

Spatial biodiversity patterns in a large New Zealand braided river

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Abstract At the catchment scale, braided rivers are recognised as physically unstable, dynamic landscapes, yet at finer spatial scales they are a mosaic of micro-habitats including physically unstable braided channels and more stable spring-sources, spring creeks, and groundwater zones. We investigated benthic invertebrate communities at 103 sites in braided channels, springs and hillslope streams in the Waimakariri River, New Zealand over 3 months. One hundred taxa were identified, including a number of rare phreatic species. Highest total taxonomic richness occurred in springs (81 taxa), whereas main braids and hillslope streams had fewer taxa (54 and 56, respectively). Spring-fed habitats also had the highest diversity of unique taxa (22), whereas main channels had five and hillslope streams 11 taxa, respectively. Several taxa including the mayfly *Deleatidium* and orthoclad chironomids were ubiquitous, whereas others such as the flatworm

Prorhynchus had restricted habitats. Our results highlight the high spatial heterogeneity of braided river habitats and the importance of springs as centres of invertebrate diversity within braided river catchments.

Keywords braided river; benthic habitat; springs; benthic invertebrates; biodiversity

INTRODUCTION

Braided rivers are among the most dynamic and complex of all riverine systems (Ward et al. 2002). They are the product of high-energy environments where highly variable discharge regimes and heavy sediment loads interact to produce dynamic riverscapes (Bristow & Best 1993). Braided rivers typically have extensive floodplains which are often hydrologically connected to the river (Brunke & Gonser 1997; Ward et al. 1999; Woessner 2000), making them spatially complex and temporally variable in groundwater-surface water exchanges (Stanford & Ward 1993; Brunke & Gonser 1997; Poole et al. 2002). Consequently, braided rivers and their floodplains include micro-habitats that are in a state of continual successional change (Arscott et al. 2000; van der Nat et al. 2003). Interactions between these conditions create a complex mosaic of heterogeneous micro-habitats with important consequences for spatial patterns of benthic invertebrate biodiversity (Ward et al. 2002).

Historically, stream ecologists have considered braided river channels to be relative biological deserts (Percival 1932), with communities characterised by low species diversity, and dominated by a few common, generalist species (Sagar 1986; Scrimgeour & Winterbourn 1989). However, a more holistic view of the “river” which includes the wider floodplain and underlying groundwaters, has revealed high spatio-temporal habitat heterogeneity in which spatially minor habitats contribute disproportionately to corridor biodiversity (Stanford 1998; Digby 1999; Ward et al. 1999).

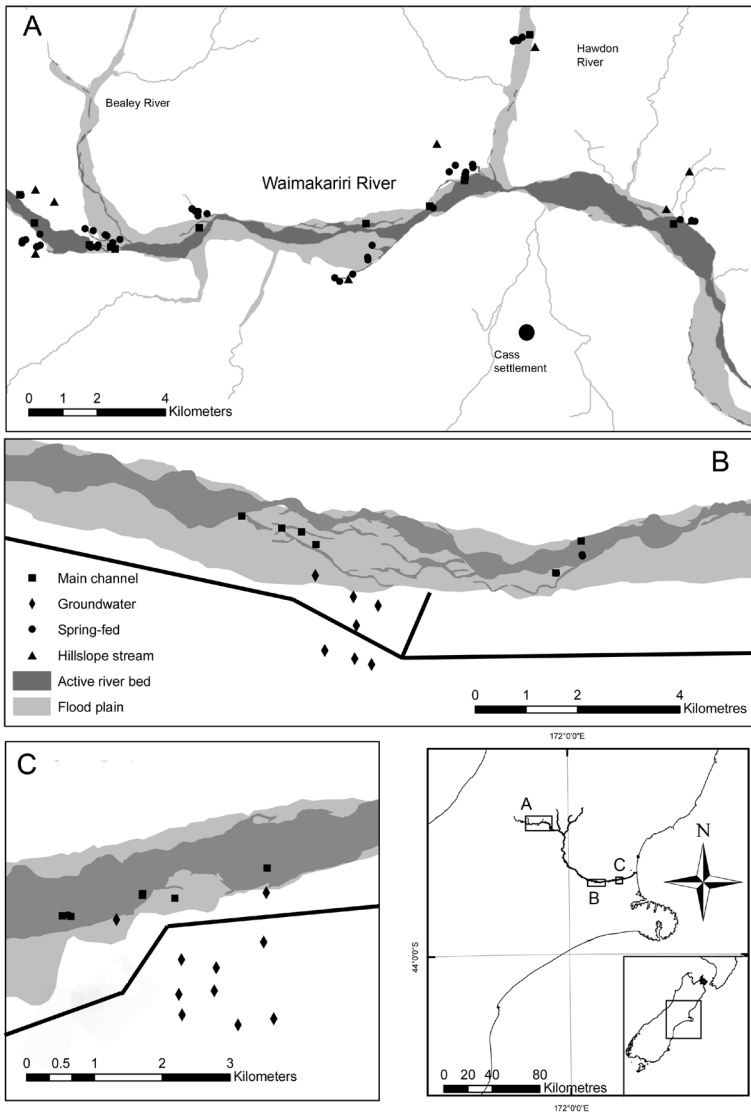


Fig. 1 Waimakariri River catchment, South Island, New Zealand, showing the locations of 103 sampling sites according to habitat type. **A**, Upper river near Cass; **B**, Halkett; **C**, Crossbank.

The habitat mosaic within braided rivers provides an ideal environment for studying biological and physico-chemical interactions within patchy landscapes. In Europe, ecological studies in the braided Val Roseg and Tagliamento river ecosystems have identified distinct landscape-scale patterns in the arrangement of aquatic habitats and have documented the importance of connectivity between habitat types in determining biodiversity patterns (Arscott et al. 2005; Malard et al. 2006). The lessons learned in the Val Roseg and Tagliamento rivers suggest that management of braided rivers should

account for the habitat diversity and connectivity that characterises these rivers (Arscott et al. 2005).

Large braided rivers are important features of the South Island, New Zealand landscape and many are facing increasing and competing demands for recreation, gravel extraction, and for irrigation and electricity generation (Young et al. 2004). With these growing human demands there is an increased need for sustainable management based on a sound understanding of braided river ecology. Little research has been published on the indigenous biota of these rivers in New Zealand, and investigations

of the patterns of biodiversity in these landscapes are almost non-existent. However, there is a small body of literature on the habitat requirement and feeding of insectivorous wading birds that inhabit the rivers (Pierce 1979; Hughey 1989) and these studies highlight the importance of small spring-fed channels and backwaters, as sites of high invertebrate productivity and diversity. Digby (1999) also demonstrated the importance of multiple habitat types for secondary production within a braided river and found that it increased as habitat stability increased. Accordingly, secondary production was lowest in unstable main braids, and highest in small spring-fed channels within the floodplain (Digby 1999).

The objectives of our study were to determine the relative contributions of different habitats to the benthic invertebrate diversity of the braided river corridor. In addition to main and side braid habitats, we investigated spring-fed channels flowing lateral to the main channels, hillslope streams which generated alluvial fans feeding the braided river, and groundwater wells adjacent to the river floodplain.

MATERIALS AND METHODS

Study area

The Waimakariri River arises in the glaciated Southern Alps at c. 2100 m a.s.l., and discharges into the Pacific Ocean on the east of the South Island (Fig. 1). The river is c. 150 km long and has a catchment area of 3560 km² (Reinfelds & Nanson 1993). In its upper reaches the river flows through a relict glacial valley and has an extensive, braided floodplain upstream of a heavily incised bedrock gorge. Below the gorge the floodplain of the river can be up to 2 km wide and the riverbed is extensively braided. Lithologically, the catchment is dominated by greywacke sandstone (45%), but includes smaller amounts of limestone, volcanics, conglomerates, and coal measures (North Canterbury Catchment Board 1986). The riverbed comprises alluvial and glacial outwash deposits primarily derived from greywacke. Mean annual flow is 121 m³ s⁻¹ and major floods that may occur at any time of the year average 1500 m³ s⁻¹ annually (Reinfelds & Nanson 1993). About 11% of the annual precipitation in the upper catchment is stored as snow and ice in winter and is released during spring and summer (October to February) when it contributes about 30% of the flow (Reinfelds & Nanson 1993).

Site selection

The purpose of this study was to investigate and compare the biodiversity values of the aquatic habitat types found within the braided river corridor. Ten river sections (c. 200 m in length) were initially selected from topographical maps based on accessibility. Sites were chosen to include, wherever practicable, the full range of micro-habitats available across the braided river floodplain. Where possible each river section included a spring complex, mainstem and braided channel riffles, a hillslope stream riffle and access to groundwater (groundwater sites were only available in the lower river) (Fig. 2). A total of 103 sites were sampled in 10 river sections, eight in the upper river near Cass and two in the lower river at Halkett and Crossbank (Fig. 1). Several spring habitat types were identified: spring-sources, spring creeks, and active-bed springs. Spring-sources were defined as upwellings in the mature, vegetated floodplain, whereas spring creeks were sites >40 m downstream from the source, and are hereafter referred to as floodplain springs. Active-bed springs were upwellings within the disturbed bed of the river, with no surrounding terrestrial vegetation (see Digby 1999 for descriptions). Groundwater was sampled from two well arrays adjacent to the lower river at Halkett and Crossbank.

Sampling

All sites were sampled on a single occasion during the summer (December to February) 2003-04. All sampling occurred under baseflow conditions. At each site temperature and conductivity were measured with an Oakton pH/conductivity/temperature 10 meter or a Horiba multi-meter. Groundwater chemistry was measured by retrieving a water sample from the well, which was then immediately sampled. Meters were calibrated before sampling to manufacturers' specifications.

Benthic invertebrate samples were collected using a kick-net (mesh size 250 μ m), and five samples taken over c. 2.5 m² were pooled into a single composite sample following the semi-quantitative procedure of Stark et al. (2001). Groundwater wells were sampled with a plankton net (250 μ m mesh). The net was dropped into the well within a stainless steel bomb, and after bottom sediments were disturbed it was pulled up through the water column. The net fitted tightly within the 100 mm well casing, so the entire water column was sampled. Contents of the bomb and net were rinsed through a 250 μ m sieve. This procedure was repeated twice at each well. Samples were preserved in 70% ethanol in the field and

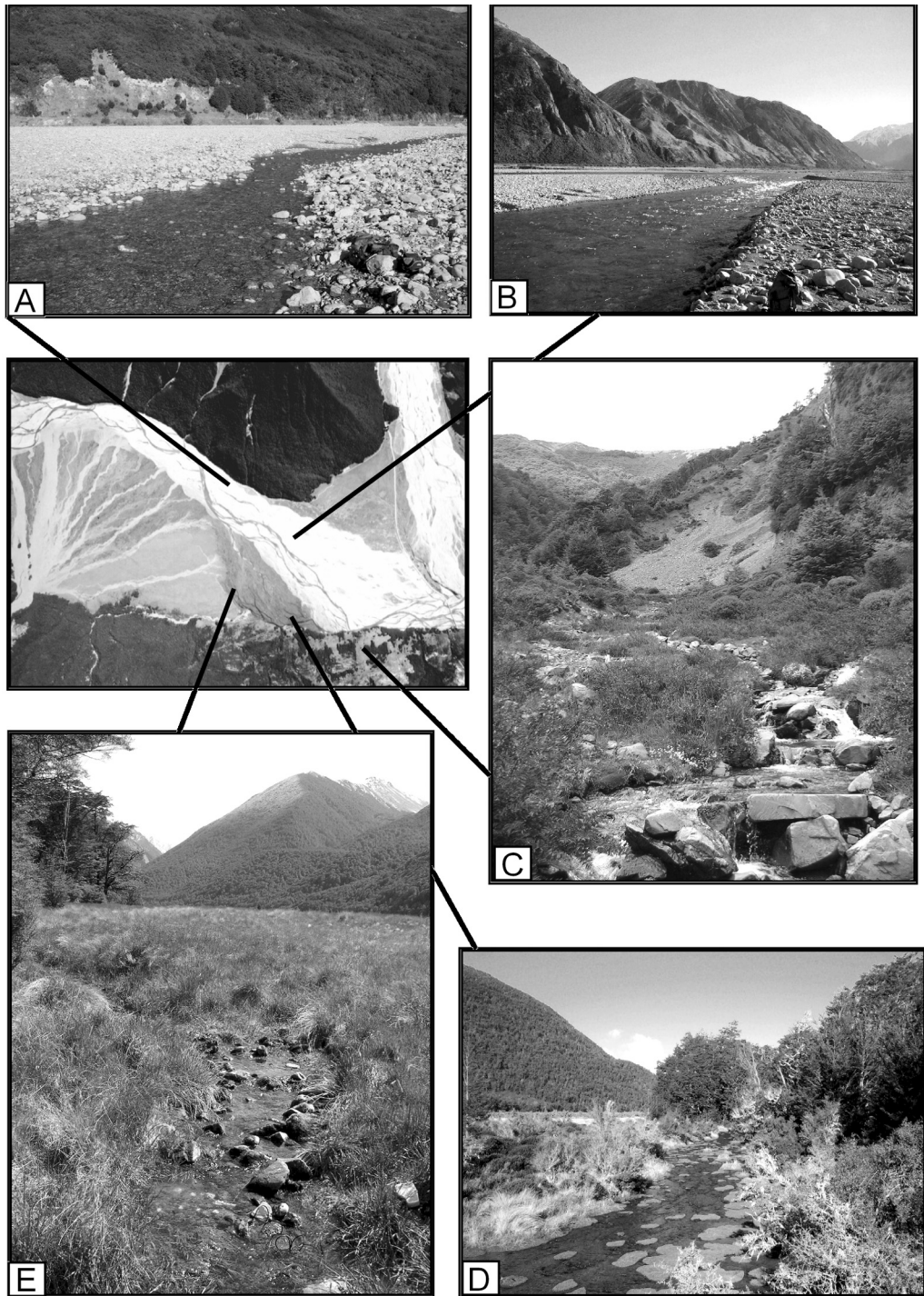


Fig. 2 Typical sites included in this survey and the approximate position of examples around Turkey fan (at the confluence of the Waimakariri and Bealey rivers) on the Waimakariri River floodplain, South Island, New Zealand. **A**, active bed spring; **B**, main channel of the Waimakariri River; **C**, hillslope stream; **D**, spring creek; **E**, floodplain spring.

sorted in the laboratory under 40× magnification. Identifications were made to the lowest taxonomic level possible, except for Oligochaeta, which were not differentiated below order, and Chironomidae, which were not separated below tribe, using keys by Winterbourn et al. (2000) and a description by Percival (1945).

Statistical analyses

Significant differences ($P < 0.05$) between physico-chemical characteristics of habitat types were identified using a Kruskal-Wallis test for non-normally distributed data. Pairwise Mann-Whitney tests were used to perform *post-hoc* testing (Zar 1999). Benthic invertebrate samples were analysed based on presence/absence and relative abundance data. Semi-quantitative coded abundance were estimated for each taxa (Stark 1998). Rarefaction of taxonomic richness was performed, standardising by the lowest number of sites sampled of any habitat, to account for the differences between the number of sites sampled (PRIMER 5; Clarke 1993). Non-metric multi-dimensional scaling (MDS) was performed to examine patterns in community composition (PRIMER 5; Clarke 1993). The Bray-Curtis distance measure was used to determine similarities between sites, after $\log_e(x + 1)$ transformation of coded abundance data, which was used to down-weight dominant taxa and place greater emphasis on taxonomic diversity (Clarke & Warwick 1997). To determine the significance of invertebrate community differences a one-way analysis of similarities (ANOSIM) was performed (PRIMER 5; Clarke 1993).

RESULTS

Physico-chemical characteristics

Active-bed springs, main channels and lower river groundwater sites were on average the warmest

habitats, but they also showed the greatest between-site variability (Table 1). In contrast, floodplain springs were the coolest and showed least variation, being consistently about 8°C, which approximated the annual average air temperature and the groundwater temperature in the upper Waimakariri floodplain (Gray 2005). The high temperatures in lower river groundwater sites (average c. 15.1°C) compared to headwater floodplain springs reflect the difference in mean annual air temperature between upper and lower reaches. Spring creeks and hillslope streams were on average warmer than the floodplain springs, but also relatively stable. Conductivity was generally low, although it was markedly higher in the hillslope streams than all other sites (Table 1).

Benthic invertebrates

A total of 100 invertebrate taxa were identified from the 103 sites, 81 in spring-groundwater habitats (i.e., active-bed springs, spring creeks, floodplain springs, and groundwater), 56 in hillslope streams, and 57 in main channel habitats, respectively (Fig. 3). Thirty-two taxa were found in all habitats across the braided river (Fig. 3). Spring habitats included a high proportion of taxa unique to springs (22%), but only 5% and 11% of taxa were found exclusively in main channel and hillslope streams, respectively. Of the spring habitats, spring creeks had the most unique taxa (6) and only two taxa were found in all spring habitats (active-bed, floodplain, and spring creeks). No taxa were found in only groundwater. Rarefied taxonomic richness confirmed the high diversity of springs, and the comparatively high diversity of spring creeks and floodplain springs (Table 2).

Insects dominated the fauna of all surface habitats, whereas Crustacea and mites were the most abundant groups in groundwater samples (Fig. 4, Table 3). Main channel sites were dominated

Table 1 Mean (\pm SE) temperature and conductivity values for six habitat types surveyed (single measurement) in summer 2003–04 in the Waimakariri River, New Zealand. Results of pairwise Mann-Whitney *post-hoc* test comparisons following Kruskal-Wallis test are shown.

Habitat	No. of sites	Temperature (°C)	$P < 0.001$	Conductivity ($\mu\text{S cm}^{-1}$ @ 25°C)	$P < 0.05$
Main channel	24	14.0 (0.2)	b	61 (0.5)	b
Hillslope stream	9	8.5 (0.1)	ac	85 (0.1)	a
Active-bed spring	11	15.3 (0.3)	b	61 (1.2)	b
Floodplain spring	16	7.8 (0.1)	a	62 (0.7)	b
Spring creek	26	9.5 (0.1)	c	61 (0.8)	b
Groundwater	17	15.1 (0.3)	b	54 (3.2)	b

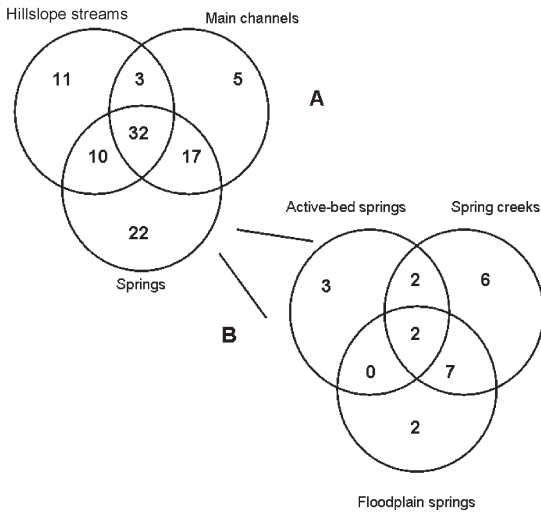


Fig. 3 Taxonomic richness in different braided river habitats. Numbers of taxa common in different habitats are indicated by overlapping sections of circles. **A**, number of taxa found in three braided river macro-habitat types. **B**, Micro-habitat allocation of taxa unique to spring/groundwater habitats. All taxa found in groundwater habitats were also found in springs.

by mayflies, predominantly *Deleatidium* (Fig. 4, Table 3). Dipterans were also common and diverse in main channel habitats (16 taxa), whereas caddisflies were taxonomically diverse (23 taxa), but accounted for less of the community. Hillslope streams had similar community composition to main channel sites, and were dominated by mayflies (*Deleatidium*) and Diptera (Chironomidae and Simuliidae). Stoneflies (particularly *Zelandoperla* and *Zelandobius*) made a greater contribution to the communities of hillslope streams than main channels (Table 3). Active-bed springs were also dominated by mayflies and dipterans, however, the amphipods *Paraleptamphopus*, *Phreatogammarus*, and *Paracrangonyx* were also common (Fig. 4, Table 3). Floodplain spring habitats differed from other surface waters in being dominated by Diptera (particularly the chironomids Orthoclaadiinae and Diamesinae) and having few mayflies.

Whereas main channel and hillslope sites were mostly devoid of aquifer-dwelling taxa, groundwaters were entirely inhabited by hypogean invertebrates, almost exclusively Crustacea (Table 4). Floodplain springs and spring creeks had few aquifer dwelling taxa, but the more recent active-bed springs had more hypogean taxa than other surface habitats.

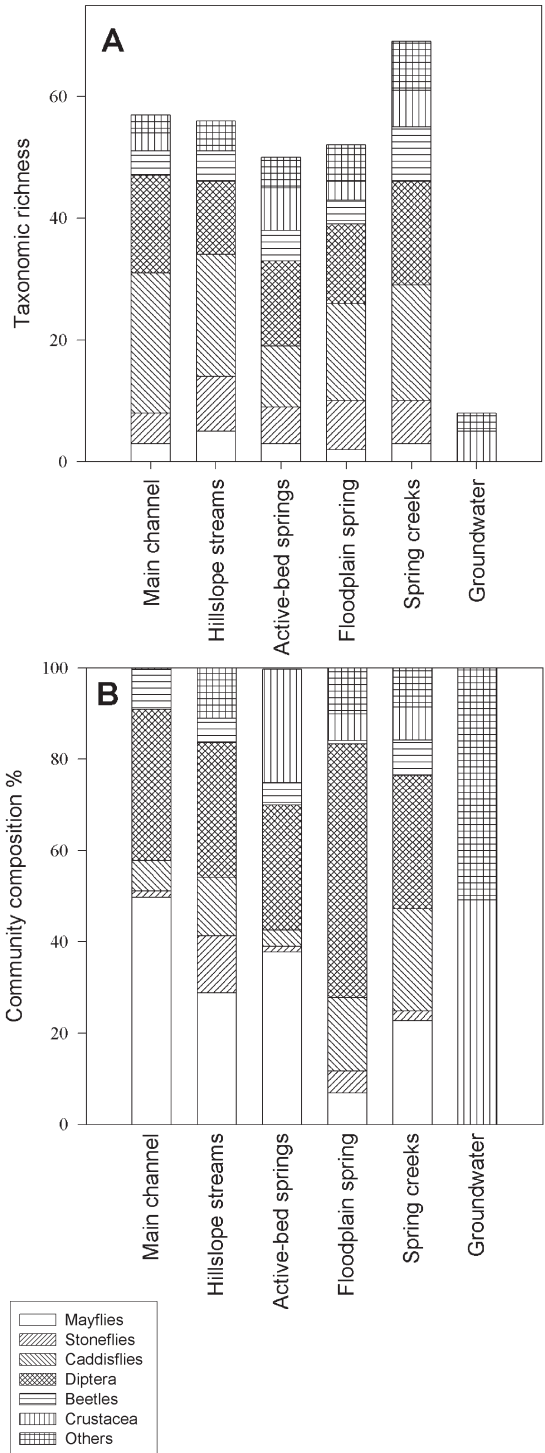


Fig. 4 **A**, Taxonomic richness, and **B**, community composition of invertebrate communities in six braided river habitats.

MDS ordination of invertebrate communities from all habitats showed that groundwater communities were distinctly different from surface-water communities (Fig. 5). Within the surface-water communities, main channel and active-bed spring communities had higher Axis 2 scores, whereas floodplain and hillslope streams tended to have lower Axis 2 scores. ANOSIM indicated that despite some overlapping of sites, invertebrate communities among

habitats were significantly different overall (Global R -statistic = 0.509, $P = 0.001$). However, pairwise comparisons indicated that spring creek assemblages did not differ significantly from either floodplain springs ($R = -0.017$, $P = 0.574$) or hillslope streams ($R = 0.149$, $P = 0.082$) (Table 5).

The Waimakariri River floodplain contained several taxa restricted to springs and groundwater, specifically the flatworm *Prorhynchus putealis*,

Table 2 Absolute and rarefied species richness (ES(n)) for different braided river habitats. Rarefied values were standardised by the lowest number of sites sampled within each category (in bold). Rarefied taxonomic richness for each of the spring/groundwater habitats based on the 22 taxa found only in these habitats.

Habitat	No. of sites	Total taxonomic richness	ES(n)
All habitats			
Main channel	24	57	4.15
Hill slope	9	56	6.07
Springs and groundwater	70	81	6.71
Total	103	100	
Springs and groundwater only			
Active-bed springs	11	7	2.02
Floodplain springs	16	11	4.84
Spring creek	26	17	5.35
Groundwater	17	3	3.00
Total unique taxa		22	

Table 3 Most common taxa in different braided river habitats. Percentage of the community accounted for by that taxon are shown in parentheses.

Main channel	Hillslope stream	Active-bed spring
<i>Deleatidium</i> (50)	<i>Deleatidium</i> (27)	<i>Deleatidium</i> (33)
Chironominae (18)	Orthocladiinae (19)	<i>Paraleptamphopus</i> (16)
Orthocladiinae (13)	<i>Potamopyrgus antipodarum</i> (10)	Orthocladiinae (12)
Elmidae (8)	<i>Zelandoperla</i> (4)	Eriopterini (9)
<i>Hydrobiosis parumbripennis</i> (2)	Elmidae (4)	<i>Coloburiscus humeralis</i> (5)
<i>Austrosimulium</i> (1)	Diamesinae (3)	<i>Paracrangonyx</i> (5)
Scirtidae (1)	<i>Zelandobius</i> (3)	<i>Phreatogammarus</i> (4)
<i>Hydrobiosis frater</i> (1)	<i>Austrosimulium</i> (3)	Chironominae (3)
Eriopterini (1)	Tanypodinae (2)	Scirtidae (2)
Floodplain spring	Spring creek	Groundwater
Orthocladiinae (25)	<i>Deleatidium</i> (22)	Hydracarina (51)
Diamesinae (17)	Orthocladiinae (15)	<i>Paraleptamphopus</i> (32)
<i>Potamopyrgus antipodarum</i> (8)	<i>Pycnocentodes</i> (11)	Copepoda – Cyclopoida (13)
Chironominae (6)	Elmidae (4)	Isopoda (3)
<i>Deleatidium</i> (6)	<i>Potamopyrgus antipodarum</i> (4)	Ostracoda (1)
<i>Pycnocentodes</i> (5)	Diamesinae (4)	<i>Paracrangonyx</i> (1)
<i>Paraleptamphopus</i> (4)	<i>Pycnocentria</i> (3)	
<i>H. parumbripennis</i> (4)	<i>Austrosimulium</i> (3)	
Tanypodinae (4)	<i>Oxyethira albiceps</i> (3)	

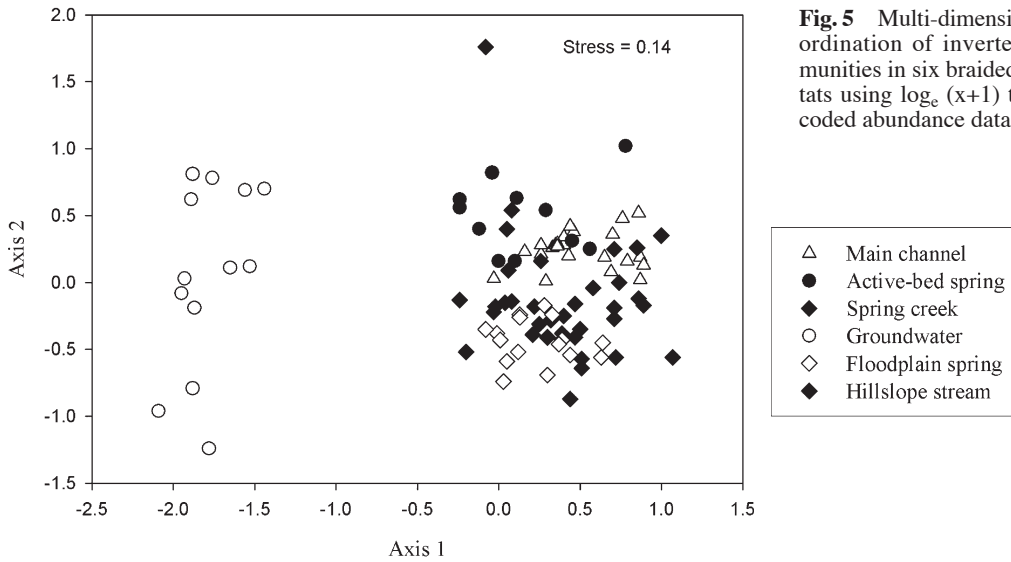


Fig. 5 Multi-dimensional scaling ordination of invertebrate communities in six braided river habitats using $\log_e(x+1)$ transformed coded abundance data.

Table 4 Occurrence of taxa unique to spring and groundwater habitats among the 103 sites sampled in this study. Taxa included were present in >5% of each habitat type.

	Active-bed springs	Floodplain springs	Spring creeks	Groundwater
<i>Zelolessica cheira</i>		X	X	
<i>Philorheithrus agilis</i>		X		
<i>Zelandotipula</i>		X	X	
Stratiomyidae		X	X	
<i>Huxelhydrus syntheticus</i>			X	
<i>Prorhynchus</i>		X	X	
<i>Paracrangonyx</i>	X			X
<i>Crurugens fontanus</i>	X			
Isopoda (other than <i>Cruregens</i>)	X			X
Ostracoda	X	X	X	X

the isopod *Crurugens fontanus*, and the amphipod *Paracrangonyx*.

DISCUSSION

The traditional view of New Zealand braided rivers as highly unstable ecosystems with low benthic invertebrate diversity and communities dominated by disturbance-tolerant species (Sagar 1986; Scrimgeour & Winterbourn 1989) does not take into account the diverse array of non-braided aquatic habitats present in their floodplains. Our study and recent work by

Digby (1999) and Gray (2005) have shown that New Zealand braided river systems, as a whole, are frequently physically complex, with a mosaic of habitats of varying stability supporting markedly different benthic communities. In particular, the results of the present study show that spring systems embedded within a braided river floodplain can have comparatively high invertebrate diversity, and taxa different from those in the unstable braids. Craig & McCart (1975) described spring-fed rivers in Alaska as “green oases in the polar environment”; spring habitats in this braided river landscape similarly provide islands of stability and diversity.

An assessment of taxonomic diversity in highly contrasting habitats, large braided rivers versus small spring and hillslope streams, is difficult. In this study, sampling was standardised across habitats in terms of area and time sampled. However, this design does not account for differences in the absolute area of each habitat within the river valley and seasonal changes in these areas. Malard et al. (2006) reported a decline in the density of benthic invertebrates with increasing area of main channel habitat. This dilution-concentration effect might reduce the density and more importantly diversity of samples taken from the main channel. However, the use of pooled composite kick-net samples and sampling during summer low flow (concentration) periods meant that our findings are likely to be representative of actual diversity values in braided river main channels.

Physico-chemical conditions

Temperature patterns in the upper catchment reflected the likely sources of hydrological connectivity in the floodplain. Main channel sites, which are predominantly sourced from surface waters, were warmest. By December, the main channels in this river are probably fed by run-off high in the catchment and water temperatures are controlled by air temperature. The active-bed springs also had higher water temperatures which are probably controlled by main channel water temperatures. Their flow probably derives from shallow hyporheic water from the main channel as indicated by the

Table 5 Pairwise comparisons of significantly different habitats by one-way analysis of similarities (global *R*-statistic = 0.509, *P* = 0.001). (Mc, main channel; sc, spring creek; abs, active-bed springs; gw, groundwater; fps, floodplain springs; hs, hillslope streams.)

Habitat types	<i>R</i> value	<i>P</i> value
mc, sc	0.297	< 0.001
mc, abs	0.422	< 0.001
mc, gw	0.898	< 0.001
mc, fps	0.796	< 0.001
mc, hs	0.461	< 0.001
sc, abs	0.346	< 0.001
sc, gw	0.869	< 0.001
abs, gw	0.705	< 0.001
abs, fps	0.862	< 0.001
abs, hs	0.646	< 0.001
gw, fps	0.806	< 0.001
gw, hs	0.789	< 0.001
fps, hs	0.633	< 0.001

similar conductivities between the two habitats. Floodplain springs and spring creeks were cool and comparatively similar, although exposure to the air temperatures increased the average temperature in spring creeks. The hillslope streams were also consistently cooler as these were alpine-fed and predominantly forested. The relatively higher conductivities of this water may result from forested inputs. Groundwater temperatures beneath and adjacent to the lower Waimakariri River were warmer and had highly variable temperature and conductivity when compared with springs in the upper river. Lower river groundwater temperatures were more similar to temperatures in the main channel, a finding that we are not able to adequately explain but which may be an artefact of the well design.

Biological patterns

Spring habitats in the Waimakariri floodplain contained the highest overall diversity and the greatest number of unique taxa of any habitats sampled in this study. In contrast, several European and North American studies that compared benthic invertebrate communities in springs and surface-fed streams have found the highest diversity in the latter (Ward & Dufford 1979; Barquin 2004). However, in a braided reach of the glacial Roseg River, Switzerland, Burgherr et al. (2002) found higher taxonomic diversity in groundwater-fed channels than in the main channel, consistent with our findings, and proposed that high levels of disturbance in glacial outwash rivers may be a reason for the lower diversity in the main braids. Lower diversity in Northern Hemisphere springs has been attributed to the high abundance and numerical domination of predatory amphipods in springs which reduce overall diversity, and the negative effects of temperature constancy upon taxa with seasonally synchronised lifecycles (Barquin & Death 2004). We can only speculate on the reasons for differing results in New Zealand. However, it is possible that some combination of high disturbance, asynchronous life histories widely documented for New Zealand benthic invertebrates (Winterbourn 1981), and relative numerical paucity of predators create the conditions in which communities are more diverse.

Groundwater habitats in the Waimakariri were dominated by hypogean taxa, but very few aquifer-dwelling invertebrates were found in main channel or hillslope streams. Hillslope streams rarely have a contiguous, stable aquifer and although hyporheic

species may occur below the main channel they are unlikely to withstand hydraulic extremes and substrate disturbance closer to the surface. However, small numbers of groundwater invertebrates were found in both springs and spring creeks. That spring complexes act as centres of high diversity within the braided river is partially an artefact of the combination of surface-water and groundwater fauna which can exploit these stable habitat islands.

Although in this study the groundwater communities had limited taxonomic diversity, taxon richness is likely to have been underestimated as the level of taxonomic resolution possible was coarse, and by their nature well samples were small. Groundwater communities below river systems elsewhere have been shown to be extremely diverse. For example, in the Rhône River, France, Gibert et al. (1994) identified 38 stygofaunal (obligate groundwater dwellers) species, of which 23 were Crustacea. Stanford et al. (1994) identified over 80 groundwater taxa in the alluvial aquifer of the Flathead River, United States, including taxa that exploit both surface and groundwater habitats.

The most diverse group of stygofauna in New Zealand are the Hydracarina, which contain 70 formally described taxa (Scarsbrook & Fenwick 2003). Hydracarina were the dominant taxa in groundwater communities in our study, but we were unable to confidently separate them taxonomically.

Despite the presence of a core of ubiquitous taxa found in all New Zealand streams (Winterbourn et al. 1981), ordination of community assemblages revealed differences between the fauna within different habitats in the Waimakariri River. These differences are likely to be a consequence of the combined effects of substrate stability, micro-habitat diversity, the presence or absence of macrophytes, and the relative influence of groundwater chemistry (Death 1995; Gray 2005). Furthermore, biological interactions have the potential to structure invertebrate assemblages at physically stable sites, via competitive exclusion, founder effects, and predation (Death 1995; Townsend et al. 1997). Determining the relative contribution of each of these drivers was beyond the scope of this survey and more intensive sampling would be required to elucidate the drivers of these patterns.

Unique taxa: crenobionts or crenophiles?

The number of taxa restricted to springs (crenobionts) in New Zealand is low by comparison with world standards (Death et al. 2004), and none of the

taxa found in this study can be considered true crenobionts. However, we did identify a number of groundwater and spring taxa, and the absence of these in other habitat types in this extensive sampling of the Waimakariri River, suggest that they can be described as crenophiles, i.e., taxa that preferentially exploit spring habitats.

Within our data set, the major dichotomy among communities was between the non-insect groundwater taxa and surface-water dwelling insects. The presence of groundwater taxa such as the flatworm *Prorhynchus* and various stygobitic amphipods and isopods in surface-water (spring) communities indicate the presence of hydrologic connections between surface and groundwaters along the length of the Waimakariri River floodplain.

Our results provide compelling evidence that springs markedly enhance the diversity of braided river corridors, and that spring-fed habitats are hotspots of diversity within the river landscape. We suggest that springs constitute not only a stable habitat for invertebrates unable to colonise unstable, flood-prone environments of the main channel, but also constitute an ecotone between surface waters and groundwaters, providing the opportunity for mixing of hypogean and epigean taxa.

The high degree of endemism of New Zealand's benthic invertebrate fauna (Boothroyd 2000) means that many of the taxa inhabiting uncommon ecotones are likely to be globally unique. Poorly-known taxa, including some species of the Crustacea *Crurugens*, *Phreatogammarus*, and the flatworm *P. putealis* are likely to be dependent on the integrity of upland groundwater ecosystems for their survival. As braided river systems come under greater pressure to be used for water and gravel extraction and hydro-electric development, the need to improve our understanding of the diversity of braided rivers and their interactions with aquifer hydrology and ecology increases.

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