

Michaelis (1974) provided a thorough description of the flora of five coldwater springs in New Zealand (Appendix 1). She identified 50 species (19 algae, 13 mosses, 11 vascular plants and 7 liverworts), and Waikoropupu Springs was found to be the most diverse spring, with 35 species.

Kilroy et al. (2004) noted that 25 of 99 algal taxa found in the Waimakariri River catchment were restricted to spring habitats. Overall, diatoms were the most diverse group (65 taxa), and 21 of these (33%) were found only in spring-fed habitats. Collier & Smith (2006) noted the distinctive flora of rockface seepages in the western Waikato.

There does not seem to be any bryophyte assemblage that is specific to spring-fed streams (A. Suren, NIWA Christchurch, pers. comm.). Substrate stability is an important factor determining the distribution of bryophytes (Suren & Duncan 1999) and, therefore, many freshwater springs provide suitable habitat for them. Given a stable substrate, bryophyte species assemblage depends on a spring's water chemistry, flow permanence and the surrounding geology (Suren 1996). However, in a small alpine springbrook, Cowie & Winterbourn (1979) noted a distinct zonation of bryophyte species, with *Fissidens rigidulus* occupying the mid-channel, *Pterygophyllum quadrifarium* along the banks and *Cratoneuropsis relaxa* in the outer spray zone.

The most commonly collected bryophyte taxa in springs have been *F. rigidulus* and *C. relaxa*, both of which are widespread species in New Zealand streams (Suren 1993, 1996). The moss *Hypnobartlettia fontana* is known only from Waikoropupu Springs (Fife et al. 2004).

Long periods with stable bed sediments and infrequent high-velocity events are required for significant macrophyte colonisation of lotic (flowing) environments (Reeves et al. 2004), and thus macrophytes are frequently found in the stable beds of springs (Biggs et al. 2001). Good examples of this are *Nasturtium officinale* and *Callitriche stagnalis* (Appendix 1), which are commonly found in cold clear-water springs (Coffey & Clayton 1988). Some pest plant species, of genera such as *Salvinia*, *Elodea*, *Egeria* and *Lagarosiphon*, have also been found in springs (Coffey & Clayton 1988). Most exotic macrophytes have been classified as having ruderal strategies (Riis & Biggs 2001), meaning they are effective colonisers of disturbed sites, and may also displace natives at sites with high nutrient concentrations. However, given stable conditions, macrophytes can segregate depending on water velocity, depth and substrate composition (Riis & Biggs 2003), which means that macrophyte diversity can be highly dependent on the physical diversity of the spring habitat (see Michaelis 1977).

3.4 THE CONTRIBUTION OF SPRINGS TO BIODIVERSITY IN BRAIDED RIVER LANDSCAPES

Braided rivers develop in high-energy environments, where highly variable discharge regimes and heavy sediment loads interact to produce dynamic riverine landscapes (Richards 1982; Mosley 2004). Within the braided river landscape important physical, chemical and biological interactions occur

across three spatial dimensions: longitudinal interactions from source to sea (e.g. sediment transport, fish migration), lateral interactions with banks and flood plain (e.g. braiding pattern, vegetation dynamics) and vertical interactions with underlying groundwaters (e.g. aquifer recharge, flood-plain springs). The interactions within and among these three dimensions over time create a dynamic mosaic of aquatic habitats: groundwaters, springs, turbulent main channels, spring-fed streams and relatively calm side channels and backwaters. This dynamic mosaic of inter-connected habitats plays an important role in determining the structural and functional biodiversity of braided rivers (Ward et al. 2002).

In a recent review of the invertebrate ecology of New Zealand's braided rivers, Gray & Harding (2006) identify a relatively small body of literature that has described invertebrate biodiversity patterns in these systems. However, most of this published research has focused on main channel habitats (e.g. Sagar 1986; Scrimgeour & Winterbourn 1989), and within braided river landscapes the importance of springs and spring-fed channels has received little attention until recently (see section 3.4.1).

There is a small body of literature on the habitat requirements and feeding of insectivorous wading birds in braided rivers (e.g. Pierce 1979; Hughey et al. 1989; Sanders 2000), which highlights the importance of small spring-fed channels, and backwaters, as habitats with high invertebrate productivity and diversity. In his thesis work, Digby (1999) further highlighted the importance of multiple habitat types for secondary production within a braided river landscape (Rakaia River). He found that invertebrate productivity increased across a gradient relating to habitat stability, with secondary production lowest in unstable main braids, and highest in small spring-fed channels within the flood plain. He also provided a typology of habitats within the braided river landscape, which has been useful in recent research identifying biodiversity values across different spring habitats of a braided riverscape (Gray et al. 2006).

3.4.1 Invertebrate diversity patterns

Over the last 4 years, two separate studies of spatial biodiversity patterns within the braided Waimakariri River have been carried out. The following results arise from a combination of these datasets (see also Gray et al. 2006). The principal aim of both studies was to assess the relative contribution of different habitat types to aquatic biodiversity. In summer 2003, NIWA biologists surveyed invertebrate and algal distribution patterns in multiple habitat types (springs, groundwaters and main channel) along three reaches of the Waimakariri River. During 2004, a similar survey of invertebrate communities in surface lotic habitats in the upper Waimakariri was performed by Gray (2005).

These studies assessed longitudinal, lateral and vertical patterns in the structural biodiversity of a large braided river. Five main habitat types were sampled for macroinvertebrates. In addition to the main channel and braids, which form the dominant components of a braided river by area, habitats that reflect the important groundwater-surface-water interactions in braided rivers were included. Invertebrates were sampled from spring-fed

channels lateral to the main channels, and from the springs at the heads of these channels. Hill slope tributaries of the main river were also sampled. In addition, invertebrates were sampled from two groundwater well arrays adjacent to the river flood plain.

A total of 119 invertebrate taxa were identified from 103 sites, which included 30 springbrooks, 27 springs, 17 groundwater wells, 22 main channel/braids and seven hill slope stream habitats. Hill slope streams (50 taxa) were dominated by *Deleatidium* and *Nesameletus* mayflies, the stoneflies *Stenoperla* and *Zelandoperla* and various chironomids; the main channel sites (65 taxa) were dominated by *Deleatidium*, oligochaete worms and chironomids. Groundwater samples contained a low richness of specialised taxa (6 taxa), comprising predominantly amphipods, copepods and mites. Springs and springbrook sites had the greatest taxonomic richness (80 and 84 taxa, respectively) and were dominated by the ubiquitous *Deleatidium*, oligochaetes and orthoclad chironomids. The springbrooks also contained high numbers of the trichopteran *Pycnocentroides* sp. In contrast, springs had a high relative abundance of the amphipods *Paraleptambopus* spp.

A Venn analysis of invertebrate communities revealed several important features of biodiversity in a braided river landscape (Fig. 13A). Spring and springbrook habitats contained the greatest number of taxa (37) unique to any one broad habitat type. The highly disturbed main channels and hill slope streams each contained only eight unique taxa, the majority of their taxonomic diversity being shared with springs. A core group of ubiquitous taxa (30) were found at all sites and constitute the well-documented, highly abundant, habitat generalists that characterise many New Zealand streams (Winterbourn et al. 1981; Scarsbrook 2000). Overall, 84% of taxa were found in springs compared to 54% in the main channels and 42% in hill slope streams. Hence, springs, despite being small discrete habitats, not only contained the greatest diversity, but also the greatest number of unique taxa.

A further analysis of patterns in invertebrate communities within springs and groundwater revealed that springbrooks and springs contained high numbers of unique taxa, whereas all the invertebrates collected within groundwater samples were also found in surface habitats (Fig. 13B). The generalist core was quite small, and was represented by the aquifer-dwelling organisms, all

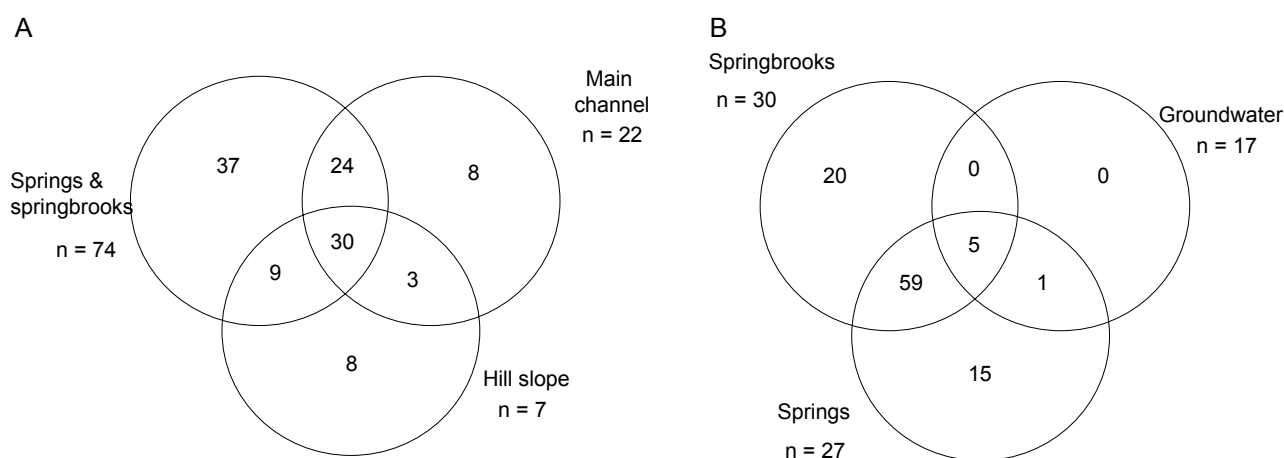


Figure 13. Numbers of invertebrate taxa (A) unique to spring, main channel and hill slope streams and combinations of the above, and (B) unique to springbrooks, springs, groundwater and their combinations.

of which were found across the spectrum of groundwater-dominated surface habitats, with the exception of *Paracrangonyx* sp., which was only found in groundwater and springs. The considerable overlap between springbrook and spring sites is apparent, as are the number of taxa unique to both habitats.

3.4.2 Algal diversity patterns

In a 2003 study, 98 algal taxa were found in three habitat types within two reaches (Upper = Klondyke/Mt White; Lower = Halkett/Crossbank) of the Waimakariri River (Kilroy et al. 2004). Of the 98 species, 65 were diatoms, 18 chlorophytes, 13 cyanobacteria, one tribophyceae and one rhodophyte.

In the Upper reach, main channel and springbrook habitats both had diverse and distinct algal assemblages (Fig. 14A). Only seven taxa were found in all three habitat types. In contrast, springs had fewer species and only a few taxa were exclusive to that particular habitat. These included four diatoms (e.g. *Rhoicospenia curvata*), three cyanobacteria (e.g. *Chaemosiphon* sp.) and an unidentified colonial chlorophyte.

In the Lower reach, the main channel habitat was the most diverse (Fig. 14B), although it should be noted that sampling intensity varied significantly between habitats. However, results suggest a greater proportion of shared taxa in the Lower reach (19% of 67 taxa shared) compared with the Upper reach (9% of 75 taxa). Only four taxa were found exclusively in springs in the Lower reach, with all belonging to the Diatomaceae.

3.4.3 Conclusions

The springs and main channel habitats considered in our studies of the Waimakariri River represent extremes in terms of their physico-chemical characteristics (Gray 2005; Gray et al. 2006), and yet both are part of a single body of water moving along the Waimakariri River flood plain. Hydrological connectivity mediated by the flood-plain aquifer, and maintained by flood-induced fluvial dynamics, results in stable spring habitats occurring amidst highly disturbed braided channels (Ward et al. 1999). These disparate habitats are united as parts of an expanded 3-dimensional view of the ‘river’ within the landscape (Stanford 1998).

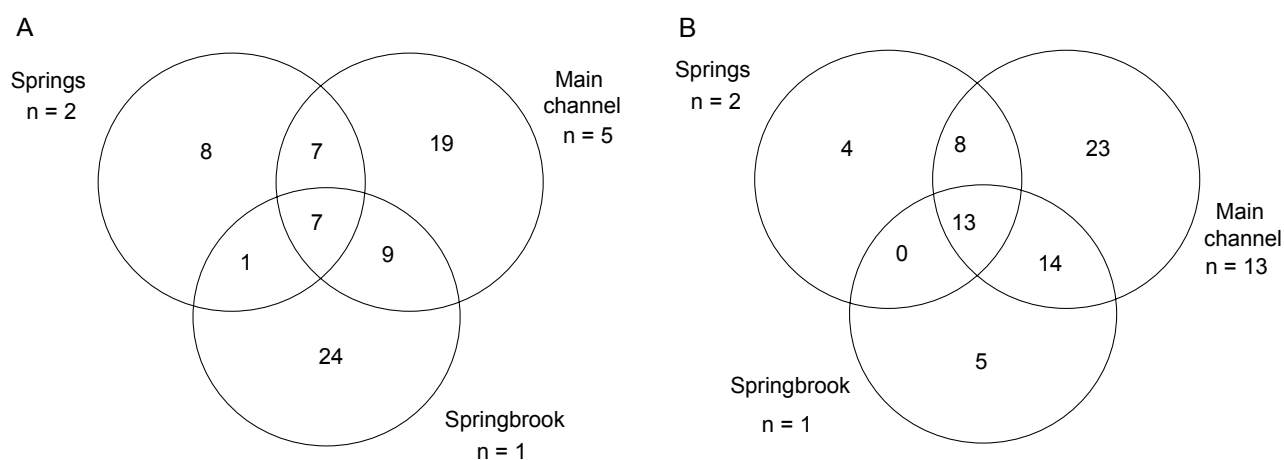


Figure 14. Numbers of algal taxa unique to spring, springbrook and main channel habitats, and combinations of the above at sites in the (A) upper, and (B) lower Waimakariri River.

Our results indicate that hydrological connectivity and habitat diversity enhances invertebrate and algal diversity in a braided river, and that spring-fed habitats are hotspots of invertebrate diversity within this landscape. They appear to constitute a stable habitat for invertebrates unable to colonise unstable, flood-prone environments, but also provide an ecotone, or zone of mixing between surface waters and groundwater, where a number of phreatic taxa may exist. Consequently, springs contained more taxa overall than any other habitat, and also the highest number of taxa unique to any one habitat.

Management of braided rivers should recognise, and seek to protect, the significant biodiversity values associated with inter-connected aquatic habitats (e.g. springs, springbrooks and main channels) within the riverscape. Protection will require a holistic approach, since the different habitats, including springs, cannot be managed as spatially-isolated entities. Managers must also be aware of the temporal dimension, expressed through the flow regime of the river. Throughout a braided river system, the distribution and permanence of springs will vary over time with river and groundwater levels—a reflection of the multi-dimensional nature of the rivers (Poole et al. 2002). Changes in river and groundwater levels through human interference with the natural flow regime are likely to influence spring distribution and permanence, although we currently lack empirical evidence of this. Further research is required to assess the effects of fluctuating flows on the invertebrate communities of spring and spring-fed habitats, so that future water allocation decisions in braided rivers will be made without ignoring an important component of the ecosystem.

4. Environmental drivers of spring communities

Springs constitute discrete habitats with relatively constant physico-chemical conditions (van der Kamp 1995), but they also exhibit ecotonal characteristics, including sharp environmental gradients, driven by their location at the interface of groundwater, surface water and terrestrial ecosystems. The physical habitat template of springs, controlled to a large extent by hydrogeology and topography, can be expected to play a major role in determining community structure.

The primary driver of spring invertebrate communities is flow permanence (Danks & Williams 1991; Erman & Erman 1995; Smith & Wood 2002). Within permanent springs, the drivers of communities may be predominantly biogeographic at large spatial and temporal scales whereas, at the local scale, conditions such as substrate, flow regime, velocity and water chemistry are important (Glazier 1991; Williams 1991; Hoffsten & Malmqvist 2000; Smith & Wood 2002; Smith et al. 2003; Barquín & Death 2006). Overlaying these effects will be human impacts, which act at a range of scales, from large-scale effects on groundwater quality through to localised impacts on the spring.

In sections 4.1–4.4 we summarise several bodies of research that have focused on describing environmental drivers of spring communities at different spatial scales. The first piece of research aggregates spring data from throughout New Zealand, in order to identify broad-scale environmental drivers. In contrast, work by Gray (2005) provides an insight into environmental drivers at the catchment scale (section 4.2). Section 4.3 provides information from studies on flow permanence as a driver of stream communities in the Selwyn River/Waikirikiriri. The final section (4.4) summarises further detailed studies focusing on land use as a key driver of spring communities.

4.1 A BROAD-SCALE ASSESSMENT OF ENVIRONMENTAL DRIVERS IN NEW ZEALAND

In order to identify distinct spring community assemblages and their environmental drivers at a broad spatial scale, we collated biological and physico-chemical data from 82 springs from around New Zealand (Fig. 15). This dataset included data from Barquín (2004), Collier & Smith (2006), Scarsbrook & Haase (2003) and data from a study of springs along the base of the Kaimai Ranges (see section 4.4.2). All biological samples (invertebrate relative abundance) were collected with 0.25-mm-mesh nets and sampling was carried out in late summer/autumn.

The River Environment Classification (REC; Snelder & Biggs 2002) was used to generate a range of environmental variables for each spring, based on its physical coordinates. The variables calculated included altitude, distance to sea, rainfall and surrounding land use. For each spring, an estimate of natural land cover (%) in the contributing catchment was calculated by pooling together the relative proportions of natural land cover categories (i.e. native forest, tussock and scrub) based on the Landcover Database (LCDB2) GIS layer. Conductivity and temperature were recorded at the 82 selected sites at the time of sampling.

To maintain consistency across the dataset, taxonomic resolution was reduced to the genus or family level. Despite this lowered resolution, a total of 108 taxa were included in the dataset. The majority (89%) of these taxa were insects, but Oligochaeta and Amphipoda were the most commonly recorded taxa, found in 70 and 51 springs, respectively. Other common invertebrates were snails of the genus *Potamopyrgus* and chironomid larvae of the subfamily Orthocladiinae and the genus *Polypedilum*, which were found in 47 and 36 springs, respectively. The number of invertebrate taxa recorded at each site varied between 3 and 44.

The existence of distinct spring assemblages around the country was determined using cluster analysis. Relative Sorensen distances were calculated on the invertebrate relative abundance dataset and Ward's variance method was used to build the cluster dendrogram within the PC-ORD statistical package (McCune & Mefford 1997). The cluster analysis identified five major site groupings based on community composition (Table 1). Insect taxa dominated Clusters 1 and 3, while non-insect taxa made up more than 70% of the invertebrate community in Clusters 2, 4 and 5. Larvae of the mayfly *Zephlebia* and the

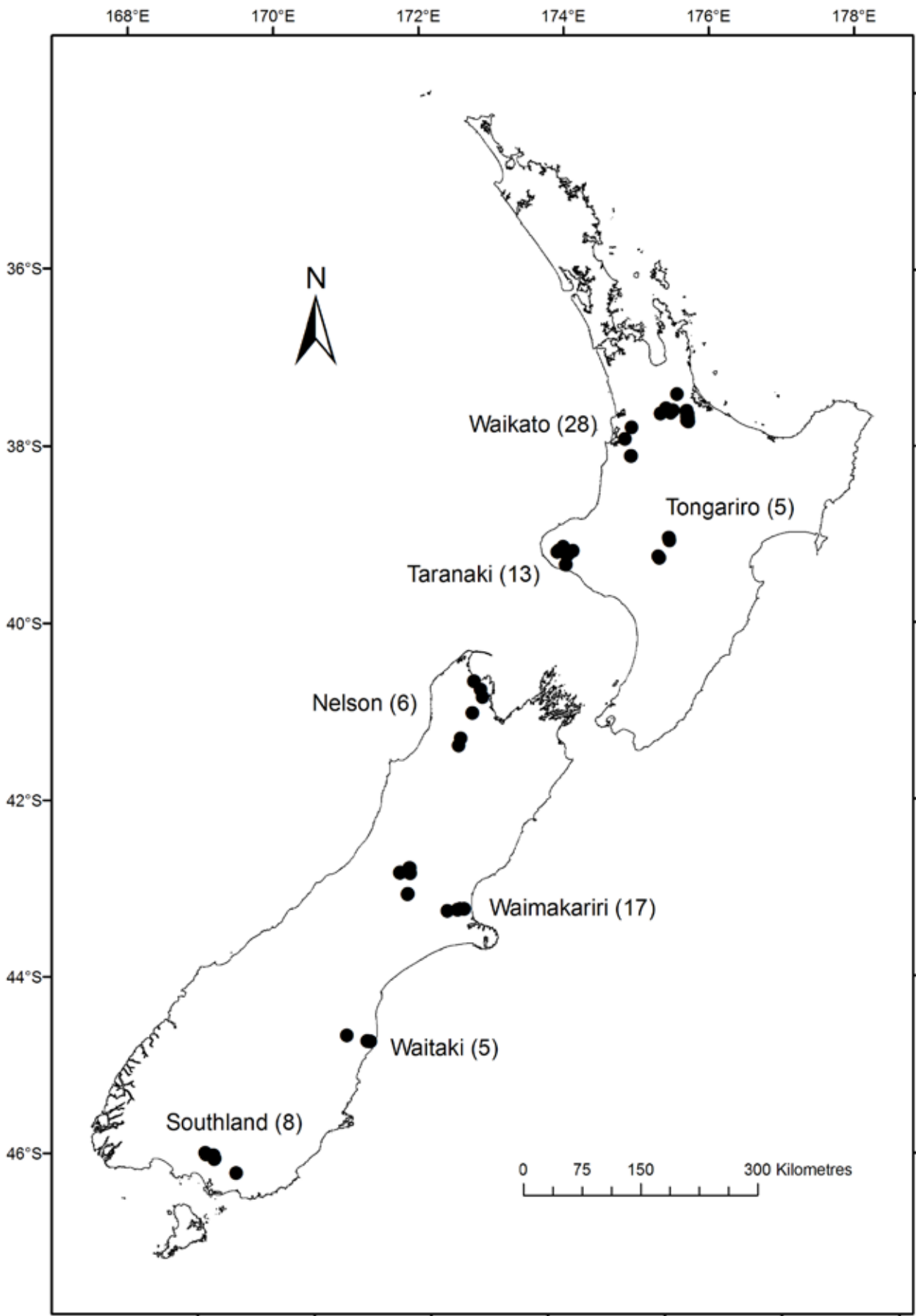


Figure 15. Locations of springs used for broad-scale analyses of environmental drivers of spring biodiversity patterns.

TABLE 1. DOMINANT TAXA (LISTED IN DECREASING RELATIVE ABUNDANCE) IN EACH OF FIVE INVERTEBRATE COMMUNITY CLUSTERS, INCORPORATING DATA FROM 82 SPRING SITES.

SPECIES	CLUSTER 1	CLUSTER 2	CLUSTER 3	CLUSTER 4	CLUSTER 5
Number of springs	21	11	22	7	21
Dominant taxa (5 most common)	<i>Polypedilum</i> <i>Zephlebia</i> Acarina <i>Potamopyrgus</i> Amphipoda	<i>Potamopyrgus</i> Amphipoda <i>Austroclima</i> <i>Oligochaeta</i> Acarina	<i>Deleatidium</i> <i>Maoridiamesa</i> <i>Naonella</i> <i>Pycnocentria</i> <i>Eukiefferiella</i>	Oligochaeta <i>Naonella</i> <i>Potamopyrgus</i> Sphaeriidae Amphipoda	Amphipoda Oligochaeta <i>Potamopyrgus</i> Orthocladinae Tricladida
Average taxon richness	13	11	26	17	11
Proportion Insecta (%)	74	28	87	26	25

TABLE 2. AVERAGE PHYSICO-CHEMICAL CHARACTERISTICS OF SPRINGS IN EACH OF FIVE INVERTEBRATE COMMUNITY CLUSTERS, BASED ON RELATIVE ABUNDANCE DATA FROM 82 SPRING SITES. RESULTS OF ANOVA ANALYSIS TESTING FOR DIFFERENCES BETWEEN CLUSTER GROUPINGS ARE ALSO GIVEN. * $P = 0.05-0.01$, ** $P < 0.01$.

PHYSICO-CHEMICAL VARIABLE	CLUSTER 1	CLUSTER 2	CLUSTER 3	CLUSTER 4	CLUSTER 5	$F_{4,77}$
Average catchment elevation (m a.s.l.)	301	250	884	382	252	14.1**
Distance to sea (km)	81.5	86.2	142.7	81.8	68.2	2.7*
Catchment rainfall (mm/y)	1891	1408	2227	1230	1323	6.5**
Percentage natural land cover (%)	37	30	89	44	28	9.7**
Temperature (°C)	14	14	11	14	14	6.3**
Conductivity ($\mu\text{S}/\text{cm}$ @ 25°C)	181	200	116	171	207	3.3*

chironomid *Polypedilum* dominated invertebrate communities in springs from Cluster 1, whereas *Deleatidium* and the chironomids *Maoridiamesa* and *Naonella* dominated invertebrate communities in Cluster 3. *Potamopyrgus*, oligochaetes and amphipods dominated spring invertebrate communities in Clusters 2, 4 and 5, respectively (Table 1). Average numbers of invertebrate taxa were more than two times higher in springs from Cluster 3 than in springs from Clusters 1, 2 and 5.

Springs from different clusters showed significant differences in physico-chemical attributes (Table 2). In particular, Cluster 3 stood out from the others, because of high elevation, high rainfall, high percentage natural land cover and low temperatures. This cluster also had the highest average taxon richness, and highest percentage Insecta (Table 1). Several univariate measures of community composition were also significantly associated with these broad-scale variables. For example, simple regression analysis showed a significant positive association ($R^2 = 0.54$; $P < 0.001$) between taxon richness and percentage natural land cover (Fig. 16A). In addition, there appeared to be a threshold effect, with higher taxon richness (i.e. > 20) only observed at springs where natural land cover exceeded 30%. There was also a significant positive association between Insecta (%) and elevation ($R^2 = 0.31$; $P < 0.001$). Again, there appeared to be a threshold effect, whereby insect dominance became increasingly pronounced at springs above 300 m a.s.l. (Fig. 16B).

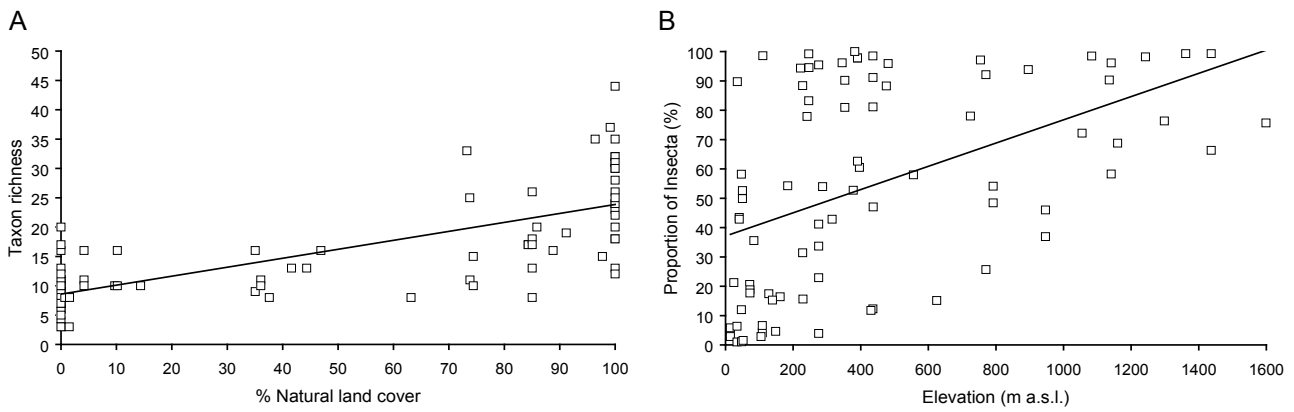


Figure 16. (A) Association between percentage natural land cover and taxa richness in springs. (B) Association between spring elevation and proportion of Insecta across 82 spring sites.

4.2 ENVIRONMENTAL DRIVERS IN A BRAIDED RIVER LANDSCAPE

In a study of 41 springs within the braided flood plain of the upper Waimakariri River, Gray (2005) examined the influence of flow permanence on spring invertebrate community structure. Sites were visited on six occasions, and permanence was measured as the proportion of site visits when water was found to be flowing at the sites. A Multi-Dimensional Scaling (MDS) ordination on coded abundance data (Fig. 17) showed a separation of spring sites of varying permanence along Axis 1. The spring with the lowest permanence had only a single species, the dytiscid beetle *Huxelbydrus syntheticus*. This species is commonly found in shallow temporary pools on the shingle beds of rivers on the eastern flanks of the Southern Alps (Winterbourn et al. 2000). The three sites exhibiting 66% permanence were numerically dominated by various chironomids and larvae of the sandfly *Austrosimulium*. The two sites that were 85% permanent were also numerically dominated by chironomids and sandfly larvae. However, they also contained numerous caddisfly, dipteran and mayfly larvae, taxa that dominated at the permanent sites.

In Fig. 17, permanent springs formed a large, variable cluster. In an attempt to identify environmental factors that might contribute to the variation observed in permanent springs within a braided river landscape we used a composite dataset from a total of 51 springs combined from two separate studies on spring habitats in the upper Waimakariri River (Gray 2005; Kilroy et al. 2004).

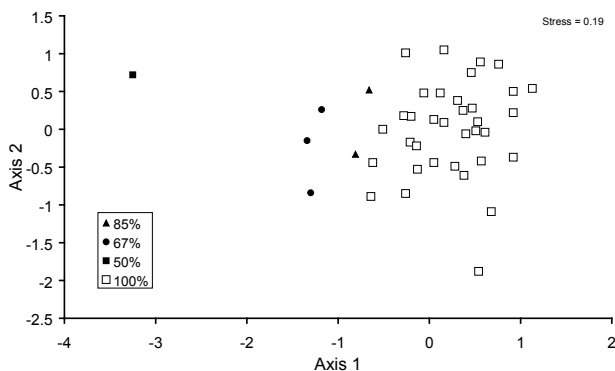


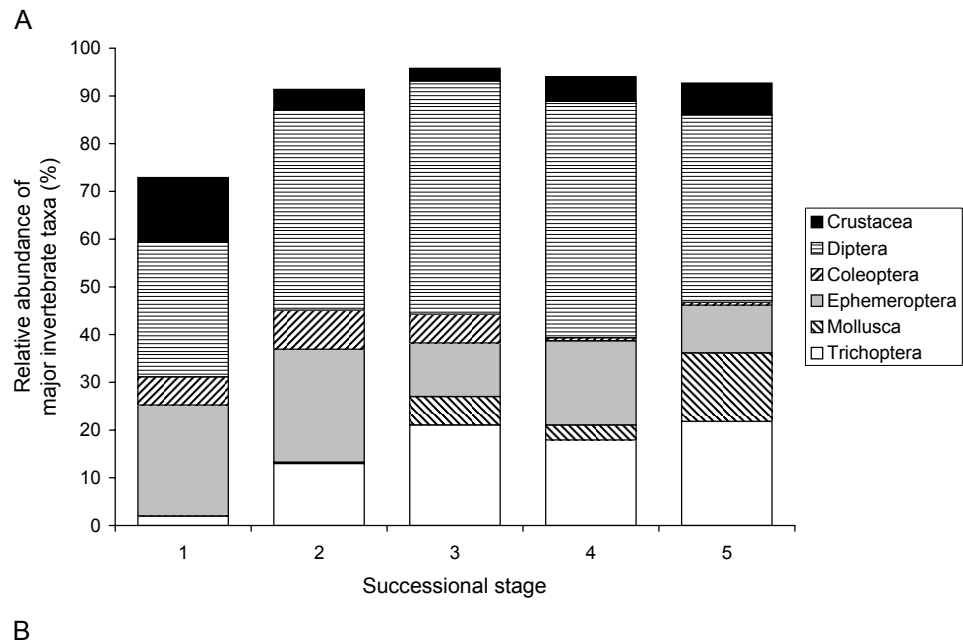
Figure 17. MDS ordination of benthic invertebrate communities in springs. Sites are delineated according to permanence of flow. The majority of sites were always flowing and thus exhibited 100% permanence.

Sites were classified in terms of their successional stage, based on vegetation types surrounding the spring (Reinfelds & Nanson 1993). Briefly, Reinfelds & Nanson (1993) identified a successional gradient of river floodplain habitats in the Waimakariri River based on dendrochronology and time-lapse aerial photography. Stage 1 habitats were in the active bed of the river and might be expected to be reworked within any one year (age 0). Stages 2–5 represent increasing times between flood-controlled reworking, with ages of 3–30, 30–50, 50–150 and 150–300 years respectively. Percentage cover of macrophytes was also estimated by eye for each spring.

Invertebrate community composition varied markedly with successional stage (Fig. 18A). Mayflies, dipterans and Crustacea were the main components of the community in the youngest springs. These habitats were within the active channel of the river and were characterised by an absence of macrophytes (Fig. 18B). It is interesting to note that this class had the highest proportion of Crustacea, with hypogean taxa (e.g. *Paraleptamphopus* spp. and *Phreatogammarus* sp.) dominating. Relative abundance of Trichoptera, particularly cased-caddis, and Mollusca increased significantly along the successional gradient of spring habitats (one-way ANOVA, $P < 0.05$). Conversely, Coleoptera were a significant faunal component in springs of an early successional stage (i.e. Stages 1-3), but were rare in older springs (i.e. Stages 4-5).

Macrophyte cover also varied with successional stage of springs in the Waimakariri River (Fig. 18B), and the presence of macrophytes may have been a contributor to changes in invertebrate communities. To separate the potential interacting effects of macrophyte cover and successional stage on invertebrate communities, Gray (2005) carried out a controlled macrophyte

Figure 18. (A) Relative abundance of major invertebrate taxa across successional stage in upper Waimakariri River floodplain springs. (B) Percentage cover of macrophytes within springs habitats varying in successional stage (as defined by Reinfelds & Nanson 1993).



removal experiment in four late-successional stage springs. The removal of macrophytes resulted in a reduction in invertebrate abundance, but an increase in community evenness. Invertebrate communities shifted from dominance by Diptera and *Potamopyrgus* in undisturbed macrophyte quadrats, to communities dominated by Ephemeroptera and Trichoptera on the inorganic substrates remaining after macrophyte removal.

Gray (2005) suggested that observed differences in community composition over successional stage in springs were probably due to differences in dispersal ability (i.e. differences among species in their ability to colonise more frequently disturbed, early successional stage springs) and habitat preference (i.e. preferences for organic v. inorganic substrates). Other studies have also shown successional gradients based on time since major disturbance, e.g. glaciation or river channel migration, owing to the variable dispersal abilities of invertebrates (Hoffsten & Malmqvist 2000; Milner et al. 2000; Barquín 2004). However, local-scale factors, such as presence/absence of aquatic plants, may also play an important role in structuring spring invertebrate communities in New Zealand.

4.3 FLOW PERMANENCE AND SPRING BIODIVERSITY

Flow permanence is a critical factor in determining biological diversity in springs (Danks & Williams 1991; Erman & Erman 1995). For example, Smith & Wood (2002) found that flow permanence had a greater influence on invertebrate communities of limestone springs in the United Kingdom than any other physical or chemical variable examined. They found clear differences in the macroinvertebrate communities observed in perennial and intermittent springs. Several authors have suggested that permanent springs have a distinctive fauna, with particular traits that limit them to these permanent habitats (e.g. Erman & Erman 1995; Erman 2002; Gray 2005). These authors hypothesise that strong dispersal ability is the critical factor in determining persistence of particular taxa in ephemeral spring habitats, whereas biota with low dispersal abilities are expected to be more common in permanently flowing springs. Recent research in the Selwyn River/Waikirikiri has investigated the influence of flow permanence of lotic habitats within the river, and some preliminary data from spring-fed remnant channels along a permanence gradient in the river allows us to test this hypothesis.

Three permanent springs and three ephemeral springs were sampled along the Selwyn River/Waikirikiri on two occasions (November 2003 and October 2004) using a Hess sampler (mesh size = 0.25 mm). Average taxon richness (\pm SD) was higher in permanent springs (37.6 ± 5.1) than in ephemeral channels (21.7 ± 2.9), and this difference was statistically significant (two sample *t*-test; $P=0.016$). The permanent sites included taxa of relatively low mobility (e.g. conoesucid caddisflies: *Olinga feredayi*, *Pycnocentroides* sp.) and longer generation times (e.g. *Stenoperla prasina*). In contrast, the ephemeral sites were dominated by multivoltine taxa such as chironomids (e.g. *Cricotopus* sp.) and species with high mobility (e.g. *Deleatidium* sp.). A number of taxa were entirely absent from the ephemeral sites and these can be considered to be potential indicators of flow permanence in springs (Table 3). The limited data from the Selwyn River/Waikirikiri provides further support for the conclusions of Gray (2005) that spring permanence have significant influences on spring community composition.

TABLE 3. POTENTIAL INDICATORS OF FLOW PERMANENCE IN SPRINGS. TAXA ARE SHOWN IN ORDER OF DECREASING RELATIVE ABUNDANCE.

TAXA EXCLUSIVE TO PERMANENT SPRINGS	TAXA EXCLUSIVE TO EPHEMERAL SPRINGS
<i>Olinga feredayi</i> (Trichoptera: Conoesucidae)	<i>Polypedilum</i> spp. (Diptera: Chironomidae)
<i>Potamopyrgus antipodarum</i> (Rissooidea: Hydrobiidae)	Scirtidae (Coleoptera)
<i>Pycnocentroides</i> sp. (Trichoptera: Conoesucidae)	Oligochaeta
<i>Polyplectropus</i> (Trichoptera: Polycentropodidae)	Staphylinidae (Coleoptera)
<i>Xantboenemis zelandica</i> (Odonata: Coenagrionidae)	<i>Ephydrella</i> (Diptera: Ephydriidae)
<i>Stenoperla prasina</i> (Plecoptera: Eustheniidae)	<i>Antiporus</i> sp. (Coleoptera: Dytiscidae)
<i>Neozeplebia scita</i> (Ephemeroptera: Leptophlebiidae)	
<i>Archibauliodes diversus</i> (Megaloptera: Corydalidae)	

4.4 LAND-USE EFFECTS ON SPRING BIODIVERSITY PATTERNS

In section 2.3 it was noted that more than 50% of springs in the existing database were found within catchments dominated by pastoral agriculture. This highlighted a need for information on the effects of land-use, and pastoral agriculture in particular, on the biodiversity values of springs.

In comparison with streams fed by run-off in agricultural landscapes, permanent springs may be buffered to some extent against land-use effects. They receive a constant supply of clear, cool groundwater, so invertebrate communities may not be subject to some of the major stressors present in streams in agricultural catchments (e.g. Quinn 2000). Conversely, the absence of floods may make springs more susceptible to other land-use stressors, such as the smothering of habitats by fine sediments. This may be particularly prevalent in areas where stock access may lead to bank collapse.

Spring research by NIWA over the last 3 years has included two complementary studies of land-use effects on spring biodiversity patterns. The first study provided a broad-scale assessment of the effects of riparian vegetation types on spring communities (Scarsbrook & Haase 2003). A second, more intensive study, focused on separating the potentially interacting effects of riparian land use and stock access on spring ecosystems (MS, 2004, unpubl. data).

4.4.1 A broad-scale survey of land use and spring communities

Early in the NIWA springs research programme we surveyed springs in dairying landscapes. The Department of Conservation and New Zealand Dairy Industry funded this research, and full results are presented in Scarsbrook & Haase (2003).

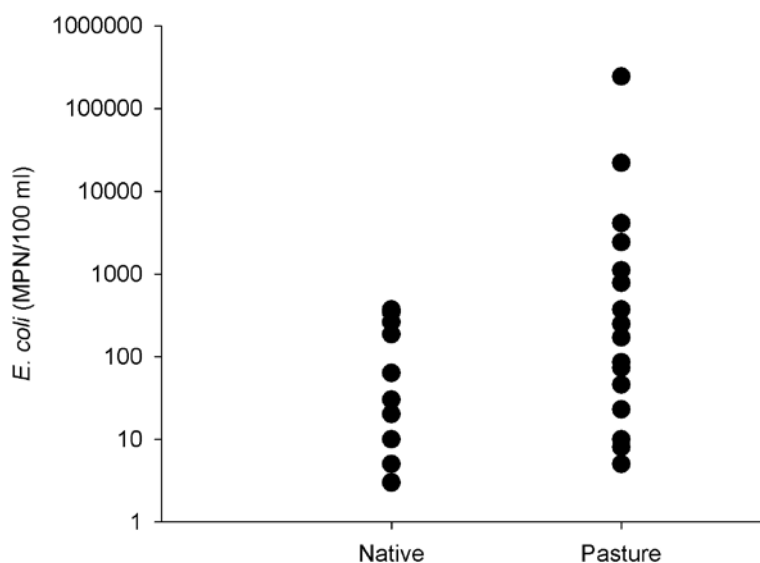
A total of 34 spring sites in four regions were sampled in January and February 2003 (Table 4). Each spring site was classified as having a riparian zone with either native vegetation or pasture. All sampled springs were small, with discharges estimated to be generally less than 10 L/s.

Levels of the faecal bacterium *Escherichia coli* were measured to provide an indicator of land-use intensity/disturbance (Fig. 19). Scarsbrook & Haase (2003) assumed that elevated levels of *E. coli* reflected stock access and subsequent spring disturbance. In fact, they found that the three springs with highest

TABLE 4. LOCATION AND LAND USE DESIGNATIONS OF 34 SPRINGS FROM FOUR REGIONS AROUND NEW ZEALAND.

SITE NAME	EASTING	NORTHING	ELEVATION (m a.s.l.)	RIPARIAN VEGETATION
Waikato 1	2742341	6379151	100	Pasture
Waikato 2	2762719	6381230	80	Pasture
Waikato 3	2762735	6381485	80	Pasture
Waikato 4	2762688	6381295	80	Pasture
Waikato 5	2742012	6379626	80	Pasture
Waikato 6	2745617	6382047	80	Pasture
Waikato 7	2745607	6381947	80	Pasture
Waikato 8	2736329	6384534	40	Pasture
Waikato 9	2736423	6384530	40	Pasture
Waikato 10	2765201	6372183	390	Native
Waikato 11	2729466	6378231	60	Pasture
Taranaki 1	2610365	6201210	380	Native
Taranaki 2	2610378	6201293	380	Native
Taranaki 3	2608919	6201195	380	Pasture
Taranaki 4	2613258	6202808	360	Native
Taranaki 5	2613258	6202808	380	Native
Taranaki 6	2607802	6186932	100	Pasture
Taranaki 7	2616983	6204533	360	Native
Taranaki 8	2609321	6198453	310	Native
Taranaki 9	2613440	6203202	380	Native
Taranaki 10	2611096	6201434	380	Native
Canterbury 1	2353700	5584700	40	Pasture
Canterbury 2	2353300	5584900	40	Pasture
Canterbury 3	2327070	5592110	120	Native
Canterbury 4	2357300	5584600	40	Pasture
Canterbury 5	2357000	5584500	40	Pasture
Southland 1	2156477	5440509	100	Pasture
Southland 2	2156477	5440509	100	Pasture
Southland 3	2145883	5443277	50	Pasture
Southland 4	2157150	5435620	180	Native
Southland 5	2146775	5441484	50	Pasture
Southland 6	2156356	5439346	100	Native
Southland 7	2157771	5436460	120	Pasture
Southland 8	2185089	5417855	20	Pasture

Figure 19. Levels of *Escherichia coli* bacteria collected at 34 spring sources around New Zealand with either a native vegetation or pasture riparian zone. Scarsbrook & Haase (2003).



levels of *E. coli* were in pasture where stock were excluded. However, waterfowl (mallard ducks, *Anas platyrhynchos*) were present at all three springs, and it is likely they were the source of faecal contamination.

Comparison of community composition across the 34 springs indicated that riparian vegetation type (native or pasture) at the spring may be an important determinant of community composition, as shown in a multidimensional scaling ordination of invertebrate relative abundance data (Fig. 20). An Analysis of Similarities (ANOSIM; Primer 5) identified a significant separation of pasture and native sites in ordination space (Global $R=0.49$; $P=0.001$). Native sites are generally to the right, whereas pasture sites are to the left of Axis 1 of a 2-dimensional non-metric multidimensional scaling ordination. The pattern was particularly strong in Taranaki, where two pasture sites are at the left of Axis 1, whereas the other eight sites, all with native riparian vegetation, cluster to the right. Axis 1 scores were negatively correlated with temperature ($r_s = -0.42$; $P < 0.05$), which suggests that springs in pasture may be exposed to thermal stress. Spot measurements of temperature ranged from 21.7°C (Waikato 9) to 9.9°C (Southland 4).

Despite overall similarities in community structure associated with riparian vegetation type, Scarsbrook & Haase (2003) also found regional differences in spring community structure. For example, taxa belonging to the Ephemeroptera, Plecoptera and Trichoptera were relatively diverse in Taranaki springs, with the exception of those lacking canopy cover. Across all 34 springs, %EPT_{taxa} (i.e. the proportion of taxa belonging to Ephemeroptera, Plecoptera and Trichoptera) varied from 0% to 41% (Taranaki 9). In the Taranaki springs with native riparian vegetation, the average was 26%, which was the highest of the four regions. Within the Taranaki landscape, small gullies containing remnant bush appear to be relatively common, and held distinctive spring faunas (e.g. *Zephebia nebulosa*, *Pseudoeconesus* spp.). We suggest that these small bushy gullies form important areas of 'natural' biodiversity within the dairying landscape of this region. It is interesting to note that the one Waikato site with intact

Figure 20. MDS ordination plot of invertebrate relative abundance data from 34 spring sites in four regions (WAI = Waikato, TAR = Taranaki, CAN = Canterbury, SOU = Southland). Open symbols denote pasture, and filled symbols denote native riparian vegetation.

