



New Zealand coldwater springs and their biodiversity

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Mike Scarsbrook, José Barquín and Duncan Gray

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ABSTRACT

Coldwater springs are a significant component of the New Zealand landscape, yet they have received little attention from freshwater ecologists and conservation managers. Recently, a major research effort has been directed towards understanding the invertebrate biodiversity values of coldwater springs, identifying key environmental drivers of biodiversity patterns, and setting out a framework for spring management. Coldwater springs contain a highly diverse invertebrate fauna, including species from both surface and groundwater ecosystems, and also species that appear to be restricted to spring habitats (e.g. some hydrobiid snails and isopods). Biodiversity patterns are strongly influenced by flow permanence, disturbance history, elevation, catchment land use and riparian vegetation structure. Springs and their biota face significant threats from unsustainable use of groundwaters and the destruction of spring habitats. Management of springs, particularly on lowland alluvial plains, should be intimately linked with groundwater management so that spring flows and groundwater quality are maintained at the aquifer scale. Protection and rehabilitation of springs may also be required at the local scale, especially on private land, so that representative habitats are maintained within the landscape. A number of knowledge gaps are identified that may affect our ability to effectively manage and protect coldwater springs. This report identifies coldwater springs as important components of New Zealand's freshwater ecology that require more conservation attention than they have received to date; ways to address these omissions are suggested.

Keywords: springs, macroinvertebrates, biodiversity, land use, ecotones, conservation, knowledge gaps

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1. Introduction

Springs are formed when the water table intersects with the earth's surface, or groundwater rises to the surface through rock faults, fractures or depressions (Death et al. 2004). Springs form groundwater-dependent ecosystems (GDEs) (Hatton & Evans 1998). As they occur when groundwater flow paths intersect the earth's surface, their defining physico-chemical characteristics (e.g. thermal and hydrological stability) are controlled by the hydrogeological properties of their parent aquifer (van der Kamp 1995). Springs occur throughout the landscape, but vary greatly in morphology and size, ranging from minor seepages from bedrock faces, to alluvial springs in braided river landscapes, to resurgences in karst (e.g. Riwaka River resurgence, near Motueka), up to very large vents discharging many thousands of litres per second (e.g. Waikoropupu Springs, Takaka). A unique characteristic of springs is that they form a three-way zone of interaction between groundwater, surface water, and terrestrial ecosystems.

Environmental stability, and the location of springs at the interface between several distinct ecosystems, has led ecologists to suggest that springs are 'hot spots' for aquatic biodiversity. A good example of the important contribution of springs to aquatic (and terrestrial) biodiversity is illustrated by research in arid areas of inland Australia (Knott & Jasinska 1998) and the United States (Sada 2005). Springs provide small mesic (moist) refuges in arid landscapes and have been critical to the survival of indigenous peoples, European explorers and settlers, and their livestock. They also have a distinctive flora and fauna, with high levels of local endemism (Knott & Jasinska 1998), particularly among animals with restricted powers of dispersal (e.g. hydrobiid snails, amphipods and some fish). For example, Ponder & Clark (1990) identified 12 hydrobiid species of a single genus (*Jardinella*) in just four mound spring groups of southwestern Queensland. All species were endemic to a particular spring group.

The positioning of springs at the interface of groundwater, surface water and terrestrial ecosystems has led to inevitable conflicts between human resource use within these ecosystems and the natural ecosystem integrity of springs (Sada 2005). Human activities can have significant effects on the parent aquifer (e.g. effects on water quantity and quality), the spring (e.g. water supply takes and riparian habitat modification by stock grazing and trampling) and the connectivity between the spring and other aquatic habitats (e.g. isolation of springs in a degraded landscape) (Smith 2002). Overall, spring habitats, and the biological diversity they support, can be regarded as controlled by a natural environmental template that is overlain by varying levels of human impact. Conservation of spring systems will generally depend on two issues: maintenance of groundwater quantity and quality and minimisation/mitigation of anthropogenic disturbance to the springs themselves and their associated habitats (Knott & Jasinska 1998).

During the 1990s a number of reviews of spring ecology were published in countries other than New Zealand (Williams & Danks 1991; Ferrington 1995; Botosaneanu 1998). These reviews have provided a solid knowledge base

for the development of management strategies to protect the biodiversity values inherent in springs (e.g. Sada et al. 2001), and have also provided an impetus for more focused ecological studies that address particular knowledge gaps (e.g. Hoffsten & Malmqvist 2000; Smith & Wood 2002; Sada 2005). In New Zealand, our knowledge of coldwater springs has lagged far behind that of North America, Europe and Australia. There have been very few published ecological studies of coldwater springs, and this lack of knowledge is recognised as a constraint to management and protection of these valuable resources.

Over the last 5 years a significant research effort has been directed at addressing this knowledge gap. Funding from the Department of Conservation (DOC), the Foundation for Research, Science and Technology (FRST) and the New Zealand Dairy Industry has supported spring biodiversity research by the National Institute of Water & Atmospheric Research (NIWA). In addition, postgraduate studies at Massey University and the University of Canterbury have added significantly to our ecological understanding of pristine spring systems. Barquín (2004) sampled invertebrate communities from springs and springbrooks in four National Parks around New Zealand (Arthur's Pass, Kahurangi, Tongariro and Egmont). Gray (2005) focused his studies on the ecology of braided river springs, with much of the research located in the upper Waimakariri River catchment, Canterbury, South Island.

1.1 OBJECTIVES

The principal aims of this report are to summarise the state of our knowledge regarding the ecology of New Zealand coldwater springs, and to utilise this knowledge to identify management approaches. This report is structured around four specific objectives:

- Identify biodiversity values of coldwater springs in New Zealand
- Determine key environmental drivers of spring biodiversity
- Identify anthropogenic threats to spring ecosystems and quantify effects
- Determine appropriate spatial scales and strategies for conservation and management of spring habitats

In this report we summarise the major findings of research under each objective, and draw on international published literature to summarise our state of knowledge with respect to biodiversity values in springs. We also provide recommendations for more effective conservation of spring biodiversity and suggest a framework for management of New Zealand's coldwater springs.

1.2 DEFINITIONS AND SCOPE OF REPORT

A spring is a defined area where a natural discharge of groundwater returns to the surface (van Everdingen 1991; White 2005). One significant area of confusion in the literature is caused by misuse of the term 'spring' when referring to 'springbrooks' (Erman & Erman 1995). Springs have distinct

physico-chemical and biological characteristics, which become modified as groundwater mixes within a surface water body (e.g. changes with distance downstream in a springbrook; Barquín 2004). However, defining the point at which a spring becomes a springbrook, or a spring-fed wetland, is problematic, as changes occur gradually and vary with the environmental variable being measured. Also, the transition from spring to springbrook depends on the size of the spring and its receiving waterbody (e.g. springbrook, river, wetland or lake). McCabe (1998) introduced a definition based on thermal characteristics, using temperature variation to define the transition from spring to springbrook as the point at which temperature variation exceeds 2°C. This definition requires intensive monitoring of each spring, which is often impracticable. Throughout this report we refer to springs wherever our sampling occurred within a few metres of a defined source of groundwater discharge, and where physico-chemical conditions were assumed to reflect groundwater influence; otherwise, we use the term springbrook.

Throughout this report we refer to springs as ‘ecotones’. This reflects the unique position of springs at the interface between groundwater, surface water and terrestrial ecosystems (Fig. 1). An ecotone is a zone of interaction and exchange between adjacent ecosystems. Ecotones possess specific physical and chemical attributes, biotic properties, and energy and material flow processes, but each is unique in its interactions with adjacent ecosystems (Naiman & Decamps 1997). Contemporary stream ecology recognises an important role for ecotones in the structural (e.g. community structure, biodiversity) and functional attributes (e.g. carbon and nutrient dynamics) of freshwater ecosystems (Naiman & Decamps 1997; Ward & Tockner 2001).

As groundwater-dependent ecosystems (GDEs), springs are controlled by groundwater level, discharge flux from the aquifer and groundwater quality (Sinclair Knight Mertz 2001). These ecosystems include terrestrial vegetation communities, river base flow systems, aquifer and cave ecosystems, wetlands, and springs. In Australia, management of GDEs is a state and federal issue and a number of management recommendations have been identified to protect them from a range of anthropogenic threats. We suggest that the GDE framework will be useful for managing springs and other groundwater habitats in New Zealand.

Biological diversity (biodiversity) is much more than species or genetic diversity. It also includes functional (process) diversity and habitat diversity (Ward et al. 1999). The New Zealand Biodiversity Strategy (DOC 2000)

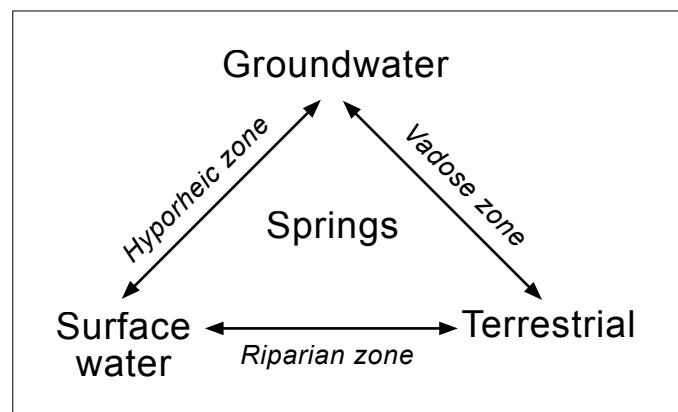


Figure 1. Springs form a three-way ecotone, or zone of interaction, between groundwater, surface water and terrestrial ecosystems. Other ecotones include the riparian zone (stream banks), the vadose zone (unsaturated soils) and the hyporheic zone (streambed interstices).

defines biodiversity as ‘the variability among living organisms from all sources including, inter alia, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species, and of ecosystems’. Components include genetic diversity, species diversity and ecological (ecosystem) diversity. In this report we address all three of these aspects of biodiversity as they relate to springs habitats.

Our report is restricted to describing biodiversity in coldwater springs (i.e. springs in which temperatures do not exceed 20°C). We do not include mineral springs (i.e. springs having Total Dissolved Solids >1000 mg/L), or thermal springs (i.e. springs with a mean annual temperature more than 5°C greater than mean annual air temperature). Death et al. (2004) provide a useful review of the biodiversity values occurring in New Zealand’s geothermal springs.

2. Springs in the landscape

Springs are surface expressions of groundwater flow processes which, in turn, are controlled by geology, climate and topography (Fetter 1980). Hence, the location of a spring in the landscape, and its environmental characteristics (e.g. discharge rate, flow permanence, temperature, water chemistry and substrate) are controlled by the hydrogeological setting of the spring and its parent aquifer (van der Kamp 1995).

Hydrogeologists recognise a wide variety of spring types, and several physical classification schemes have been developed to describe the interaction between springs, the underlying groundwater and the surrounding landscape. The most basic classification separates gravity springs (in which water flows down an elevation gradient) and artesian springs (in which the potentiometric level of groundwater is higher than the land surface and the water discharges under pressure). Fetter (1980) described five main classes of springs:

- *Depression spring*—A topographical depression intersects an unconfined aquifer.
- *Contact spring*—A permeable, water-bearing stratum overlies an impermeable stratum. Water discharges where the contact zone between the strata intersects the land surface.
- *Fault spring*—A faulted, impermeable rock stratum is located downslope of a groundwater flow path.
- *Sinkhole spring*—The process of dissolution of carbonate rocks (karstification) has led to the development of a sinkhole that has intersected the water table.
- *Fracture spring*—The fracture zone between two opposing rock strata provides a flow path for groundwater to discharge.

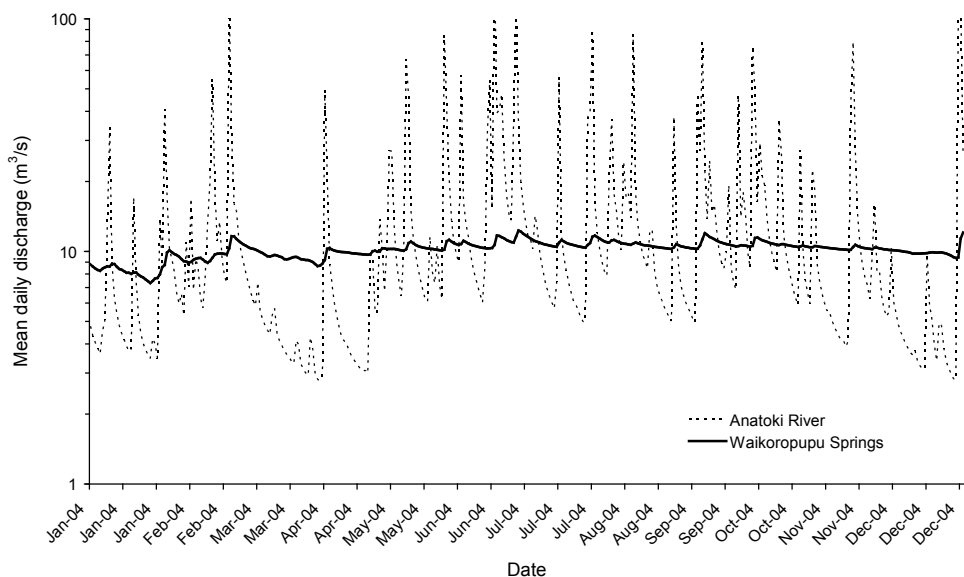
In addition to classifications proposed by hydrogeologists, some classification schemes have also been proposed by aquatic biologists (e.g. Zollhöfer et al. 2000). The most common of these was first proposed by Steinman (1915), who developed a typology based on flow patterns:

- *Limnocrene*—A spring discharges through the bed of a pond or lake (e.g. Waikoropupu Springs).
- *Rheocrene*—A spring's discharges form a flowing stream (e.g. Riwaka Resurgence).
- *Helocrene*—Small springs (seepages) form a spring-fed marsh.

It is interesting to note that classifications proposed by biologists tend to stress the role of springs as source of surface water habitats, whereas definitions put forward by hydrogeologists tend to focus on springs as the endpoint of groundwater flow paths. In this report we do not provide a full classification of spring types. Instead, we characterise springs by their underlying geology and land-use characteristics. In terms of underlying geology, we recognise three major types of springs in the New Zealand landscape:

- *Karst springs*—Springs are a conspicuous feature of karst areas, because groundwaters tend to become concentrated in relatively large fissures or conduits that are found in these areas (Williams 2004). The largest karst spring complex in New Zealand is Waikoropupu, which drains the karst aquifer of the Takaka Valley (Williams 2004). Other main areas of karst in New Zealand include the King Country (central North Island) and the Punakaiki area (West Coast, South Island). Karst springs tend to be more permanent than other spring types, because of their size and the age and stability of the geological formations they drain. Karst springs also tend to have lower hydrological stability than other spring types, often subtly tracking changes of flow in the catchment (Fig. 2), as a result of high levels of connectivity between the catchment, the caves and conduits within the aquifer and the spring outlets (White 2005).

Figure 2. Discharge hydrograph for the main vent of Waikoropupu Springs (site 52903) and the nearby Anatoki River (site 2870013). Data supplied by Tasman District Council.



- *Volcanic springs*—Different types of aquifers can feed volcanic springs. They may form in a variety of volcanic situations, for example in andesitic lava flows (e.g. Ohinepango Springs, Ruapehu) or fractured basalts (e.g. Western Springs, Auckland). Water in this latter type of aquifer travel through cracks and fissures formed when the once-liquid magma solidifies and cools. Springs usually originate where there is a change in the geology, for example from confining lava flows to volcanic breccia (e.g. Bubbling Springs, Taranaki). The age of these springs will be highly dependent on the history of the volcanic region. For example, springs located on the western flanks of Mt Ruapehu rest on lahars and river sediments that have not been disturbed or highly altered for 20 000 years (Thornton 1985) (e.g. Waitaiki Spring), whereas springs on the eastern side of the mountain have experienced a series of major disturbances in the last 200–4000 years (Neall et al. 1999) (e.g. Ohinepango Springs and Waihohonu Springs). Mt Taranaki presents a similar example. Springs on the southeast side of the mountain rest on deposits that have remained undisturbed for the last 10 000 years, whereas springs on the eastern side (e.g. Bubbling Springs) may have received lahars some 500–1000 years ago (Soons & Selby 1992). Volcanic springs tend to have high permanence and exhibit a high degree of hydrological stability.
- *Alluvial springs*—Aquifers feeding alluvial springs have a sedimentary origin (unconsolidated glacial and fluvial alluvium). The sediments have intergranular porosity which allows water to move through them. Springs from alluvial aquifers usually form where the water table meets the ground surface (i.e. they are usually depression springs). As a consequence, alluvial springs tend to migrate along channels as groundwater levels rise and fall. This type of spring was termed a ‘linear spring’ in the typology of Zollhöfer et al. (2000), and is commonly observed in alluvial river valleys (e.g. Waimakariri River and Selwyn River/Waikirikiriri, Canterbury). Alluvial springs often arise where groundwater flow paths are forced upwards by impermeable strata. Examples are seen along the eastern edge of Ruataniwha Plains, in the southern Hawke’s Bay area, where the underlying aquifers are forced upwards by the limestone strata of the Raukawa Range to the east of the plains (HBRC 2004). Most alluvial springs originated after the deposition of glacial colluvium from the upper Quaternary, which implies that the oldest of these springs may be 15 000–10 000 years old. The permanence of alluvial springs is strongly controlled by the characteristics of the parent aquifer—springs draining shallow, unconfined aquifers will tend to have lower permanence than artesian springs fed by deeper, confined aquifers.

2.1 ENVIRONMENTAL TEMPLATE OF SPRINGS

Spring habitats are characterised by thermal constancy, and relative hydrological stability (van der Kamp 1995). These features vary among spring types, but in comparison with streams which are dominated by run-off, springs are highly stable environments. There are few flow recorders in springs in New Zealand. One exception is the main vent of Waikoropupu Springs, which is closely monitored because of concerns about the effects of upstream water abstraction and land use on flows in this internationally recognised system.

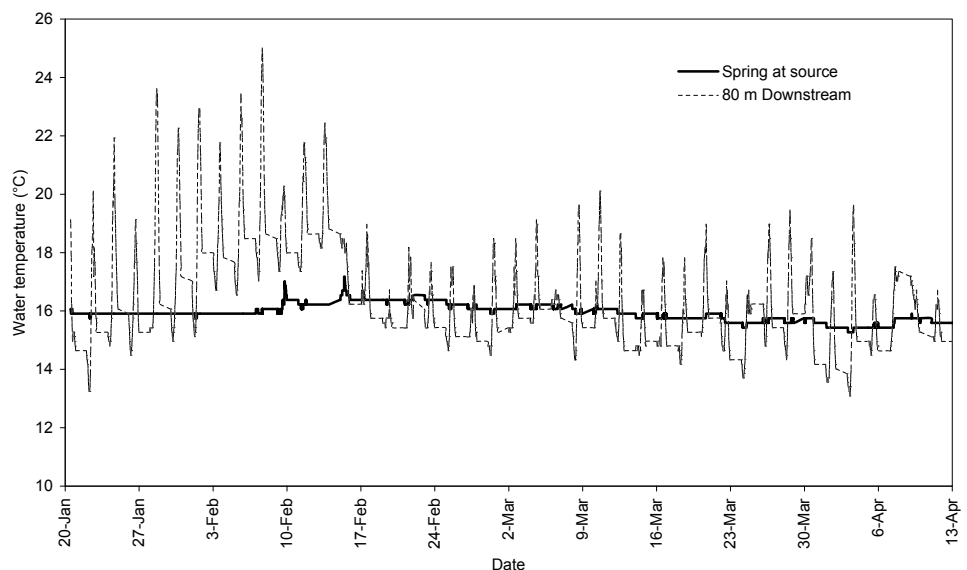
By comparing the springs' discharge with that of the nearby Anatoki River (Fig. 2), it is clear that the springs respond relatively quickly (albeit subtly) to rainfall and exhibit flow recession during drier periods (note that the log scale tends to exaggerate the variation in the spring flows and under-represent those of the river).

Hydrogeologists use spring hydrographs to measure spring permanence, using the flow recession time constant. This is the time required for flow to decrease to 37% of the initial value during prolonged dry periods (van der Kamp 1995). The recession times of springs may vary from a few hours to decades and are strongly related to the hydrogeological context of the underlying aquifer. Spring permanence is proportional to aquifer storage capacity and residence time, and inversely proportional to permeability of the parent formations (van der Kamp 1995). Evapotranspiration loss around springs, particularly those surrounded by heavy natural vegetation, can have significant effects on spring permanence, with some springs drying up completely during hot, dry weather when evapotranspiration losses are greatest.

The characteristic thermal stability of springs reflects the constant temperature of groundwater below about 10 m depth (van der Kamp 1995). The average water temperature for most springs is approximately equal to the average mean air temperature of the area (van der Kamp 1995). This provides a simple means of separating coldwater and thermal springs based on temperature alone.

The thermal stability of springs is also used to delineate springs from springbrooks (Barquín 2004), although the extent of the spring will depend on discharge, the residence time (rheocrenes have lower residence time than helocrenes) and the amounts of solar radiation reaching the water (controlled by factors such as shade and altitude). The change in thermal regime downstream of a spring is illustrated in Fig. 3. Water temperature measured during summer 2004 in a small spring and springbrook at the base of the Kaimai Ranges, northern North Island (MS, unpubl. data), shows significant increases in temperature variation within 80 m of the spring (Fig. 3).

Figure 3. Water temperature variation along a small Waikato springbrook. Time period covered 40 days in summer 2004.



Spring water chemistry is often very different from the water chemistry of streams fed by run-off in the same region (McCabe 1998). In addition, spring water chemistry often changes significantly over relatively short distances. Such sharp environmental gradients are a characteristic feature of ecotones (Naiman & Decamps 1997). Water chemistry in springs reflects the chemical signature of the parent aquifer that has been modified by interactions with soils and air as it resurfaces. An example of this interaction is provided by spring water pH. Groundwaters tend to have increased levels of acidity, as the CO₂ that is abundant in them is transformed through dissolution into carbonic acid. As water wells up at springs, it immediately comes into contact with the atmosphere, where CO₂ levels are lower. The process of equilibration leads to increases in pH (van der Kamp 1995). For example, average pH (\pm SD) for five springbrooks at the base of the Kaimai Ranges increased from 5.84 (0.46) at the source to 7.08 (0.33) c. 80 m downstream (MS, 2004, unpubl. data). Similar, but inverted responses, are often seen with levels of dissolved oxygen in springs. Oxygen-poor groundwaters quickly equilibrate with the oxygen-rich atmosphere at springs. Where iron-rich, acidic, oxygen-poor groundwaters emerge, springs are often highlighted by obvious iron flocculation and the presence of iron bacteria.

2.2 NEW ZEALAND SPRINGS

In some areas of New Zealand, springs have always provided Maori with a reliable supply of fresh water and the value of this resource has been reflected in a wealth of legends and traditional practices (F. Thorne, Ngati Hikairo, 2005, pers. comm.). Recent work by NIWA with Tainui iwi around Kawhia Harbour on the west coast of the North Island has identified significant historical and cultural values assigned to springs by the local people. In pre-European times, springs provided the only reliable source of fresh water on the Kawhia peninsula, which is underlain by a series of small sand aquifers. From earliest settlement of the area, the springs around Kawhia peninsula have also provided significant food gathering and growing sites, e.g. tuna (eels, *Anguilla* spp.) and taro, (*Colocasia esculenta*), and water sources for irrigation of kumara (sweet potato, *Ipomoea batatas*) crops. It is highly likely that other iwi throughout New Zealand have had a long history of association with coldwater springs, and their cultural and historical values may provide a useful addition to assessments of biodiversity value. For example, current research on karst ecosystems (FRST Contract No. C01X0503) is utilising traditional knowledge of Ngati Maniapoto iwi to build a database of culturally and historically significant sites around Waitomo, central North Island. Many of the sites are associated with caves (e.g. burial sites) and springs (e.g. water sources).

Springs are an important source of human water supply in contemporary New Zealand (White 2001). The communities of Whangarei, Pukekohe and Rotorua, along with many smaller localities, use springs as water supplies (see Fig. 4A, B). Other important uses include bottling of water (e.g. Blue Spring, Putaruru, central North Island), and water supplies for fish farming (e.g. Waikoropupu Springs). Tourist operations also make use of coldwater spring complexes, particularly around Rotorua (e.g. Paradise Valley springs,

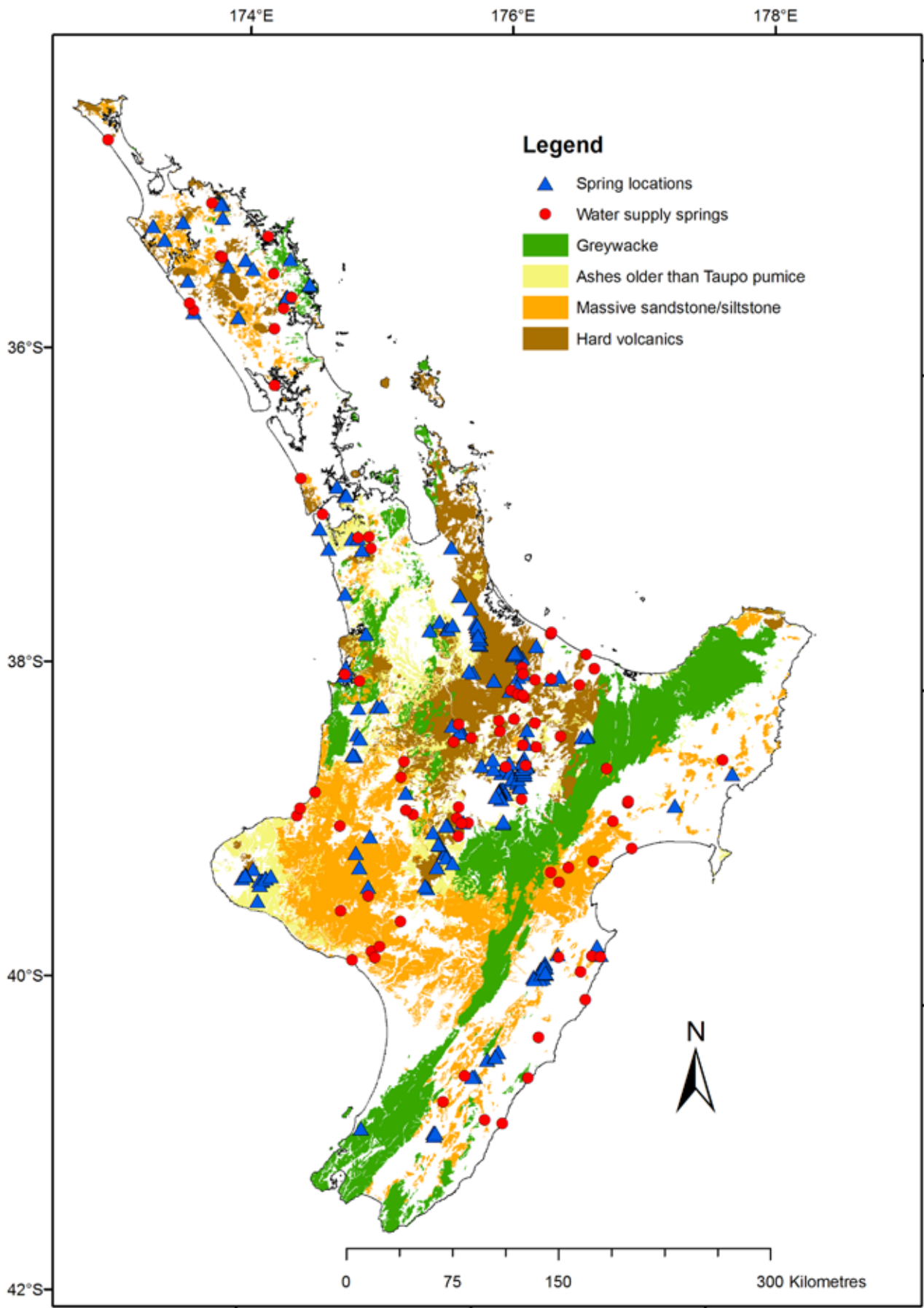


Figure 4A. Location of North Island springs and dominant baserock types (NZ Land Resource Inventory). Locations of water supply springs (Register of NZ Community Drinking-Water Supplies) are also given.

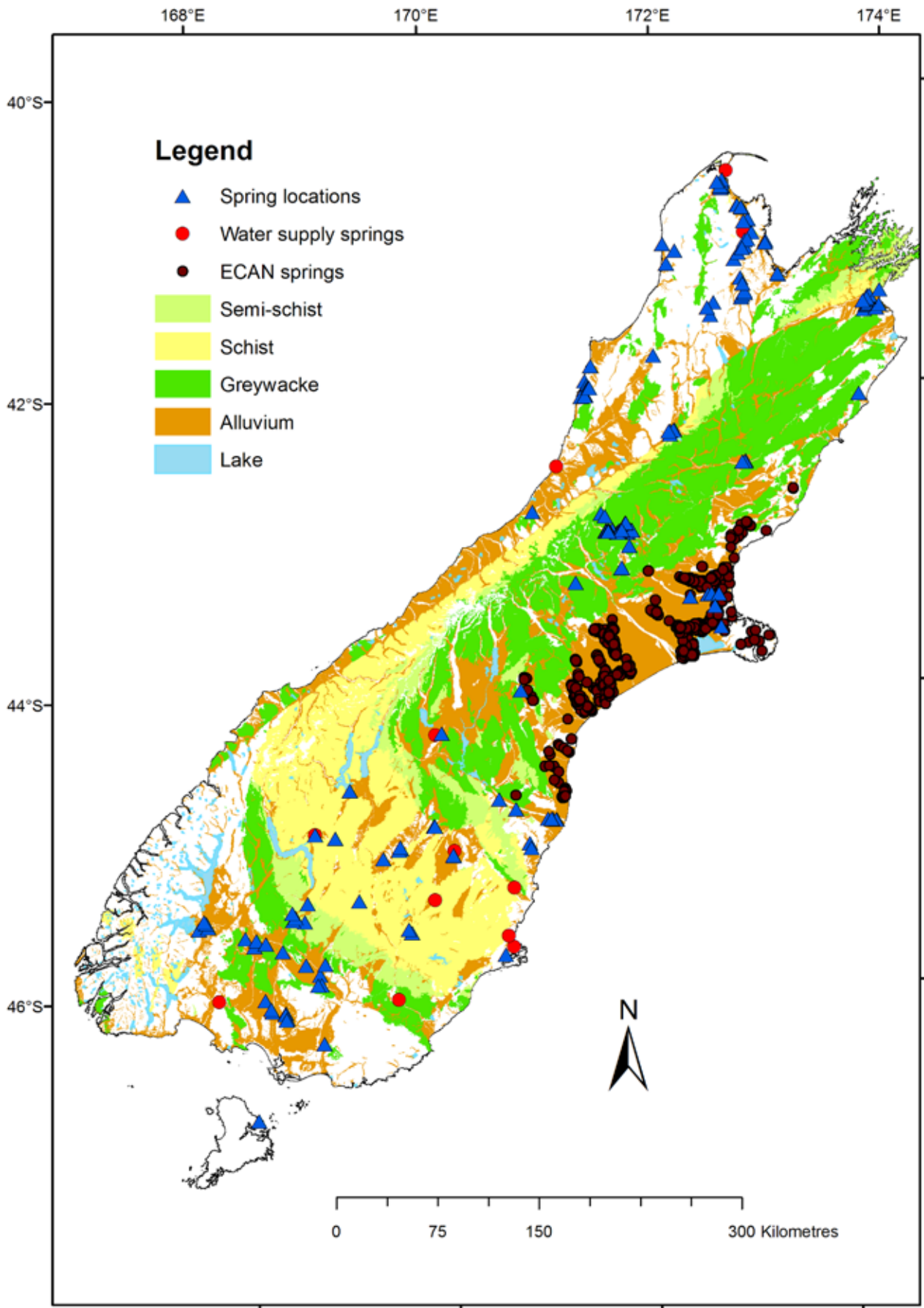


Figure 4B. Location of South Island springs and dominant baserock types (NZ Land Resource Inventory). Locations of water supply springs (Register of NZ Community Drinking-Water Supplies) are also given.

Rainbow Springs). Luxuriant growths of watercress are often associated with springs (e.g. Waikoropupu Springs), and this plant is utilised throughout the country as a food source (Michaelis 1976b).

2.3 A SPATIAL DATABASE OF NEW ZEALAND SPRINGS

A key step in managing spring habitats is to identify and map their spatial distribution. Once the resource has been mapped, intrinsic values and potential anthropogenic threats can be identified. However, mapping all springs throughout the country is a huge task. We have made a significant start to mapping spring resources through searches of literature and New Zealand topographical data, and requests for information on the location of springs from NZ Freshwater Sciences Society listserver members and DOC conservancy staff. These searches resulted in the identification of 426 springs in New Zealand. In addition, Environment Canterbury (ECAN) maintains a spring database of over 1500 locations in their region. (www.ecan.govt.nz/EcanGIS/news.html, viewed May 2006). The locations of all identified springs are plotted on Fig. 4A (North Island) and 4B (South Island).

Each of the 426 springs located was assigned a reach number, based on the River Environment Classification (REC) (Snelder & Biggs 2002). This then allowed all springs to be linked to catchment characteristics, including geology, elevation, land use and climate. No ground-truthing was carried out to determine the validity of assignment of a given spring to a reach number, and this should be taken into account when interpreting the spring environmental summaries given below.

More than 50% of the springs were located at elevations <400 m a.s.l. and were within 100 km of the coast (Fig. 5). This suggests that a large proportion of springs are located in lowland areas, where they are potentially most at risk from water quality deterioration and physical habitat modification associated with agricultural intensification. Taking the ECAN database into consideration further supports this conclusion (Fig. 4B).

In terms of geology, most springs (over 60%) were located in either alluvial or acidic volcanic areas¹ (Fig. 6A). This reflects the widespread coverage of these two geological classes, with volcanic rocks dominating the central North Island (Fig. 4A) and alluvium forming a major component of the South Island (Fig. 4B).

Land-use patterns indicate that more than 50% of springs are associated with stream reaches that fall under the pastoral land-use category of the REC (Fig. 6B). It should be noted that the REC reaches are classified as pastoral if the proportion of upstream pastoral land-use exceeds 25%. The REC does not provide information on local land use, which appears to be very important in determining the level of impact on springs (see section 4.4).

¹ Acidic volcanic is one of seven geology classes used to classify streams under the River Environment Classification (REC), see Snelder & Biggs (2002).

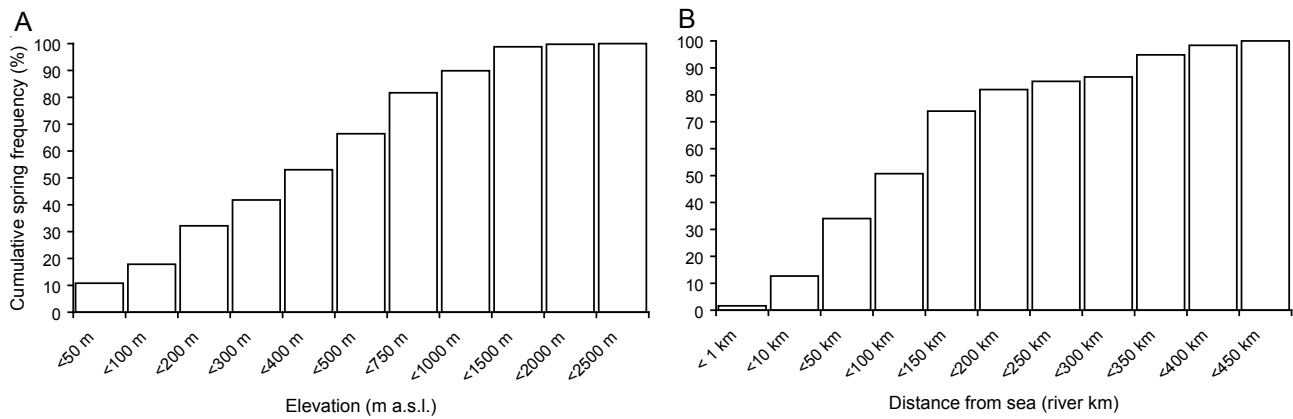


Figure 5. Frequency of 426 springs categorised by (A) elevation and (B) distance from the sea.

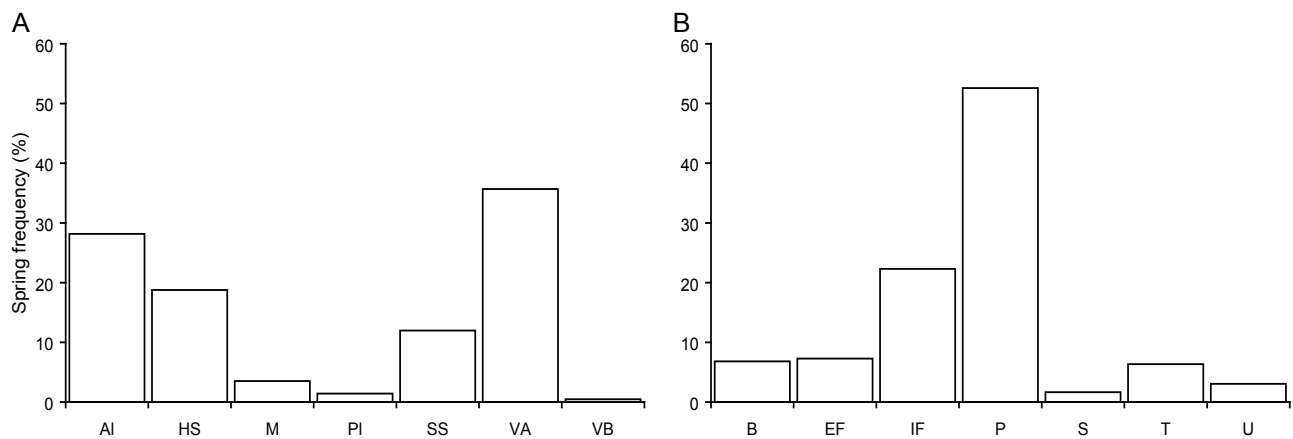


Figure 6. Frequency of 426 springs categorised by (A) geology and (B) land use. Key to REC geology codes: AI = alluvium, HS = hard sedimentary, M = miscellaneous, PI = plutonics, SS = soft sedimentary, VA = volcanic acidic, VB = volcanic basic. Key to REC Land-use codes: B = bare ground, EF = exotic forest, IF = indigenous forest, P = pastoral, S = scrub, T = tussock, U = urban. These codes are explained in Snelder & Biggs (2002).

2.4 ALLUVIAL SPRINGS IN BRAIDED RIVER LANDSCAPES

Braided rivers occur throughout the world, most frequently in arctic and alpine regions with a distinct flood season, but they also occur in arid and Mediterranean climates subject to torrential rain, and in some tropical regions subject to monsoonal rains (Bravard & Gilvear 1996). The braided rivers of the South Island of New Zealand have been formed over the last 20 000 years as a result of glacial action, rainfall and snow melt (Gage 1977). The rivers are characterised by large, unpredictable floods, and by some of the highest sediment yields of the world's rivers (Winterbourn et al. 1981). For each river, these factors combine to produce an extensive, flat, alluvial flood plain across which the active channel of the river migrates back and forth. The active river channel is highly unstable, but is bounded by a mosaic of more stable elements, which can be classified according to their sedimentary deposits (Bravard & Gilvear 1996) or successional stage of the vegetation (Burrows 1977). Flood plains are recognised as being extremely patchy environments in terms of successional stage and habitat structure (Poole 2002). They also tend to have high hydraulic conductivity, allowing the formation of an alluvial aquifer and high levels of groundwater-

surface-water exchange (Woessner 2000). This shifting 3-dimensional mosaic provides a range of inter-connected aquatic habitat types within braided river landscapes.

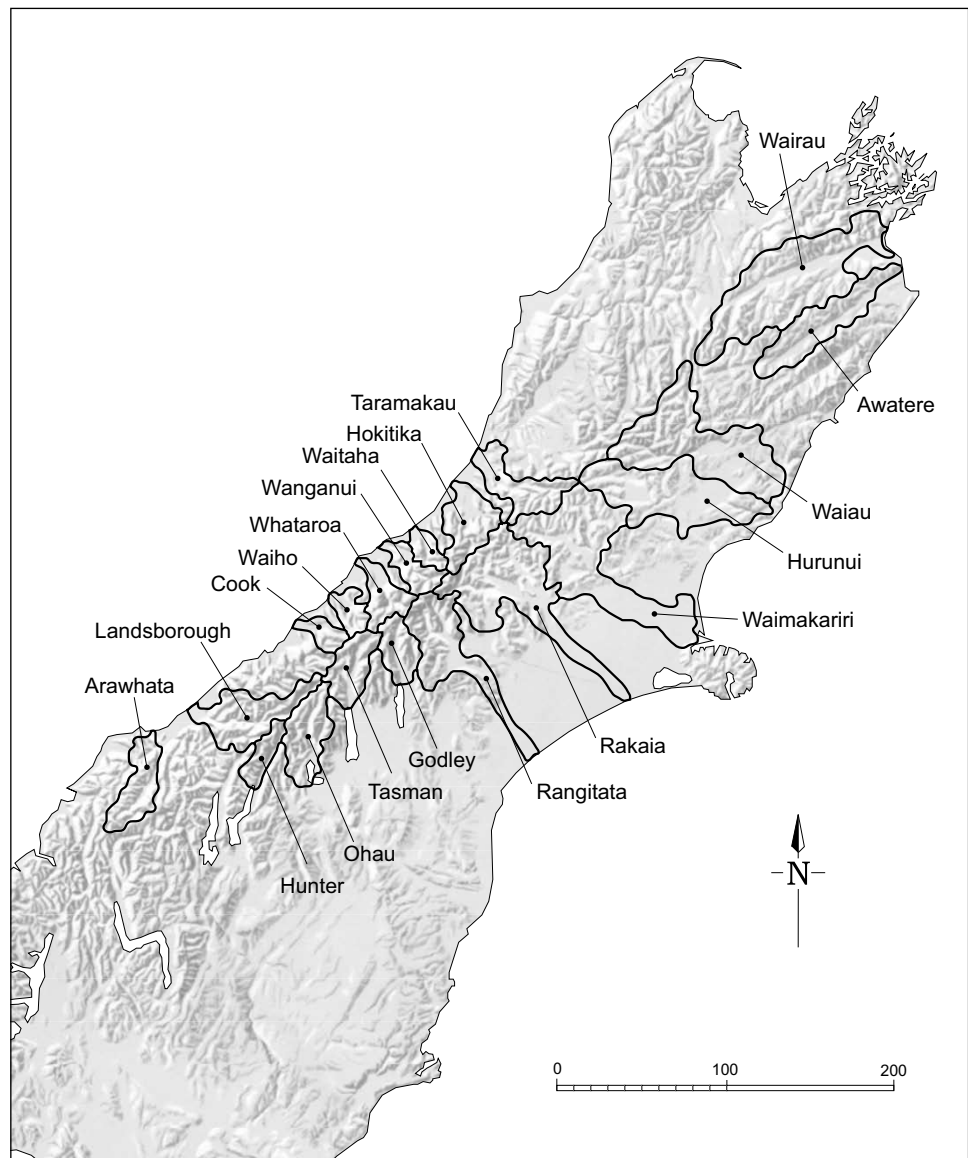
The location and relative age of springs in braided river landscapes are functions of the movement of water through the alluvium, which is determined by hydraulic pressure, depositional structure and the parent lithology of alluvial deposits (Stanford & Ward 1993; Valett et al. 1996; Woessner 2000). In general, the upper reaches of braided rivers are characterised by down-welling surface water, whereas the lower reaches exhibit up-welling. However, a flood-plain topography, valley constriction or the presence of impermeable layers within or beneath the aquifer can result in local patterns of aquifer recharge and discharge. This hydraulic connectivity results in a blurring of the perceived boundaries between the river and aquifer. Consequently, flood plains comprise a wide variety of aquatic habitats, many of which are linked by surface and sub-surface flow paths. Hydrological connectivity links a wide range of aquatic habitats, forming, in essence, a single body of water moving at variable speeds by multiple pathways through the flood-plain system.

The high connectivity generates flood-plain springs in areas of localised up-welling. These springs exhibit physico-chemical characteristics in complete contrast to those of the river main channel and constitute important habitats within the riverine landscape (Burgherr et al. 2002; Ward et al. 2002; Gray & Harding 2006).

Very little is known about the distribution and occurrence of braided river springs in New Zealand. However, Reinfelds & Nanson (1993) made an extensive investigation of stable flood-plain elements within the Waimakariri River catchment and found that the most extensive stable areas occurred in the upper river, in the lee of outcropping bedrock or alluvial tributary fans. These sites were characterised by late successional stage vegetation and numerous springbrooks, which flowed within the depressions formed by abandoned braid channels. Such streams, existing on stable, sheltered areas of flood plain, may remain undisturbed by river migrations for long periods of time. Reinfelds & Nanson (1993) suggested a period of 250 years might elapse before the entire Waimakariri River flood plain is re-worked.

Gray (2005) performed a mapping survey of springs within the braided reaches of 20 South Island braided rivers (Fig. 7). Springs were identified by eye from topographical maps (1:50 000 scale) as channels arising on the river flats with no surface link to a recognisable hill slope stream or no upstream connection to the main river. Spring permanence was indicated by the presence of vegetation and used to distinguish spring channels from backwaters and flood channels with an intermittent upstream connection to the main river. Springs were also classified according to the valley type within which they occurred (confined or flowing across plains), and according to any natural or human-made features with which they appeared to be associated, e.g. tributary fans, bluffs or flood retention works. A considerable number of springs occurred on vegetated islands within the main channel network of rivers, and were classified as being exposed to the destructive, eroding effects of the river.

Figure 7. South Island of New Zealand showing the 20 braided river systems analysed by Gray (2005). Catchments were delineated using the hydrological modeling tool within ARC GIS 8.2 (Environmental Systems Research Institute, Redlands, CA, USA) and the New Zealand 500 m Digital Elevation Model.



An important criterion driving the formation of braided reaches is slope. Braiding is found in valleys with gradients of 0.04–0.17°; an abundance of bed material; and a hydrological regime marked by major flood peaks (Bravard & Gilvear 1996). Interestingly, no springs were recorded in braided reaches with a gradient exceeding 0.9°. Possibly, the reaches exhibiting braiding with slopes above 0.9° and below the supposed braiding maximum slope of 1.7° are too unstable for the development of vegetated flood-plain elements and associated stable spring creeks.

Overall, Gray (2005) found that 65% of springs occurred within 0.5 km of a physical sheltering structure, such as a bluff, tributary alluvial fan or flood retention works, whereas the remaining 35% appeared to be exposed. Within four Canterbury rivers, alluvial fans and rocky bluffs were rare along the plains reaches. Exposed springs increased from approximately 20% of all springs in confined inter-montane reaches to being the predominant type on plains. However, in both valley types, the actual number of exposed springs was very similar. Consequently, the confined, inter-montane reaches of braided rivers contained the greatest number and diversity of springs by virtue of the presence of both exposed and sheltered sites.

16% of springs identified by Gray (2005) were within 0.5 km of flood retention works. This suggests that human activities can be constructive as well as destructive in terms of spring habitat and, therefore, biodiversity; but it also raises concerns about the extent of our knowledge of the long-term effects of activities such as gravel extraction and flood bank construction on the distribution of springs within braided rivers (see section 5.1).

Gray (2005) also undertook a comparison of spring types across catchments, and observed a correlation between mean reach slope and spring type. Rivers with a mean slope of less than 0.3° had a higher percentage of exposed springs than steeper rivers. Unfortunately, the pattern was blurred by the effects of flood retention works, particularly in the Taramakau and Wanganui Rivers on the west coast of the South Island. Despite this, the pattern suggests that stable, exposed flood-plain springs may be more common in lower-gradient rivers, or lower-gradient reaches of rivers. This relationship can also be seen in four Canterbury rivers, where the highest number of exposed springs are in the lower-gradient reach of the Rakaia River plains.

Although the exact mechanism of spring formation is not known, it seems likely that springs are a product of factors operating at multiple spatial and temporal scales. Porous alluvial flood plains characterised by high sediment loads and flood events are the result of glacial and fluvial action over thousands of years. At the local scale, up-welling and down-welling of water are regulated by the relative position of the flood-plain surface and the water table. Relative depressions in the flood-plain surface formed in the lee of large geomorphologic structures (i.e. fans and bluffs) result in up-welling at the point where the surface intersects the water table. In addition, the presence of impermeable barriers within the aquifer, or the constriction of the aquifer above a gorge, may produce positive hydraulic pressure and up-welling such that the water table rises to meet the surface of the flood plain. A final, but not mutually exclusive, possibility is that springs are fed by a shallow network of highly permeable preferential flowpaths embedded in a matrix of low-permeability substrate. Cut and fill riverbed erosion and zones of uniform deposition created these channels. Water flows rapidly along preferential flowpaths until the zone of high porosity intersects the surface, possibly within an abandoned braid channel, scoured lower than the surface of the surrounding flood plain.

It is highly likely that all these mechanisms are in operation simultaneously along the reaches of braided rivers and that different spring types show variable levels of permanence, stability and successional stage, resulting in a further increase in the habitat heterogeneity available across the flood plain. In terms of prediction, springs are likely to be more abundant in confined inter-montane valleys with complex geomorphology. Although springs appear to occur throughout braided river systems, the mechanisms and characteristics of the springs will alter with the morphology of the valley, thereby influencing the biological communities within the springs and the reach and landscape-scale contribution of these habitats to biodiversity.

3. Biodiversity values of New Zealand springs

3.1 HISTORICAL ECOLOGICAL STUDIES OF NEW ZEALAND FRESHWATER SPRINGS

The study of the biota of springs (crenobiology) is well established overseas (see reviews in Ferrington (1995) and Botosaneanu (1998)). In contrast, there have been few studies on the ecology of New Zealand's coldwater spring habitats. The first studies describing the biological communities inhabiting New Zealand freshwater springs were of Western Springs, Auckland (Johnstone 1972); Avon River/Otakaro, Christchurch (Marshall 1973); and Waikoropupu Springs and five other coldwater springs elsewhere in New Zealand (Michaelis 1974, 1976a,b, 1977). At the end of the 1970s, Russell & Rodgers (1977) characterised the waters of Western Springs and Cowie & Winterbourn (1979) investigated the biota at the spring source of Middle Bush Stream, an alpine springbrook near Cass, central South Island. During the next 20 years, there were no studies characterising biological communities or spring habitats, although the origin of some springs of the east coast of the North Island was studied (Hunt & Glover 1995) and some ecological studies compared springbrook biota with invertebrate communities of unstable streams fed by run-off (e.g. Death & Winterbourn 1994; Death 1995) or included them as sites in experimental work (Rounick & Winterbourn 1983; Rounick & James 1984; Winterbourn & Fegley 1989; Suren 1991).

In the last 5-10 years there has been a marked increase in interest in New Zealand freshwater springs, with a variety of topics being addressed. For example, studies have been undertaken on the ecology of Spring Creek (Young et al. 1999) and of other spring-fed streams on the Wairau River plain, Marlborough (Young et al. 2002), the effects of land use on freshwater springs (Scarsbrook & Haase 2003), and the spatial and longitudinal patterns of invertebrate communities in springs (Barquín 2004). A chapter in the book 'Freshwaters of New Zealand' (Death et al. 2004) draws together what is known about both coldwater and geothermal springs. An identification guide to bryophytes and algae of Waikoropupu Springs has also been published (Fife et al. 2004), and several spring studies have been published recently (Barquín & Death 2006; Collier & Smith 2006).

In the only published biodiversity survey of coldwater springs to date in New Zealand, Michaelis (1976a, 1977) focused on Waikoropupu Springs, but also sampled five other coldwater springs in the North and South Islands. Michaelis (1977) found 16 species of algae, seven species of moss, three species of liverworts, five angiosperms and 40 species of aquatic invertebrates. The snail *Potamopyrgus antipodarum* was found at all six cold springs sampled, and made up 88%-96% of total invertebrates at Waikoropupu Springs.

Springs also contribute to functional diversity of ecosystems. For example, Digby (1999) found that levels of secondary production in spring habitats in the Rakaia River were an order of magnitude higher than in the main

braid or side braid habitats. These springs contained relatively high numbers of invertebrate species, provided habitat for native fish and were important foraging areas for native wading birds (Hughey et al. 1989; Hughey 1998).

3.2 INVERTEBRATE FAUNA OF NEW ZEALAND SPRINGS

A range of studies over the last 5 years has provided a wealth of information on the faunal biodiversity of springs. The key faunal elements of springs, and some of their particular characteristics, including levels of endemism and genetic diversity, are outlined below. We also provide a brief review of the floral diversity of springs (see section 3.3).

3.2.1 Hydrobiidae (spring snails)

The gastropod snails of the family Hydrobiidae are referred to as ‘spring snails’, because they tend to have a high affinity for springs and groundwater habitats. Haase (in press) carried out a revision of New Zealand’s spring snails based on genetic and morphological data from museum material as well as new collections from throughout New Zealand. His results show an extensive radiation of these small snails in New Zealand, mirroring previous work in Australia (Ponder & Clark 1990) and New Caledonia (Haase & Bouchet 1998). Prior to the revision, there were 16 described hydrobiids in New Zealand, including the ubiquitous *P. antipodarum*. There are now 64 described species in 15 genera, with 49 of the species recorded as occurring in springs (including cave resurgences and seepages) (Haase in press). Furthermore, Haase suggests that several long branches observed in constructed phylograms may be indicative of an even greater extant (or extinct) diversity yet to be discovered. This makes New Zealand part of a global centre of hydrobiid diversity, and confers significant biodiversity value on our springs.

The importance of spring habitats for hydrobiid diversity is highlighted by the fact that New Zealand’s hydrobiids exhibit a large number of narrow-range endemics. Of the 64 known species, 30 are restricted to their type locality (Fig. 8), and 70% (21 species) of these local endemics are found in the Northwest Nelson region (Northwest Nelson-Paparoa and Motueka units of the Waters of National Importance (WONI) classification (Chadderton et al. 2004). Another feature of the available distribution data is that there is a distinct overlap between hydrobiid diversity patterns and areas of karst, or limestone, geology. However, it is interesting to note that no locally endemic snails were found in areas of limestone to the northeast and east of the Central Plateau. Spring snails tend to have poor dispersal characteristics and the observed distributions may reflect speciation in glacial refugia (e.g. Northwest Nelson) and in areas not heavily affected by more recent volcanic eruptions.

Given the localised distribution of many species, low levels of migration and gene flow between populations of spring snails (Haase 2005) and the susceptibility of springs and groundwaters to modification from land-use change and water abstraction, New Zealand’s spring snail fauna should be considered at risk, and urgent attention is required to incorporate habitats of these snails into conservation planning and management.

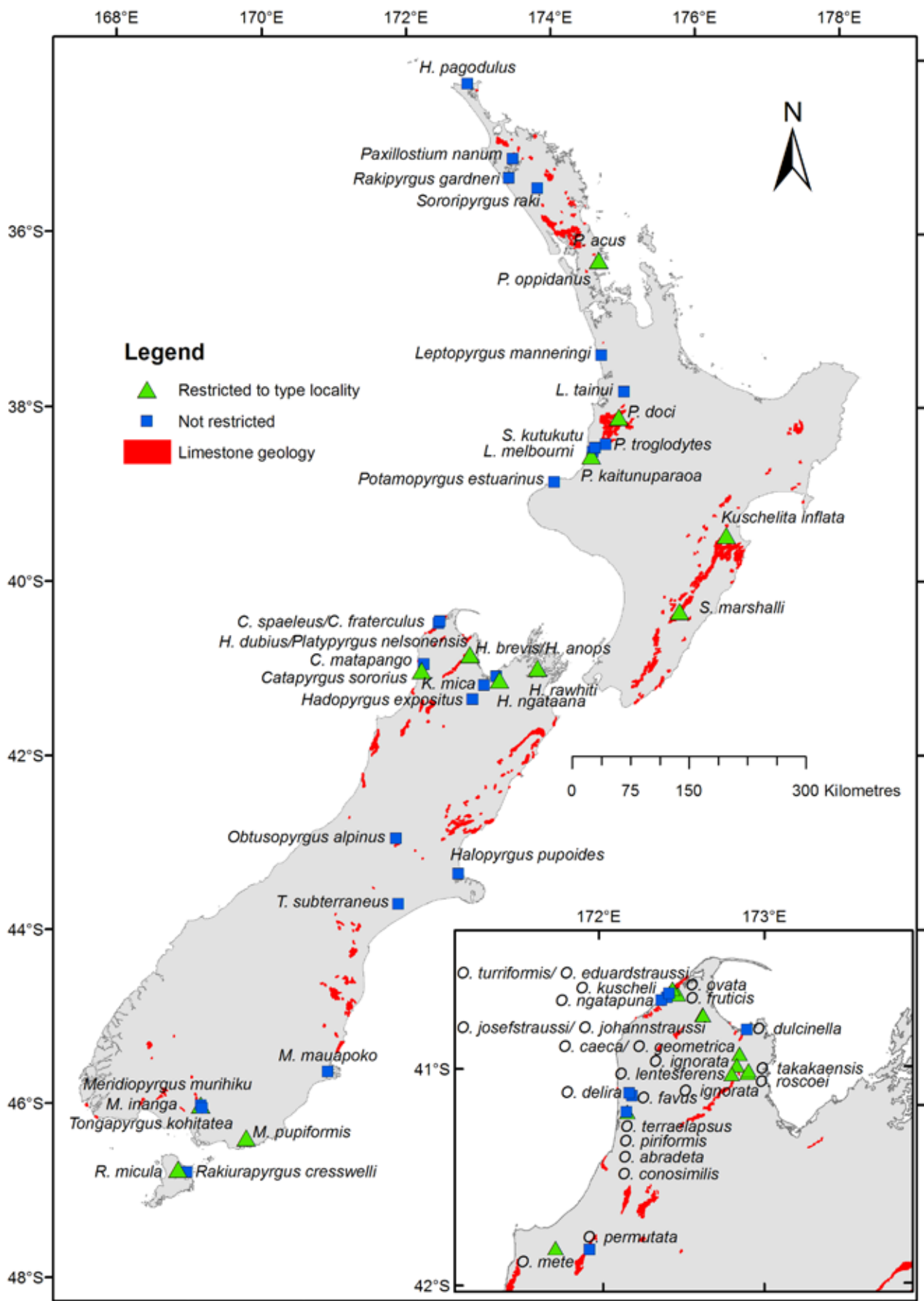


Figure 8. Type localities for 38 species of New Zealand hydrobiids (not including *Potamopyrgus antipodarum* (type locality = New Zealand) and *P. dawbini* (Auckland Is), which are not shown) overlain on limestone geology. Inset shows 24 species of *Opacuticola* distributed in Northwest Nelson and Buller.

3.2.2 Peracaridean crustaceans (amphipods and isopods)

Amphipods and isopods dominate many spring habitats around the world (Gooch & Glazier 1991; Webb et al. 1998). In New Zealand, there appears to be a high level of diversity within the families Paraleptamphopiidae (Amphipoda) and Phreatoicidae (Isopoda). Both these families include groundwater and surface-water forms, with springs as an area of overlap and, hence, greater diversity.

Paraleptamphopiidae

The genus *Paraleptamphopus* currently consists of two described freshwater species endemic to New Zealand (Scarsbrook et al. 2003), although the group is currently the focus of several studies by NIWA and University of Waikato taxonomists. *Paraleptamphopus subterraneus* is a blind, subterranean species that was described in 1882 from Canterbury aquifers (Chilton 1894), whereas *P. caeruleus* is an epigeal (surface) species found in the central and southern portion of the South Island (Hurley 1975). It has long been suspected that there are additional species and genera in the group (Watson 1972; Chapman & Lewis 1976; Bousfield 1983).

In a recently completed PhD thesis, Sutherland (2005) used mitochondrial and nuclear DNA analyses to describe variability within the genus *Paraleptamphopus*. His work supports on-going morphological taxonomy. Sutherland (2005) sampled 421 freshwater habitats around the North and South Islands. He found *Paraleptamphopus* species at 49 of these sites, with most in small springs and streamside ditches. *Paraleptamphopus subterraneus* was found only at two Hawke's Bay sites. *Paraleptamphopus caeruleus* was present at 14 sites. At least six other morphologically distinct taxa were collected.

Sutherland (2005) found several genetically distinct lineages within the genus *Paraleptamphopus*, and concluded that up to 28 species may be present. The area containing the greatest genetic diversity was the upper West Coast of the South Island (i.e. Paparoa–Northwest Nelson). Of note was the absence of *Paraleptamphopus* from the northeast and east of the North Island (Bay of Plenty, East Cape, and northern Hawke's Bay). This gap in distribution mirrors that of hydrobiid snails. It is possible that volcanism may have led to extirpation of these poorly dispersing taxa.

In a study of 34 spring habitats from four regions around New Zealand, Scarsbrook & Haase (2003) collected a wide diversity of amphipod taxa. Fenwick (NIWA, Christchurch) identified 13 morphologically distinct species of '*Paraleptamphopus*' from these samples. These 'morphospecies' ranged from those with strong pigmentation and distinct eyespots (epigeal forms), through to unpigmented and eyeless (hypogean, or sub-surface) forms (Fig. 9). In addition to high diversity, it appears that there may also be a high level of local endemism, as six of the 13 taxa were found at single locations (Fig. 10). Eight of the paraleptamphopiids were restricted to samples from Southland, suggesting that this region, like Northwest Nelson (Sutherland 2005), is another hotspot of amphipod diversity.

Taxonomic descriptions and biosystematics research of the paraleptamphopiid group are on going, but it is clear that there is a much greater level of diversity than is currently recognised. Many of these taxa appear to preferentially

Figure 9. Three morphotypes of amphipods collected from lowland springs in Southland: darkly pigmented surface stream form (top), possible spring specialist—crenobiont (middle), and unpigmented and eyeless groundwater form (bottom). All specimens are about 5 mm long.

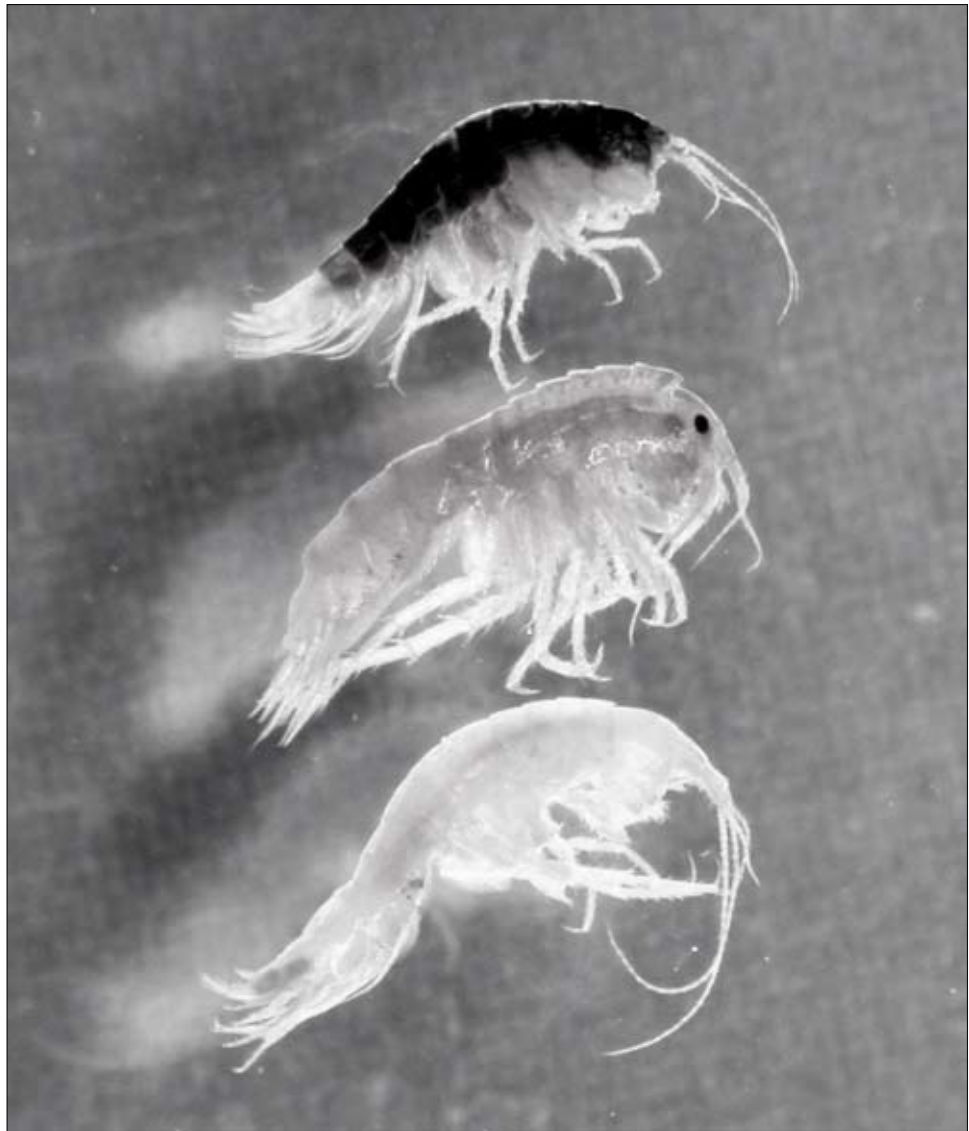
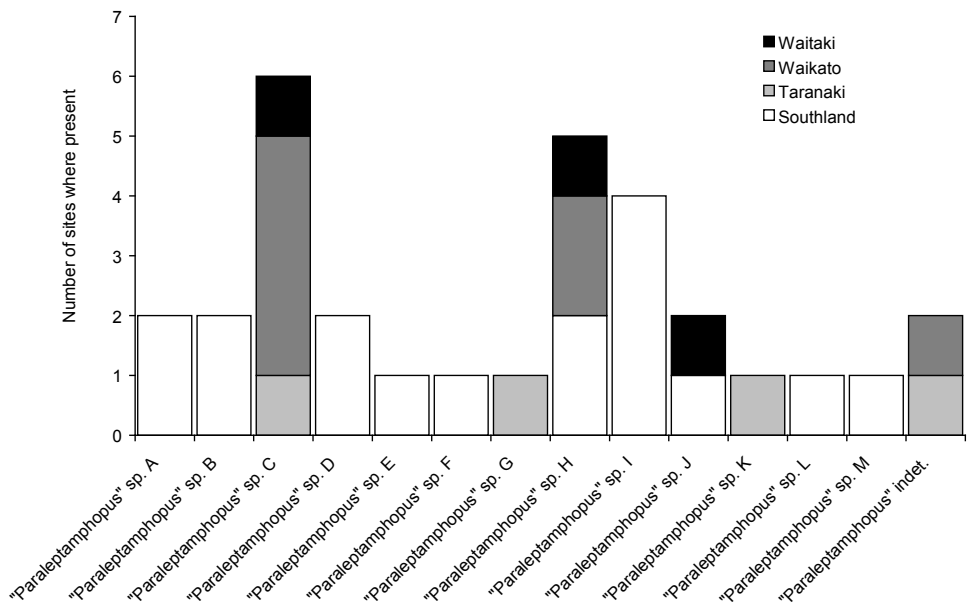


Figure 10. Frequency of occurrence of *Paraleptamphopus* spp. (Crustacea) at 34 spring sites around New Zealand by region.



inhabit small springs (Sutherland 2005) and other places where groundwater and surface water mix (e.g. hyporheic zones) (Burrell & Scarsbrook 2004). As such, this group is a key component of the New Zealand spring fauna.

Phreatoicidae

There are currently nine described species in three genera within the Phreatoicidae in New Zealand (Scarsbrook et al. 2003). Species in the genera *Phreatoicus* and *Neophreatoicus* are found in groundwaters in Canterbury. The remaining genus, *Notamphisopus* (Fig. 11), contains six species. Initial descriptions of the species in the genus (Nicholls 1944) suggest that these organisms may be spring specialists, but few specimens have been observed since they were first described. They appear to be restricted to the southern South Island and Stewart Island/Rakiura (Chapman & Lewis 1976). Scarsbrook & Haase (2003) sampled eight Southland springs and six of these contained *Notamphisopus*. A revision of New Zealand Phreatoicidae is underway with funding provided through the Department of Conservation's TIFBIS Fund (G. Fenwick, 2006, pers. comm.)

3.2.3 Decapod crustaceans

Freshwater shrimps are often found in lowland streams and are usually associated with aquatic plants (Carpenter 1976). It is thought that young shrimp may undergo their early development in brackish water before migrating upstream (Carpenter 1983). In New Zealand, shrimps (*Paratya curvirostris*) have been recorded in Waikoropupu and Western Springs (Michaelis 1974), and in spring-fed tributaries of the Wairau River plains (Young et al. 1999, 2002). All of these are lowland springs close to the sea. *Paratya* has also been collected from springs around Kawhia and Aotea harbours (MS, 2005, unpubl. data). Studies are underway to identify spatial patterns in genetic diversity of *Paratya* (P. Smith, NIWA Wellington, 2005, pers. comm.).

New Zealand crayfish (koura, *Paranephrops* spp.) are likely to be found in streams less than 6–8 m wide, with water depths of 0.2–0.3 m and velocities under 0.4 m/s (Parkyn 2004). Moreover, their abundance is closely linked

Figure 11. A specimen of the phreatoicid genus *Notamphisopus* from a Southland spring. Specimen is 8 mm long.



to the presence of cover such as wood, undercut banks, tree roots and macrophytes. Floods can drastically reduce crayfish abundances (Parkyn & Collier 2004), and crayfish seem to avoid streams with strong seasonal temperature variation (Parkyn 2004). Thus, spring habitats may favour crayfish populations by providing constant temperature and flow patterns along with abundant macrophyte growth. Koura (*P. planifrons*) have been recorded in Waikoropupu, Otangaroa, Hamurana (near Rotorua) and Western Springs (Michaelis 1974), and in spring-fed tributaries of the Wairau River plains (Young et al. 1999, 2002). They have also been recorded in springs along the base of the Kaimai Ranges (MS 2004, unpubl. data). *Paranephrops zelandicus* was observed in a number of Southland springs sampled by Scarsbrook & Haase (2003).

3.2.4 Crustacean diversity patterns

Scarsbrook & Haase (2003) used data from 34 spring sites around New Zealand to identify regional patterns of crustacean biodiversity. Their broad-scale survey indicated that Southland has a distinctive spring fauna, which was often dominated by Crustacea and Mollusca. Across all 34 sites there was a negative correlation between the species richness of Crustacea and Ephemeroptera-Plecoptera-Trichoptera (EPT) (Pearson correlation coefficient, $r = -0.456$; $P < 0.01$) (Fig. 12A). This may partly reflect larger-scale biogeographical factors, since few EPT taxa were found in Southland, where Crustacea dominated. Phreatoicid isopods, spring snails and eight of the 13 morphologically distinct forms of paraleptamphopiid amphipod were found only in Southland (Fig. 10). In contrast, the diversity of mayflies, stoneflies and caddisflies was very low in the sampled springs. The dominance of Crustacea and the absence of EPT taxa are intriguing. Further investigation is needed to determine whether this is a true biogeographical pattern, or a pattern caused by bias in the choice of sampling sites.

Scarsbrook & Haase (2003) found that the total number of taxa (i.e. insects, molluscs and crustaceans) collected from springs in each region varied from 29 at Waitaki sites to 61 in Southland and Waikato. When the total number of taxa was divided by the number of sites sampled, Southland had the greatest spring biodiversity (7.6 taxa/site), whereas the other three regions had similar numbers of taxa per unit effort (5.2-5.8 taxa/site). Because of

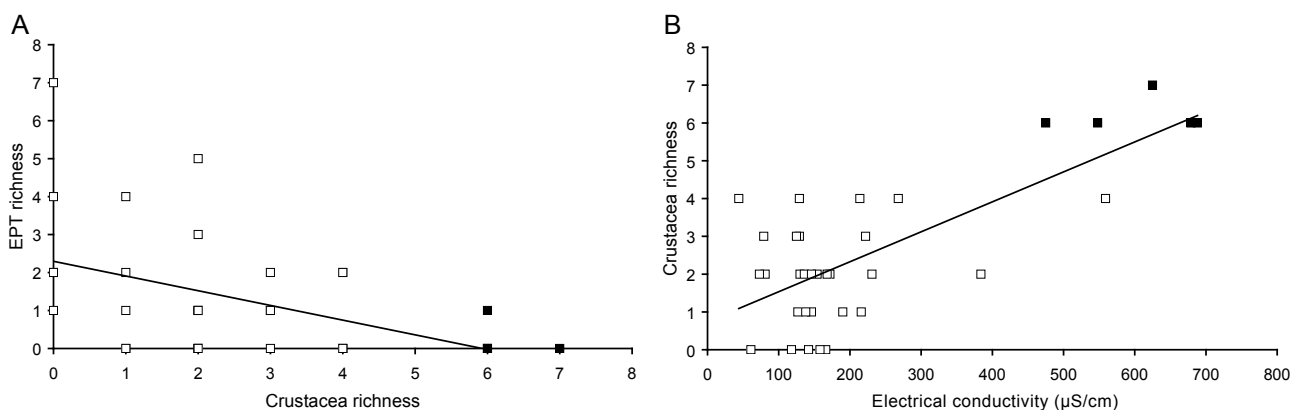


Figure 12. (A) Relationship between number of Crustacea and number of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa across 34 spring sites (N.B. There are several overlapping datapoints); (B) Relationship between conductivity and diversity of Crustacea at 34 spring sites. Filled squares are limestone springs in Southland.

this diversity, we suggest that Southland may be an excellent locality for further, more detailed, investigations of biodiversity patterns in springs and their underlying groundwaters.

Scarsbrook & Haase (2003) also found that the diversity of Crustacea in the 34 sampled springs was strongly correlated with conductivity ($r=0.748$; $P<0.001$). Crustacean diversity was greatest at the five limestone springs sampled in Southland (Fig. 12B). No other limestone springs were sampled, and it is probable that the high diversity of Crustacea seen in Southland reflects this sampling bias to some extent.

3.2.5 Insect taxa relevant to springs

The mayfly *Zephlebia nebulosa* is known to occur in small streams, springs and on wet rock faces in the northern North Island (Townes & Peters 1996). Scarsbrook & Haase (2003) found it at four spring sites: three in Taranaki and one in the Waikato. All of these sites had intact, native forest riparian areas, and limited stock access. According to a recent study of mainly undisturbed springs forming rock-face seepages around the western Waikato, *Z. nebulosa* was relatively widespread, occurring at 11 of the 21 sampling sites (Collier & Smith 2006). All of these sites were shaded by native vegetation. During sampling at 15 springs along the base of the Kaimai Ranges, *Z. nebulosa* was found at three springs surrounded by native riparian vegetation and at two sites in pasture, but with stock excluded (MS, 2004, unpubl. data).

The trichopteran family Oeconesidae contains a number of taxa that are known to be spring specialists. In particular, larvae of *Pseudoeconesus* and *Oeconesus* are often found in small springs amongst leaf litter and other organic detritus (Winterbourn et al. 2000). Scarsbrook & Haase (2003) found *Pseudoeconesus* larvae at three spring sites in Taranaki and five sites in Waikato. They were present in a range of spring conditions, including those where stock had full access. Oeconesidae were also found at five springs along the base of the Kaimai Ranges, with the group absent only from springs in pasture with open stock access (MS, 2004, unpubl. data).

The chironomid *Polypedium opimus* is known from small streams and seepages (Winterbourn et al. 2000). Scarsbrook & Haase (2003) found it at two forested spring sites in Taranaki. In a study of land-use effects on springs along the base of the Kaimai Ranges, an unidentified species of *Polypedium* was found at all 15 springs, suggesting it is not sensitive to habitat degradation (see section 4.4).

3.2.6 Distinctive fauna of rock-face seepages

Collier & Smith (2006) measured water quality, physical habitat characteristics and invertebrate community structure in 17 small springs forming rock-face seepages, five larger springs and five streams in western Waikato. All sites were bordered by native vegetation. A total of 147 taxa were collected, 53% of which were recorded only from seepage samples. Seepage faunas tended to be numerically dominated by Mollusca, but Trichoptera and Diptera were the most diverse groups. Insects made up 23% of total invertebrate abundance in seeps, 77% in springs and 93% in streams. Species restricted to rock-face seepages included *Zephlebia nebulosa*, *Zelandotipula ?novarae* (Tipulidae) and *Austrothaumalea appendiculata* group (Thaumaleidae).

A number of species new to science were also recorded, including a cased chironomid belonging to the genus *Stempellina* (Tanytarsini), and two species of hydrobiid snails.

Invertebrate community composition reflected underlying geology, aquatic moss cover and riparian shade. Maintenance of riparian plant cover over seepages should help sustain supplies of organic matter, moss cover and shade, providing habitat complexity and low water temperatures (Collier & Smith 2006).

The work of Collier & Smith (2006) has highlighted rockface seepages as an important subset of springs, with communities forming valuable components of freshwater biodiversity. In terms of community composition, taxonomic distinctiveness and average phylogenetic and taxonomic diversity, seepage faunas were also significantly different from those of larger springs, emphasising that hygropetric (vertical water surface) habitats support fundamentally different assemblages of aquatic invertebrates. Such habitats do not appear on 1:50 000-scale topographical maps, and are seldom explicitly considered as water bodies. Protection of the distinctive faunas of these habitats will require a more inclusive approach to managing freshwaters.

3.2.7 Groundwater fauna

Occurring at the interface between surface and groundwater, springs often harbour a range of groundwater fauna. Despite considerable work in the late 19th and early 20th centuries by Charles Chilton (e.g. Chilton 1894), our knowledge of the groundwater fauna must still be considered to be in its infancy (Scarsbrook et al. 2003). However, it is clear that the fauna is diverse, and has features that contribute to New Zealand's distinctive natural heritage.

A species not mentioned by Scarsbrook et al. (2003) is the phreatic flatworm *Prorhynchus putealis*, which was first collected from deep groundwater wells in Canterbury (Haswell 1898). Percival (1945) went on to describe the discovery of *Prorhynchus* in a variety of habitats close to the surface, and includes some brief notes on biology. Initially collected beneath stones and amongst macrophytes in a shallow spring near Cass, Arthur's Pass, further specimens were found within trout redds in the up-welling reaches of the Selwyn River/Waikirikiri, Canterbury, and the Otapiri River, Southland. A second species, *P. haswelli*, was also described from the lower Selwyn River/Waikirikiri, although nothing more is known about its distribution. More recently, specimens of *Prorhynchus* spp. have been found in numerous spring-fed habitats along the flood plain of the upper Waimakariri River (Gray 2005), and in shallow groundwater wells installed along the flood plain of the Selwyn River/Waikirikiri (MS, 2005, unpubl. data).

3.3 THE FLORA OF SPRINGS

The distribution of algae, bryophytes and macrophytes in New Zealand fresh waters is strongly controlled by light and nutrient availability, substrate stability and flow regime (Suren & Duncan 1999; Biggs & Kilroy 2004; Reeves et al. 2004). Springs often provide excellent habitats for both native and introduced aquatic plants, which may be abundant.

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

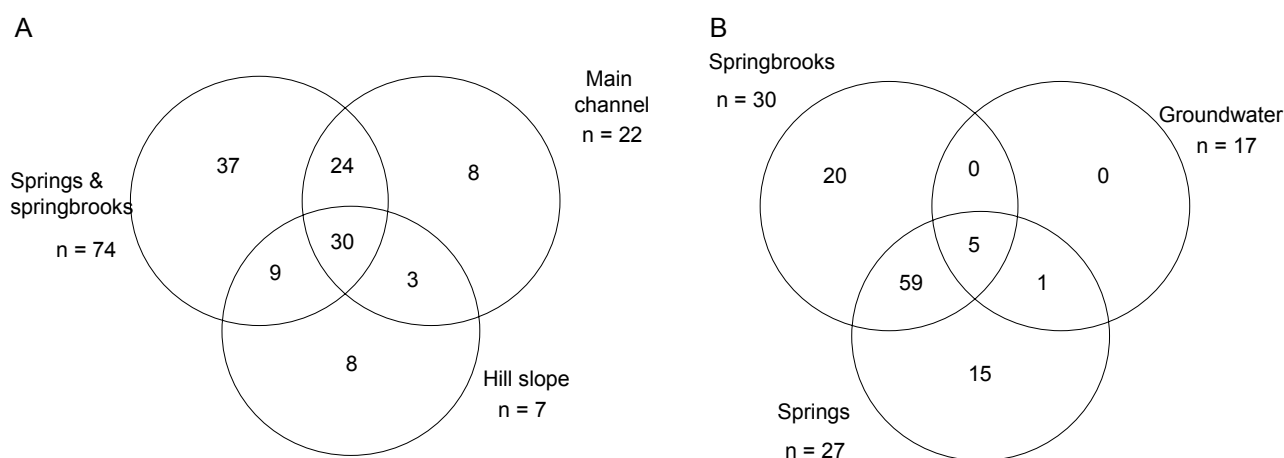


Figure 13. Numbers of invertebrate taxa (A) unique to spring, main channel and hill slope streams and combinations of the above, and (B) unique to springbrooks, springs, groundwater and their combinations.

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).

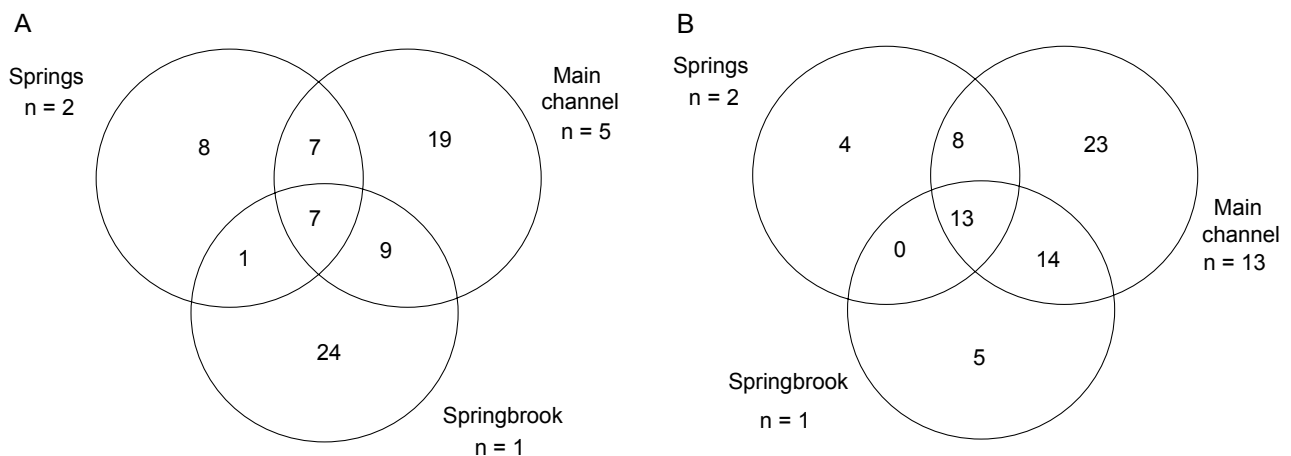


Figure 14. Numbers of algal taxa unique to spring, springbrook and main channel habitats, and combinations of the above at sites in the (A) upper, and (B) lower Waimakariri River.

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

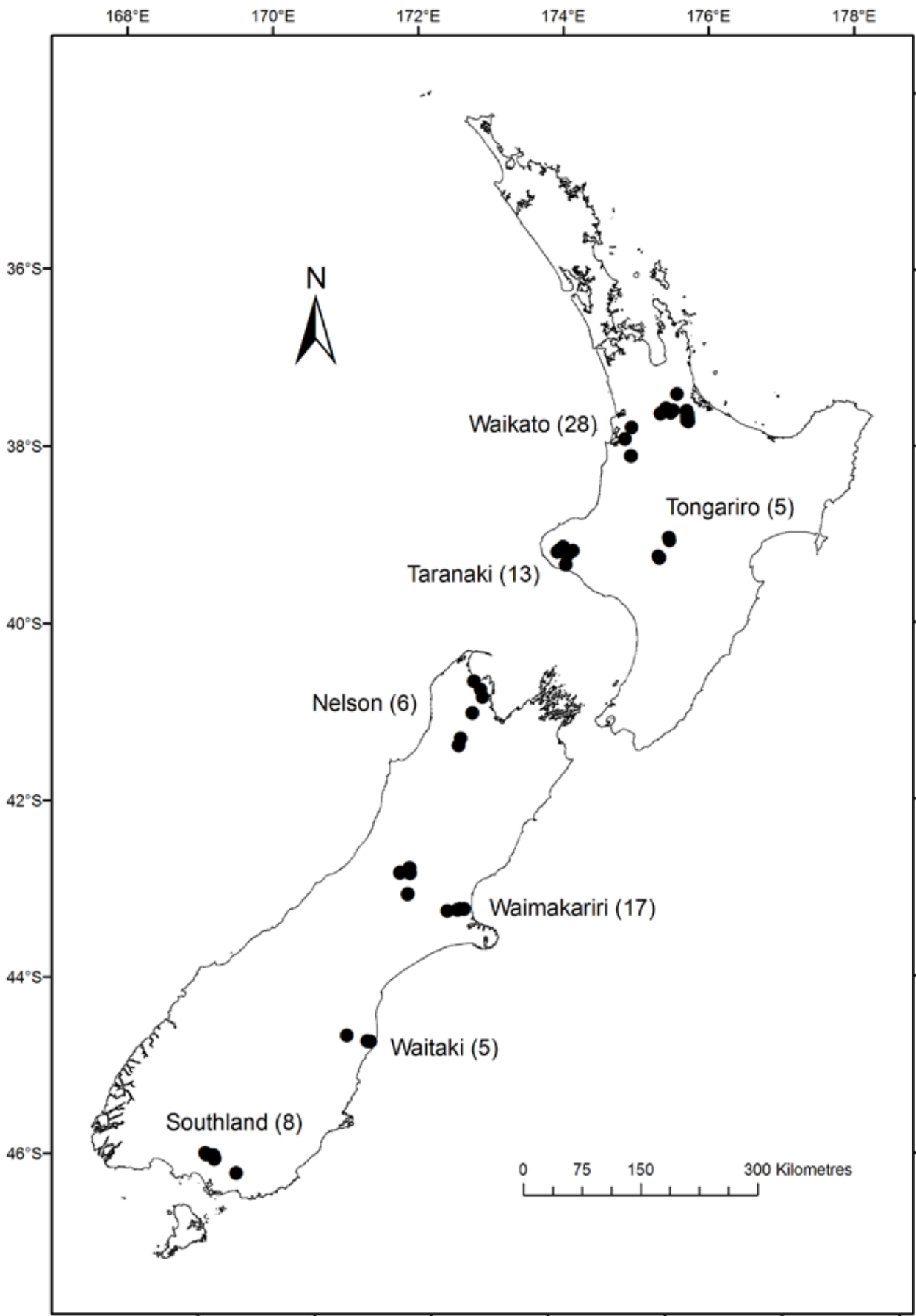


Figure 15. Locations of springs used for broad-scale analyses of environmental drivers of spring biodiversity patterns.

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).

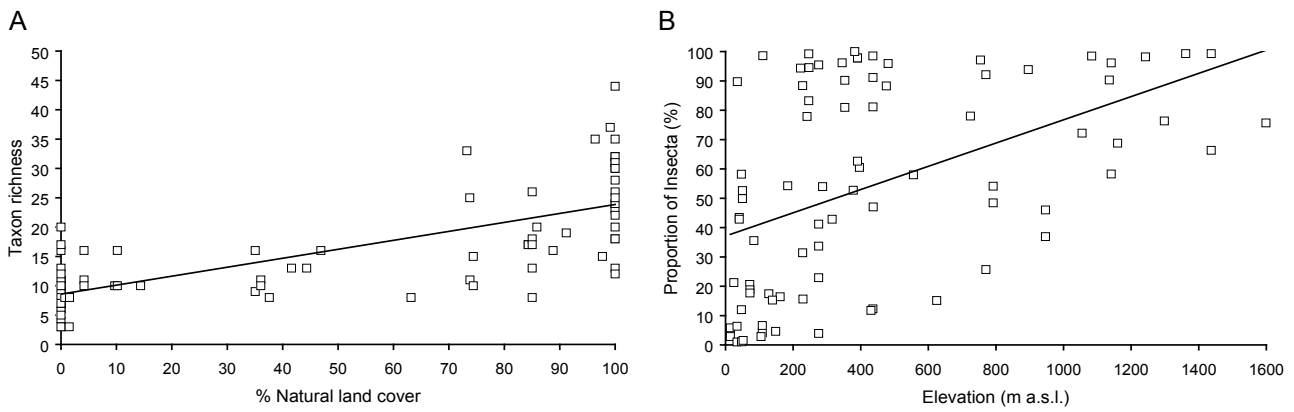


Figure 16. (A) Association between percentage natural land cover and taxa richness in springs. (B) Association between spring elevation and proportion of Insecta across 82 spring sites.

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).

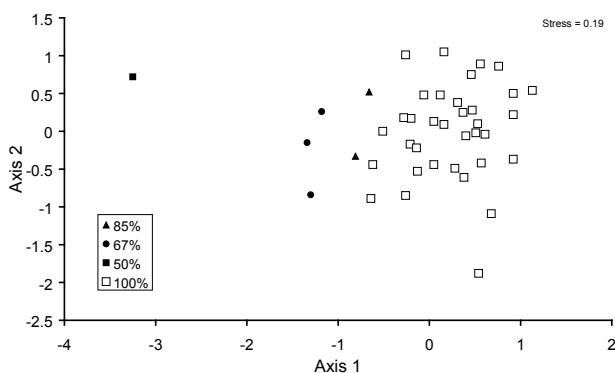


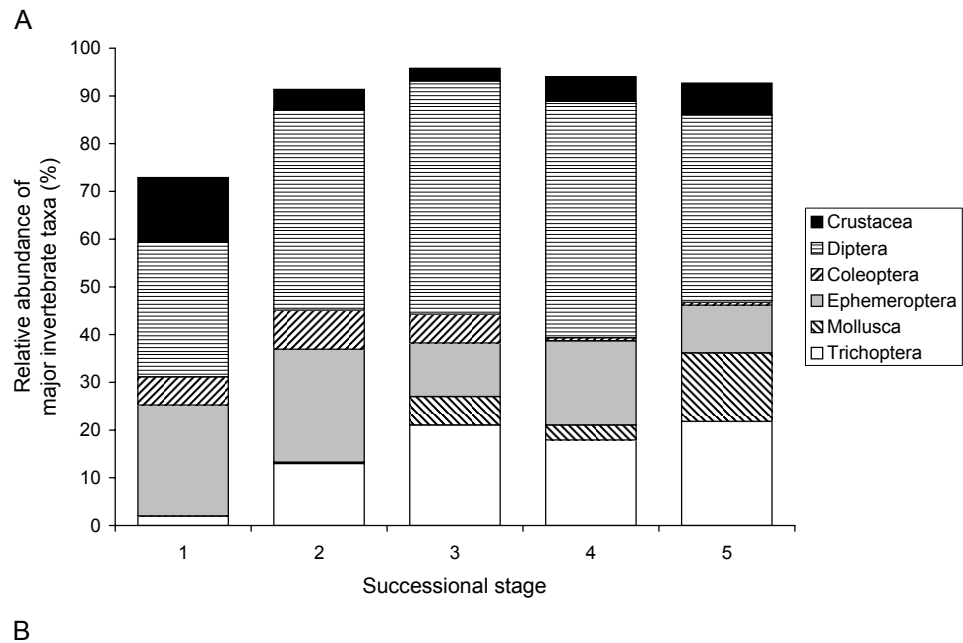
Figure 17. MDS ordination of benthic invertebrate communities in springs. Sites are delineated according to permanence of flow. The majority of sites were always flowing and thus exhibited 100% permanence.

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>Polypeditum</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).

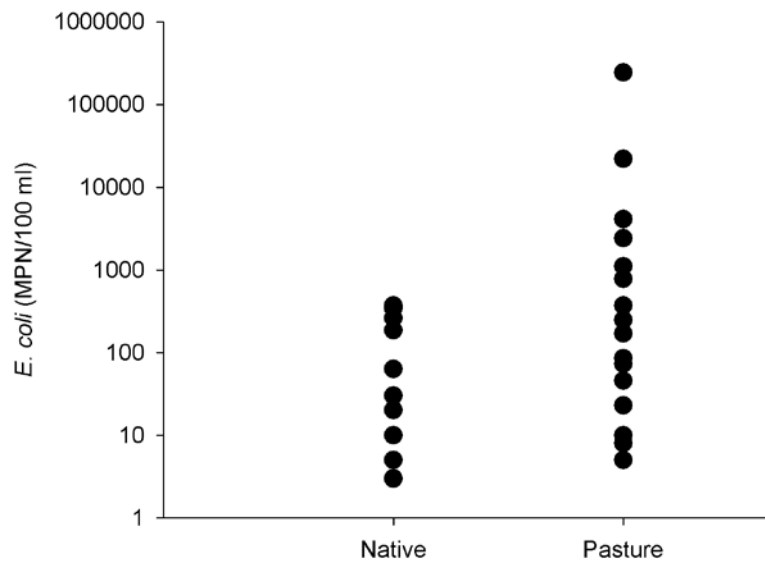
A total of 34 spring sites in four regions were sampled in January and February 2003 (Table 4). Each spring site was classified as having a riparian zone with either native vegetation or pasture. All sampled springs were small, with discharges estimated to be generally less than 10 L/s.

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).

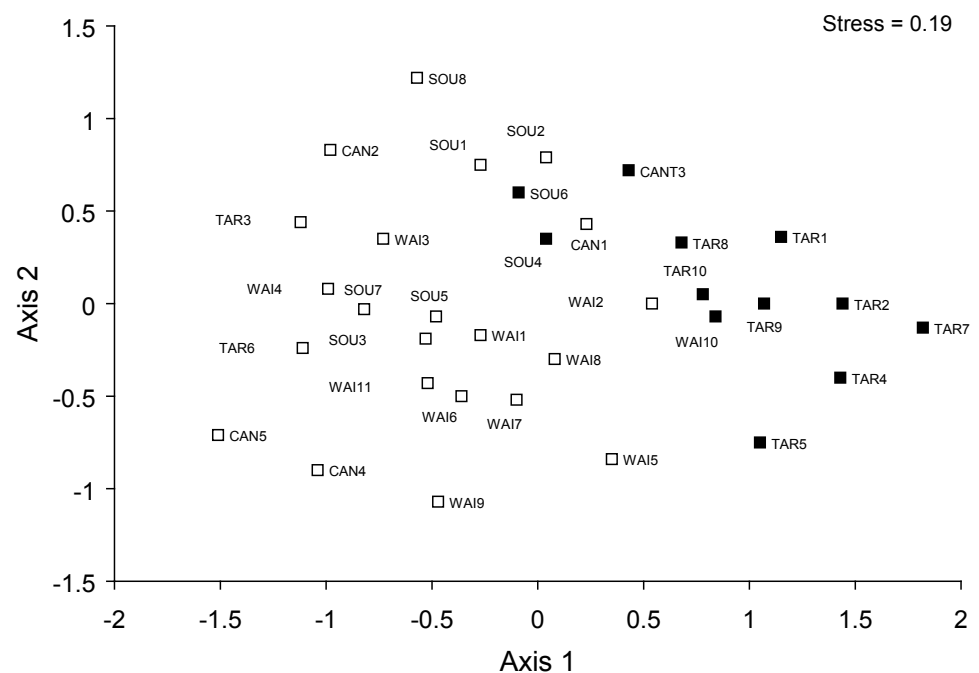


levels of *E. coli* were in pasture where stock were excluded. However, waterfowl (mallard ducks, *Anas platyrhynchos*) were present at all three springs, and it is likely they were the source of faecal contamination.

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, $\%EPT_{\text{taxa}}$ (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.



native riparian vegetation (Waikato 10) had a fauna that was very similar to that found in the remnant bush gullies in Taranaki. Unfortunately, there are very few such remnants in the highly modified Waikato landscape.

4.4.2 Separating the effects of riparian vegetation type and stock access on springs

The broad-scale survey of Scarsbrook & Haase (2003) indicated associations between community composition and riparian land use, but regional differences, and other sources of variation (e.g. variation in substrate type, underlying geology, stock access) precluded strong inferences on land-use effects. During the summer of 2004, a separate, complementary study was carried out to identify the interacting effects of type of riparian vegetation (native bush v. pasture) and stock access on springs. Sources of variation in other factors were minimised by selecting study sites within a particular hydrogeological setting (i.e. rheocene springs arising along a narrow elevation gradient along the base of the western Kaimai Ranges; Fig. 21). Springs were chosen to reflect four different land uses:

- Native forest riparian zone with no stock access (NNS; $n = 4$)
- Native forest riparian zone with stock access (NS; $n = 3$)
- Pasture riparian zone with no stock access (PNS; $n = 4$)
- Pasture riparian zone with stock access (PS; $n = 4$)

Invertebrate community composition varied significantly with riparian vegetation type (i.e. native v. pasture), whereas stock access appeared to produce additional, cumulative effects. There was evidence of a disturbance gradient across the four treatments, with the numbers of taxa unique to a particular treatment decreasing from 20 at native sites without stock access, through to only six at pasture sites with stock access (Fig. 22A).

Relative abundance of the dominant taxon—an indicator of community stress (Barbour et al. 1999)—increased along the disturbance gradient (Fig. 22B). The chironomid *Polypedilum* sp. was the dominant taxon overall, making up 20% on average of all samples. The relative abundance of EPT individuals decreased from an average 44% at native forest springs without stock access, through to only 2% at pasture springs with stock access. Mayflies (e.g. *Zephlebia dentata*, *Z. nebulosa*) and stoneflies (e.g. *Austroperla cyrene*) were major components of the fauna in the native forest springs, whereas amphipods, chironomids and molluscs dominated the pasture springs.

In a study in Switzerland, Zöllhöfer (1999) compared the invertebrate faunas of natural springs with those of springs grazed by cattle. He found significant differences in taxon richness between the two spring types. One distinct pattern was that mayflies were absent from springs with unlimited cattle access. In the present study we found a strong land-use effect on the relative abundance of leptophlebiid mayflies. The relative abundance of leptophlebiid mayflies averaged 24% in springs in native forest with no stock access, and was similar at native forest sites with stock access (20%), but decreased to 7% at pasture sites with no stock, and to less than 1% at pasture sites with stock access. Therefore, we suggest that riparian vegetation type may be the principal determinant of mayfly abundance in our Kaimai springs, but stock access can cause additional losses, particularly in open pasture springs.

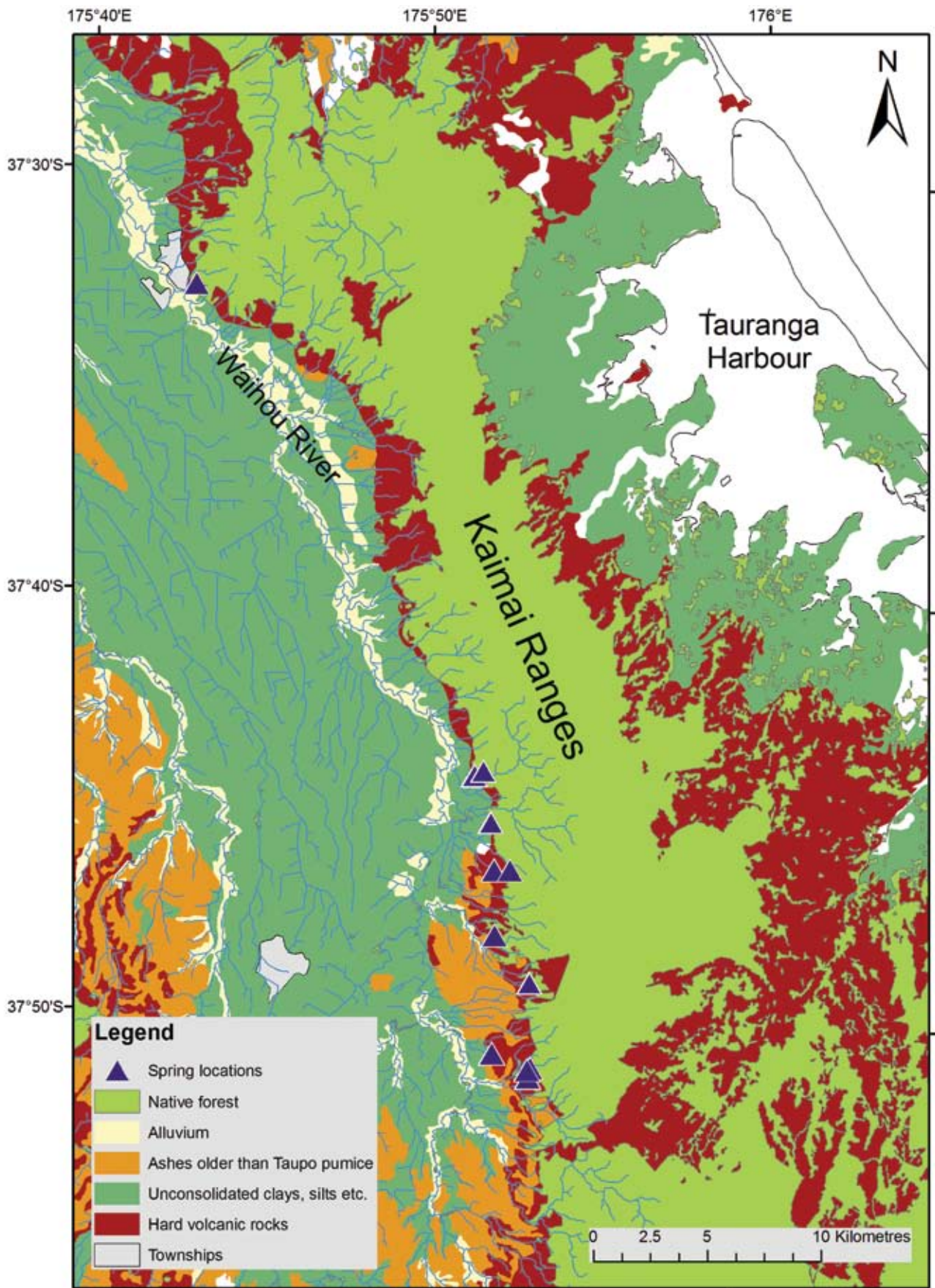


Figure 21. Locations of 15 springs along the base of the Kaimai Ranges.

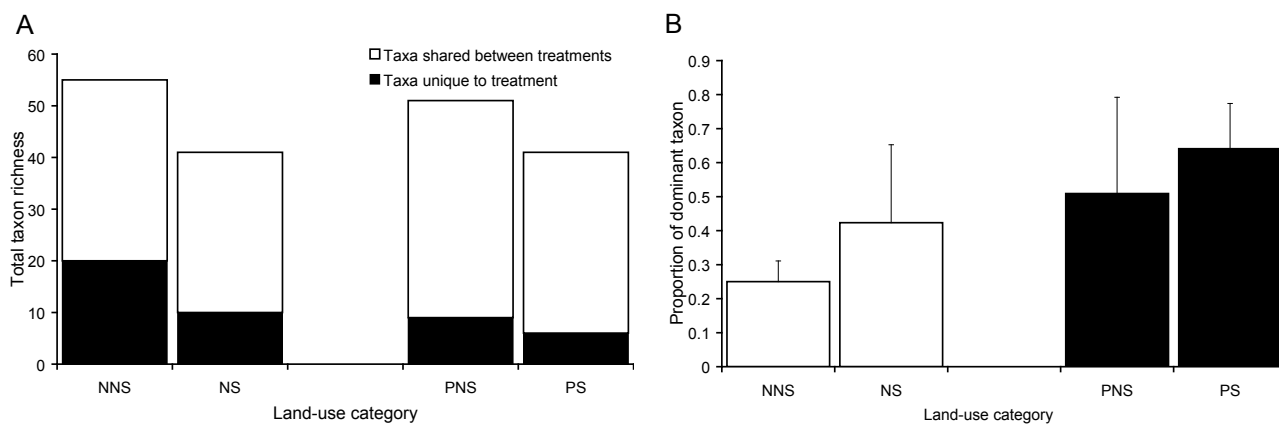


Figure 22. (A) Taxon richness patterns across springs in different land-use categories; (B) Proportions of dominant taxon across springs in different land-use categories.

5. Anthropogenic threats to springs

As ecotones, springs integrate ecological processes occurring in groundwater, surface water and terrestrial ecosystems. However, this integrating property also makes springs particularly vulnerable to impacts caused by a range of direct and indirect human activities (Fig. 23). The range of threats has been summarised by a number of authors (e.g. Danks & Williams 1991; Smith 2002). Water permanence is a key factor influencing the number of crenobiontic species, endemism and biodiversity in spring habitats (Danks & Williams 1991; Erman & Erman 1995). Thus, many threats to the integrity and biodiversity of spring ecosystems are related to the reduction of their flow. Groundwater abstraction for mining and pastoral purposes is the major threat to the mound springs of the Great Artesian Basin (GAB), Australia, and has already led to the extinction of many springs and their associated flora and fauna (Fatchen 2000; Ponder 2002). Land drainage for agricultural and forestry activities has caused a fall in water table levels which, in turn, has reduced the density of springs to less than half on the Swiss Plateau and in the Jura Mountains (Zollhöfer 1999). In the USA, water extraction for municipal and irrigation uses has reduced springs to approximately 15% of historical levels in the Funeral Mountains, Death Valley (Erman 2002), and water abstraction for municipal supply is the major threat to numerous springs of the state of Florida (Hartnett 2000). Modification of surface flows can also alter spring flow. For example, canalisation and regulation of rivers can reduce the inter-connectivity between surface flows and groundwater storage (Hancock 2002) and negatively affect spring flows, especially of alluvial springs. Urbanisation upstream from a source of the Avon River/Otakaro, Canterbury, has produced a downstream shift of its springs as land development advanced (Marshall 1973). It has been suggested that water extraction impacts on spring flows may be a greater problem in valley and desert systems, which depend largely on artesian-regional aquifers, than in mountainous areas (Sada et al. 2001; Erman 2002).

The value of natural spring waters is illustrated by the growth of the bottled water industry, both in New Zealand and internationally. However, Smith (2002) suggested that the capture of springs for bottled water operations is a significant threat, worldwide, to their integrity and persistence.

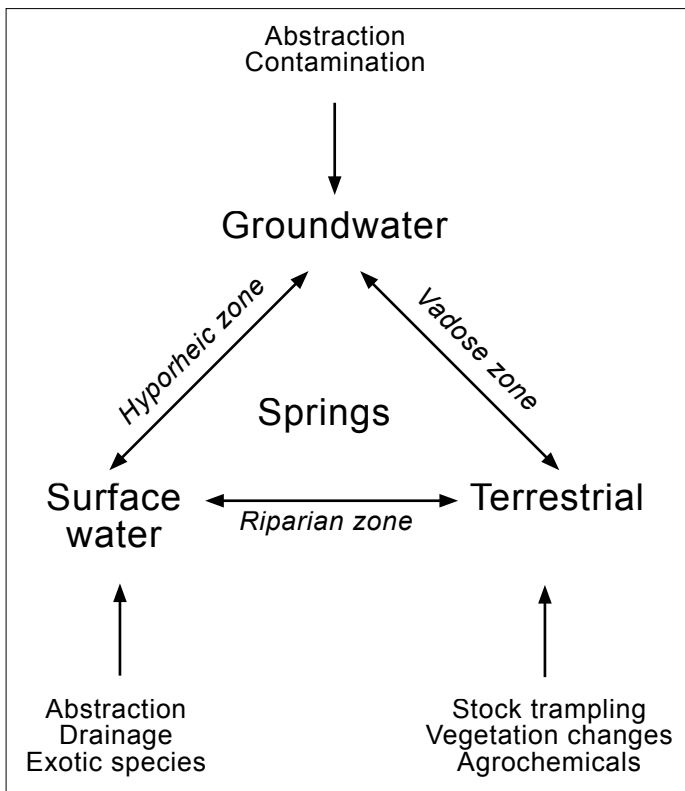


Figure 23. Diagram showing how springs integrate anthropogenic impacts on groundwater, surface water and terrestrial ecosystems.

Spring water quality largely depends on the underlying geology and the land uses of the recharge basin (van der Kamp 1995). Contamination can occur from point sources such as septic tanks (e.g. Blue Spring, Florida) (Hartnett 2000), or from diffuse sources such as the application of agrochemicals (e.g. springs of the Wairau River plains) (Young et al. 2002). Additionally, heavy metals and other chemicals associated with mining can pollute groundwaters and aquifers (Hancock 2002), and are the cause of water contamination in some western USA springs (Sada et al. 2001). Another source of pollution can be road and urban runoff. For example, water quality in Sulphur Springs, Florida, was seriously impaired after the city of Tampa directed stormwater into sinkholes connected to the spring (Hartnett 2000).

Removal of riparian vegetation affects invertebrate community composition in New Zealand springs (Scarsbrook & Haase 2003) and Californian (USA) springs (Erman 2002). The absence of riparian cover changes

stream energetic budgets (Quinn 2000) and temperature patterns (Collier et al. 2001), and can produce algal and macrophyte blooms as more light reaches the channel (e.g. springs of the Wairau River plains) (Young et al. 2002). Elimination of riparian forest also destabilises banks and diminishes the filtration properties of the riparian zone, which contribute to increased nutrient and sediment loads from surface run-off (Quinn 2000; Parkyn & Wilcock 2004). Finally, logging activities have the potential to damage the physical environment of a spring, by increasing the sediment load reaching the spring channel (Erman & Erman 1995; Zollhöfer 1999; Erman 2002), and reducing woodland environments, which can provide shelter, feeding and mating areas for some adult aquatic insects (Collier & Smith 1998, 2000).

Livestock affect streamside vegetation, stream channel morphology, shape and quality of the water column and the structure of stream-bank soil (Kaufmann & Krueger 1984; Fleischner 1994). In arid regions, cattle grazing changes riparian vegetation community composition (e.g. at mound springs) (Fatchen 2000; Ponder 2002), and overgrazing can virtually eliminate all riparian vegetation (e.g. springs in the western USA) (Sada et al. 2001; Erman 2002). Moreover, livestock trampling erodes spring banks, and degrades habitats for aquatic flora and fauna by filling the interstitial spaces around rocks and gravel and by compacting mud and clay (Minckley & Unmack 2000; Sada et al. 2001; Erman 2002). In contrast, it has been suggested that coarse substrate (cobbles, boulders and bedrock) may provide some protection from stock trampling in some New Zealand springs (Scarsbrook & Haase 2003).

Piping and diversion of spring flows is one of the most common threats to the physical diversity of spring habitats (Shepard 1993; Erman & Erman 1995; Cianficconi et al. 1998; Fatchen 2000; Sada et al. 2001), and can reduce or

eliminate flows altogether (Erman 2002). Many high-discharge springs are sites for swimming, fishing and camping (Shepard 1993; Hartnett 2000). The recreational use of springs often involves capture of the spring and water diversions for aesthetic reasons, damming of spring pools, removal of riparian vegetation, compaction of soils and usage of chemicals such as chlorine (van Everdingen 1991; Shepard 1993; Zollhöfer 1999; Sada et al. 2001).

All but one of the 12 spring-associated hydrobiid species described from artesian springs in Queensland by Ponder & Clark (1990) were considered to be endangered because the springs they reside in had no conservation status and are threatened by pastoral activities and extraction from parent aquifers. Ponder & Clark (1990) suggested that the threats posed by stock access were less serious than those posed by the land managers themselves. Damage by stock may be short-term, whereas activities of land managers (e.g. damming, digging out, over-pumping of an aquifer) may result in the complete disappearance of a spring. Ponder & Clark (1990) noted that many of the springs surveyed by Habermehl (1980) in the late 1970s no longer existed when visited in 1984. In New Zealand, our diverse hydrobiid fauna may similarly be threatened by land-use intensification. Fig. 24 shows a small spring arising from limestone hills in central Southland. This spring contained two new species of hydrobiid snail (Scarsbrook & Haase 2003), yet was open to trampling by stock.

Introduced species can also have a significant impact on the biodiversity and ecological function of springs. For example, vertebrates such as the mosquitofish and many plant species recognised as noxious weeds are now found in springs throughout the world (Shepard 1993; Minckley & Unmack 2000; Sada et al. 2001; Ponder 2002; Young et al. 2002). Exotic plants reduce overall plant and animal diversity and alter site hydrology, whereas non-native fishes, crayfish and toads may reduce or even extirpate native aquatic species (Sada et al. 2001; Ponder 2002; Young et al. 2002).

Because springs have groundwater sources, spring water quality is obviously affected by activities that impact groundwater quality (see Close et al. (2001) for a review). This suggests that the fauna of springs may have potential as relatively inexpensive indicators of groundwater quality (Williams & Danks 1991). Indeed, springs and their fauna may act as indicators of both the sustainability of groundwater abstraction and groundwater quality.

5.1 IMPACT OF RIVER MANAGEMENT AND REGULATION ON BRAIDED RIVER SPRINGS

The springs of braided rivers, and their fauna, are dependent on the spatial and temporal dynamics of flood-plain elements, and connectivity within the braided river flood plain (Gray 2005). Different habitat types (e.g. springs, springbrooks, side braids and main channels) are maintained in more-or-less constant proportions by the natural flow regime that drives the shifting mosaic of flood-plain elements (Arscott et al. 2002; van der Nat et al. 2003; Hauer & Lorang 2004). Anthropogenic activities such as diversion, channelisation and impoundment can have severe impacts upon the relative proportions of these flood plain elements, and thereby pose a significant risk to discrete habitats such as springs.

Many large New Zealand rivers have been channelised to create farmland and prevent river migration (Young et al. 2004). Constriction of the active river channel can cause changes in local aggradation and degradation, which can affect the channel's interactions with the aquifer and thence water supply to springs. A 0.5-m drop in the bed of the lower Motueka River was predicted to reduce summer aquifer recharge by 24% (Young et al. 2004). Furthermore, disconnection of the river from its flood plain tends to reduce habitat heterogeneity at the landscape scale and alter successional dynamics within existing flood-plain habitats (e.g. springs). Following the construction of flood control barriers, extant springs are likely to have a reduced probability of disturbance, and the formation of new springs by the reworking of alluvial gravels and river channel migration is likely to be reduced. Spring-fed habitats therefore will tend towards later successional stages (see section 4.2), with subsequent implications for biodiversity across the riverscape.

The effects of flood retention works are not universally negative. In the lower Selwyn River/Waikirikiri, flood retention practices have included both the construction of retention banks and planting of riparian willows to constrict the active channel. Spring habitats often occur at the head of

Figure 24. A small Southland spring showing obvious damage from stock trampling. Despite the damage from stock, the spring contained two new species of hydrobiid snail.



remnant channels, which form adjacent to active channels. These springs are formed by the constricted river cutting down into the alluvium, and intersecting the water table, rather than spreading laterally. Bank vegetation is the principal control on lateral channel movement (M. Hicks, NIWA, pers. comm.) and, hence, deep scouring by constricted flows. In the lower Selwyn River/Waikirikiri, springs that occur in the scoured beds of remnant channels likely provide refugia for fish and invertebrates during summer low-flow periods in the river, although this hypothesis has yet to be tested. Gray (2005) noted spring up-welling complexes formed in the lee of flood retention works in the upper Waimakariri River at Klondyke Corner. Kilroy et al (2004) collected 42 algal taxa in one of these sites, by far the highest diversity of any of the 24 sites sampled. Whilst it is interesting that human activities can be constructive as well as destructive in terms of habitat, we must recognise our lack of knowledge of the long-term effects of activities such as gravel extraction, flood bank construction and riparian planting of exotic trees on the distribution and permanence of springs. In general, construction of flood control barriers results in the reduction of invertebrate and habitat diversity seen in many channelised European rivers (Claret et al. 1999; Pringle 2001; Hohensinner et al. 2004).

The braided rivers of the South Island were formed in the last 20 000 years as a result of glacial action, rainfall and snow melt (Gage 1977). Continuous erosion of friable bedrock, coupled with high and unpredictable rainfall, maintains these rivers in a constant state of morphological dynamism. The alluvium that has accumulated within glacial valleys is highly permeable, and carries an alluvial aquifer within a sinuous lattice of preferential flow paths (Huggenberger et al. 1994; Woessner 2000; Poole et al. 2002). This aquifer provides stable inputs of water for springs, despite the irregularity of precipitation in each catchment.

Over time, reductions in porosity and hydraulic conductivity may occur because of the intrusion of fine sediments into interstitial spaces, or through bed-armouring processes. The clogging of the top layer of the channel sediments with fine sediment is termed 'colmation' (Brunke 1999). Under natural flow regimes, fine sediment is removed by high-flow events involving bed load movements, thereby resetting the colmation process (Brunke & Gonser 1997). Impoundment of the River Spol in Switzerland resulted in decreased discharge and a flow regime unable to effect bed mobilisation, leading to clogging of the bed interstices (Murle et al. 2003). A similar experiment conducted in the River Rhone flood plain revealed the importance of high-flow events for maintaining connectivity between surface waters and groundwaters (Claret et al. 1999). The pristine headwaters and natural flow regimes of many rivers are critical to groundwater-surface-water connectivity, as they maintain the aquifer recharge required to supply flow to many springs found along flood-plain reaches (Poff et al. 1997).

Impoundment is a feature of many large rivers. Since 1950, 10 000 km³ of water (more than five times the volume of water in all the world's rivers) have been impounded in reservoirs globally (Rosenberg et al. 2000). Despite the damming of many of New Zealand's largest rivers, such as the Clutha, Waitaki, Waikato, Rangitaiki and Waiau, little research has been undertaken on the geomorphological and ecological consequences for groundwater-surface-

water exchange, or their spring complexes. However, there is a wealth of international and New Zealand literature summarising the general downstream effects of flow regulation brought about by impoundment (e.g. see Henriques 1987; Rosenberg et al. 2000). Overall, dams and river diversions have proven to be severely detrimental to aquatic habitat, contributing to the destruction of fisheries, extinction of species and the loss of ecosystem services vital to the human economy (Pringle et al. 2000; Rosenberg et al. 2000). In particular, the negative impact of flow regulation upon the morphological and successional diversity of flood plains has been highlighted (Ward & Stanford 1995; Gilvear 2004; Hohensinner et al. 2004; Choi et al. 2005). A reduction in channel-forming flows and sediment load reduces the rate of channel migration, which is important for maintaining high levels of habitat diversity. High biodiversity in flood-plain ecosystems is a function of the diversity of water bodies with differing degrees of connectivity with the main channel, and the range of successional stages present due to historic channel migrations (e.g. Reinfelds & Nanson 1993). The effect of flow regulation is similar to that of channelisation, in that it truncates the fluvial system and disconnects the river from its flood plain (Hohensinner et al. 2004).

Since the 1930s, the morphology of the lower Waitaki River in the southern South Island has been significantly altered, predominantly by impoundment for hydro-electrical power generation. The reduction in flow variability and sediment input due to impoundment has caused an increase in channel stability. In the Duntroon area, encroachment of the river by exotic vegetation has reduced the width of the un-vegetated flood channel by 250 m (Meridian Energy 2003). Over the same time period the river has changed from a braided system to one characterised by more stable anastomosing channels (Meridian Energy 2003). The changes in channel morphology have resulted in a reduction in flood-plain area and associated habitat heterogeneity, with potential for loss of species adapted to life within the shifting habitat mosaic of braided rivers (Gray 2005). Although groundwater-fed channels were recorded in the lower Waitaki in 2003 (Meridian Energy 2003), the long-term effects of channel morphology changes on them are unknown.

Natural flow regimes maintain a mosaic of variable groundwater-surface-water exchange and contribute to the formation of braided river springs. Without high levels of disturbance in the main channel, vertical and lateral hydrological connectivity are reduced, and result in the loss of springs, which can be considered 'hotspots' of biodiversity within the braided river corridor (Gray et al. 2006). Anthropogenic activities such as diversion, channelisation and impoundment can have severe impacts upon the balance of dynamic riverine systems. Consideration of the biodiversity values of a river system must take into account habitat diversity and functional integrity of the whole system. The 3-dimensional aspect of flood plains, longitudinal linkages and connectivity between adjacent elements in the landscape mosaic should be central features of our management of braided rivers (Pringle 1997; Ward et al. 1999; Pringle 2001; Malard et al. 2002; Wiens 2002).

6. Management and conservation of springs

Direct (e.g. water abstraction) and indirect (e.g. domestic animal grazing) utilisation of springs by society produces a wide variety of benefits to humans, but these uses may also be associated with significant costs to the environment, including biodiversity loss and deterioration of water quality, which threaten the ecological integrity of spring ecosystems. Effective management of springs will be achieved by recognising the full range of environmental and societal values associated with these habitats, understanding threats to the sustainability of these values and formulating strategies that provide a balance between potentially conflicting uses.

Throughout the world there is a growing recognition of the value of springs, and several initiatives have been implemented to ensure their protection and sustainable management. In the eastern USA, the Florida Springs Task Force has outlined steps for protecting and restoring Florida's springs and underground aquifers (Hartnett 2000), while in the west a conference focusing on spring-fed wetlands in Las Vegas, Nevada, has helped to unite visions on spring habitat management (Sada & Sharpe 2004). Moreover, the Bureau of Land and Management, USA, has also produced a guide to effectively manage and protect western freshwater springs (Sada et al. 2001). In Germany, the Society of Spring Ecology and Conservation (SSEC) has played an important role in producing valuable information related to spring habitats with the creation of the journal *Crunoecia*. SSEC also organised the first European symposium on spring ecology and conservation. In Australia, the Great Artesian Basin (GAB) is the focus of a group of researchers that meets annually to discuss questions related to the management and protection of springs. Furthermore, the South Australian Department for the Environment has published a plan for the management of Australian mound springs (Fatchen 2000). More broadly, the Australian federal government has developed national strategies for the management of groundwater-dependent ecosystems (GDEs; Sinclair Knight Mertz 2001). The goal is to provide water for the environment to sustain and where necessary restore ecological processes and biodiversity of GDEs, such as springs.

6.1 SPRINGS AS GROUNDWATER-DEPENDENT ECOSYSTEMS

We believe that a GDE management framework (Hatton & Evans 1998) may be applicable and beneficial to springs management in New Zealand, although it will form only part of a complete management framework. Recognition of springs as GDEs is essential to their management and protection, because groundwater abstraction and consumptive use, as well as land-use practices impacting on aquifer quality, are key threats to the integrity of spring habitats.

Hatton & Evans (1998) recognised five classes of ecosystem dependency on groundwater attributes (e.g. flux, level, pressure, quality): entirely dependent, highly dependent, proportionally dependent, opportunistically dependent and not dependent. Many springs can be classified as falling into the 'entirely dependent' category, because even slight changes in groundwater attributes can lead to their demise. However, some spring types (e.g. linear alluvial springs) may be also classified under the 'highly dependent' category, as these ecosystems may be adapted to naturally varying groundwater levels.

There are four key steps to developing GDE management strategies:

1. Identify potential GDEs
2. Determine the degree of ecosystem dependency on groundwater
3. Assess the water regime in which dependency operates
4. Determine the environmental water requirement

With regard to the management of springs, Steps 1 and 2 are implicit, whereas Steps 3 and 4 require assessments of the full range of existing groundwater water uses and the effects different uses have on ecosystem integrity. As is the case with freshwater ecosystems throughout the world, determining a spring's environmental water requirements is a challenging task. In springs, complete loss of flow would be devastating, but the ecosystem may be able to function at reduced levels of groundwater flux, pressure or quality.

6.2 KEY ELEMENTS OF A SPRING MANAGEMENT FRAMEWORK

As with any management strategy, the clear definition of management goals for springs is a precursor to effective conservation, protection and restoration. Set out below, we provide a synopsis of steps followed in spring management worldwide, and recommend key elements that we believe should form the basis of a spring management strategy in New Zealand.

6.2.1 Spring mapping

Mapping of springs is essential to estimate spring densities and describe broad-scale environmental characteristics. In New Zealand, the first attempt to create a national spring database has yielded 527 springs over a 2-month period (see section 2.2.1). Spring locations were obtained through polling of management agency staff and the freshwater science community. This database is complemented by an additional 1400-1500 springs in the pre-existing ECAN database. Further work is required to expand the spring database, and to link it to available physico-chemical and biological data. It should be noted that current freshwater classification schemes in New Zealand (e.g. REC) do not explicitly include spring habitats. Further development of a spring database may allow this to be rectified in the future.

Several spring mapping surveys have also been carried out on a regional level in Germany (Groever et al. 1996; Hotzy 1996; Krueger 1996). In the district of Gueterlosh (220 km²), 203 springs were located in a 12-month period (Groever et al. 1996), whereas 700 springs were recorded over 3 years in Brandenburg (29 000 km²), although this has been suggested to be only

10% of the estimated total number (Krueger 1996). Extrapolation of spring densities and types from one region to another is likely to generate significant errors, as spring numbers and typology are highly influenced by regional hydrogeology (van Everdingen 1991; van der Kamp 1995). Moreover, locating spring sites and collecting information (i.e. past disturbances, land uses) involves extensive public consultation with locals and private landowners, and thus must be tackled at a regional level. GIS techniques have proved quite efficient for the retrieval of information on springs such as land uses, vegetation, underlying geology and climate data, but ground-truthing of such information is vital.

6.2.2 Spring habitat assessment

A full-scale scientific investigation of all springs within a region is unlikely to be justifiable. However, the evaluation of spring ecosystem conditions is necessary to record basic information, which will be used to establish management and restoration priorities. This information should include discharge characteristics, habitat structure, flora, fauna and water chemistry. Different methods can be used for spring habitat assessment. In Australia, the GDE approach (see section 6.1 above) has been useful for spring management (e.g. Fatchen 2000), and this approach may also be useful in New Zealand. In Germany, environmental quality indices are in widespread use (Hinterlang & Lischewski 1993), with specific evaluation methods for spring flora and riparian vegetation (Hinterlang et al. 1993), fauna (Fischer 1996; Zollhöfer & Gonser 1998) and water chemistry (Andree et al. 1996) currently in use. Assessment of proper functioning condition of spring habitats can also be used for rheocene (Prichard et al. 1998) or limnocrene and helocene (Prichard et al. 1999) spring types as suggested by Sada et al. (2001). Recording of exotic and rare species, disturbance conditions and conflicting issues with management objectives is highly desirable (Sada & Pohlmann 2003). The assessment process should also clearly identify existing and potential threats to the range of values provided by springs.

6.2.3 Management priorities and direction

Once spring biotic and abiotic characteristics have been evaluated, and the management needs identified, then management priorities and direction can be developed. Examining habitat condition and determining whether a spring needs protection or restoration will determine management responses. Priority should be assigned to protecting unaltered spring habitats and restoring habitats with a high potential for recovery (Sada et al. 2001). Selected habitats may also need protection to prevent further degradation until restoration activities start to take effect.

There are many factors that can be considered in setting up management priorities, and resource agencies must decide which ones are most appropriate for their region and conservation programmes (Sada & Pohlmann 2003). Springs within a region can be ranked according to their resource values and restoration needs using matrix analysis (Sada et al. 2001). This would indicate the relative importance of each spring and how each one can be considered during management and restoration programmes (Sada et al. 2001; Sada & Pohlmann 2003). Consequently, resources can be allocated according to the management priorities that have been set.

6.2.4 Spring monitoring

The efficiency of management strategies and progress towards stated goals can be assessed through monitoring programmes. These programmes should be designed to quantitatively describe biotic communities, riparian habitats and spring flow characteristics, accounting for their spatial and temporal variability. Moreover, monitoring surveys should become less intensive as more information is gathered on biotic and abiotic natural variability (Sada & Pohlmann 2003). Changes outside natural ranges can be determined as excessive, while those within the natural range are likely to be acceptable. Site selection for monitoring is crucial and appropriate reference sites for intermittent and/or altered springs will be required to allow separation of changes associated with anthropogenic and natural changes (Sada & Pohlmann 2003). Because spring habitats can be sensitive to disturbance, particularly where local endemics may occur, the frequency and destructiveness of sampling techniques used in the monitoring programme should be carefully considered (Resh 1983). Monitoring programmes should be part of any management plan in order to review and update management strategies to achieve desired goals. Monitoring methods would also need to be consistent with initial assessment methods so as to have comparable baseline and post-management datasets.

6.3 PROTECTION, ENHANCEMENT AND RESTORATION OF SPRING HABITATS

The environmental context (e.g. hydrogeological properties, land use) of a given spring should be carefully considered when determining management actions to protect, enhance or restore ecological integrity. For example, fencing and exclusion of cattle from spring habitats have different effects on springs in arid and temperate regions. In temperate regions, cattle exclusion, which is one of the first measures implemented by spring restoration programmes in Germany (e.g. 'Aktionsprogramm Quellen', J. Römheld, Bayerisches Landesamt für Wasserwirtschaft, München, 2005, pers. comm.), helps to re-establish woodland vegetation, which contributes to enhanced habitat quality. In contrast, exclusion of livestock reduced plant diversity and free water areas in springs of the GAB because of large increases in vegetation biomass of the most competitively superior species (Fatchen 2000). The appropriate management regime should take into account the natural condition of a spring with respect to exclusion of grazing animals. A grazing/non-grazing rotation programme or the maximisation of desirable outcomes can be the solution to manage spring habitats successfully in arid regions (Fatchen 2000).

In pre-human times (1000 years BP), most of New Zealand was heavily forested and ungulate grazers were absent. Therefore, the natural condition of most springs in New Zealand would have included extensive riparian vegetation and a very different grazing regime from that found now, so protection and restoration of these habitats should take this into account.

Delineation of the spring recharge basin is desirable in order to protect spring water quality (Jensen et al. 1997), despite it being difficult to achieve—it requires a detailed knowledge of underlying geology and groundwater flows. However, it will help to identify possible areas that may act as sources of groundwater pollution, and to develop best management practices through local land-use planning. Areas adjacent to spring sources, or in their recharge basins, have been purchased as part of restoration programmes in Florida (Hartnett 2000) and Germany (Buechler & Hinterlang 1993; Hurck 1996).

Springs and a portion of their associated springbrooks should be protected from activities that decrease biological diversity and cause functional changes. Groundwater abstraction close to the spring and development around the spring should be carefully controlled. Diversions, impoundment or other types of habitat modifications, when necessary, should not be done within the first 50 m of the spring and should stop drawing water when it is not needed (Sada et al. 2001; Sada & Pohlmann 2003). Where fish access to springs is a desired management goal, appropriate measures should be taken to ensure uninterrupted access (e.g. fish-friendly culvert design). Appropriate native riparian vegetation (i.e. woodland vegetation or grasses) should be planted or allowed to grow to restore sediment and nutrient run-off filtering and to stabilise spring banks (Collier et al. 1995). Proper management practices, such as construction of sign-posted walkways, toilet facilities and rubbish containers will also protect springs on public lands from damage associated with recreational use (Fatchen 2000; Hartnett 2000).

Populations of non-native plants and animals need to be controlled, and it is important that control efforts are specific to these species. Application of more generic treatments such as rotenone, or broad-spectrum herbicides, can have deleterious effects on spring biodiversity and ecosystem functioning (Sada et al. 2001; Erman 2002). Methods that minimise impacts such as manual removal, targeting only a small portion of habitat during a single treatment, or confining natives where they are protected from treatment effects, are preferred (Sada et al. 2001). Elimination of noxious weeds can be effectively achieved by a combination of mechanical methods and proper riparian management (i.e. providing shade) (Young et al. 1999), without the extirpation of other native flora.

Finally, education programmes can assist in improving community understanding of the relationship between land uses and the quality and quantity of spring water. Thus, a coordinated educational programme, employing a range of educational materials (e.g. brochures, pamphlets, booklets, slide exhibitions, videotapes, school field trips or regional and international conferences) will help to communicate this understanding and facilitate spring ecosystem protection (Laukoetter et al. 1992; Hartnett 2000).

Habitat restoration is an important aspect of managing spring resources, although it may take lower priority than protection of unmodified springs, where these unmodified habitats are under threat and contain significant biodiversity values. Restoration may include removal of barriers between groundwater, spring and springbrook, including man-made structures such as pipes, troughs, spring boxes or dams for impoundments, all of which impede the natural movement of water. Restoration may also include active transfer

of fauna or flora from one spring to another, although it does create risks for genetic diversity (Erman 2002), particularly for groups with high levels of local endemism (e.g. hydrobiid snails). Such threats to genetic diversity can be minimised by developing a detailed knowledge of the spring fauna and flora of the region (Sada et al. 2001). However, it would seem safer to favour natural recolonisation processes than to play an active role (Waechter & Ruether 1994; Glattfeld et al. 1996), except where natural recolonisation may be precluded by limited dispersal ability.

6.4 PROTECTION OF NEW ZEALAND'S COLDWATER SPRINGS

Many of New Zealand's largest springs are afforded some level of protection because they are part of the conservation estate (e.g. Waikoropupu Springs; Ohinepango Springs), or through their use for public water supply (e.g. Hamurana Springs). However, large springs are rare features in the landscape, and most springs are small and inconspicuous.

Based on springs' distributional density, their poor representation in the conservation estate and their high potential for anthropogenic disturbance through water abstraction and land-use intensification, we suggest that small, lowland springs are most at risk of degradation and further loss of biodiversity. Many of these small lowland springs are already impacted, and active rehabilitation and restoration will be required. However, many of these springs will also be located on private land, so their protection will be very dependent on the motivation of the landowner. Education of landowners on the values and services provided by intact, functioning springs will play an important role in protection or restoration of these systems.

We have identified three major spring types based on their underlying geology which may provide a useful basis for determining management approaches to the conservation and protection of spring biodiversity. These are:

- *Karst springs*—These exhibit a relatively high degree of permanence, although their discharge may be variable. Throughout New Zealand, but especially in Northwest Nelson, karst springs are a centre of hydrobiid snail and amphipod diversity. The high levels of local endemism observed in karst springs suggest that they may require management at relatively small spatial scales. For example, protection of individual springs will be required where maintenance of local endemics is a management priority.
- *Volcanic springs*—These are a major feature of the North Island, particularly around the Central Plateau and Mt Taranaki. Volcanic springs tend to have relatively high permanence and flow stability, but their history of large-scale disturbance tends to reduce their biodiversity values, and spring assemblages tend to be dominated by vagile insect taxa. Management of such springs should focus on protection of representative spring habitats within particular biogeographic regions.
- *Alluvial springs*—These tend to be concentrated in intensively farmed, lowland areas, especially in Canterbury and Southland. These springs are at risk from groundwater abstraction, river management and habitat

destruction. Management of alluvial springs should be intimately linked with groundwater management, so that spring flows and groundwater quality are maintained at the aquifer scale. Protection and rehabilitation of springs may also be required at the local scale, so that representative habitats are maintained within the landscape.

The key to the protection of small springs is to raise awareness of the values associated with spring habitats, so that landowners see them as valued landscape features. Raising awareness should be a deliberate, but gradual process. Organisations such as the QE II National Trust will have an important role to play. The Trust facilitates the protection of habitats of significant natural values on private lands. At present the Trust's database of covenants includes c. 350 wetlands, many of which will include springs (R. Allibone, QE II National Trust, 2005, pers. comm.).

Regional council activities will also be crucial to raising public awareness of the values associated with springs. Examples include work on the ecology of spring-fed systems in the Wairau River valley (e.g. Young et al. 2002), the extensive spring database produced by ECAN, and recent work detailing sustainable management of water resources of the Ruataniwha Plains (HBRC 2004).

7. Conclusions and future directions

Springs occur at the interface of groundwater, surface water and terrestrial ecosystems. As ecotone habitats, they are characterised by sharp gradients in physico-chemical characteristics (e.g. dissolved gases, temperature), but their defining characteristics (thermal and hydrological stability) are controlled by the hydrogeological context of their parent aquifer. Spring size, permanence, water quality and substrate type are all controlled by aquifer hydrogeology.

Springs throughout New Zealand contain a diverse fauna and flora. There is a significant spring specialist fauna, which includes a significant diversity of spring snails (Hydrobiidae), isopods of the family Phreatoicidae, amphipods of the family Paraleptamphopiidae, and a number of insect taxa (e.g. the mayfly *Zephlebia nebulosa*, the cased-caddis *Pseudoeconesus* spp.). The hydrobiid snail fauna of springs is of particular importance, as New Zealand is a significant hotspot of hydrobiid diversity. The high levels of local endemism observed in spring snails and amphipods indicate that springs are important centres of genetic diversity and radiation for poorly-dispersing taxa. At the regional level, Northwest Nelson and Southland appear to be hotspots for spring biodiversity. In braided river catchments, springs provide stable habitats in otherwise harsh aquatic environments. As a result, springs and the brooks they feed are important centres of biodiversity for both algae and invertebrates in these landscapes. Overall, the biodiversity values associated with New Zealand coldwater springs dictate that protection is required, particularly to halt the decline in indigenous biodiversity, and protect a full range of aquatic habitats.

Spring community structure is controlled, first and foremost, by spring permanence. In permanent springs, community structure varies with geology, elevation and disturbance history. Research on the Waimakariri River indicates that successional stage (which is determined by vegetation types and reflects time since disturbance) is a key factor influencing community structure in braided river catchments, although the presence/absence of macrophytes is important at local scales. At a range of spatial scales we have found that catchment land use and riparian vegetation composition are significant factors associated with spring invertebrate biodiversity patterns. Springs shaded by native vegetation have greater relative abundance of mayflies and stoneflies, and stock access appears to act as an additional, or cumulative source of disturbance. In general, lowland springs in pastoral landscapes with unlimited stock access can be expected to have reduced biodiversity values, although local factors, such as substrate composition, may mitigate impacts.

The key anthropogenic threats to the biodiversity values of New Zealand's coldwater springs are the unsustainable use of groundwaters through over-pumping, or chemical contamination, and the destruction of spring habitats through vegetation clearance and stock trampling. At the local scale, we suggest that spring protection on private land might be easily achievable, given sufficient landowner motivation, because springs are generally of small size, and their protection can provide a number of additional benefits to the landowner (e.g. water supply, nutrient trapping). At the regional scale, protection of the underlying aquifers to maintain spring flows constitutes a more difficult process, particularly in groundwater-dependent regions such as Canterbury and Hawke's Bay.

The key steps to improving our management of springs include an effective mapping of spring resources, identification of biodiversity values and other services, provision of methods for assessing spring habitat quality and biological integrity, definition of management goals for springs within different hydrogeological and land-use settings, monitoring to assess management effectiveness, public education and the provision of information on effective approaches for spring restoration or rehabilitation in degraded landscapes.

7.1 KEY KNOWLEDGE GAPS

Based on our review of available knowledge pertaining to New Zealand springs, we have identified a number of knowledge gaps that should be addressed in future studies. These are:

- *Spring classification*—There is a pressing need to recognise groundwater-dependent ecosystems (GDEs), such as springs, within national freshwaters classifications systems (e.g. River Environment Classification, REC). At present the REC system does mention spring-fed sources of flow, but these must be user defined. We recommend that efforts be made to include groundwater dependence within the GIS framework of the Source of Flow class of the REC. This should enhance our ability to map and better manage springs and spring-fed systems. The springs database developed during this programme may provide a useful starting point for inclusion of a springs GIS layer within the REC.

- *Identification tools*—Recent detailed biosystematics research has identified a huge diversity of spring fauna, particularly within the Hydrobiidae (Mollusca) and Paraleptamphopiidae (Amphipoda). Much of this detailed knowledge is relatively inaccessible to ecologists and managers, because of the highly specialised nature of species identification in these groups. Provision of identification tools even to genus level would help ecologists increase the taxonomic resolution of their spring research projects and more clearly identify biodiversity hotspots.
- *Springs as refugia*—Several authors have suggested a refugial role for springs in the landscape (e.g. Mosley 1983; van Everdingen 1991). We suggest that springs may provide significant thermal refugia for native fish and invertebrates in some regions of New Zealand. This is probably most likely to occur in alluvial springs in lowland areas of New Zealand (e.g. Canterbury Plains and Ruataniwha Plains, southern Hawke’s Bay), where river temperatures can exceed critical temperatures for key stream invertebrates. Research testing this hypothesis may help increase the profile of springs, and increase public perceptions of their value.
- *Restoration ecology of springs*—To our knowledge, no work has tracked spring restoration in New Zealand. In addition to the obvious management need for information on restoration processes, research on the restoration of springs would provide a test of the importance of dispersal characteristics in determining spring recolonisation dynamics. For example, in alluvial springs, the importance of groundwater as a pathway for dispersal could be tested—i.e. does the aquifer represent a continuous, navigable habitat or are organisms restricted in their movement by phreatic dispersal barriers or contemporary anthropogenic impacts.
- *River management effects on springs*—Recent preliminary work on the occurrence of springs within braided river systems has shown that flow regulation, channelisation and flood protection works can have severe impacts on flood-plain habitat heterogeneity. We suggest that further research is required to identify linkages between biocomplexity in braided rivers and large-scale human interventions in flow and habitat characteristics.
- *Development of methods to measure spring habitat quality and biotic integrity*—Such methods will be required for biomonitoring of springs. Closely aligned to this would be work to assess the use of spring fauna as indicators of sustainable use of groundwaters, both in terms of groundwater quantity (i.e. spring permanence) and quality (i.e. spring fauna as indicators of contamination).

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Appendix 1

ALGAL AND MACROPHYTE TAXA FOUND IN A SURVEY OF FIVE COLDWATER SPRINGS

This survey was carried out by F.B. Michaelis in 1974. Presence of a species is denoted by 'x'. '*' indicates introduced vascular plants. Sites are: A = Hamurana Springs (Rotorua), B = Lake Hayes spring (Queenstown), C = Otangaroa Springs (Putaruru), D = Three Springs (Fairlie), E = Waikoropupu Springs (Takaka), and F = Western Springs (Auckland).

	A	B	C	D	E	F
Diatoms						
<i>Achnanthes</i> spp.					x	
<i>Cocconeis</i> spp.					x	x
<i>Cymbella</i> spp.					x	
<i>Fragilaria</i> spp.						x
<i>Gomphonema</i> spp.					x	x
<i>Navicula</i> spp.					x	x
<i>Synedra</i> spp.					x	x
Cyanobacteria						
<i>Entophysalis rivularis</i>					x	
<i>Nostoc parmeloides</i>					x	
<i>Nostoc verrucosum</i>					x	
Microcoleus?					x	
Oscillatoria?					x	
Filamentous green algae						
<i>Ulobrrix zonata</i>						x
<i>Stigeoclonium</i> spp.						x
Chlorophyta						
<i>Chaetophora elegans</i>					x	
<i>Spirogyra</i> spp.					x	x
Chrysophyta						
<i>Vaucheria</i> spp.					x	x
Rhodophyta						
<i>Batrachospermum</i> sp.					x	
<i>Hildenbrandia rivularis</i>					x	
Mosses						
<i>Acrocladium cuspidatum</i>					x	
<i>Bryum blandum</i>					x	
<i>Calliergonella cuspidata</i>					x	
<i>Cratoneuroopsis relaxa</i>				x	x	
<i>Cyatophorum bulbosum</i>					x	
<i>Drepanocladus aduncus</i>					x	
<i>Drepanocladus fontinaliopsis</i>						x
<i>Echinodium hispidum</i>					x	
<i>Fissidens rigidulus</i>		x			x	
<i>Hypnobarilettia fontana</i>					x	
<i>Hypopterygium filiculaeforme</i>					x	
<i>Thamnum pandum</i>	x					
<i>Thuidiopsis furfurosa</i>	x					

Continued on next page

Appendix 1 continued.

	A	B	C	D	E	F
Liverworts						
<i>Chiloscyphus austrigenus</i>					x	
<i>Lophocolea austrigena</i>					x	
<i>Lophocolea minor</i>					x	
<i>Neostoscypbus pboenicorbizus</i>					x	
<i>Radula</i> sp.					x	
<i>Riccardia</i> sp.	x					
<i>Ricciocarpus natans</i>						x
Vascular plants						
<i>Callitriche stagnalis</i>	x		x		x	x
* <i>Elodea</i> spp.						x
* <i>Egeria</i> spp.						x
* <i>Juncus microcephalus</i>					x	
* <i>Lagarosiphon major</i>	x		x			
<i>Lemna minor</i>		x	x		x	
<i>Myriophyllum elatinoides</i>					x	x
<i>Myriophyllum porpinquum</i>	x					
* <i>Nasturtium officinale</i>	x	x	x	x		
<i>Potamogeton</i> spp.	x					x
* <i>Salvinia</i> spp.						x

What are the biodiversity values of coldwater springs?

Coldwater springs are formed when the water table intersects with the earth's surface, or groundwater rises to the surface through rock faults, fractures or depressions. Springs are a significant component of the New Zealand landscape, yet they have received little attention from freshwater ecologists and conservation managers. Recently, a major research effort has been directed towards understanding the invertebrate biodiversity values of coldwater springs. This report summarises the state of our knowledge regarding the ecology of New Zealand springs, and identifies the approaches that are required to manage, protect and rehabilitate springs.

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