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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.

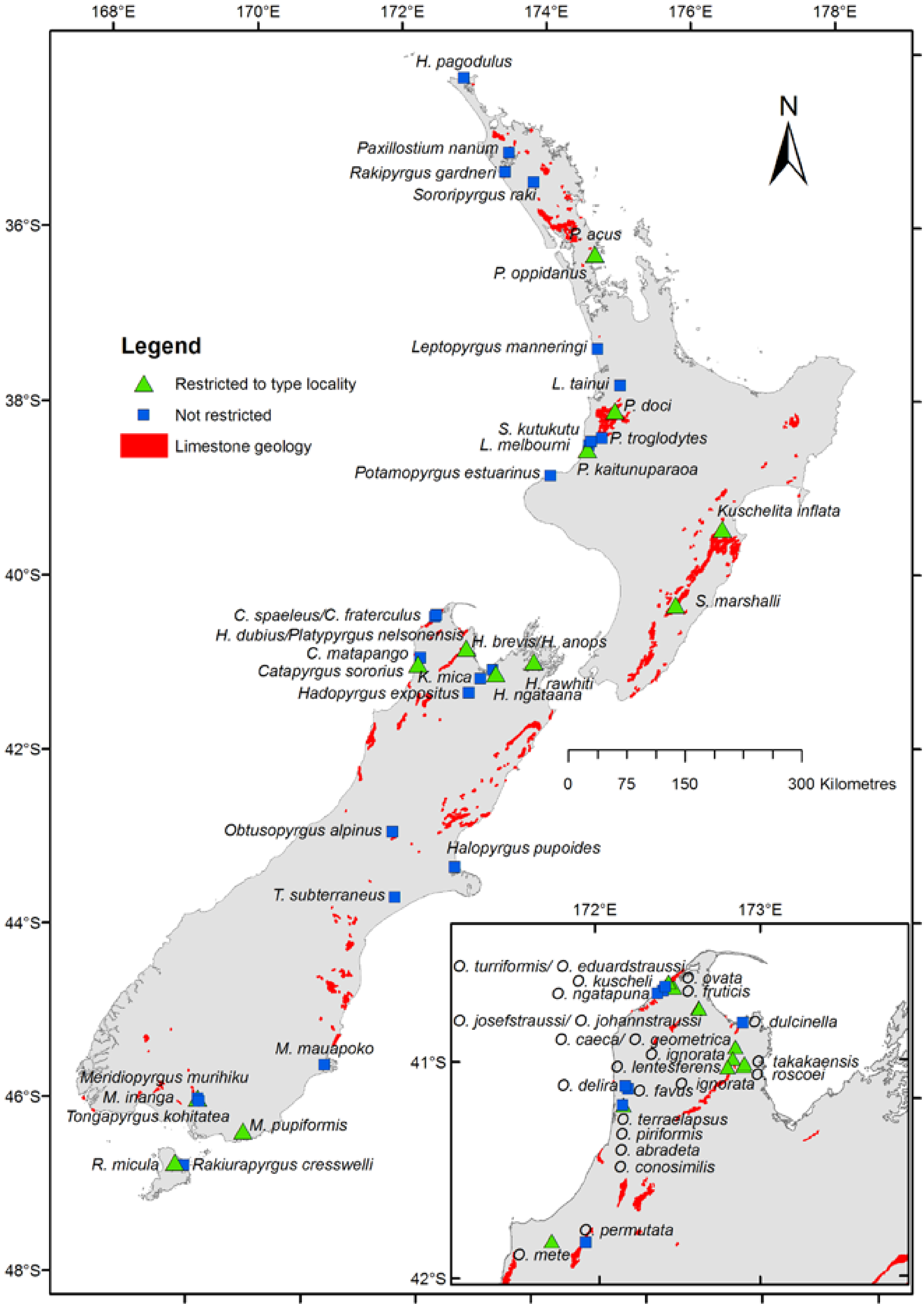

Figure 8. Type localities for 38 species of New Zealand hydrobiids (not including *Potamopyrgus antipodarum* (type locality = New Zealand) and *P. dawbini* (Auckland Is), which are not shown) overlain on limestone geology. Inset shows 24 species of *Opacuincola* distributed in Northwest Nelson and Buller.

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 epigean (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 subterranaeus* 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 (epigean 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

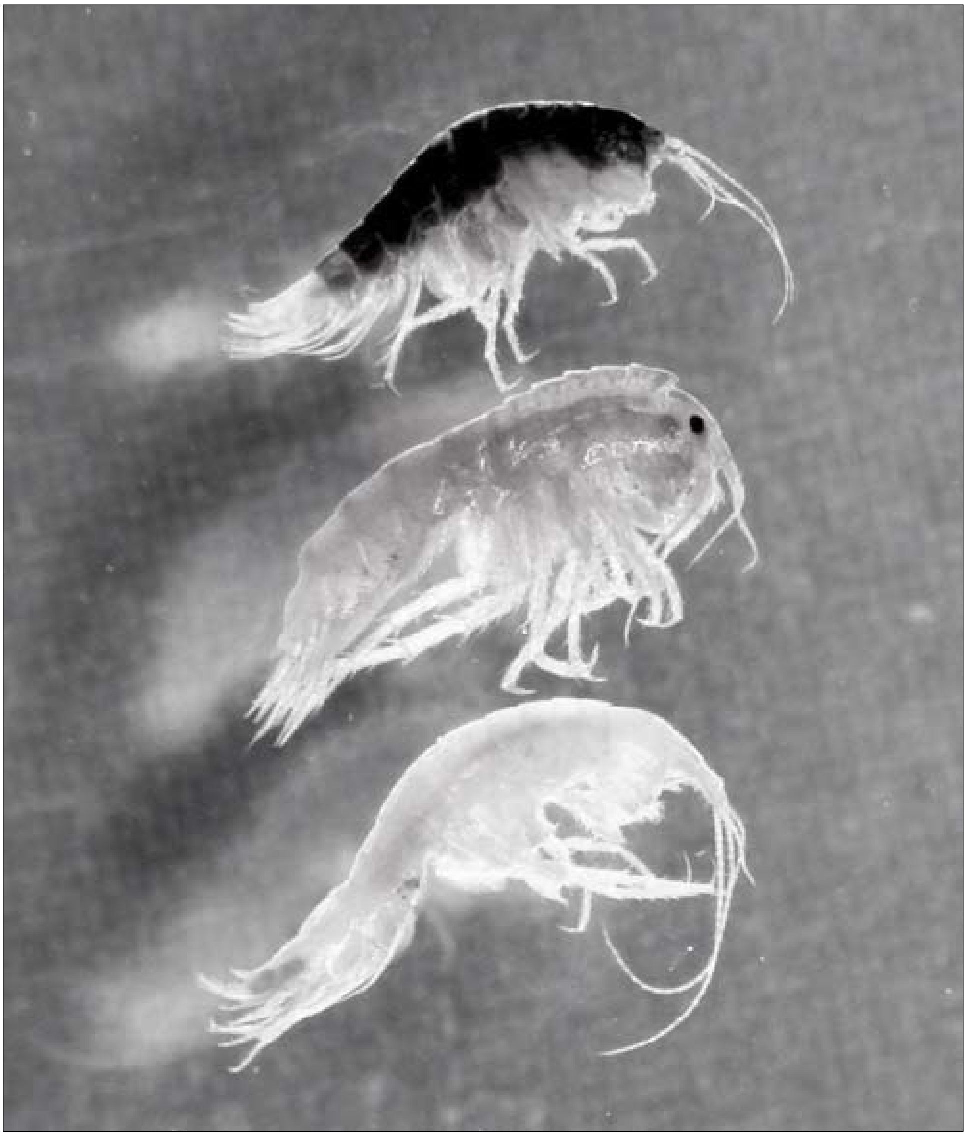

Figure 9. Three morphotypes of amphipods collected from lowland springs in Southland: darkly pigmented surface stream form (top), possible spring specialist—crenobiont (middle), and unpigmented and eyeless groundwater form (bottom). All specimens are about 5 mm long.

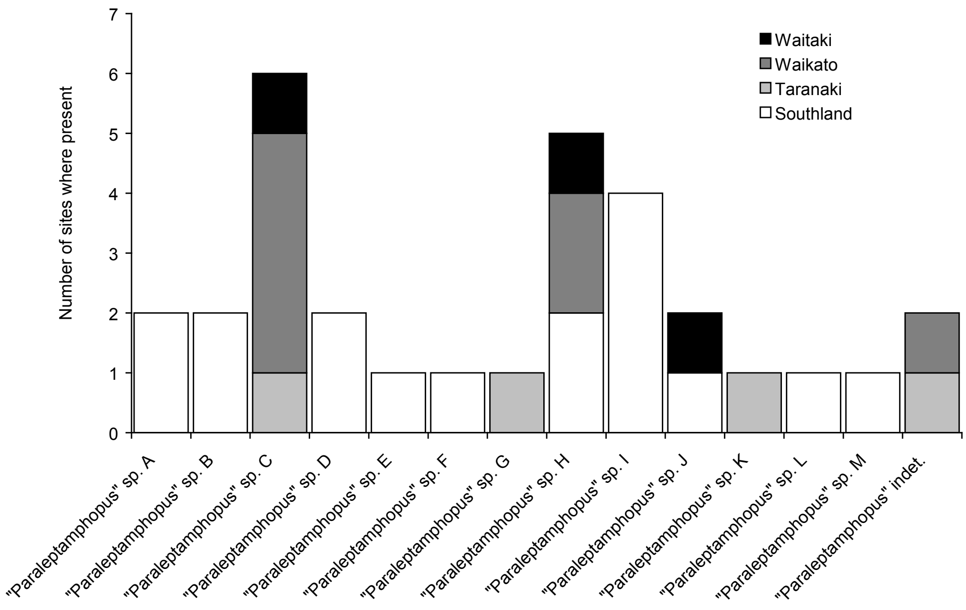

Figure 10. Frequency of occurrence of *Paraleptamphopus* spp. (Crustacea) at 34 spring sites around New Zealand by region.

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

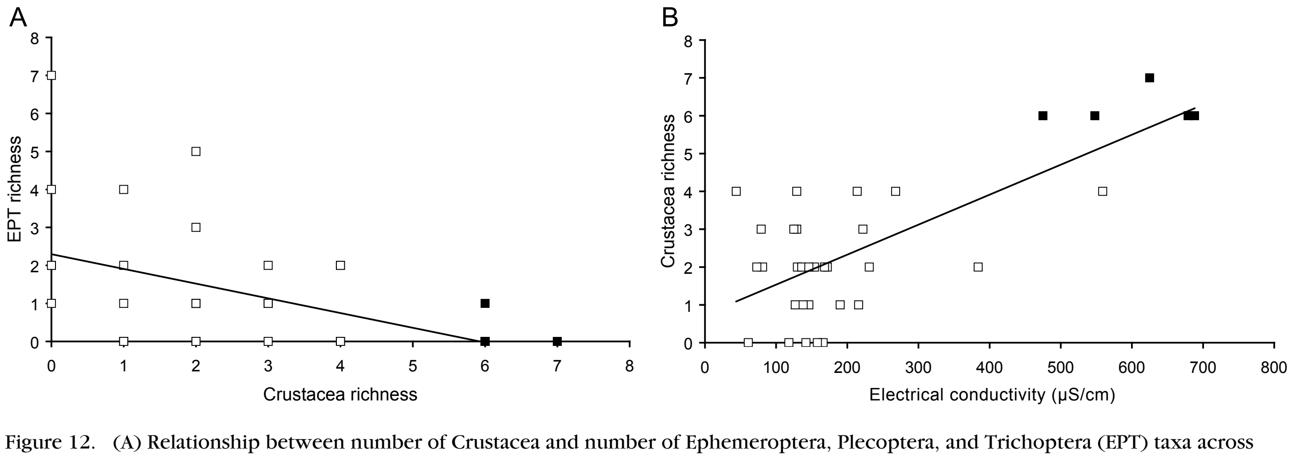

Figure 12. (A) Relationship between number of Crustacea and number of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa across 34 spring sites (N.B. There are several overlapping datapoints); (B) Relationship between conductivity and diversity of Crustacea at 34 spring sites. Filled squares are limestone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

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