62	0.68	0.69	4.32	4.11	5.39
Day 28	21	77	33	0.72	0.73	0.64	4.46	5.80	4.78
Day 42	53	72	62	0.55	0.64	0.53	4.59	3.56	4.26

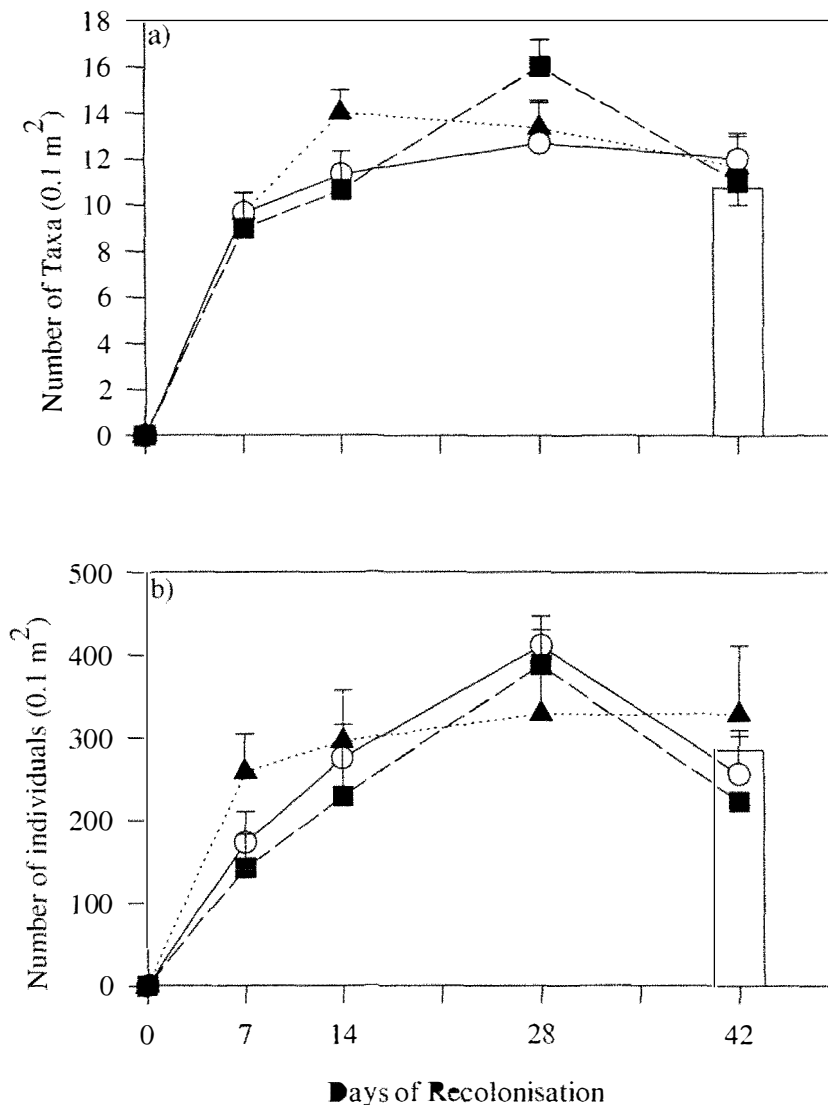


Fig 1. Mean (± 1 SE) number of taxa (a), and total number of individuals (b) for artificial substrate baskets allowing hyporheic entry only (squares), drift entry only (triangles) and control treatments allowing both (circles) from the Makaretu River, Southern Hawkes Bay collected between 30 March and 2 May, 1997. Bars in each graph represent Surber samples collected at day 42.

Community Composition

Control (Fig. 2a) and drift treatments (Fig. 2b) had similar community composition during the 42 day experiment, while hyporheic treatments (Fig. 2c) had different relative abundance of individual taxa. Numerically, within the control and drift treatments *Elmidae* was dominant, while *Deleatidium* was most abundant within the hyporheic treatment. However, *Deleatidium* increased in abundance in all treatments through time, dominating all treatments at day 42. In contrast, the density of *Elmidae* increased to day 28 (mean number at day 28; H = 56, D = 241, C = 258), before declining by day 42 in all baskets

(mean; H = 13, D = 116, C = 122) (see Table 2). Overall, abundance of Elmidae was low in the hyporheic treatment and declined in the drift and the control treatments from day 7 to day 42. Overall number of animals such as Eriopterini and *Neppia* sp. were rare in all treatments, but increased in numbers through time (see Table 2).

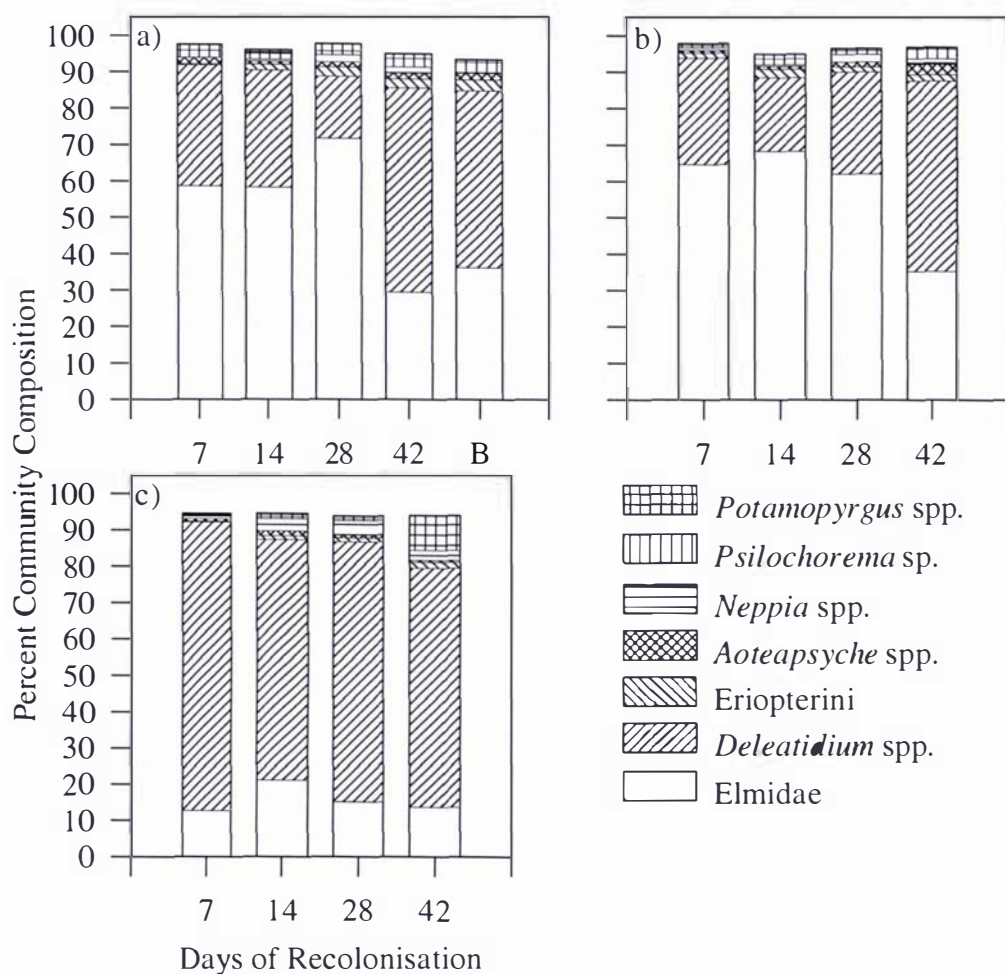


Fig 2. Percent community composition for the seven most abundant taxa within Control (a), Drift (b), and Hyporheic (c) treatments collected between 30 March and 2 May, 1997 in the Makaretu River, Southern Hawkes Bay. Percent composition bar 'B' in the control graph represents Surber samples collected at day 42.

Ordination of assemblage structure separated treatments into two broad groups (Fig. 3), the control (and additional Surber controls) plus drift treatments to the middle and left, with the hyporheic samples grouped to the middle and top right. Sites were separated according to taxon abundance, with hypogean taxa (*Paraleptamphopus subterraneus*, *Cruregens fontanus*, Acarina sp3 and Collembola sp1); less mobile (*Psilochorema* sp. and *Pycnocentroides* spp.) and mobile benthic taxa (*Deleatidium* spp.) associated with hyporheic treatments. In contrast, benthic taxa associated with control and drift treatments

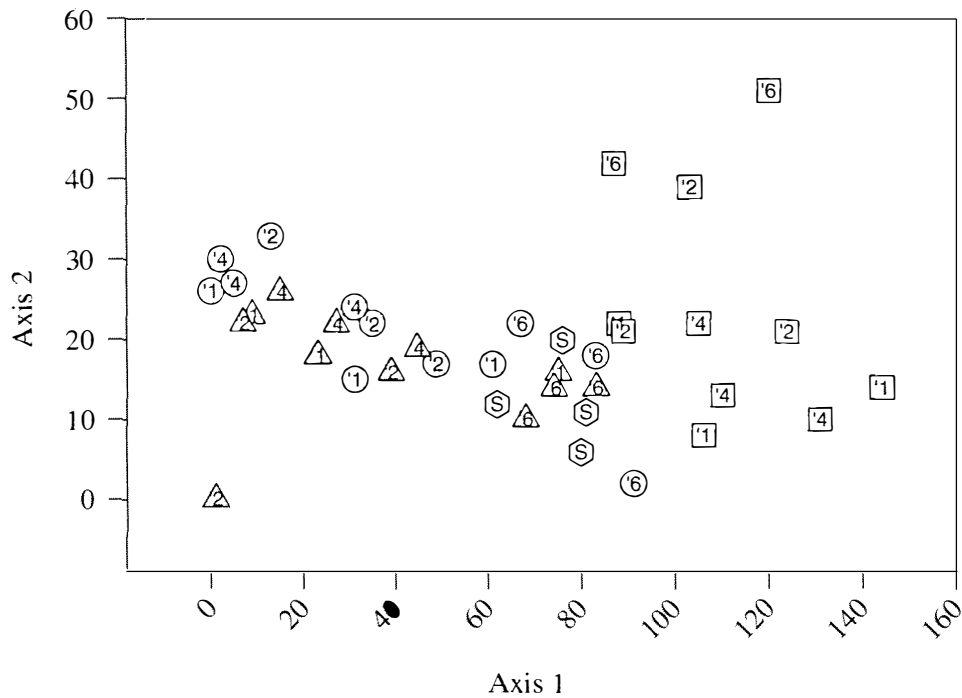


Fig 3. DECORANA analysis of samples collected from Hyporheic (squares), Drift (triangles) and Control (circles) treatments in the Makaretu River, Southern Hawkes Bay between 30 March and 2 May, 1997. Numbers '1', '2', '4' and '6' represent the duration (in weeks) of colonisation and hexagons (with S) represent Surber samples collected on day 42.

Table 2. 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 March 30 and May 2, 1997 in the Makaretu River.

Invertebrate	Mean count (0.1 m ²)			Sampling occasion d.f., = 3, 18		Treatment d.f., = 2, 6		Site × Treatment d.f., = 6, 18	
				F value	P value	F value	P value	F value	P value
Elmidae	475	104	545	14.92	< 0.01	19.36	< 0.01	0.74	0.62
<i>Deleatidium</i> spp.	270	451	312	1.36	0.29	7.39	0.02	2.14	0.10
<i>Neppia</i> spp.	10	20	12	10.86	< 0.01	2.57	0.16	2.11	0.10
<i>Aoteapsyche</i> spp.	12	6	14	0.67	0.58	2.25	0.19	0.47	0.82
Eriopterini	17	6	16	7.37	< 0.01	16.93	< 0.01	1.46	0.25
<i>Potamopyrgus</i> spp.	12	10	6	2.57	0.09	4.25	0.07	2.47	0.06
<i>Psilochorema</i> sp.	14	3	15	2.07	0.14	9.06	0.02	1.58	0.21

were Elmidae, Eriopterini and *Costachorema xanthoptera*. Axis 1 accounted for 55.1 % of the variation in the data while Axis 2 accounted for 15.2 %. A Multi Response Permutation Procedure (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 drift ($r = 0.18$, $P = 0.06$) and hyporheic treatments ($r = 0.11$, $P = 0.11$) was consistent throughout the experiment. Moreover, benthic samples collected at day 42 using a Surber were not different in composition from the control treatment sampled at day 42 ($r = 0.23$, $P = 0.12$).

DISCUSSION

Colonisation was rapid in all treatments, with all taxa present within the first 7 days of colonisation. However, it was only after 14 and 42 days, respectively, that density and community composition were comparable to the benthos. These results are comparable to other studies in New Zealand, indicating that although all taxa colonise rapidly, pre-existing community composition may not be achieved for up to one month (Sagar 1983; Scrimgeour et al. 1988). Species diversity increased through time until day 42 when the artificial substrate baskets had similar diversity to the benthos. This duration for species recovery is consistent with a number of studies that show taxa number recover within a few weeks (Sagar 1983; Boulton et al. 1991; Mathooko & Mavuti 1992) to periods exceeding one month (Williams & Hynes 1976; Meier et al. 1979; Scrimgeour et al. 1988). Colonisation was not complete until at least 28 days after colonisation began.

The number of invertebrates colonising the benthos is known to vary with the source of invertebrates (Townsend & Hildrew 1976; Williams & Hynes 1976; Boulton et al. 1991). However, the number of taxa and density was not different among treatments in this study. The type of taxa colonising and the subsequent community composition within each treatment did differ, with drift and control communities distinct from baskets colonised solely from beneath the stream bed. Community composition was not different

after 42 days between treatments (and Surber control samples) when *Deleatidium* was the most abundant taxa. *Deleatidium* also dominated the hyporheic treatments throughout the experiment, while Elmidae dominated the drift (and control) baskets until day 28. However, after 42 days *Deleatidium* was the most abundant taxon in all treatments, suggesting *Deleatidium* colonised by vertical movement from within the bed and Elmidae 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.

Habitat preferences by Elmidae and *Deleatidium* may also have affected the preference of the former to colonise by drift and crawling, while the latter may colonise predominantly from the hyporheic zone. Elmidae, which prefer finer sediments (Death 2000), may be more likely to enter the drift because smaller substrates are more likely to move with changes in flow. Overall, the movement of bed substrates declines with increasing particle size (Carling 1983; Carson & Griffiths 1987), so any invertebrate inhabiting large substrates may enter the drift less often compared to those that favour smaller substrates. Elmidae larvae may also be more prone to removal from bed substrates because these animals are less streamlined compared to *Deleatidium*. In contrast, *Deleatidium* is more abundant on larger substrates (i.e., 12-26 cm) (Quinn et al. 1990; Jowett & Richardson 1990; Death 2000), is more streamlined and may be less prone to be lost into the drift because it inhabits the boundary layer near the stream bed.

In the absence of dominance among species, 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 colonists early that declined later, while *Deleatidium* density was low initially but increased later suggests *Deleatidium* may be more competitive for space and resources (functionally dominant) than Elmidae in the benthos (see also chapter 4). Therefore, community composition may have changed during the experiment because *Deleatidium* may be functionally dominant in New Zealand streams. In addition, the proportion of *Deleatidium* and Elmidae may have remained constant in the hyporheic treatment because the functionally dominant taxa favoured colonising from the hyporheic

zone and was abundant in these baskets early. Removing the influence of a colonisation source (i.e., the hyporheic zone) may alter community composition 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 and abundance resembling the benthos after 14 days. However, community composition was not consistent with the surrounding benthos until the last 2 weeks of colonisation, suggesting number of taxa and density recovers rapidly but composition may not recover for some time. Community recovery was not complete until at least 28 days after colonisation began. Communities unrestricted by colonisation sources were distinct from communities colonised only from the hyporheic zone until day 42 when *Deleatidium* became most abundant in all treatments. Differences among treatments were perhaps related to Elmidae entering in greater numbers through drift and crawling, while *Deleatidium* colonised from the hyporheic zone.

CHAPTER 6

INTERSTITIAL COMMUNITY COMPOSITION OF UP AND DOWN WELLINGS: A STUDY IN THREE BRAIDED RIVERS



ABSTRACT: This chapter investigates whether up-welling regions provide a more suitable refuge for benthic invertebrates sensitive to elevated water temperatures than down-wellings. At three up and three down-welling regions in each of the braided Makaretu, Tukituki and Waipawa Rivers, hyporheic water samples were collected from 2 well depths (30 cm and 60 cm) between March 24 and 27, 1999. The percent abundance (40 %) and density (29 individuals pers 2L sample) of epigeal animals was highest in down-wellings in all rivers, but only constituted 25% (23 individuals per 2L sample) of the animals at up-wellings. Up-wellings in the Makaretu where chemical conditions were least like surface water, had a fauna where only 6 % of the community comprised epigeal animals compared to 36 % in the Tukituki and Waipawa. Despite similar substrate characteristics to the other rivers, the low epigeal abundance within up-wellings in the Makaretu was probably linked to the groundwater fed conditions at this site. In contrast, the higher epigeal abundance in the Tukituki and Waipawa up-wellings may be due to greater surface water infiltration into the hyporheic zone because both the rivers have significant groundwater recharge at the sites sampled. There was not enough evidence to support the assumption that the hyporheic zone acts as a temperature refuge, as there was little difference in temperature sensitive or tolerant epigeal animals between up and down-wellings. The groundwater recharge hydrological conditions in the Tukituki and Waipawa Rivers provided favourable conditions for benthic animals because surface water infiltration at downwellings produced chemical conditions similar to the surface channel. In contrast, up-wellings were less suitable for benthic animals because hyporheic water chemistry was strongly influenced by the groundwater (e.g., lower dissolved oxygen and temperature, higher conductivity), or through solutes interacting with sediments in the groundwater discharge conditions of the Makaretu, where up-welling water chemistry was similar to the groundwater.

INTRODUCTION

Chemical and thermal conditions fluctuate in the hyporheic zone because of the interaction between surface and groundwater (Schwoerbel 1961; Triska et al. 1989). Spatial patterns of interstitial communities also change in response to hydrology (Stanley & Boulton 1993; Newbury 1984; Dole-Oliver et al. 1997) because movement of water between the hyporheic zone and the surface stream creates areas of high and low resource availability (Boulton et al. 1998). Surface water enters the hyporheic zone in areas of down-welling when the hydraulic head of surface water is greater than the groundwater. In contrast, water exits the hyporheic zone at up-wellings where upward pressure of the groundwater is greater than that of the river channel (Hendricks 1993; Stanford & Ward 1993; White 1993). The changing chemical conditions in the hyporheic zone from surface and groundwater mixing alters the extent of the hyporheic zone (Williams 1993; Fraser & Williams 1998), which in turn may affect the composition of the resident hyporheos (Triska et al. 1989; Findlay 1995; Fraser & Williams 1998).

In contrast to stream flow, interstitial water movement is relatively slow (Thackson & Schnelle 1970), with change in the chemical composition of interstitial water occurring through longer interstitial residence time (Cooling & Boulton 1993; chapter 4). This chemical change is the result of the storage and cycling of solutes in the hyporheic zone (Kennedy et al. 1984; Bencala 1993). However, the concentration and subsequent release of these resources to the river channel is dependent on stream discharge and slope, substrate permeability, depth of alluvium and bed surface profile (heterogeneity) (Vaux 1968; Kennedy et al. 1984). Residence time of interstitial water and subsequent resource availability must therefore depend on geomorphology, substrate characteristics, hydrology and the rate of chemical exchange in the hyporheic zone (Kennedy et al. 1984; Bencala 1993; chapter 2 and 4).

It has been suggested that benthic invertebrates move into the hyporheic zone to seek refuge during disturbances such as floods (Williams & Hynes 1974, 1976), droughts (Williams 1977, Delucchi 1989) or temperature extremes (Boulton et al. 1998). However, because temporal variation in the chemical nature of interstitial water alters the boundaries of the hyporheic zone (Williams 1993), movement of benthos into the substrate will depend

on the presence of suitable physicochemical conditions (e.g., dissolved oxygen and temperature). Regions of down-welling may provide passively drifting invertebrates with areas of hyporheic water similar in chemical composition to the river channel occurs; while up-wellings which may differ chemically from surface conditions, will be less suitable for benthic invertebrates (Cooling & Boulton 1993) and more suitable for hypogean taxa. However, during summer when high water temperatures are common in the river channel, benthic invertebrates intolerant of elevated water temperatures may move into the hyporheic zone in response to lower water temperatures because of cooler groundwater infiltration.

A number of studies have shown taxa common to the benthos are more abundant where hyporheic water is more similar chemically to the surface (i.e., down-welling), while hypogean taxa are more abundant when chemical conditions are distinct from the river channel (i.e., up-welling) (Cooling & Boulton 1993; Dole-Oliver et al. 1997; chapter 4). However, there has been no comparison between up and down-wellings in New Zealand river systems. In this chapter, hyporheic community composition between up and down-wellings in three braided rivers is examined to assess whether up-wellings provide a more suitable refuge for benthic invertebrates sensitive to elevated water temperatures than down-wellings. That is, are a greater proportion and density of benthic taxa intolerant of elevated water temperatures present in up-wellings (e.g., *Deleatidium* spp., *Aoteapsyche* spp., *Pycnocentria funerea*) compared to temperature tolerant taxa (e.g., Elmidae, *Potamopyrgus antipodarum*) (Quinn et al. 1994).

STUDY SITES

The three braided rivers in this study are part of the Tukituki River catchment in the Southern Hawkes Bay. The Tukituki (39°90'S, 176°11'E) and Waipawa Rivers (39°10'S, 176°35'E) were sampled in fourth order braided sections meandering freely within fluvial deposits up to 150 m wide and up to 40 m deep (HBRC 1999). The Makaretu River (40°01'S, 176°21'E) is a third order braided river flowing within fluvial deposits 20 m to 25 m wide and 30 m deep (HBRC 1999). Substrate characteristics in the Tukituki and Waipawa Rivers comprised 5% boulders (> 26 cm), 30% large cobbles (13-26 cm), 30%

small cobbles (6-12 cm), 30% gravels (0.2-6 cm) and 5% sand/silt (<0.2 cm). The Makaretu has slightly smaller substrates comprising 5% boulders, 10% large cobbles, 30% small cobbles, 40% gravel and 15% sand/silt greywacke particles (Hawkes Bay Regional Council unpublished data). The rivers originate in the Ruahine Ranges and run through predominantly pastoral landuse, with willows (*Salix* sp.) present along the banks.

METHODS

Miniature Piezometers

Hydraulic head was measured with a 0.41 cm ID translucent polyethylene tube (piezometer) with a perforated tip encased with 300 µm mesh. The mesh provides a screen preventing influx of sediment into the tube. Each piezometer was inserted 40 cm into the substrate by first driving a 2 cm diameter steel tube (casing) loosely fitted with lag bolts at each end to prevent sediment entry and impact damage from the hammer. The piezometer was then inserted and held in place while the casing was removed leaving the lag bolt in the sediment near the piezometer tip. Raised above the water level, the translucent piezometer allowed measurement of head differential with respect to the surface water using a ruler. Once water levels in the tube stabilises, the difference between the tube level and the surface water can be estimated (Lee & Cherry 1978). Head differential for each site recorded in this study and groundwater fluxes documented in HBRC (1999) are shown in Table 1.

Table 1. Piezometer measurements estimating hydraulic exchange at up and down-welling regions in 3 Southern Hawkes Bay Rivers sampled between March 24 and 27 1999. S1-3 represents sample sites for each river. Positive (+ve) groundwater flux denotes discharge from the underlying aquifer and water races to the river channel (river gain), while negative groundwater flux (-ve) represents rivers recharging the groundwater conditions (river loss).

	Makaretu			Tukituki			Waipawa		
Site	S1	S2	S3	S1	S2	S3	S1	S2	S3
Down-welling (mm)	-18	-7	-44	-16	-17	-10	-32	-32	-14
Up-welling (mm)	24	5	28	20	19	10	38	33	15
Groundwater Flux (From HBRC 1999)	+ve	+ve	+ve	-ve	-ve	-ve	-ve	-ve	-ve

Sample Collection

At three up-welling (river gain) and three down-welling (river loss) regions (S1-3) within each river, hyporheic water samples were collected from 2 wells of different depth (36 bores in total) between March 24 and 27, 1999. Pump sampler similar to that described by Boulton et al. (1992) was used to collect samples. A 1.5 metre long metal rod (13 mm diameter) with a 14 mm PVC tube sleeve was forced into the substrate to 30 or 60 cm and a 4 litre water sample was extracted from each well using a hand operated bilge pump. The water samples were then sieved through 150 μ m mesh and stored in 70% ethanol for later sorting and identification using the keys of Chapman & Lewis (1976) and Winterbourn & Gregson (1989). If taxa could not be identified using the available keys they were assigned to apparent morphospecies.

Temperature, conductivity, pH and dissolved oxygen were measured from each well depth and in the river channel using an Orion 122 portable conductivity meter, an Orion model 250A pH meter and a YSI 59 dissolved oxygen meter, respectively.

Data analysis

To assess whether the welling region, well depths and rivers differed with respect to univariate community characteristics, variables were analysed with a three-level nested analysis of variance (ANOVA) (site nested within river) using SYSTAT (SYSTAT 1996). Individual taxon counts were log transformed to decrease heterogeneity of data prior to analysis. Visual inspection of plotted means was used post hoc to assess differences between welling region, well depth and river. Diversity was assessed using species number, Simpson's index of equability or evenness (Simpson 1949) and Margalef's index of species richness (Clifford & Stevenson 1975).

Multi Response Permutation Procedure (MRPP), with Sorensen's distance measure, was performed using the PC-ORD statistical package (McCune & Mefford 1995) to assess variation in community composition among rivers, welling regions and well depth. Beals smoothing was performed on community composition data to reduce the influence of zeros in the data set. 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.

RESULTS

Environmental Characteristics

The pH ($F_{1,6} = 7.16$, $P < 0.01$) (Fig. 1a) and temperature ($F_{1,6} = 8.39$, $P = 0.03$) (Fig. 1b) of hyporheic water were similar to the river channel in down-wellings and distinct from the surface water at up-wellings. In contrast, conductivity was highest at up-wellings and lowest at down-wellings ($F_{1,6} = 7.96$, $P = 0.01$) and 10 % higher than the surface water in up-wellings (Fig. 1c). Dissolved oxygen (Fig. 1d) was similar between up and down-wellings ($F_{1,6} = 11.60$, $P = 0.82$). In addition, dissolved oxygen ($F_{2,6} = 11.60$, $P = 0.01$), temperature ($F_{2,6} = 9.98$, $P = 0.01$), conductivity ($F_{2,6} = 7.96$, $P = 0.01$) and pH ($F_{2,6} = 140.83$, $P < 0.01$) were different among rivers, with conductivity and pH consistently higher in the Makaretu and dissolved oxygen and temperature higher in the Tukituki and Waipawa. However, temperature ($F_{6,6} = 16.17$, $P < 0.01$), conductivity ($F_{6,6} = 4.88$, $P = 0.04$) and pH ($F_{6,6} = 191.20$, $P < 0.01$) were not consistent between sample sites within each river (i.e., S1-3). Refer to Table 2 for raw environmental data for the three rivers.

Table 2. Mean (± 1 S.E) environmental conditions for the 3 up-welling and 3 down-welling sites in the Makaretu, Tukituki and Waipawa Rivers. r = samples from the river channel, while h = samples from the hyporheic zone.

		Makaretu				Tukituki				Waipawa			
		D30	D60	U30	U60	D30	D60	U30	U60	D30	D60	U30	U60
pH	r	7.9	7.9	8.2	8.1	7.5	7.5	7.1	7.1	7.3	7.3	7.2	7.2
	h	7.9	7.9	7.9	7.9	7.7	7.7	7.7	7.7	7.5	7.5	7.5	7.5
DO (mg/L)	r	9.4	9.3	9.0	7.7	8.6	8.4	8.8	8.7	7.7	7.7	8.2	7.9
	h	12.0	12.0	11.6	11.6	11.3	14.3	10.1	10.1	9.5	9.5	9.7	9.7
Temp (°C)	r	16.3	15.9	16.7	17.6	20.5	21.0	20.4	20.1	23.3	23.3	19.8	20.4
	h	15.9	15.9	16.0	16.0	20.1	20.1	19.1	19.1	21.9	21.9	21.3	21.3
Cond (µScm)	r	85.1	87.9	93.8	100.6	101.9	102.1	101.7	103.4	118.6	122.5	120.1	123.3
	h	83.1	83.1	83.3	83.3	101.0	101.0	101.8	101.8	119.0	119.0	118.2	118.2

Diversity patterns

Twenty six taxa were identified from the three braided rivers, with invertebrates such as Copepoda sp1., *Deleatidium* spp., Oligochaeta and *Paraleptamphopus subterraneus* most numerous. The number of taxa was similar among rivers ($F_{2,6} = 1.79$, $P = 0.25$) and well depths ($F_{1,6} = 0.0$, $P = 0.98$). Higher taxa counts occurred at down-wellings in the Makaretu and Waipawa Rivers (mean = 5 and 6, respectively) and up-wellings from the Tukituki (mean = 6) overall ($F_{2,6} = 6.76$, $P = 0.03$) (Fig. 2a). The number of individuals was similar between rivers ($F_{2,6} = 0.48$, $P = 0.64$) (Fig. 2b) and well depths ($F_{1,6} = 0.88$, $P = 0.38$). However, at down-wellings the number of individuals was twice that of up-wellings in the Tukituki and Waipawa, while the density was three times greater at up-wellings than down-wellings in the Makaretu ($F_{1,6} = 8.90$, $P = 0.02$).

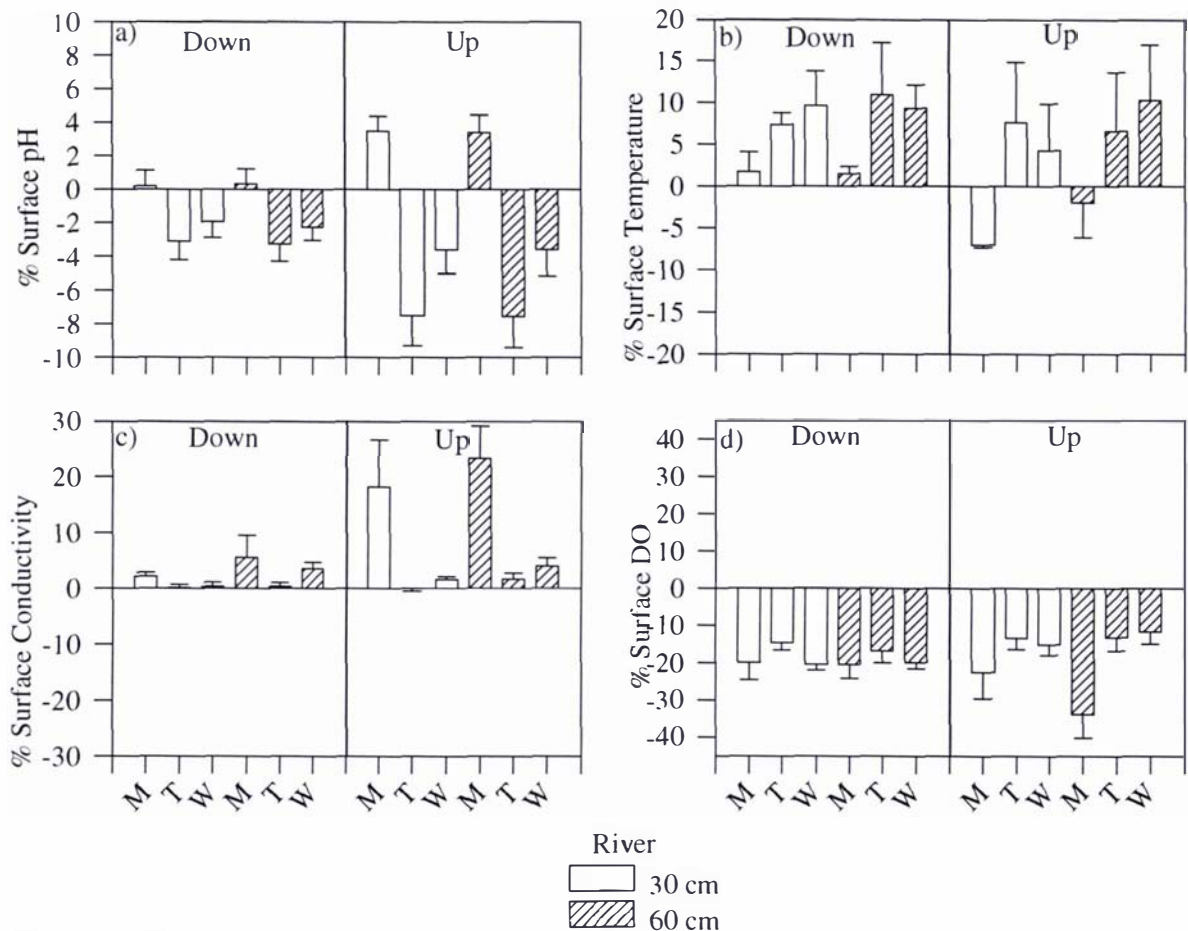


Figure 1. Mean (± 1 S. E.) pH (a), temperature (b), conductivity (c) and dissolved oxygen (d) expressed as a percentage of the equivalent surface measures from the hyporheic zone of the Makaretu (M), Tukituki (T) and Waipawa (W) Rivers in the Southern Hawke's Bay sampled between March 24 and 27, 1999.

Margalef's index of species richness did not differ among rivers ($F_{2,6} = 1.30$, $P = 0.34$), between up and down-wellings ($F_{1,6} = 0.05$, $P = 0.83$) (Fig. 2c) or with well depth ($F_{1,6} = 1.39$, $P = 0.28$). However, there was a significant interaction between river and up/down-wellings ($F_{2,6} = 6.53$, $P = 0.03$) because of 15 % higher species richness in the Makaretu River down-wellings, compared to 10 % higher richness in the Tukituki and Waipawa up-wellings. Species evenness was also similar among rivers ($F_{2,6} = 0.62$, $P = 0.57$), between up and down-wellings ($F_{1,6} = 0.01$, $P = 0.91$) (Fig. 2d) and well depths ($F_{1,6} = 0.63$, $P = 0.46$).

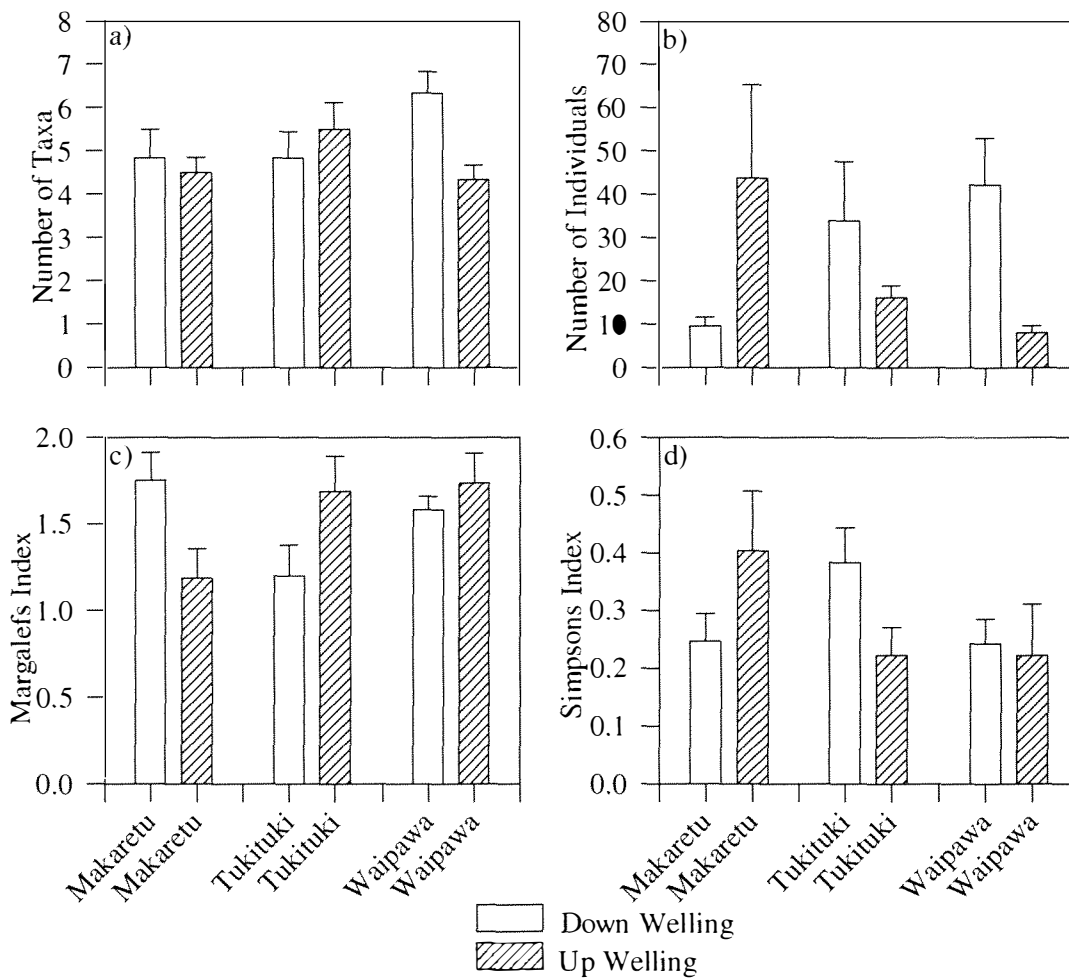


Figure 2. Mean (± 1 S. E.) number of taxa (a), number of individuals (b), Margalef's index (c) and Simpson's index (d) collected from up and down-wellings in 3 braided rivers in the Southern Hawkes Bay sampled between March 24 and 27, 1999.

Community Composition

Half of the animals collected (54 %) from the hyporheic zone in the three rivers were common to the benthos. Epigeal taxa collected were *Aoteapsyche* spp., *Hydrobiosella stenocerca*, *Hydrobiosis parumbripennis*, *Pycnocentria funerea* and *Oxyethira albiceps*; five Chironomidae (Tanypodinae and morphs A, C, D and G); Eriopterini, Elmidae, *Deleatidium* and *Potamopyrgus antipodarum*. The density (Table 2) and percent abundance (Fig. 3) of epigeal animals was highest at down-wellings ($F_{1,6} = 18.62$, $P < 0.01$). However, the number of epigeal animals at down-wellings was not consistent within each river (range for Makaretu = 0-16, Tukituki = 0-107, Waipawa = 0-74) despite an average of 40% of the hyporheos being epigeal taxa at down-wellings and 25 % at up-wellings. The number of epigeal animals did not appear to be related to piezometer

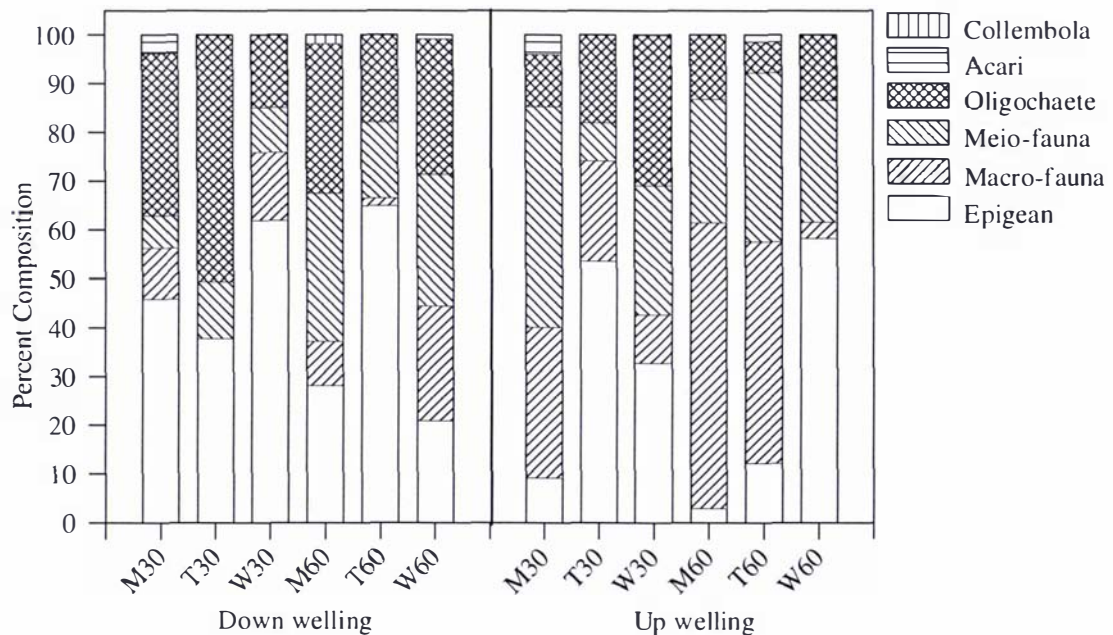
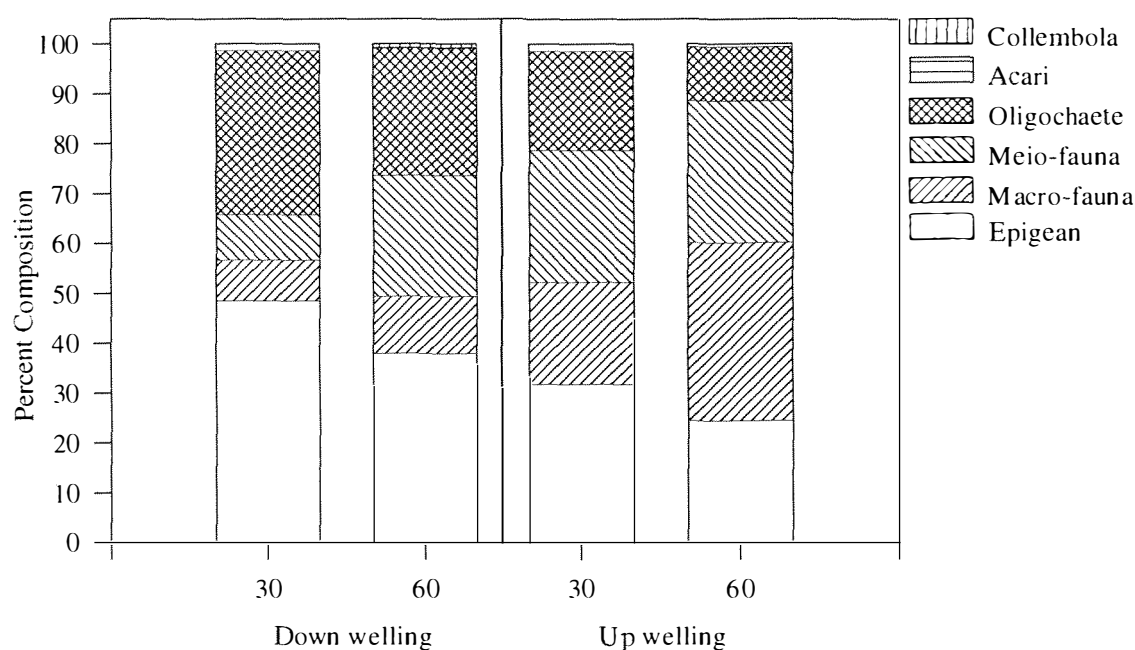


Figure 3. Percent community composition for hyporheic samples collected from 3 braided rivers in the Southern Hawkes Bay sampled between March 24 and 27, 1999. Macrofauna include Amphipoda and Isopoda, while meiofauna comprise Ostracoda, Copepoda and Syncarida. M = Makaretu samples (at 30 and 60 cm), T = Tukituki samples (at 30 and 60 cm) and W = Waipawa samples (at 30 and 60 cm).

heights (hydraulic head). With the exception of the Tukituki River where the greatest number of epigeal animals occurred at 60 cm, the number of epigeal animals declined with increasing depth in both up and down-wellings ($F_{1,6} = 6.55$, $P = 0.04$) (Fig. 4). Of the 14 epigeal taxa collected, *Aoteapsyche*, Chironomidae G, Tanypodinae, *P. antipodarum* and *P. funerea* were collected exclusively from down-wellings, while Chironomidae C and

O. albiceps were collected only from up-wellings (see Table 2). However, with the exception of Chironomidae C and G, these taxa were rare in all samples collected (i.e., < 6 animals in total). Hypogean taxa constituted the remaining 46 % (12 taxa) of the taxa collected from the hyporheos. Hypogean taxa included 2 Acarina (morphs 1 and 8); 3 phreatic Amphipoda (*P. subterraneus*, *Phreatogammarus* sp. and one undetermined Amphipoda), 2 Copepoda (Morphs 1 and 2); the Isopoda *Cruregens fontanus*; a stygocarid Crustacea (Syncarida), one Ostracoda, a Collembola and one Oligochaeta. The most numerous animals in the hyporheos were macro (e.g., Amphipoda and Isopoda) and meio

Figure 4. Percent community composition for hyporheic samples at two sample depths (data pooled) from 3 braided rivers in the Southern Hawkes Bay sampled between March 24 and 27, 1999. Macrofauna include



Amphipoda and Isopoda, while meiofauna comprise Ostracoda, Copepoda and Syncarida.

fauna, with macro ($F_{1,6} = 14.40$, $P < 0.01$) and meiofauna ($F_{1,6} = 6.07$, $P = 0.04$) comprising 60 % of the invertebrates in up-wellings and 25 % at down-wellings. The numerical abundance of macrofauna was not consistent between up and down-wellings for each river (i.e., between S1-3) ($F_{2,6} = 9.98$, $P = 0.01$) and the density of meiofauna was highest in the Makaretu and lowest in the Tukituki ($F_{6,6} = 8.71$, $P = 0.01$). The proportion of macro ($F_{1,6} = 3.68$, $P = 0.10$) and meiofauna ($F_{1,6} = 3.82$, $P = 0.10$) was similar between well depths. Number of Oligochaeta was similar between well depths ($F_{1,6} = 1.89$, $P = 0.22$), but was twice as high in down-wellings (30 % by abundance) as in up-wellings (15 %) ($F_{1,6} = 5.34$, $P = 0.04$).

Table 2. Total number of epigeal animals collected in up and down-wellings in the braided Makaretu, Tukituki and Waipawa Rivers in the Southern Hawkes Bay. Sites were sampled between March 24 and 27, 1999. Temperature tolerant taxa are represented by (*), while temperature sensitive taxa are represented by (**) (Quinn et al. 1994). Invertebrate abundance is expressed as total number of each taxon collected from the 36 bores.

Epigeal Taxa	Down-welling	Up-welling	Welling difference d.f., = 1, 6
** <i>Deleatidium</i> spp.	159	38	$F = 56.1, P < 0.01$
Chironomidae (4 taxa)	69	9	$F = 7.25, P = 0.04$
*Elmidae	11	9	$F = 0.01, P = 0.96$
<i>Hydrobiosis/Hydrobiosella</i>	6	5	$F = 0.02, P = 0.91$
Eriopterini	7	3	$F = 0.90, P = 0.40$
Tanypodinae	6	-	$F = 1.00, P = 0.36$
<i>O. albiceps</i>	-	1	$F = 1.00, P = 0.36$
** <i>Pycnocentria</i> spp.	3	-	$F = 9.00, P = 0.02$
** <i>Aoteapsyche</i> spp.	1	-	$F = 1.00, P = 0.36$
* <i>P. antipodarum</i>	1	-	$F = 1.00, P = 0.36$

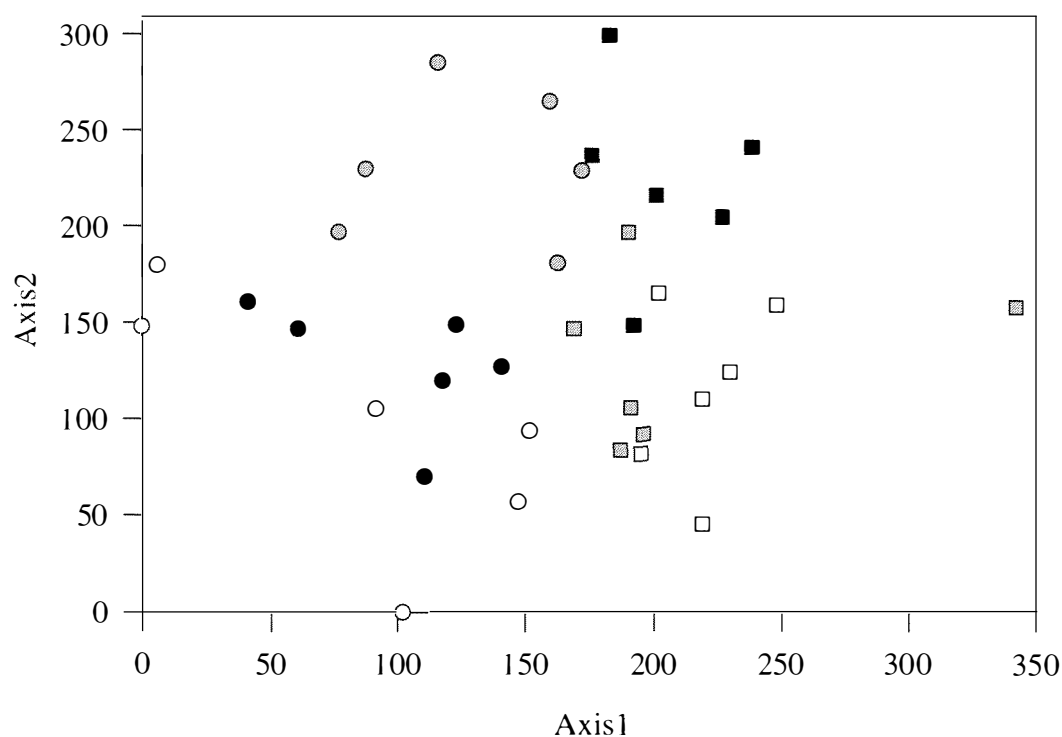


Figure 5. DECORANA analysis of community composition between the Makaretu (black), Tukituki (clear) and Waipawa (grey) Rivers sampled between March 24 and 27, 1999. Circles represent up-wellings, while down-wellings are represented by squares.

Overall, community composition was different between rivers (MRPP, $r = 0.04$, $P < 0.01$) and between up- and down-wellings (MRPP, $r = 0.02$, $P = 0.03$), but similar between well depths (MRPP, $r = 0.01$, $P = 0.29$).

Ordination of assemblage structure separated samples into up and down-welling groups (Fig. 5). Down-welling samples to the right were associated with greater numbers of Chironomidae D, Tanypodinae, *C. fontanus* and Oligochaeta 1. In contrast, up-welling samples to the left were associated with greater numbers of *P. subterraneus*, Amphipoda sp7 and Copepoda sp1 & 2. None of the environmental characteristics were associated with either axis, but epigeal taxa were more numerous in down-welling samples (i.e., to the right of axis 1), while Crustacea and Oligochaeta were more abundant in up-wellings (i.e., to the left of axis 1). Axis 1 accounted for 59.2 % of the variance of the data and Axis 2 accounted for 21.7 %.

DISCUSSION

Wells collecting samples further from the influence of surface water (e.g., up-wellings and 60 cm wells) had a lower abundance and density of epigeal animals and Oligochaeta than when hyporheic water was more similar to that from the surface (i.e., down-wellings). Benthic invertebrates such as *Deleatidium*, Chironomidae, Elmidae and Eriopterini were the most abundant animals in down-wellings, while *P. subterraneus*, *Phreatogammarus* and copepods were most common in up-wellings. Density of animals in the hyporheos increased in relation to the numerical abundance of hypogean animals in the Makaretu River and the numerical abundance of epigeal animals in the Tukituki and Waipawa Rivers. However, epigeal animals were always more numerous in down-wellings than hypogean animals in up-wellings within all rivers. Thus, although there was a variable response of invertebrates to hydraulic gradient between rivers, community composition was distinct between up and down-wellings within each river.

Differences in the response of invertebrates to up or downwellings in the 3 rivers may be related to different water chemistry in the hyporheic zone of each river as substrate and discharge characteristics are similar between rivers. Both the Tukituki and Waipawa

Rivers had higher water temperature, but lower conductivity and pH in both up and downwelling zones than the Makaretu. Groundwater discharges water into the river channel from the underlying aquifer in the Makaretu (HBRC 1999), thus interstitial water was chemically more dissimilar (i.e., lower dissolved oxygen, higher pH and conductivity) to the surface water than in the other two rivers. Groundwater chemistry is more stable because it generally flows within a closed system with fewer environmental interactions (e.g., change in temperature, flow regime and sediment) that alters surface water chemistry (see Domineco & Schwartz 1990; Appelo & Postma 1994; Fetter 1994). The Tukituki and Waipawa in contrast lose surface water to the underlying aquifer (groundwater recharge), so water chemistry (i.e., conductivity, dissolved oxygen, pH and temperature) will be more similar to the river channel, particularly during the time of sampling (summer) (HBRC 1999). Thus, although down-welling regions in the Makaretu had a similar percent abundance and density of epigeal animals (river mean = 40 %) to the Tukituki (47 %) and Waipawa Rivers (40 %), epigeal animals were rare in Makaretu up-wellings (river mean = 6 %) compared to the Tukituki (35 %) and Waipawa Rivers (38 %).

Epigeal animals were more abundant in down-wellings (mean = 40 %) because water flow may passively move benthic taxa into the hyporheic zone (Marmonier & Dole 1986; Cooling & Boulton 1993). However, the presence of epigeal animals (mean = 25 %) in up-wellings must be via mechanisms other than passive movement because the flow direction is out of the hyporheic zone. Any benthic invertebrates present in up-wellings must move actively in response to a change in the environmental conditions of the surface water or river channel (i.e., physical or chemical disturbance). In contrast, hypogean taxa (i.e., Crustacea, Oligochaeta) may be more abundant at up-wellings because of their small size and tolerance to conditions like low dissolved oxygen (Danielopol 1989; Cooling & Boulton 1993).

Greater mixing of the groundwater with surface water would alter the chemical nature of the hyporheic zone, such that epigeal animals would become less abundant and hypogean taxa more abundant. For example, up-wellings in the Makaretu had the highest pH (more alkaline than the surface), higher conductivity ($> 100 \mu\text{S cm}^{-1}$ indicative of groundwater infiltration) (Scarsbrook pers comm), and lower temperature and dissolved oxygen than the surface (also indicating groundwater influence) (White 1993) and the

lowest epigeal density (i.e., 6 %). Conductivity was similar to the surface in up and down-wellings of the Tukituki and Waipawa (i.e., $< 100 \mu\text{S cm}^{-1}$), dissolved oxygen was higher and epigeal abundance was greater (i.e., 30 %). It has been suggested that hypogean animals are excluded from areas most densely populated by epigeal animals, while hypogean animals may dominate where resource supply is limiting to epigeal taxa (Brunke & Gosner 1999). The abundance of epigeal animals at down-wellings may therefore reflect more suitable habitat and potential food resources drifting into the hyporheic zone from the surface water. In contrast, the abundance of hypogean animals at up-wellings may reflect biotic interactions such as absence of competition from epigeal animals and water chemistry these taxa may favour.

Rivers in the Southern Hawkes Bay undergo summer surface water temperatures up to 24 °C during March (Fowler & Death 2000; chapter 2), and as temperatures were cooler in up-wellings, the presence of benthic animals in up-wellings may be an attempt to seek a temperature refuge (Boulton et al. 1998). However, there was insufficient evidence to suggest that temperature sensitive (i.e., *Deleatidium*) or tolerant (i.e., Elmidae) (Quinn et al. 1994) benthic taxa collected showed any consistent preference for up or down-welling (either in terms of percent abundance or density) to support this idea. Epigeal animals may be present in up-wellings because animals are actively moving into up-wellings for reasons other than high surface water temperature avoidance. Alternatively, epigeal animals may be present in up-wellings to avoid elevated flows (velocity and/or discharge); or feed off the microbial biofilm established in response to high nutrient supply from greater groundwater mixing.

In summary, the density and percent abundance of epigeal animals was highest in down-wellings from all rivers, but only constituted one quarter of the animals at up-wellings. Up-wellings in the Makaretu, where chemical conditions were least like the surface water, had epigeal animals comprising only 6 % of the community compared to 36 % in the Tukituki and Waipawa. Despite similar substrate characteristics to the other rivers, the low epigeal abundance within the Makaretu River up-wellings was most likely linked to the groundwater fed hydrology in the Makaretu. Whereas, the higher abundance of epigeal animals in the Tukituki and Waipawa up-wellings may be due to greater surface water infiltration into the hyporheic zone through groundwater recharge hydrology. The

abundance of epigeal animals in the hyporheic zone may be influenced more by surface/groundwater mixing than temperature exclusively. Despite the lack of evidence to support the hyporheic zone as a temperature refugium in these rivers, the results suggest differences in epigeal abundance between up (active migration) and down (passive movement) wellings are in response to factors other than temperature. These factors include surface/groundwater interactions (i.e., pH and conductivity changes) and habitat suitability (e.g., resource supply and/or competition), which may influence the spatial distribution of refugium for benthic taxa.

CHAPTER 7

SYNTHESIS



Mangatewai Stream, April 1996. Site 3 (refer chapter 2).

Benthic communities are subject to constant disturbance from fluctuations in flow, bed movement and temperature variation. Community composition in such a system relies on the resilience and resistance of the biota and the ability of invertebrates to colonise a physically changing environment (Mackay 1992; Hildrew & Giller 1994). In contrast, hyporheic communities may not experience the same disturbance regime because the hyporheic zone is only physically disturbed during large bed moving events (Kochel 1988; Komar 1988). Environmental conditions such as lower dissolved oxygen or high conductivity may therefore be more important in determining hyporheic community composition (Dole-Oliver & Marmonier 1992; Boulton et al. 1998) than physical disturbance alone because the physicochemical characteristics are more likely to be influenced by temporal fluctuations in the water table (Williams 1993). This thesis examined the influence of a number of abiotic characteristics (including disturbance) on hyporheic community composition, and whether these same environmental characteristics also affect benthic communities. Disturbances considered were bed movement and the duration of channel dewatering, both common events in Hawkes Bay streams that could potentially alter both hyporheic and benthic communities.

In this study, both broad (between river) and fine (within river) scale environmental factors was found to influence the composition of the hyporheos. Local geomorphology appeared to have a significant effect on the hyporheos by markedly increasing the proportion of epigeal animals in sites with young geomorphology, with a contrasting dominance of hypogean animals at sites with older bed deposits. This effect may reflect differences in disturbance regime between sites as a result of alteration of substrate composition, substrates stability, the type and extent of alluvial deposition and in turn, the interstitial flow patterns.

The shallow hyporheos (i.e., 30 cm) is more likely to be influenced by physical disturbance than the community at 60 cm because it will take more intense events to scour greater than 60 cm of a streambed. The depth of scour associated with floods was not assessed in this study and future work should examine the depth of scour during floods and the response of the hyporheos (Matthaei et al. 1999). Nonetheless, the greater epigeal abundance from 30 cm wells in these studies may reflect invertebrates seeking refuge in the upper streambed. Epigeal animals also dominated communities of unstable sites. In

contrast, older sites may have more stable substrates, so site characteristics other than physical disturbance (e.g., substrate compactness or organic matter supply) may be more important in determining community composition. Thus, physical disturbance may be the most important factor determining community composition in sites with young sediments, while factors other than physical disturbance may be more important in determining community composition at older sites.

Geological age appeared to influence hyporheic community composition, but it is unlikely that the age of alluvial deposits determined community composition alone. For example, older sites may have the greatest density and abundance of hypogean taxa because of greater groundwater infiltration (e.g., decreased dissolved oxygen concentration and increased conductivity) (Williams 1993; Boulton et al. 1998; Fraser & Williams 1998). In contrast, sites with young substrates harboured a more diverse epigean fauna because benthic taxa may seek refuge in the hyporheic zone during bed movement events (Williams & Hynes 1976; Boulton 1989; Boulton et al. 1998). Moreover, unstable substrates may be less compact and allow greater infiltration of surface water into the hyporheic zone. Thus, water chemistry comparable to the river channel may produce conditions more suited to benthic taxa and less favourable to hypogean taxa in the hyporheic zone of unstable sites. The reverse would be the case at stable sites where water chemistry similar to the groundwater (i.e., low dissolved oxygen and high conductivity) may increase the abundance of hypogean animals. Substrate compactness would also be greater with less bed movement thereby increasing interstitial water residence times. Therefore, geomorphologic factors such as interstitial flow rates, surface and groundwater mixing and physical disturbance, may be more important in determining hyporheic community composition directly.

Species diversity was highest in the hyporheic zone at sites with intermediate levels of bed movement where both epigean and hypogean species are able to coexist. Physical abrasion and discharge variance in the surface channel alters diversity patterns in the benthos (e.g., Townsend et al. 1987; Resh et al. 1988; Scarsbrook & Townsend 1993; Death & Winterbourn 1995), but may only alter hyporheic community composition indirectly by siltation, increased groundwater pressure and increases in the proportion of benthic animals seeking refuge. The braided Waipawa River, had a less diverse benthic

community than the Tukipo River probably because of the lower discharge variance in the latter (Fowler & Death 2000). However, this was not the case for the hyporheos where greatest diversity (especially epigeal taxa) was found in the unstable Waipawa. The shift in benthic diversity patterns between rivers of contrasting stability may be related to less bed movement in the Tukipo and higher discharge variance and bed movement in the Waipawa. Such unstable conditions may increase the proportion of benthic animals seeking refuge in the hyporheos (Marmonier & Cru  z des Ch  telli  rs 1991; Dole-Oliver et al. 1997) and produce environmental conditions similar to the surface of the Waipawa. In contrast, at more stable sites conditions may be least like the surface water, have less surface water infiltration and thus increased abundance of hypogean animals.

Differences in the hyporheos within each river (i.e., between well depths) and between seasons (i.e., temporally) were related to dissolved oxygen, temperature and conductivity conditions in those seasons and/or rivers (Dole-Oliver et al. 1992; Boulton et al. 1998; Brunke & Gosner 1999). Differences in the composition of the hyporheos are related to habitat preferences of the different taxa. For example, water chemistry that was similar to the surface at down-wellings was associated with significantly higher numbers of benthic animals in a similar manner to young and unstable substrates. Conversely, hypogean animals dominated up-wellings in a similar manner to older and stable substrates where physicochemical conditions were least like the surface (e.g., low dissolved oxygen and high conductivity). Thus, despite similar substrate characteristics between rivers, hyporheic community composition was linked primarily to thermal and chemical characteristics at a given site.

Greater substrate compactness in the hyporheic zone (e.g., the Ongaonga Stream) may reduce surface water infiltration, reduce surface/groundwater mixing and thereby increase the abundance of hypogean taxa. This may be the case for the constrained Ongaonga Stream community where animals such as ostracods, which can tolerate lower flow and oxygen conditions were more abundant. Alternatively, greater organic matter supply (i.e., dense overhead vegetation in the Tangarewai Stream) may increase the abundance of invertebrates that can utilise this food source. The dominance of Amphipoda in the Tangarewai may have been in response to this, although the actual diet of hyporheic Amphipoda would need to be established. In contrast, unstable sites may have a greater

proportion of epigeal animals seeking refuge in the hyporheic zone because of less compact substrates and greater bed movement.

Dewatering of the river channel will likely disturb the hyporheic zone by reducing interstitial flow, increasing desiccation and decreasing the abundance of invertebrates colonising from the hyporheic zone. Removing this source of invertebrates will alter colonisation patterns, as invertebrates can no longer seek refuge in the hyporheic zone during disturbance in the channel. Other studies have found that benthic invertebrate density changes in response to the source of colonists after disturbance such as floods or dewatering (Sagar 1983; Williams 1977). However, the density and recovered benthic community composition was not affected by altering the source of colonists in this study. The benthos was affected more by the duration of disturbance (in this case dewatering) because the mayfly *Deleatidium* colonised more slowly at sites dewatered for longer periods (i.e., greater than 10 weeks). In contrast, the riffle beetle Elmidae colonised rapidly in all sites before being replaced by *Deleatidium* as the dominant benthic taxon. The recovery of diversity and abundance in this thesis after dewatering for up to 4 months was consistent with other short dewatering duration studies (e.g., Wood & Petts 1999; Wright & Symes 1999), but was much more rapid compared to dewatering conditions greater than 3 years (i.e., chalk streams in England) (refer Wood & Petts 1999). Restricting the type of some colonising taxa by disturbance duration may thereby reduce the rate of recovery of certain taxa (e.g., *Deleatidium*) and increase the abundance of earlier successional taxa (e.g., Elmidae) (see Bond 1993). Nonetheless, removing the hyporheic zone as a colonisation source did not alter benthic communities in the long term, but changed community recovery patterns in the short term by restricting the source of some colonists.

Difficulties arise during assessment among a small number of streams over time because limited replication leads to highly variable community composition within and between sites. This variability is the result of the hyporheic zone being a very patchy resource (Dole-Oliver et al. 1997). By sampling a greater number of sites in this thesis, time restrictions lead to a reduction in the number of replicate samples collected. Future studies undertaking similar surveys at a number of sites should seek to increase sample replication to reduce variability between samples within and between sites. Future research should seek to identify differences in hyporheic community composition at sites differing

in geology (age and type). However, to alleviate sampling bias at sites with different substrate composition a suitable sampling device should be designed. Research should also seek to identify and expand on the significance of the hyporheic zone refuge from disturbance such as elevated surface water temperatures and physical bed movement, respectively. The depth of scour may also be important in determining the vertical distribution of the hyporheos, so the influence of depth of bed movement and the vertical composition of the hyporheos should also be examined.

The hyporheic zone may provide refugia for benthic invertebrates during environmental disturbance (e.g., bed movement, discharge variance and dewatering) and may be an important refuge for the benthos in frequently disturbed sites (e.g., Williams & Hynes 1976; Sedell et al. 1990; Lancaster 1999). The proportion of epigeal animals may therefore increase with increasing physical disturbance (e.g., bed movement), but decline during stable conditions because the environment becomes less like the surface. Thus, stable sites did not harbour as many epigeal species in this study because factors other than disturbance (e.g., greater substrate compactness, lower dissolved oxygen concentration or increased organic matter supply) may be more important in determining invertebrate community composition than physical disturbance alone. In contrast, hypogean animals are least abundant when bed movement is common and environmental conditions are similar to the surface. There is a diverse hyporheos in New Zealand rivers, the composition of which was determined by interstitial flow patterns, water chemistry, and the frequency of bed movement.

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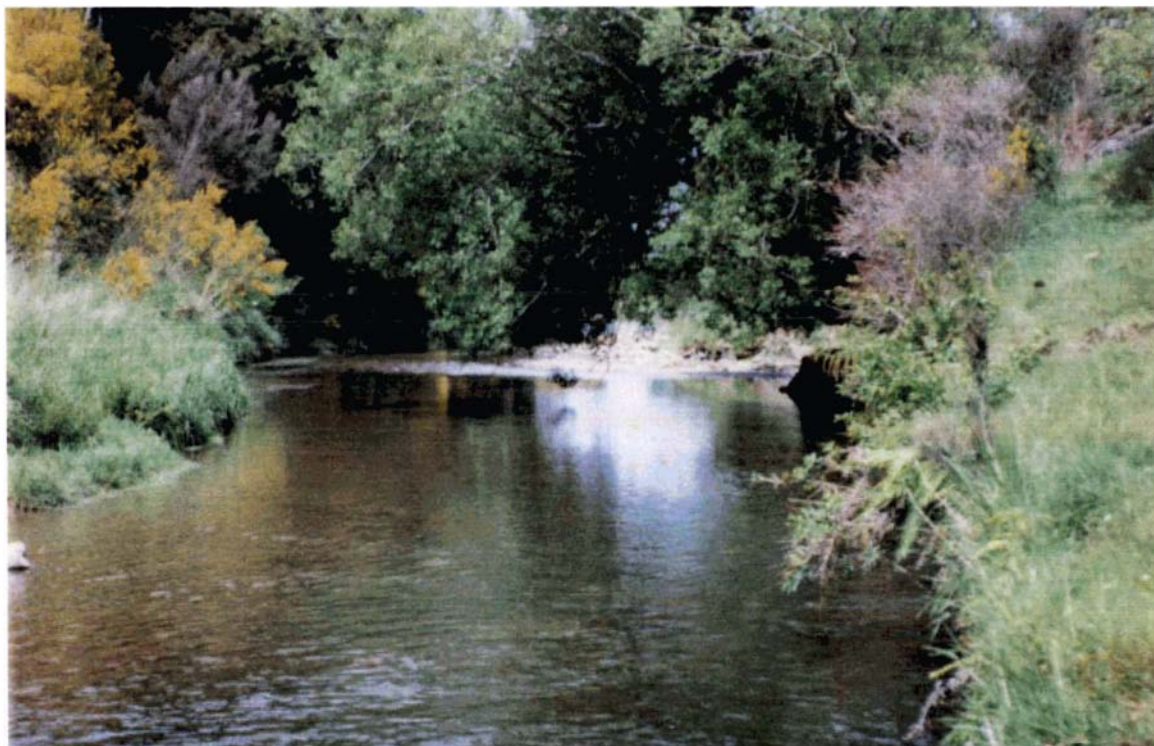
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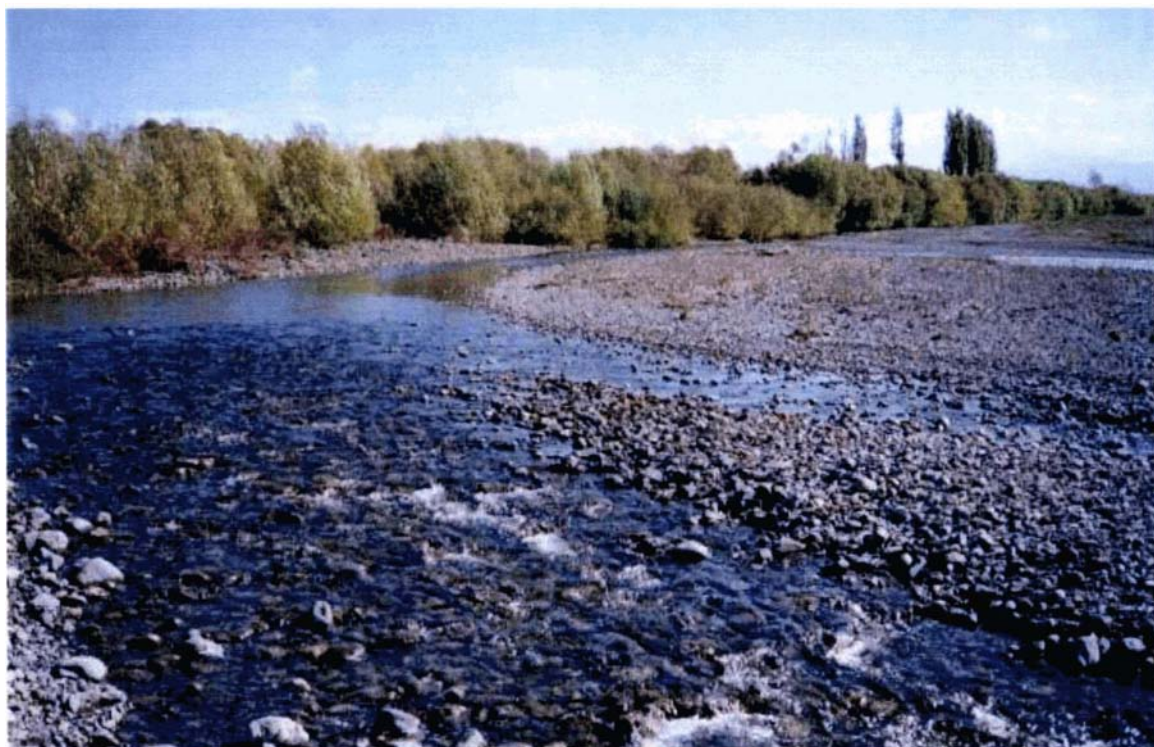
Waipawa River. April 1996 at 8:00am. Site 8 (refer chapter 2).



Waipawa River. April 1996 at 8:30am. Site 8 (refer chapter 2).



Tukipo Stream, February 1997. Site 4 (refer chapter 2).



Tukituki River, March 1998. Site 6 (refer chapter 2).

APPENDIX 1

Fowler, R. T.; Death, R. G. 2000: Effects of channel morphology on temporal variation in invertebrate community structure in two North Island, New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* 34: 231-240.

APPENDIX 2

Fowler, R. T.; Death, R. G. 2001: The effect of environmental stability on hyporheic community structure. *Hydrobiologia* 445: 85-95.

APPENDIX 3

HYPORHEIC AND BENTHIC INVERTEBRATE DATA:

The invertebrate datasheets presented on pages 11 – 20 have the following abbreviations for invertebrates collected (mean of replicates) for sites surveyed:

Chapter 2:

Numerically, rivers are as follows:

1 = Makaretu; **2** = Mangatewai; **3** = Mangatewainui; **4** = Ongaonga;
5 = Tangarewai; **6** = Tukipo; **7** = Tukituki; **8** = Waipawa.

Sites labelled a, b or c represent autumn (April 1996), winter (September 1996 and summer (February 1997) sampling occasions respectively.

Chapter 3:

Rivers are as follows:

ww = Whitewater; **po** = Porter; **ss** = Slip Spring; **mb** = Middle Bush;
cl = Cora Lynn; **cr** = Craigieburn Cutting; **br** = Bruce; **ko** = Kowai.

Samples labelled as **0.3** and **0.6** represent samples collected at 30 and 60cm respectively.

Chapter 4:

Rivers are labelled as **T** = Tukituki; **W** = Waipawa; **M** = Makaretu.

Dewatering duration is labelled as **0** = controls; **1** = 6 weeks; **2** = 10 weeks; **3** = 14 weeks.

Days after rewatered are labelled as **A** = 7 days; **B** = 14 days; **C** = 28 days; **D** = 42 days.

Chapter 5:

Artificial substrate treatments are labelled as **c** = controls; **h** = hyporheic entry only; **d** = drift entry only.

S = the Surber control samples collected at the end of the experiment.

Sample since first colonisation (i.e., when the baskets were placed into the stream) are **1** = 7 days; **2** = 14 days; **4** = 28 days; **6** = 42 days.

Chapter 6:

Rivers are labelled as **T** = Tukituki; **W** = Waipawa; **M** = Makaretu.

Welling region replicate is labelled as **1**, **2** and **3**.

Depth is labelled as **30** (30cm) and **60** (60cm) for up (**U**) and down (**D**) welling regions.

		1a	1b	1c	2a	2b	2c	3a	3b	3c	4a	4b
Acarina	Acari 1	-	0.5	0.5	3	-	-	-	-	0.5	-	-
	Acari 2	-	-	-	-	-	-	-	-	-	1	-
	Acari 3	-	-	-	-	-	-	-	-	-	-	-
	Acari 4	-	-	-	-	-	-	0.5	-	-	-	-
	Acari 5	-	-	-	-	-	-	0.5	-	-	-	-
	Acari 6	-	-	-	-	-	-	1	-	-	-	-
	Acari 7	-	-	-	0.5	0.5	-	-	-	-	-	-
	Acari 9	-	1	1.5	-	-	-	-	-	-	-	-
	Acari 10	-	-	-	-	-	-	-	-	-	-	-
	Stygocarida (Syncarida)	-	-	-	-	2	-	-	-	-	-	-
Crustacea	<i>Phreatogammarus</i> spp.	2	6	4.5	-	5	5.5	2.5	0.5	4	-	-
	<i>Cruregens fontanus</i>	-	0.5	-	-	-	-	0.5	0.5	-	-	-
	Phreatoicidae	-	-	-	-	-	-	-	-	-	-	-
	Amphipoda 7	-	-	-	-	0.5	-	-	-	-	-	-
	Copepoda 1	-	-	-	-	-	-	-	-	-	-	11.5
	Copepoda 2	-	0.5	-	-	-	-	-	-	-	-	0.5
	Copepoda 3	-	-	-	-	-	-	-	-	-	-	0.5
	Isopoda 1 (Lote type)	-	-	-	-	0.5	-	-	-	-	-	8
	Ostracoda 1	-	-	-	-	-	-	-	0.5	0.5	-	-
	Ostracoda 2	-	-	-	-	-	-	1	-	-	1.5	2.5
	Ostracoda 4	-	-	-	-	-	-	-	-	-	0.5	216
	Ostracoda 5	-	-	-	-	-	-	-	-	-	-	1
	Ostracoda 6	-	-	-	-	-	-	-	-	-	-	-
	Ostracoda 7	-	-	-	-	-	-	-	-	-	-	50.5
	Ostracoda 8	-	-	-	-	-	-	-	-	-	-	0.5
	Ostracoda 9	-	-	-	-	-	-	-	-	-	-	1.5
Collembola	Collembola 1	-	-	-	-	-	-	-	0.5	0.5	6	-
	Collembola 2	-	-	-	-	-	-	-	-	-	0.5	-
	Collembola 3	-	-	-	-	-	-	-	-	-	-	-
	Collembola 4	-	-	-	-	-	-	-	-	-	-	-
	Collembola 5	-	-	-	-	-	-	-	-	-	-	-
	Collembola 7	-	-	-	-	-	-	-	-	-	-	-
	Collembola 9	-	-	-	-	-	2.5	-	-	-	-	-
Coleoptera	Elmidae	0.5	2	-	4	-	6	3.5	5.5	4	-	-
Diptera	Chironomid A	-	-	-	-	-	-	-	-	0.5	1	-
	Chironomid B	-	-	-	-	-	-	-	-	-	0.5	-
	Chironomid C	-	3.5	-	-	-	-	-	1.5	0.5	-	-
	Chironomid D	-	-	-	-	-	-	-	-	-	-	-
	Chironomid E	-	-	-	-	-	-	-	-	-	-	-
	Chironomid F	-	-	-	-	-	-	-	1	-	-	-
	Chironomid G	-	-	-	-	-	-	-	-	-	-	-
	<i>Eriopterini</i>	-	-	0.5	-	-	-	-	-	0.5	-	-
	Hexatomini	-	-	0.5	-	-	-	-	-	-	-	-
Ephemeroptera	<i>Austroclima</i> spp.	-	5	0.5	-	-	-	-	2.5	-	-	-
	<i>Coloburiscus humeralis</i>	-	-	-	-	-	-	0.5	-	-	-	-
	<i>Deleatidium</i> spp.	-	-	-	0.5	0.5	-	0.5	-	-	-	-
	<i>Neozephlebia</i> spp.	-	0.5	-	-	-	-	-	-	-	-	-
	<i>Nesameletus</i> sp.	-	-	-	-	-	0.5	-	-	-	-	-
Mollusca	<i>Physa</i> spp.	-	-	-	-	-	-	-	-	-	-	-
	<i>Potamopyrgus antipodarum</i>	-	-	-	1.5	-	-	-	-	-	0.5	3.5
Nematoda	Nematoda	-	-	1.5	-	0.5	-	-	-	-	-	-
Megaloptera	<i>Archichauliodes diversus</i>	-	-	-	-	-	-	-	0.5	-	-	-
Planarian	<i>Neppia</i>	-	-	-	-	-	-	-	-	-	-	-
Oligochaeta	<i>Oligochaeta</i>	1	5	6	0.5	0.5	2	-	1	0.5	-	20.5
Plecoptera	<i>Zelandoperla</i> spp.	-	-	-	-	-	0.5	-	-	-	-	-
	<i>Zelantobius</i> spp.	-	-	-	-	-	-	1	-	-	-	-
Polychaeta	<i>Namanereis tiriteae</i>	-	-	-	-	-	-	2	-	-	-	-
Trichoptera	<i>Aoteapsyche</i> spp.	-	-	-	-	-	-	-	-	-	-	-
	<i>Hydrobiosis parumbripennis</i>	-	0.5	-	-	-	-	-	-	-	-	-
	<i>Hydrobiosella stenocerca</i>	-	0.5	1.5	0.5	0.5	-	0.5	-	1.5	-	-
	<i>Oxyethira albiceps</i>	-	-	-	-	-	-	-	-	-	-	-
	<i>Polypsectropus</i> spp.	-	-	-	-	-	-	-	-	1.5	-	-
	<i>Pycnocentria</i> spp.	-	-	-	-	-	-	-	-	-	-	-
	<i>Pycnocentrella</i> spp.	0.5	-	-	1	-	0.5	-	-	-	-	-
	<i>Pycnocentrodes</i> spp.	-	-	-	-	0.5	-	-	-	-	-	2

	4c	5a	5b	5c	6a	6b	6c	7a	7b	7c	8a	8b	8c
Acari 1	-	2	2	0.5	-	-	-	-	-	-	-	-	-
Acari 2	-	-	-	-	1	-	-	-	-	-	-	-	-
Acari 3	-	-	-	-	-	-	-	-	-	-	-	-	1
Acari 4	-	-	-	-	-	-	-	-	-	-	1	-	1
Acari 5	-	-	-	-	-	-	-	-	-	-	-	-	-
Acari 6	-	-	-	-	-	-	-	-	-	-	-	-	-
Acari 7	-	-	-	-	-	-	-	-	-	-	-	-	-
Acari 9	-	-	-	-	-	-	-	-	-	-	-	-	-
Acari 10	-	-	1	-	-	-	-	-	-	-	-	-	-
Stygocarida (Syncarida)	-	-	-	-	0.5	-	0.5	1.5	6.5	0.5	-	0.5	-
<i>Phreatogammarus</i> spp.	-	26.5	73	312	-	-	-	-	0.5	16	1.5	7.5	5
<i>Cruregens fontanus</i>	-	-	0.5	6.5	-	-	-	-	-	0.5	-	1	-
Phreatoicidae	-	-	-	13	-	-	-	-	-	-	-	-	-
Amphipoda 7	-	-	-	-	-	-	-	-	-	-	-	-	-
Copepoda 1	2	2.5	16.5	-	-	-	-	-	-	-	-	-	-
Copepoda 2	-	-	1	2.5	-	-	-	-	-	-	-	-	-
Copepoda 3	-	-	-	-	-	-	-	-	-	-	-	-	-
Isopoda 1 (Lote type)	1	-	-	-	-	-	-	-	-	-	-	-	-
Ostracoda 1	10	-	0.5	-	-	-	-	-	-	-	1	-	-
Ostracoda 2	-	-	-	-	-	-	-	-	-	-	-	-	-
Ostracoda 4	24	-	-	-	-	-	-	-	-	-	-	-	-
Ostracoda 5	25	-	-	-	-	-	-	-	-	-	-	-	-
Ostracoda 6	-	-	2	-	-	-	-	-	-	-	-	-	-
Ostracoda 7	-	-	-	-	-	-	-	-	-	-	-	-	-
Ostracoda 8	-	-	-	-	-	-	-	-	-	-	-	-	-
Ostracoda 9	-	-	-	-	-	-	-	-	-	-	-	-	-
Collembola 1	-	-	-	-	-	-	0.5	-	-	-	-	-	-
Collembola 2	-	-	-	-	-	-	-	-	-	-	0.5	-	-
Collembola 3	-	-	-	-	-	-	-	0.5	-	-	1	-	-
Collembola 4	1.5	-	-	-	-	-	-	-	-	-	1	-	-
Collembola 5	-	-	-	-	-	-	-	-	-	-	0.5	-	-
Collembola 7	4.5	-	0.5	-	-	-	0.5	-	-	-	-	-	-
Collembola 9	-	-	-	-	-	-	-	-	-	-	-	-	-
Elmidae	-	-	-	-	0.5	-	-	-	0.5	2	0.5	-	1
Chironomid A	-	-	-	-	-	1	0.5	-	-	-	1.5	-	-
Chironomid B	-	-	-	-	-	-	-	-	-	-	-	-	-
Chironomid C	-	-	3.5	-	-	-	-	-	0.5	-	-	0.5	-
Chironomid D	-	-	-	-	-	-	-	-	-	-	-	0.5	-
Chironomid E	-	-	-	-	-	1	-	-	-	-	-	-	-
Chironomid F	-	-	-	-	-	-	-	-	1	-	-	-	-
Chironomid G	3.5	-	-	0.5	-	-	-	-	-	-	-	-	-
<i>Eriopterini</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
Hexatomini	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Austroclima</i> spp.	-	0.5	4.5	-	-	-	-	-	2	0.5	-	-	-
<i>Coloburiscus humeralis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Deleatidium</i> spp.	-	-	-	-	-	-	-	-	0.5	8	1.5	0.5	2
<i>Neozephlebia</i> spp.	-	-	3.5	-	-	-	-	-	-	-	-	-	-
<i>Nesameletus</i> sp.	-	-	-	2	-	-	-	-	-	-	-	-	-
<i>Physa</i> spp.	7	-	-	-	-	-	-	-	-	-	-	-	-
<i>Potamopyrgus antipodarum</i>	-	-	0.5	-	-	-	-	-	-	-	-	-	-
Nematoda	-	-	-	1	-	2	1.5	-	-	-	-	-	-
<i>Archichauliodes diversus</i>	-	-	0.5	-	-	-	-	-	-	-	-	-	-
<i>Neppia</i>	0.5	-	-	-	-	-	-	-	-	-	-	-	-
Oligochaeta	16	-	-	7.5	-	0.5	-	-	-	4.5	-	0.5	-
<i>Zelandoperla</i> spp.	-	-	-	-	-	-	-	-	0.5	-	-	-	-
<i>Zelanobius</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Namanereis tiriteae</i>	0.5	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aoteapsyche</i> spp.	-	-	-	-	-	-	0.5	-	-	-	-	-	-
<i>Hydrobiosis parumbripennis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hydrobiosella stenocerca</i>	-	0.5	-	1	-	-	-	-	-	-	-	-	-
<i>Oxyethira albiceps</i>	2	-	2	0.5	-	-	-	-	-	-	-	-	-
<i>Polyplectropus</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pycnocentria</i> spp.	-	-	1.5	-	-	-	-	-	-	-	-	-	-
<i>Pycnocentrella</i> spp.	-	0.5	-	-	-	-	-	-	-	-	-	-	-
<i>Pycnocentroides</i> spp.	-	0.5	-	-	-	-	-	-	-	-	-	-	-

		ww 0.6	ww 0.3	po 0.6	po 0.3	ss 0.6	ss 0.3	mb 0.6	mb 0.3	cl 0.6	cl 0.3	cr 0.6	cr 0.3	br 0.6	br 0.3	ko 0.6	ko 0.3
Acarina	Acari 11	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-
Crustacea	Amphipoda 6	-	-	4.5	-	-	-	-	-	-	-	-	-	-	-	-	-
	Amphipoda 7	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-
	Copepoda 1	-	-	54.5	3	-	-	-	-	0.5	-	-	-	-	-	-	-
	<i>Daphnia</i> sp.	-	-	-	1.5	-	-	-	-	-	-	-	-	-	-	-	-
	Ostracoda 1	-	-	3.5	-	-	-	-	2.5	-	-	-	-	-	-	-	-
	Ostracoda 10	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-
	Ostracoda 11	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Phreatogammarus</i> spp.	-	-	17	5	8.5	-	-	-	-	-	-	-	-	-	-	-
	<i>Paraleptamphopus subterraneus</i>	0.5	-	1	0.5	-	-	-	2	-	-	-	-	-	-	-	-
	Stygocarida (Syncarida)	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-
Coleoptera	Elmidae	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diptera	Chironomid F	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
	Chironomid G	-	1	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-
	Chironomid H	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-
	<i>Eriopterini</i>	0.5	-	-	-	-	-	-	0.5	-	-	0.5	-	-	-	-	-
	<i>Stictocladius</i> sp.	-	-	-	-	-	-	-	2	-	-	1	-	-	-	-	1
Ephemeroptera	<i>Deleatidium</i> spp.	-	-	-	2	-	-	-	-	-	-	-	-	0.5	0.5	0.5	-
Mollusca	<i>Potamopyrgus antipodarum</i>	-	-	0.5	0.5	3	-	-	-	-	-	-	-	-	-	-	-
Oligochaeta	Oligochaete	1	1	30.5	12.5	-	0.5	4.5	3	0.5	1	1	5.5	-	-	-	0.5
Planarian	<i>Neppia</i> sp.	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-
Plecoptera	<i>Cristaperla fimbria</i>	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-
Trichoptera	<i>Aoteapsyche</i> spp.	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Hydrobiosidae</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-
	<i>Olinga feredayi</i>	-	-	3	-	-	-	-	1	-	-	-	1	-	-	-	-

		TA0	TA1	TA2	TA3	TB0	TB1	TB2	TB3	TC0	TC1	TC2	TC3	TD0	TD1	TD2	TD3	WA0	WA1	WA2	WA3
Coleoptera	Elmidae	10.3	17.7	13.0	36.3	56.0	21.0	17.3	97.3	20.0	100.7	32.3	61.3	38.0	59.7	9.7	40.7	134.7	13.7	83.3	31.3
	Hydraenidae	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diptera	Austrosimulium (austrolens gp)	0.3	-	0.3	-	-	-	0.7	-	0.3	-	-	-	0.3	-	-	-	0.3	0.3	-	0.3
	Chironomid 2	3.0	3.7	3.7	1.7	1.3	1.0	4.7	1.3	-	1.7	0.7	0.7	0.3	0.7	-	1.0	63.0	11.0	56.0	38.0
	Chironomid 5	0.3	1.0	1.3	-	3.3	2.0	0.3	-	-	2.3	1.0	0.7	6.0	24.0	8.3	9.0	6.7	8.7	3.0	19.3
	Ceratopogonidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Empididae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-
	Eriopterini	1.3	0.7	0.7	1.0	5.0	0.7	3.0	5.3	1.0	3.7	0.3	2.3	1.7	1.3	1.7	1.7	7.7	-	-	1.0
	Limnophora sp.	0.3	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Tabanidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ephemeroptera	<i>Austroclima</i> spp.	-	-	-	-	0.7	0.3	-	-	0.3	0.3	0.3	-	-	-	-	0.3	-	-	-	-
	<i>Deleatidium</i> spp.	19.3	16.7	53.0	28.0	31.0	28.3	11.0	6.0	109.7	150.3	133.3	131.0	150.7	279.7	179.3	151.3	342.3	175.7	175.7	89.3
	<i>Zephlebia dentata</i>	-	1.0	0.3	-	-	-	-	-	-	0.0	-	-	-	-	-	-	-	-	-	-
Mollusca	<i>Physa</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Potamopyrgus antipodarum</i>	-	-	-	0.3	0.3	0.3	0.3	-	1.0	0.7	0.3	-	0.3	-	0.3	0.3	0.7	0.7	6.3	-
Planarian	<i>Neppia</i>	-	-	-	-	0.3	-	-	-	1.0	1.0	0.7	-	-	1.3	-	-	2.3	2.7	8.3	1.3
Oligochaeta	Oligochaeta	0.3	-	-	-	-	-	-	-	0.3	-	-	0.7	-	-	-	-	1.0	-	1.3	-
Plecoptera	<i>Zelandobius</i> spp.	-	-	0.3	-	0.7	-	-	-	-	0.7	-	-	-	1.0	1.0	3.0	0.3	-	-	-
	<i>Zelandoperla fenestrata</i>	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-
Trichoptera	<i>Aoteapsyche</i> spp.	2.0	6.3	16.0	11.7	5.0	12.7	4.3	6.3	1.0	14.0	4.0	9.0	1.7	9.7	1.7	5.7	6.0	1.7	8.0	1.7
	<i>Hudsonema amabilis</i>	-	-	-	-	-	-	-	-	-	0.3	-	0.3	-	0.3	-	-	-	-	-	-
	<i>Hydrobiosis parumbripennis</i>	0.7	0.7	1.3	0.3	3.0	1.0	1.3	1.0	0.3	3.0	0.3	2.0	0.3	1.3	-	2.3	2.3	1.3	1.7	2.0
	<i>Oxyethira albiceps</i>	-	-	0.7	0.3	1.7	-	0.3	0.7	-	-	0.3	-	-	-	-	-	-	0.7	10.0	2.0
	<i>Olinga feredayi</i>	0.7	1.0	0.3	0.3	1.0	2.7	-	-	-	4.0	0.7	1.3	-	4.3	0.3	-	0.3	-	3.7	-
	<i>Pycnocentria funerea</i>	-	-	0.3	0.3	0.3	-	0.3	-	-	-	-	-	-	-	0.3	-	5.0	-	-	0.3
	<i>Psilochorema</i> sp.	-	0.7	-	0.3	-	1.0	-	-	1.3	3.0	-	1.3	2.3	3.0	1.3	1.3	0.7	-	0.3	-
	<i>Pycnocentrella</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.7	-	-	-
	<i>Pycnocentrodes</i> spp.	3.7	3.0	6.0	9.0	0.3	2.3	-	3.7	3.0	11.3	3.0	6.0	1.0	1.0	3.3	12.7	24.3	2.3	3.0	4.0

	WB0	WB1	WB2	WB3	WC0	WC1	WC2	WC3	WD0	WD1	WD2	WD3
Elmidae	191.0	31.7	111.3	21.0	209.3	17.3	173.7	24.3	136.0	15.3	115.0	23.3
Hydraenidae	-	-	-	-	-	-	-	-	-	-	-	-
Austrosimulium (austrolens gp)	-	0.3	-	0.3	2.0	0.3	0.3	-	0.7	0.7	-	-
Chironomid 2	11.0	2.7	6.0	13.3	19.7	3.3	3.0	4.7	38.7	2.3	8.7	9.0
Chironomid 5	0.3	1.0	0.7	2.3	10.7	2.0	-	0.3	32.7	5.7	5.0	7.7
Ceratopogonidae	-	-	-	-	-	-	-	-	-	-	0.7	-
Empididae	-	-	-	0.3	0.7	-	-	0.3	-	-	-	-
<i>Eriopterini</i>	16.0	-	1.7	1.0	6.0	0.7	2.0	1.3	4.7	1.0	2.0	0.7
Limnophora sp.	-	-	-	-	-	-	-	-	-	-	-	-
Tabanidae	-	-	-	-	-	-	-	-	0.7	-	-	-
<i>Austroclima</i> spp.	-	0.3	-	-	-	-	-	-	-	-	-	-
<i>Deleatidium</i> spp.	357.3	340.0	348.0	20.7	454.0	293.3	509.3	121.0	400.0	341.3	550.7	177.3
<i>Zephlebia dentata</i>	-	-	-	-	-	-	-	-	1.3	-	-	-
<i>Physa</i> spp.	0.3	0.3	-	0.3	0.3	0.3	-	0.7	-	-	-	0.7
<i>Potamopyrgus antipodarum</i>	1.0	1.7	-	0.3	-	-	-	-	0.7	0.3	-	0.3
<i>Neppia</i>	-	2.0	1.3	3.7	1.3	4.0	3.7	3.0	2.0	2.3	0.7	1.3
Oligochaeta	0.3	-	0.7	0.7	-	-	-	-	0.7	0.3	1.3	0.7
<i>Zelandobius</i> spp.	0.7	-	0.3	-	4.3	1.3	0.3	0.7	16.0	1.7	7.3	2.7
<i>Zelandoperla fenestrata</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aoteapsyche</i> spp.	10.3	1.7	0.3	0.3	9.7	-	0.7	2.3	15.3	0.7	2.0	0.7
<i>Hudsonema amabilis</i>	0.7	-	-	-	1.0	-	-	0.3	0.7	-	-	-
<i>Hydrobiosis parumbripennis</i>	2.0	2.0	0.3	0.3	1.3	0.7	0.3	1.3	2.7	-	1.7	0.3
<i>Oxyethira albiceps</i>	3.7	0.3	4.7	4.0	-	-	-	-	-	0.3	-	-
<i>Olinga feredayi</i>	0.7	1.7	0.7	-	1.7	0.3	-	-	1.0	0.3	-	0.7
<i>Pycnocentria funerea</i>	0.3	-	-	-	-	-	-	-	-	-	-	-
<i>Psilochorema</i> sp.	0.7	-	0.3	-	1.7	3.0	2.3	5.3	1.7	2.3	3.3	5.3
<i>Pycnocentrella</i> spp.	-	-	-	0.7	-	-	-	-	2.0	-	-	-
<i>Pycnocentrodes</i> spp.	16.3	1.0	1.0	0.7	65.0	4.0	8.3	4.0	22.7	1.3	9.7	1.0

		S	c1	c2	c4	c6	h1	h2	h4	h6	d1	d2	d4	d6
Acarina	Acari 3	-	-	-	-	-	0.3	0.1	-	-	-	-	-	-
Crustacea	<i>Paraleptamphopus subterraneus</i>	-	-	-	-	1.5	0.6	0.2	0.3	0.1	-	2.3	0.6	1.1
	Phreatocidae	-	-	-	-	-	0.3	0.1	-	-	-	0.3	0.1	-
	Amphipoda 5	-	-	-	-	-	-	-	-	-	-	1.0	0.3	0.1
Collembola	Collembola 1	-	-	-	-	-	0.5	0.1	-	-	-	-	-	-
	Collembola 2	-	-	-	-	-	-	-	0.3	0.1	-	-	-	-
	Collembola 7	-	-	-	-	-	0.3	0.1	-	-	0.3	0.1	-	-
Coleoptera	<i>Berosus</i> sp.	-	-	-	-	-	-	-	-	-	0.3	0.1	-	-
	Elmidae	105.3	102.6	145.9	258.0	121.5	44.1	47.5	56.1	37.0	133.8	184.9	226.7	143.9
Diptera	<i>Aphrophila neozelandica</i>	0.5	0.6	0.2	-	-	-	-	-	-	0.3	0.1	-	-
	<i>Austrosimulium</i> (austrolens gp)	1.0	0.5	0.4	0.1	-	0.8	0.4	0.4	0.1	0.5	0.4	0.3	0.3
	<i>Maoridiamesa</i> spp.	1.0	0.5	0.1	0.8	0.4	0.1	0.8	0.4	0.1	-	0.8	0.2	0.3
	Chironomid 3	-	-	-	-	-	-	-	0.3	0.3	0.6	0.4	0.3	0.1
	<i>Tanytarsus</i> sp.	-	-	-	-	-	-	-	-	-	0.5	0.1	-	-
	Chironomid 7	-	-	-	-	-	-	-	1.5	0.4	0.1	-	-	-
	<i>Eriopterini</i>	8.5	2.6	3.9	9.0	7.0	2.0	2.2	3.8	3.0	3.5	5.9	5.5	5.6
Ephemeroptera	<i>Austroclima</i> spp.	-	-	0.3	0.3	0.1	-	0.8	0.2	-	-	-	-	-
	<i>Coloburiscus humeralis</i>	0.5	0.4	0.1	0.3	0.1	-	-	-	-	-	0.3	0.1	-
	<i>Deleatidium</i> spp.	141.3	78.3	85.8	73.7	126.4	116.1	142.5	243.6	152.7	94.7	68.4	98.4	154.1
Hemiptera	<i>Sigara</i> sp.	-	-	-	-	-	-	0.5	0.1	-	-	-	-	-
Mollusca	<i>Physa</i> spp.	-	0.3	2.1	1.0	0.3	0.3	0.6	0.9	1.0	0.2	0.3	0.1	-
	<i>Potamopyrgus antipodarum</i>	2.0	2.5	2.4	6.1	3.8	1.4	1.9	2.5	5.4	2.1	3.0	2.3	1.3
Megaloptera	<i>Archichauliodes diversus</i>	0.5	0.4	0.3	0.3	0.3	0.1	-	-	-	-	0.5	0.4	0.3
Oligochaeta	Oligochaeta	-	0.3	0.1	2.0	0.8	0.4	0.1	1.3	0.8	0.2	1.6	1.1	0.5
Plecoptera	<i>Zelandoperla</i> sp.	1.8	0.7	0.2	-	0.3	0.1	-	0.5	0.1	-	-	1.0	0.5
Planarian	<i>Neppia</i>	0.5	0.1	1.3	6.1	4.8	1.9	6.2	13.1	10.3	3.8	2.0	6.5	5.4
trichoptera	<i>Aopteapsyche</i> spp.	5.5	3.6	2.7	5.2	4.3	1.8	2.7	2.9	2.5	2.1	2.3	4.6	8.1
	<i>Costachorema xanthoptera</i>	-	-	-	-	-	-	-	-	0.3	0.1	-	-	-
	<i>Hudsonema amabilis</i>	-	0.5	0.1	-	-	0.5	0.1	4.0	1.8	0.4	0.9	0.5	0.1
	<i>Hydrobiosis parumbripennis</i>	1.3	0.3	0.3	0.1	0.3	0.1	0.3	0.6	0.6	0.2	-	1.0	1.8
	<i>Helichopsyche</i> sp.	-	-	-	-	-	-	-	-	-	-	-	0.3	0.1
	<i>Oxyethira albiceps</i>	0.5	0.1	-	-	-	-	-	0.5	0.1	-	-	-	-
	<i>Olinga feredays</i>	-	0.3	0.8	1.7	1.2	1.3	3.1	3.5	3.9	1.2	1.8	2.5	0.6
	<i>Pycnocentria funerea</i>	1.0	0.3	0.8	0.5	0.1	0.5	1.4	0.8	0.5	0.1	-	0.8	0.2
	<i>Polypsectropus</i> spp.	-	-	-	-	-	-	0.3	0.1	-	-	-	-	-
	<i>Psilochorema</i> spp.	8.0	4.5	4.4	4.6	5.6	1.7	1.4	1.9	1.2	1.6	4.1	4.0	7.8
	<i>Pycnocentrella</i> spp.	2.0	0.5	0.9	1.0	1.2	0.3	0.1	4.3	3.1	1.0	1.0	0.8	1.3
	<i>Pycnocentrodes</i> spp.	4.5	1.4	3.3	1.1	5.5	2.6	2.7	0.9	0.7	1.7	1.4	2.6	3.9

		M1 U60	M1 U30	M1 D60	M1 D30	M2 U60	M2 U30	M2 D60	M2 D30	M3 U60	M3 U30	M3 D60	M3 D30	T1 U60	T1 U30	T1 D60	T1 D30	T2 U60	T2 U30	T2 D60	T2 D30
Acarina	Acari 1	-	1	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
	Acari 8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Crustacea	Amphipoda 7	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
	Copepoda 1	-	2	-	-	5	129	4	-	-	8	-	-	3	-	2	1	1	-	13	3
	Copepoda 2	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
	<i>Cruregens fontanus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
	Ostracoda 1	-	-	3	-	2	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-
	<i>Paraleptamphopus subterraneus</i>	3	6	2	1	3	4	-	1	45	12	1	-	2	2	-	-	2	1	-	-
	<i>Phreatogammarus</i> sp.	1	-	-	-	1	-	-	-	5	-	-	-	-	-	-	-	11	-	-	-
	Stygocarida (Syncarida)	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Collembola	Collembola 2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coleoptera	Elmidae	-	-	2	6	-	-	1	-	-	-	-	2	-	2	-	-	-	-	-	-
Diptera	<i>Eukiefferiella brundini</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	2	-	-	1	-
	<i>Stictocladius</i> 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Stictocladius</i> 1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	3	-	1	1	1
	Chironomid G	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
	<i>Eriopterini</i>	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	3	-	-	1	-
	Tanypodinae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ephemeroptera	<i>Deleatidium</i> spp.	-	-	1	-	-	4	-	1	5	5	-	-	-	2	16	4	3	10	41	9
Mollusca	<i>Potamopyrgus antipodarum</i>	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Oligochaeta	Oligochaete	3	2	8	-	-	8	-	2	1	3	3	6	-	1	2	8	2	9	44	16
Trichoptera	<i>Aoteapsyche</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Hydrobiosella stenocerca</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Hydrobiosis</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
	<i>Oxyethera albiceps</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Pycnocentria funerea</i>	-	-	1	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-

	T3 U60	T3 U30	T3 D60	T3 D30	W1 U60	W1 U30	W1 D60	W1 D30	W2 U60	W2 U30	W2 D60	W2 D30	W3 U60	W3 U30	W3 D60	w3 D30
Acari 1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acari 8	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Amphipoda 7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Copepoda 1	8	4	5	2	1	-	8	4	1	1	15	8	2	4	1	2
Copepoda 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cruregens fontanus</i>	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	1
Ostracoda 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paraleptamphopus subterraneus</i>	2	2	1	-	-	1	6	5	-	1	19	14	-	-	-	2
<i>Phreatogammarus</i> sp.	4	2	-	-	-	-	-	-	-	-	2	1	-	-	-	-
Stygocarida (Syncarida)	2	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Collembola 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elmidae	-	-	-	-	1	-	-	-	1	3	-	-	-	2	-	-
<i>Eukiefferiella brundini</i>	-	-	-	1	2	1	-	-	1	-	-	4	-	-	1	-
<i>Stictocladus</i> 2	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
<i>Stictocladus</i> 1	-	1	2	-	-	-	2	3	-	-	-	1	-	-	-	45
Chironomid G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eriopterini</i>	-	-	1	-	1	-	-	-	1	-	-	-	1	-	-	-
Tanypodinae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6
<i>Deleatidium</i> spp.	3	6	12	1	-	-	2	10	-	-	2	32	-	-	-	8
<i>Potamopyrgus antipodarum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oligochaete	2	-	-	6	4	12	10	5	-	-	4	10	-	1	2	10
<i>Aoteapsyche</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
<i>Hydrobiosella stenocerca</i>	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-
<i>Hydrobiosis</i> spp.	2	2	-	-	-	-	-	2	-	-	2	-	-	-	-	-
<i>Oxyethera albiceps</i>	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
<i>Pycnocentria funerea</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-