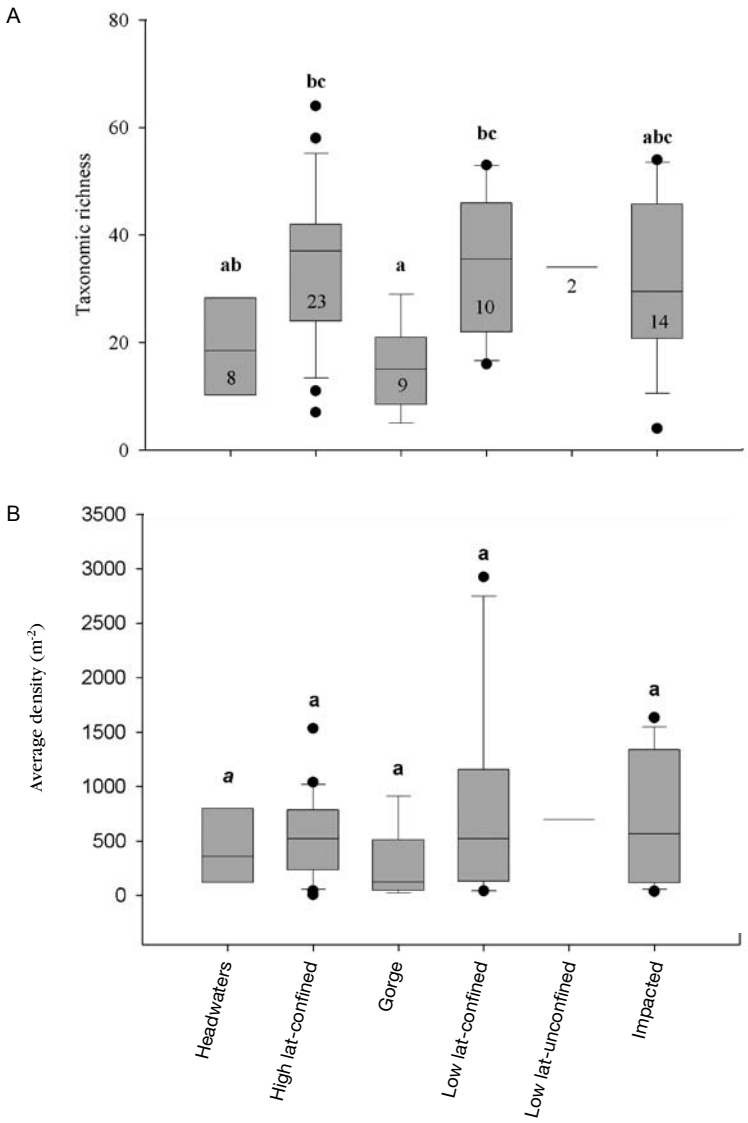

Figure 8. A. Taxonomic richness and B. mean invertebrate density (no./m^2) for each morphological reach type. Box plots show the median value, 25th and 75th percentiles, and outliers. Sample sizes are shown below the median line. Reach types that are not significantly different (Scheffe's *post hoc* < 0.05) have identical superscript letters. There was a significant difference between reach types in taxonomic richness ($F = 5.805$, d.f. = 4, 59, $P = 0.001$), but not in average density of invertebrates ($F = 1.284$, d.f. = 4, 59, $P = 0.289$). Because only two rivers had low lateral, unconfined reaches, this reach type could not be considered statistically.

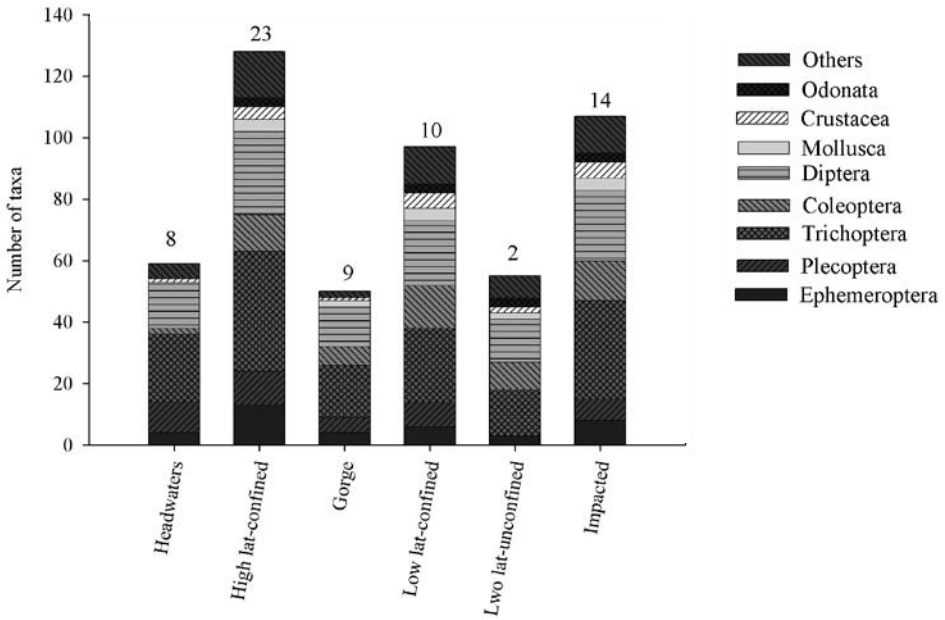

Figure 9. Numbers of ordinal (and above) taxa found in each of the six reach types. The number of sampling sites included in each category is given above each column.

3.2.4 Habitat scale

Both taxonomic richness and density varied significantly among habitat types (Fig. 10). Lateral habitats (ponds, spring creeks and spring sources) were more diverse than main channels, with side braids having intermediate richness; spring creeks had the highest mean taxonomic richness (Fig. 10A). A similar pattern was found for density, with ponds and spring creeks having higher densities of invertebrates than main channels and side braids, whereas spring sources had intermediate densities (Fig. 10B). All habitats showed considerable variation in both richness and density. Saturation analysis indicated that 86–97% of taxa were sampled in each habitat type (Appendix 3).

Most ordinal groups were represented in each habitat type, with the exception of Odonata, which were absent from the main channels of braided rivers (Fig. 11). All other groups were present in each habitat type in similar proportions. Orthocladiinae and Chironominae midges and Elmidae beetles were consistently among the ten most common taxa within each habitat type (Table 4). The ephemeropteran *Deleatidium* was ubiquitous in all habitats except ponds. Common taxa limited to a single habitat type included the plecopterans

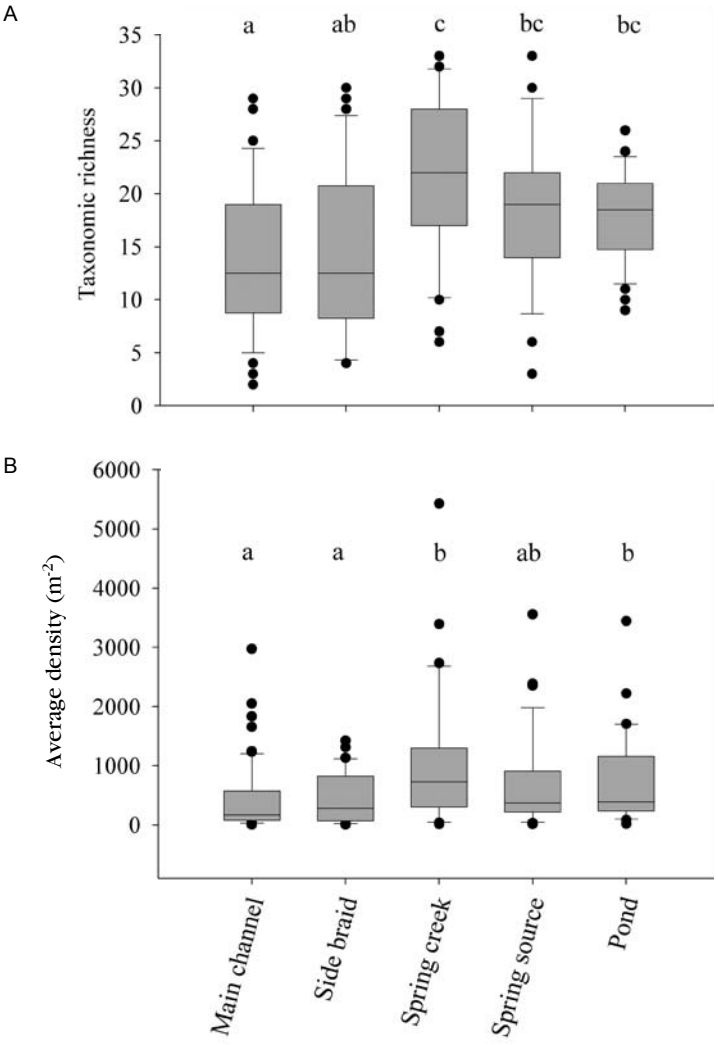

Figure 10. A. Taxonomic richness and B. average density (no./m^2) in five habitat types sampled across six reaches of 11 braided rivers. Box plots show the median value, 25th and 75th percentiles, and outliers. Habitat types that are not significantly different (Scheffe's *post hoc* < 0.05) have identical superscript letters. Density was log transformed to meet assumptions of normality, but actual values are shown on the plot. There were significant differences between habitat types in both taxonomic richness (F=9.743, d.f. = 4, 196, P<0.001) and average density (F=5.114, d.f. = 4, 196, P<0.001).

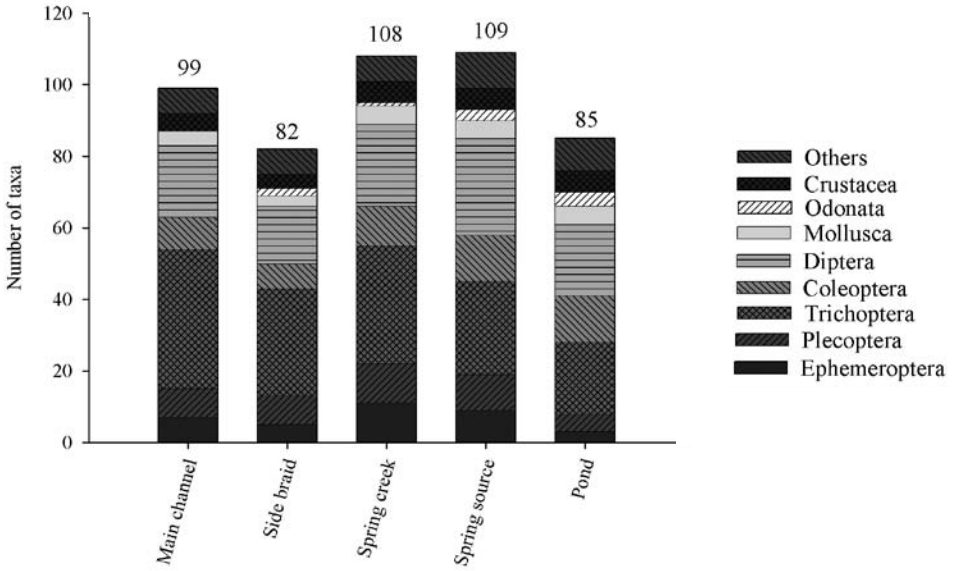

Figure 11. Numbers of ordinal (and above) taxa found in each of five habitat types in the 11 braided rivers studied. Total richness is shown above each column.

TABLE 4. THE TEN MOST COMMONLY OCCURRING TAXA WITHIN EACH HABITAT TYPE.
The percentage of habitats in which they were found and the number of those habitats sampled are shown.

MAIN CHANNELS		SIDE BRAIDS		PONDS		SPRING CREEKS		SPRING SOURCES	
TAXON	%	TAXON	%	TAXON	%	TAXON	%	TAXON	%
Zelandobius spp.	44	*Austrosimulium*	47	*Oxyethira*	53	*Potamopyrgus*	65	*Molophilus*	55
Tanypodinae	50	*Oxyethira*	50	*Berosus*	56	Tanypodinae	68	*Paraleptamphopus* spp.	55
Pycnocentrodes	52	*Aoteapsyche* spp.	53	Ostracoda	56	*Psilochorema*	71	*Oxyethira*	61
Aoteapsyche spp.	55	*Psilochorema*	53	*Xanthocnemis*	59	Chironominae	71	Chironominae	61
Chironominae	55	*Pycnocentrodes*	56	Elmidae	68	*Oxyethira*	74	Tanypodinae	63
Psilochorema	56	Chironominae	59	Oligochaeta	71	*Pycnocentrodes*	74	Elmidae	71
Eriopterini	71	*Eriopterini*	75	Chironominae	79	Oligochaeta	74	*Eriopterini*	71
Elmidae	74	Elmidae	88	*Sigara*	79	Elmidae	84	Oligochaeta	71
Orthocladiinae	94	*Deleatidium*	100	Orthocladiinae	91	*Deleatidium*	97	*Deleatidium*	89
Deleatidium	100	Orthocladiinae	100	Tanypodinae	91	Orthocladiinae	97	Orthocladiinae	89
Number of sites	**66**		**32**		**34**		**31**		**38**

Zelandoperla and *Zelandobius*, which were found only in main channels, and Muscidae (Diptera), which were only common in spring creeks. The beetle *Berosus*, a zygopteran *Xanthocnemis*, a corixid *Sigara* and ostracods were all common in ponds.

Over 70% of lateral habitats had greater invertebrate taxonomic richness than their associated main channel (Fig. 12A). All spring creeks except one had more taxa than their associated main channels, while ponds, spring sources and side braids were more variable in relative taxonomic richness, with 26%, 24% and 25% of sites, respectively, having a lower diversity than the main channel. Three ponds had over four times as many taxa as the nearby main channel. Similarly, 73% of lateral habitats had higher total invertebrate density than their associated main channel (Fig. 12B). Eighty-four percent of spring creeks had a greater density of individuals than their associated main channels, and most spring sources, ponds and side braids also displayed greater relative density than their main channels (66%, 68% and 75%, respectively).

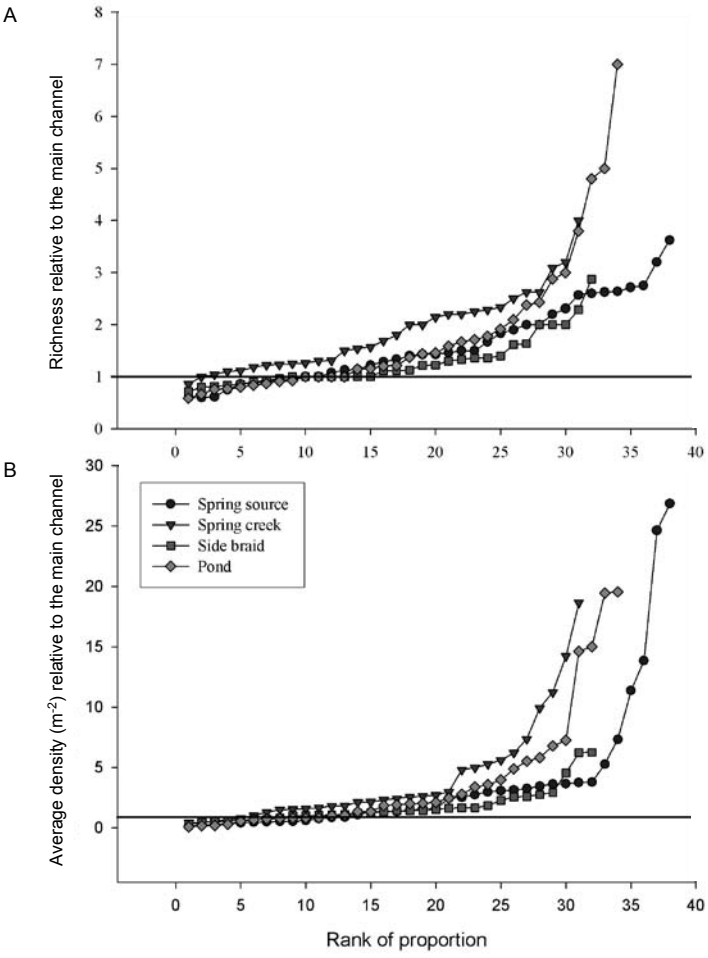

Figure 12. A. Taxonomic richness and B. average density (no./m^2) in four lateral habitats of the 11 braided rivers studied as a proportion of richness/ density in the main channel. Values greater than 1 (horizontal line) signify higher relative diversity in the lateral habitat than the main channel within that reach. All sites within each habitat type are ranked in order of increasing lateral habitat relative richness/density.

3.3 SPATIALLY RESTRICTED TAXA

Of the 144 taxa identified in our survey, 16 were found in only one river, 19 were found in two rivers and 15 were found in three (Figs 13 & 14, Table 5). Thus, 35% of taxa were only found in three or fewer river systems. These taxa were also represented by few individuals, comprising only 0.8% of all individuals. Taxa found in three or fewer rivers included 9 Ephemeroptera, 3 Plecoptera, 18 Trichoptera, 5 Diptera, 7 Coleoptera, 5 Crustacea, 1 Polychaeta, 1 Odonata, 1 Tricladida and 1 Nematomorpha (Table 5). The Tukituki River had the lowest number of spatially restricted taxa (4), while the neighbouring Ngaruroro River had the highest number (18) (Fig. 14A).

Only 13% of taxa were found in all 11 rivers. However, they comprised 80% of all individuals collected and included *Deleatidium*, Elimidae beetles, Chironominae, Orthocladiinae, Tanypodinae and Eriopterini. The spring/groundwater-associated *Paraleptamphopus* spp. and the pond-dwelling *Sigara* were also present in every river.

There was also variability in the number of taxa restricted to particular reach types (Fig. 14B). The highest numbers of spatially restricted taxa were found in the high lateral input, confined reaches and in impacted reaches further downstream in the rivers. Gorges contained very few rare taxa. Overall, braided (high lateral confined, low lateral confined, low lateral unconfined and impacted) reaches contained more spatially restricted taxa than non-braided reaches including headwater reaches.

Numbers of rare taxa were relatively evenly distributed across habitat types, with the exception of side braids (Fig. 14C). Although spring sources, creeks and ponds contained the highest number of rare taxa (16–21), 15 rare taxa were also found in main channels. The caddisfly *Neurochorema confusum* was only found in main channels, whereas ten other Trichoptera, two Ephemeroptera, a Plecoptera and a Diptera were found in main channels plus one other habitat type.

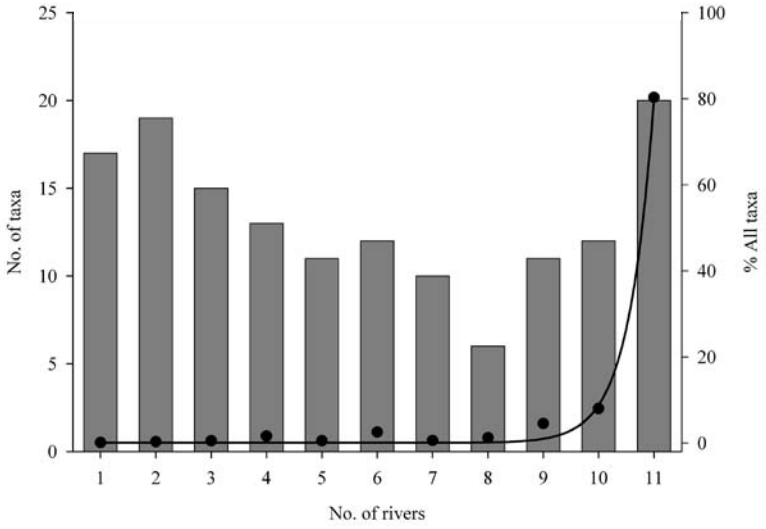

Figure 13. Numbers of taxa found only in 1, 2, 3 ... 11 rivers (histograms) and the percentage of all taxa found represented by them (closed circles).

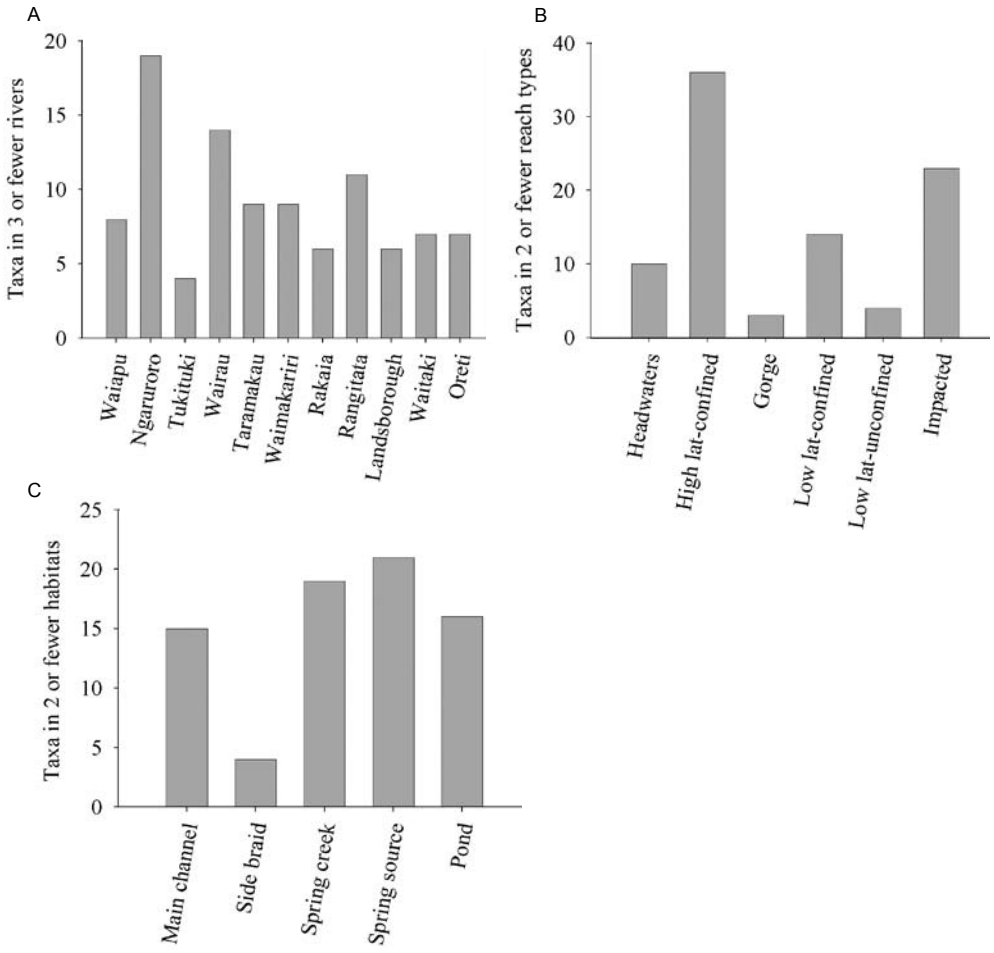

Figure 14. Numbers of taxa found in A. three or fewer river systems, B. two or fewer reach types and C. two or fewer habitat types.

TABLE 5. SPATIALLY RESTRICTED TAXA FOUND ONLY WITHIN 1, 2 OR 3 BRAIDED RIVERS.

TAXON	ORDER	WAIAPU	NGARURORO	TUKITUKI	WAIRAU	TARAMAKAU	WAIMAKARIRI	RAKAIA	RANGITATA	LANDSBOROUGH	WAITAKI	ORETI
Restricted to 1 river												
Ecnomina zealandica	Trichoptera	0	0	0	0	0	0	0	0	0	0	1
Edpercivalia	Trichoptera	0	0	0	0	0	0	0	1	0	0	0
Enochrus	Coleoptera	0	1	0	0	0	0	0	0	0	0	0
Ichthybotus	Ephemeroptera	0	1	0	0	0	0	0	0	0	0	0
Ishcnura	Odonata	1	0	0	0	0	0	0	0	0	0	0
Nematomorpha		0	0	0	0	0	0	0	0	1	0	0
Ochlerotatus antipodeus	Diptera	0	0	0	0	0	1	0	0	0	0	0
Oecetis unicolor	Trichoptera	0	0	0	0	0	0	0	0	1	0	0
Paraleptamphopus caeruleus	Amphipoda	0	0	0	0	0	0	0	0	0	0	1
Podaena	Coleoptera	0	0	0	0	0	0	0	1	0	0	0
Prorhynchus	Rabditophora	0	0	0	0	0	0	0	0	0	1	0
Staphylinidae	Coleoptera	0	0	0	0	1	0	0	0	0	0	0
Taraperla howesi	Plecoptera	0	0	0	0	0	1	0	0	0	0	0
Tiphobiosis	Trichoptera	0	0	0	0	0	0	0	1	0	0	0
Triplectides cephalotus	Trichoptera	0	1	0	0	0	0	0	0	0	0	0
Zelandobius edensis	Plecoptera	0	0	0	0	0	0	0	1	0	0	0
Restricted to 2 rivers												
Ameletopsis	Ephemeroptera	0	1	0	0	1	0	0	0	0	0	0
Antiporus femoralis	Coleoptera	1	1	0	0	0	0	0	0	0	0	0
Austroclima	Plecoptera	0	0	0	1	0	0	0	0	0	0	1
Costachorema callistum	Trichoptera	0	0	0	0	1	0	0	0	0	1	0
Cruregens fontanus	Isopoda	0	1	1	0	0	0	0	0	0	0	0
Hydrobiosella	Trichoptera	1	0	0	0	0	0	0	0	0	1	0
Hydrobiosis chalcodes	Trichoptera	0	0	0	1	0	0	0	0	0	1	0
Hydrobiosis harpidiosa	Tricoptera	0	1	0	0	0	0	0	0	0	1	0
Hydrobiosis neadelphus	Tricoptera	0	0	0	1	0	0	0	1	0	0	0
Hydrobiosis torrentis	Trichoptera	0	0	0	0	1	1	0	0	0	0	0
Hyphydrus elegans	Trichopetra	1	0	1	0	0	0	0	0	0	0	0
Mauiulus	Ephemeroptera	0	0	0	1	1	0	0	0	0	0	0
Nesameletus austrinus	Ephemeroptera	0	0	0	0	0	0	0	1	1	0	0
Neurochorema confusum	Trichoptera	0	1	0	1	0	0	0	0	0	0	0
Oniscigaster wakefieldi	Ephemeroptera	0	0	0	1	0	0	0	0	0	0	1
Paracymus	Coleoptera	1	1	0	0	0	0	0	0	0	0	0
Ptilodactylidae	Coleoptera	0	1	0	1	0	0	0	0	0	0	0
Triplectidina	Trichoptera	0	1	0	1	0	0	0	0	0	0	0
Zephlebia	Ephemeroptera	0	0	0	1	1	0	0	0	0	0	0
Restricted to 3 rivers												
Beraeoptera roria	Trichoptera	0	1	0	0	0	1	0	1	0	0	0
Copepoda		0	0	0	0	0	1	1	0	0	0	1
Corynocera	Diptera	0	0	0	0	0	1	1	0	1	0	0
Cristaperla	Plecoptera	0	1	0	0	0	0	1	1	0	0	0
Hydrobiosis frater	Trichoptera	0	0	0	0	0	0	1	1	0	1	0
Hydrobiosis silvicola	Trichoptera	0	0	0	0	0	1	1	1	0	0	0
Namanereis tiriteae	Nereididae	1	1	1	0	0	0	0	0	0	0	0
Neozephlebia	Ephemeroptera	0	1	0	0	1	0	0	0	1	0	0
Oniscigaster distans	Ephemeroptera	0	0	0	1	1	0	0	0	0	0	1
Paracrangonyx	Isopoda	1	1	0	1	0	0	0	0	0	0	0
Paratya	Atyidae	0	1	1	0	0	0	0	0	1	0	0
Pelecorhynchidae	Diptera	0	1	0	0	0	1	1	0	0	0	0
Philorheithrus agilis	Trichoptera	0	0	0	1	0	0	0	1	0	0	1
Psychodidae	Diptera	1	0	0	1	1	0	0	0	0	0	0
Traillochorema	Trichoptera	0	0	0	1	0	1	0	0	0	1	0

4. Discussion

4.1 COMPARISON OF DIVERSITY BETWEEN BRAIDED AND SINGLE CHANNEL RIVERS

New Zealand braided rivers have been considered to have depauperate invertebrate communities (Percival 1932; Gray & Harding 2007). Previous studies of main channel invertebrates have shown communities dominated by a low number of 'weedy' species, which show refuge-seeking behaviours, flexible life histories and rapid recolonisation mechanisms (Scrimgeour & Winterbourn 1989; Sagar & Glova 1992). In the main channel of the lower Rakaia River, Canterbury, Sagar (1986) found that 96% of invertebrates were larvae of the mayfly *Deleatidium*, and only identified 33 other taxa over 3 years of sampling. Thus, richness and density were described as low. Furthermore, richness and density were strongly negatively related to antecedent flooding. Regular substrate-moving floods are a feature of braided rivers and extreme physical disturbance is thought to reduce taxonomic richness, particularly of more sedentary species. In contrast, single channel rivers tend to have more stable substrates, permanent location of wetted areas and offer greater refuge for more sedentary taxa.

Our analysis of the main channels of braided and single channel rivers supported the above generalisations. However, it was found that the inclusion of hydrologically connected lateral floodplain habitats extended their diversity considerably (Gray et al. 2006; Gray & Harding 2009). In fact, our results indicate that by not sampling a full range of habitats, we may underestimate the diversity within floodplain rivers by 50%. The braided reaches of rivers should therefore be considered to be biodiversity hotspots within the riverscape. If monitoring or biodiversity assessment projects are to correctly determine the biodiversity of braided rivers, it is important that the full range of habitat types present are considered.

4.2 TAXONOMIC RICHNESS, DENSITY AND ASSEMBLAGE DIVERSITY ACROSS SPATIAL SCALES

4.2.1 Catchment scale

The 11 rivers included in this survey showed marked variation in taxonomic richness and density, as well as contrasting assemblages that were related to geographical position and topographical hydrology. The five rivers with the highest taxonomic diversity occurred in five separate regions of New Zealand, suggesting that high braided river diversity is an intrinsic feature of the rivers themselves rather than a product of regional variation in taxonomic richness. Interestingly, the rivers with the highest diversity were not necessarily those with the least impacted catchments, a pattern that has been observed previously in a number of aquatic and terrestrial systems (Englund & Malmqvist 1996; Karaus 2004; Luck 2007; Pautasso & Fontaneto 2008). Patterns in regional species

richness are difficult to explain, but dispersal ability and historic opportunities to disperse coupled with regional productivity, habitat diversity plus current and historic land-use impacts are all important (Rosenzweig 1995; Harding et al. 1998). A large-scale survey of New Zealand by Harding & Winterbourn (1997) indicated that climate, geomorphology, biogeography and vegetation cover influence both diversity and community composition. Catchment units have previously been ranked according to their level of human disturbance using the Waters of National Importance (WONI) analysis (Chadderton et al. 2004). This analysis gave each catchment a single natural heritage score, which incorporated measures of environmental representativeness, the presence of threatened species and connectivity to nationally important wetlands, but did not include aquatic invertebrate data due to a lack of available information. Using this analysis, rivers such as the Landsborough in South Westland and Rakaia in Canterbury scored highly in terms of natural heritage (WONI), whereas our data indicate that they would rank poorly in terms of benthic invertebrate richness and the presence of rare taxa. In contrast, the Ngaruroro River in Hawke's Bay scored poorly using WONI but had high invertebrate richness and the greatest number of spatially restricted taxa of any river in our survey. The Wairau River in Marlborough had the greatest taxonomic richness of the braided rivers included in our survey and a high number of spatially restricted taxa, and also scored highly in the WONI analysis. These results highlight the fact that it is not necessarily the most pristine catchments that contain the greatest diversity.

4.2.2 Longitudinal and reach scales

We found no consistent relationship between invertebrate diversity or density and distance along the 11 braided rivers, and no relationship between invertebrate density and reach type. In contrast, Arscott et al. (2005) found weak peaks in diversity at both ends of the Tagliamento River, Italy, and an increase in density downstream. Our results also conflict with the basic tenets of the River Continuum Concept (RCC) (Vannote et al. 1980), which predicts that the highest diversity should be found in the middle reaches of rivers due to increased environmental heterogeneity, and that diversity should be lower in headwaters and lower reaches. However, the RCC considers river orders 1–13, whereas our rivers ranged from order 3 to 7 and therefore can be considered 'middle reaches' in the RCC terminology.

The RCC considers only single channel rivers, whereas the flood-pulse concept (FPC; Junk 1999) extends this concept to include the intermittently inundated floodplain. In large tropical rivers, the primary driver of riverine diversity is thought to be annual inundation of the floodplain; thus, the lower reaches of large rivers should support the highest diversity as they have the largest floodplains. The original concept was developed for rivers with predictable seasonal patterns of floodplain inundation. However, the concept has also been extended to include the floodplain habitats of temperate rivers by including information derived from near-natural proglacial, headwater and lowland floodplains (Tockner et al. 2000). This extension explicitly considers expansion–contraction cycles occurring well below bank-full. Tockner et al. (2000) suggested that diversity might be greatest at intermediate levels of flood and flow pulse, but that there is insufficient evidence to make universal predictions about longitudinal patterns. The role of floodplain inundation and expansion–contraction cycles was assessed in a braided

glacial river in Switzerland by Malard et al. (2006), who found that changes in size, composition and configuration of water bodies affected biodiversity. However, the role of inundation was only considered within a single reach of the Val Roseg River and so cannot be extrapolated along an entire river.

We did not observe any obvious longitudinal diversity patterns in braided rivers, although we did observe some species replacement. Therefore, the predictions of the flood-pulse concept did not appear to apply. The RCC and FPC were proposed for pristine river systems, whereas most of the rivers included in our survey had channelised lower reaches and extensive modifications of their catchments to support pastoral agriculture in particular. The lowland reaches of many New Zealand rivers once incorporated swamps, wetlands, springs and complex groundwater/surface water exchange patterns that no longer exist (Park 2002). A good example of this is the Waimakariri River in Canterbury, which formerly had a diverse lower floodplain extending laterally from its present day mouth to Lake Ellesmere/Te Waihora (Pawson 2002).

4.2.3 Habitat

Previous studies in New Zealand and elsewhere have found that groundwater-fed channels often contain higher invertebrate richness and density than other floodplain habitats (McCabe 1998; Digby 1999; Burgherr et al. 2002; Gray et al. 2006). This finding contrasts with that of Arscott et al. (2005), who found that invertebrate richness in the braided Tagliamento River, Italy, was lower within three groundwater-fed channels than in the main channel. Furthermore, they found that the density of invertebrates in groundwater-fed channels was intermediate between that of the main channel (high) and a side braid (low). Presumably, in rivers or reaches of rivers where disturbance events are insufficiently intense or frequent to suppress taxonomic richness and density, main channel invertebrate assemblages may be similar to those in lateral habitats. This might account for the high relative invertebrate richness values seen in some main channel habitats in our survey. Conversely, lateral habitats may be regularly disturbed resulting in richness and density in some reaches remaining low relative to the main channel. This might be the case in a channelised river where a minor flood event impacts the entire floodplain habitat assemblage, e.g. the lower Waimakairi River or in the groundwater-fed channels of the Tagliamento River sampled by Arscott et al. (2005).

The lateral habitats sampled in our survey, particularly the spring creeks, had consistently greater taxonomic richness of invertebrates than their adjacent main channels. Therefore, this appears to be a general property of New Zealand braided rivers. The density of invertebrates was also greater in lateral habitats than in the main channels of any given river or reach. These findings have important implications for the bird and fish species that feed within the floodplain. Specifically, the food resource available from a braided river in terms of its capacity to support bird and fish species cannot be assumed from invertebrate density measurements in the main channels alone.

Any discussion of benthic invertebrate communities, particularly in disturbance-driven systems such as braided rivers, must be qualified with some mention of hydrology (Scrimgeour & Winterbourn 1989; Tockner et al. 2006). In general, increased disturbance from substrate-moving flows are associated with a decline in

invertebrate richness and shift in community composition (Death & Winterbourn 1995; Townsend et al. 1997). Floods can be described in terms of timing, duration, magnitude, recurrence and predictability (Poff et al. 1997; Olden & Poff 2003). Each of these factors impacts invertebrate communities and the interpretation of these results. Although all the rivers in this survey were sampled during baseflow conditions, patterns in antecedent flooding must be considered. Seasonal timing of floods—primarily spring in alpine sourced rivers versus winter in foothill rivers (Duncan & Woods 1992)—creates variation in the successional recovery state of different rivers. Thus, foothill rivers sampled in summer have had longer to recover than alpine rivers. Floods of increasing duration and magnitude result in a commensurately greater impact on invertebrate communities, which may be prevented from complete recovery by the recurrence of further flood events. Comparison of river richness values (Fig. 5) and the hydrological data in Table 1 illustrates this relationship. In general, rivers with a greater number of floods and fewer days since the last flood had lower richness, e.g. the Landsborough River. However, antecedent hydrology is not the only environmental factor influencing richness in rivers, particularly when lateral habitats, which may be unaffected by flooding, contribute so highly. The environmental drivers of braided river invertebrate communities and richness will be explored more thoroughly in a subsequent publication.

4.3 SPATIALLY RESTRICTED TAXA

The biodiversity of a habitat or river is not measured solely by the number of taxa present. Rather, consideration needs to be given to which specific taxa are present. Rare or endemic taxa might be accorded a greater conservation value than those that are common, analogous to the way that certain taxa have a higher value when calculating biotic indices such as the Macroinvertebrate Community Index (MCI) (Stark 1985). Regions of high local biodiversity and endemism characterise the New Zealand stream fauna (Harding & Winterbourn 1997; Boothroyd 2000; Harding 2003). For example, trichopteran diversity is highest in central regions and lower at northern and southern extremes of the country (Forsyth & Lewis 1987), Plecoptera are most diverse in the northwest and southwest of the South Island (McLellan 1991), and the diversity of Ephemeroptera declines from north to south (Boothroyd 2000). Furthermore, locally restricted distributions are also common, e.g. among species of *Zelandobius* (Plecoptera) (McLellan 1993). Consequently, many New Zealand taxa have limited distributions, and in some cases these taxa account for diversity differences between habitats, streams and regions, and dictate their conservation values.

The findings of this study suggest that rare taxa are found in all braided rivers and that some of them are endemics. This makes intuitive sense due to the high level of local endemism and restricted distributions nationally. Any regionally based sampling design is liable to reveal taxa unique to that region. However, the majority of taxa found to be spatially restricted were not local endemics, but simply rare. One exception is *Namanereis tiriteae*, a polychaete worm thought to be stygobiotic (subterranean dwelling), which prior to this survey was thought to be restricted to the upper Manawatu River and some easterly flowing streams in Hawke's Bay (Winterbourn 1969; Scarsbrook et al. 2003). The discovery of a

specimen in the Waiapu River extends this polychaete's known range northwards towards East Cape, but the species still appears to be restricted primarily to the east coast of the North Island (Gray et al. 2009). Another example of a regionally endemic braided river taxon is a novel species of Plecoptera found in the upper Rangitata River. *Zelandobius edensis* Gray has subsequently been confirmed as a new species within the confusus-group and has been formally described (Gray 2009). The damselfly *Ischnura aurora* is common in lakes and ponds of northern New Zealand, and was found in a pond within the floodplain of the Waiapu River during our survey. However, this species is a moderately recent immigrant to New Zealand whose potential range expansion may not yet be complete.

The distribution of taxa across the 11 regionally stratified braided rivers we examined indicates that braided rivers contain taxa that are restricted in their spatial occurrence. In some cases, these taxa are likely to be restricted to gravel bed streams (e.g. *Namanereis tiriteae*), whereas other taxa have also been recorded from other stream types (e.g. the trichopteran *Ecnomina zealandica*). Some taxa that may occur commonly in non-braided streams were found to be rare in the braided rivers (e.g. the burrowing mayfly *Ichthybotus* and the amphipod *Paraleptamphopus caeruleus*).

Rare and restricted taxa also appeared to show an affinity for the braided reaches of rivers as opposed to gorges and headwater channels. Braided reaches are more likely to contain the habitats required by these taxa due to their high physical heterogeneity. Given the broad range of physical habitats considered in our survey, it is not surprising that a number of taxa specific to those habitat types were identified. However, it is particularly interesting that main channel habitats contained comparable numbers of rare taxa to lateral habitats, despite the latter having greater diversity and density of invertebrates. This result affirms and extrapolates on that of Gray et al. (2006), who found that 5 out of 100 taxa were restricted to the main channel of the Upper Waimakariri River.

These insights indicate that it is not easy to identify rivers, reaches or habitats with the greatest biodiversity values. Rare taxa are distributed across all rivers, and most reach types and habitats. Therefore, a holistic approach to river management is almost certainly required.

4.4 IMPLICATIONS FOR CONSERVATION MANAGEMENT

Taxonomic richness and the presence of rare taxa varied considerably across spatial scales, whereas density varied significantly at the river and habitat scales only. The most predictable feature of the braided river systems analysed appeared to be the disproportionate contribution of lateral floodplain habitats to diversity. In the context of understanding dynamic floodplain systems, these results have two main implications.

Firstly, rivers are hierarchical in nature. Habitats are physically nested within reaches, which are themselves nested within rivers within a catchment, and the physical attributes of habitats are regulated by factors operating at greater spatio-temporal scales (Poff 1997). However, local geological and other idiosyncrasies create a discontinuous longitudinal continuum and propagate

physical heterogeneity along rivers, so that physical heterogeneity provides a diversity of habitat for a diversity of organisms and processes to exist. Events within the catchment will have implications for conditions within the river, reach and eventually habitat, within the constraints of local factors.

There is a high degree of inter-dependence between habitats within a reach, mediated by hydrological connectivity, which is a defining feature of floodplain systems (Woessner 2000; Poole et al. 2002, 2004). Consequently, impacts that occur at any given location have the potential to propagate effects to all habitats both up and downstream, and laterally. Our current understanding of braided river floodplains supports the contention that habitats exist in a balance described as a shifting habitat mosaic (Arscott et al. 2000, 2002; Latterell et al. 2006; Malard et al. 2006). Despite high turnover of floodplain elements, the relative proportions of habitats remain constant. Furthermore, constant rates of habitat turnover result in an array of habitats at different successional stages (Ward et al. 2002). The high biodiversity and invertebrate density of braided rivers is dependent upon the physico-chemically diverse, three-dimensional mosaic of successionally variable habitats available (Stanford & Ward 1993; Gray et al. 2006). Perturbations within a catchment, river or reach have the potential to alter this equilibrium. Flow alteration and channelisation in particular have been implicated in drastic alterations to the floodplain habitat mosaic and consequent alterations to the biodiversity of floodplains (Ward & Stanford 1995; Claret et al. 1999; Brunke 2002; Hancock 2002; Gilvear 2004; Hauer & Lorang 2004; Hohensinner et al. 2004; Choi et al. 2005). Thus, spatio-temporal hierarchical controls and hydrological connectivity must be made an integral part of management strategies. Units of a river system cannot be treated as discrete entities; rather, the biodiversity of a single reach or habitat is very much a function of the entire catchment.

Secondly, because diversity is spatially and hierarchically variable, conservation managers need to ensure that assessments of biodiversity incorporate hierarchical scales and spatial variability. It is not sufficient to categorise biotic richness or density of a river or reach by taking samples from a limited number of habitats or reaches. The apparently stochastic nature of the spatial distribution of invertebrate communities in braided rivers requires laterally and longitudinally stratified sampling. Otherwise, there is a strong possibility of spurious conclusions being drawn based on inadequate spatial sampling.

5. Conclusion

A total of 163 river systems in New Zealand have braided reaches, which account for a total floodplain habitat area of 248 400 ha. The majority of these rivers occur in Canterbury and on the West Coast of the South Island.

Braided rivers have been regarded as species depauperate 'biological deserts' when compared to more stable, single channel streams (Percival 1932). However, when the complete, hydrologically linked habitat assemblage of a floodplain river is considered, the inverse is true. The floodplain reaches of some New Zealand braided rivers can rightly be considered biodiversity hotspots in the greater riverscape, and lateral habitats may contain about 50% of the diversity of the river.

Total taxonomic richness of the 11 braided rivers included in this study was highly variable, but the composition of invertebrate assemblages corresponded broadly to geographical location, source of flow and climate. No consistent longitudinal reach-scale patterns were observed; however, braided reaches contained greater invertebrate diversity than either gorges or headwaters. The braided rivers in this survey did not conform to the theoretical concepts with respect to longitudinal diversity patterns, and it appeared that richness was regulated at the scale of the individual reach in those rivers. The five habitat types considered in this survey all showed highly variable richness values between reaches and rivers. However, the richness of lateral floodplain habitats (spring sources, spring creeks, ponds and side braids) within a specific reach was almost always greater than in the associated main channel, particularly in the case of spring creeks.

A number of taxa were both spatially and numerically rare, and such taxa were found in all rivers, most reaches and most habitats included in our survey. Some of these taxa are regionally endemic and confined to gravel bed streams, but the majority are known throughout the country whilst still being considered rare.

The hierarchical structure and high levels of connectivity that define braided rivers must be incorporated into management strategies. Braided river biodiversity is a function of the constantly shifting habitat assemblage of floodplains, which in turn is regulated by elements nested within the entire catchment, e.g. factors that affect flow and sediment input/transport at the catchment scale, and channel migration at the reach scale.

An assessment of the biodiversity and productivity values of braided rivers needs to incorporate a range of spatial scales in the study design. Because of high levels of variation between rivers, reaches and habitats, extrapolation of findings among these scales should be made with caution.

6. Acknowledgements

We thank Lindsay Chadderton and Dave Kelly for encouraging the development of this project, and the Department of Conservation (Science Investigation No. 3871) and the Miss E. L. Hellaby Grasslands Trust for funding. Numerous landowners permitted access to rivers, and Joanne Ocock provided exceptional field and laboratory assistance. Amy Whitehead, Michelle Greenwood, Myles McCauley and Richard Purdon provided valuable assistance with the fieldwork. Thanks also to Mike Winterbourn for particularly valuable comments on earlier drafts of this report.

7. References

Arscott, D.B.; Tockner, K.; van der Nat, D.; Ward, J.V. 2002: Aquatic habitat dynamics along a braided alpine river ecosystem (Tagliamento River, Northeast Italy). *Ecosystems 5*: 802–814.

Arscott, D.B.; Tockner, K.; Ward, J.V. 2000: Aquatic habitat diversity along the corridor of an alpine floodplain river (Fiume Tagliamento, Italy). *Archiv Für Hydrobiologie 149*: 679–704.

Arscott, D.B.; Tockner, K.; Ward, J.V. 2005: Lateral organization of aquatic invertebrates along the corridor of a braided river floodplain. *Journal of the North American Benthological Society 24*: 934–954.

Boothroyd, I. 2000: Biogeography and biodiversity. Pp. 30–52 in Collier, K.J.; Winterbourn, M.J. (Eds): New Zealand stream invertebrates: ecology and implications for management. New Zealand Limnological Society, Christchurch.

Brunke, M. 2002: Floodplains of a regulated southern alpine river (Brenno, Switzerland): ecological assessment and conservation options. *Aquatic Conservation: Marine and Freshwater Ecosystems 12*: 583–599.

Burgherr, P.; Ward, J.V.; Robinson, C.T. 2002: Seasonal variation in zoobenthos across habitat gradients in an alpine glacial floodplain (Val Roseg, Swiss Alps). *Journal of the North American Benthological Society 21*: 561–575.

Chadderton, W.L.; Brown, D.J.; Stephens, R.T. 2004: Identifying freshwater ecosystems of national importance for biodiversity: criteria, methods and candidate list of nationally important rivers. Discussion document. Department of Conservation, Wellington. 112 p.

Chapman, A.; Lewis, M. 1976: An introduction to the freshwater Crustacea of New Zealand. Collins, Auckland. 261 p.

Choi, S.U.; Yoon, B.; Woo, H. 2005: Effects of dam-induced flow regime change on downstream river morphology and vegetation cover in the Hwang River, Korea. *River Research and Applications 21*: 315–325.

Claret, C.; Marmonier, P.; Dole-Olivier, M.J.; Castella, E. 1999: Effects of management works on the interstitial fauna of floodplain aquatic systems (River Rhone, France). *Biodiversity and Conservation 8*: 1179–1204.

Colwell, R. 2005: EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5. Users guide and application published at http://purl.oclc.org/estimates (viewed 20 June 2007).

Cowley, D.R. 1978: Studies on the larvae of New Zealand Trichoptera. *New Zealand Journal of Zoology 5*: 639–750.

Death, R.; Winterbourn, M.J. 1995: Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology 76*: 1446–1460.

Digby, B. 1999: Invertebrate production within various habitats of a braided river. Unpublished MSc thesis, University of Canterbury, Christchurch. 66 p.

Duncan, M.J.; Woods, R. 1992: Flow regimes in New Zealand rivers. Pp. 13–28 in Moseley, P. (Ed.): Waters of New Zealand. New Zealand Hydrological Society, Wellington.

Englund, G.; Malmqvist, B. 1996: Effects of flow regulation, habitat area and isolation on the macroinvertebrate fauna of rapids in north Swedish rivers. *Regulated Rivers Research and Management 12*: 433–445.

Forsyth, D.; Lewis, M. 1987: Zoogeography of invertebrates. Pp. 265–290 in Viner, A. (Ed.): Inland waters of New Zealand. *Bulletin 241*. Department of Scientific and Industrial Research, Wellington.

Gilvear, D.J. 2004: Patterns of channel adjustment to impoundment of the upper River Spey, Scotland (1942–2000). *River Research and Applications 20*: 151–165.

Gray, D.P. 2005: Braided river springs: distribution, benthic ecology, and role in the landscape. Unpublished MSc thesis, University of Canterbury, Christchurch. 222 p.

Gray, D.P. 2009: A new species of *Zelandobius* (Plecoptera: Gripopterygidae: Antarctoperlinae) from the Upper Rangitata River, Canterbury, New Zealand. *New Zealand Journal of Marine and Freshwater Research 43*: 605–611.

Gray, D.P.; Harding, J.S. 2007: Braided river ecology: a literature review of physical habitats and aquatic invertebrate communities. *Science for Conservation 279*. Department of Conservation, Wellington. 50 p.

Gray, D.P.; Harding, J.S. 2009: Braided river benthic diversity at multiple spatial scales: a hierarchical analysis of ß diversity in complex floodplain systems. *Journal of the North American Benthological Society 28(3)*: 537–551.

Gray, D.P.; Harding, J.S.; Winterbourn, M.J. 2009: *Namanereis tiriteae*, New Zealand's freshwater polychaete: new distribution records and review of biology. *New Zealand Natural Sciences 34*: 29–38.

Gray, D.P.; Scarsbrook, M.R.; Harding, J.S. 2006: Patterns in spatial biodiversity in a large New Zealand braided river. *New Zealand Journal of Marine and Freshwater Research 40*: 631–642.

Hancock, P.J. 2002: Human impacts on the stream-groundwater exchange zone. *Environmental Management 29*: 763–781.

Harding, J.S. 2003: Historic deforestation and the fate of endemic species in streams. *New Zealand Journal of Marine and Freshwater Research 37*: 333–345.

Harding, J.S.; Benfield, E.F.; Bolstad, P.V.; Helfman, G.S.; Jones, E.B.D. 1998: Stream biodiversity: the ghost of land use past. *Proceedings of the National Academy of Sciences of the United States of America 95*: 14843–14847.

Harding, J.S.; Winterbourn, M.J. 1997: New Zealand ecoregions: a classification for use in stream conservation and management. *Department of Conservation Technical Series 11*. Department of Conservation, Wellington. 22 p.

Hauer, F.R.; Lorang, M.S. 2004: River regulation, decline of ecological resources, and potential for restoration in a semi-arid lands river in the western USA. *Aquatic Sciences 66*: 388–401.

Hohensinner, S.; Habersack, H.; Jungwirth, M.; Zauner, G. 2004: Reconstruction of the characteristics of a natural alluvial river-floodplain system and hydromorphological changes following human modifications: the Danube River (1812–1991). *River Research and Applications 20*: 25–41.

Junk, W.J. 1999: The flood pulse concept of large rivers: learning from the tropics. *Archiv Für Hydrobiologie, New Zealand 11*: 261–280.

Karaus, U. 2004: The ecology of lateral aquatic habitats along river corridors. Unpublished PhD thesis, Swiss Federal Institute of Technology, Zurich. 179 p.

Latterell, J.J.; Bechtold, J.S.; O'Keefe, T.C.; Van Pelt, R.; Naiman, R.J. 2006: Dynamic patch mosaics and channel movement in an unconfined river valley of the Olympic Mountains. *Freshwater Biology 51*: 523–544.

Leps, J.; Smilauer, P. 2003: Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge. 269 p.

Luck, G.W. 2007: A review of the relationship between human population density and biodiversity. *Biological Reviews 82*: 607–645.

Malard, F.; Uehlinger, U.; Zah, R.; Tockner, K. 2006: Flood-pulse and riverscape dynamics in a braided glacial river. *Ecology 87*: 704–716.

McCabe, D. 1998: Biological communities in springbrooks. Pp. 221–228 in Botosaneanu, L. (Ed.): Studies in crenobiology: the biology of springs and springbrooks. Backhuys Publishers, Lieden.

McLellan, I.D. (Ed.) 1991: Notonemouridae (Insecta: Plecoptera). *Fauna of New Zealand No. 22*. Manaaki Whenua Press, Lincoln. 62 p.

McLellan, I.D. 1993: Antarctoperlinae (Insecta: Plecoptera). *Fauna of New Zealand No. 27*. Manaaki Whenua Press, Lincoln. 70 p.

McLellan, I.D. 1998: A revision of *Acroperla* (Plecoptera: Zelandoperlinae) and removal of species to *Taraperla* new genus. *New Zealand Journal of Zoology 25*: 185–203.

Olden, J.D.; Poff, L.N. 2003: Redundancy and choice of hydrologic indices for characterizing streamflow regimes. *Rivers Research and Applications 19*: 101–121.

Park, G. 2002: Swamps which might doubtless easily be drained: swamp drainage and its impact on the indigenous. Pp. 176–185 in Pawson, E. (Ed.): Environmental histories of New Zealand. Oxford University Press, Melbourne.

Pautasso, M.; Fontaneto, D. 2008: A test of the species-people correlation for stream macroinvertebrates in European countries. *Ecological Applications 18*: 1842–1849.

Pawson, E. 2002: On the edge: making urban places. Pp. 238–242 in Pawson, E.; Brooking, T. (Eds): Environmental histories of New Zealand. Oxford University Press, Melbourne.

Percival, E. 1932: On the depreciation of trout fishing in the Oreti (or New River), Southland, with remarks on conditions in other parts of New Zealand. *New Zealand Fisheries Bulletin No. 5*. New Zealand Marine Department. 48 p.

Percival, E. 1945: The genus *Prorhynchus* in New Zealand. *Transactions of the Royal Society of New Zealand 75*: 33–41.

Poff, L.N. 1997: Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society 16*: 391–409.

Poff, N.; Allan, J.B.; Bain, M.B.; Karr, J.R.; Prestegaard, K.L.; Richter, B.D.; Sparks, R.E.; Stromberg, J.C. 1997: The natural flow regime. *Bioscience 47*: 769–784.

Poole, G.; Stanford, J.; Frissell, C.; Running, S. 2002: Three-dimensional mapping of geomorphic controls on flood-plain hydrology and connectivity from aerial photos. *Geomorphology 48*: 329–347.

Poole, G.C.; Stanford, J.A.; Running, S.W.; Frissell, C.A.; Woessner, W.W.; Ellis, B.K. 2004: A patch hierarchy approach to modeling surface and subsurface hydrology in complex flood-plain environments. *Earth Surface Processes and Landforms 29*: 1259–1274.

Rosenzweig, M.L. 1995: Species diversity in space and time. Cambridge University Press, Cambridge. 436 p.

Sagar, P.M. 1986: The effect of floods on the invertebrate fauna of a large unstable braided river. *New Zealand Journal of Marine and Freshwater Research 20*: 37–46.

Sagar, P.M.; Glova, G.J. 1992: Invertebrate drift in a large, braided New Zealand river. *Freshwater Biology 27*: 405–416.

Scarsbrook, M.R.; Fenwick, G.; Duggan, I.C.; Hasse, M. 2003: A guide to the groundwater invertebrates of New Zealand. *NIWA Science and Technology Series 51*. National Institute of Water & Atmospheric Research, Christchurch. 59 p.

Scrimgeour, G.J.; Winterbourn, M.J. 1989: Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia 171*: 33–44.

Smith, B.J. 2001: Larval Hydrobiosidae. Biodiversity Identification Workshop, Quick Guide. National Institute of Water & Atmospheric Research, Christchurch. 3 p.

Smith, D.; McBride, G.; Bryers, G.; Davies-Colley, R.; Quinn, J.; Vant, W. 1989: A National Water Quality Network for New Zealand. Department of Scientific and Industrial Research, Consultancy report 8016/2 (unpublished). 147 p.

Snelder, T.H.; Leathwick, J.R.L.; Dey, K.L. 2005: Definition of the multivariate environmental river classification. 'Freshwater Environments of New Zealand.' NIWA report: CHC2005-049. Department of Conservation, Christchurch.

Stanford, J.A.; Ward, J.V. 1988: The hyporheic habitat of river ecosystems. *Nature 335*: 64–66.

Stanford, J.A.; Ward, J.V. 1993: An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. *Journal of the North American Benthological Society 12*: 48–60.

Stanford, J.A.; Ward, J.V. 2001: Revisiting the serial discontinuity concept. *Regulated Rivers: Research & Management 17*: 303–310.

Stark, J.D. 1985: A macroinvertebrate community index of water quality for stony streams. *Water and Soil Miscellaneous Publication 87*: 53.

Stark, J.D.; Boothroyd, I.K.G.; Harding, J.S.; Maxted, J.R.; Scarsbrook, M.R. 2001: Protocols for sampling macroinvertebrates in wadeable streams. Ministry for the Environment, Sustainable Management Fund Project No. 5103. 57 p.

Strahler, A.N. 1957: Quantitative analysis of watershed geomorphology. *Transactions of the American Geophysical Union 38*: 913–920.

Tockner, K.; Malard, F.; Ward, J.V. 2000: An extension of the flood pulse concept. *Hydrological Processes 14*: 2861–2883.

Tockner, K.; Paetzold, A.; Karaus, U.; Claret, C.; Zettel, J. 2006: Ecology of braided rivers. Pp. 339–359 in Sambrook-Smith, G.; Best, J.L.; Bristow, C.S.; Petts, G.E (Eds): Braided rivers: process, deposits, ecology and management. Blackwell Publishers, Oxford.

Townsend, C.; Scarsbrook, M.; Doldec, D. 1997: The intermediate disturbance hypothesis, refugia and biodiversity in streams. *Limnology and Oceanography 42*: 938–949.

Vannote, R.L.; Minshall, G.W.; Cummins, K.W.; Sedell, J.R.; Cushing, C.E. 1980: The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences 37*: 130–137.

Ward, J.V.; Stanford, J.A. 1995: Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers: Research & Management 11*: 105–119.

Ward, J.V.; Tockner, K.; Arscott, D.B.; Claret, C. 2002: Riverine landscape diversity. *Freshwater Biology 47*: 517–539.

Wilson, G. 2001: National distribution of braided rivers and the extent of vegetation colonisation. Landcare Research Contract Report No. LC0001/068, Hamilton (unpublished).

Winterbourn, M.J. 1969: A freshwater nereid polychaete from New Zealand. *New Zealand Journal of Marine and Freshwater Research 3*: 281–285.

Winterbourn, M.J. 1973: A guide to the freshwater Mollusca of New Zealand. *Tuatara 20*: 141–159.

Winterbourn, M.J.; Gregson, K.L.D.; Dolphin, C.H. 2000: Guide to the aquatic insects of New Zealand. *Bulletin of the Entomological Society of New Zealand 13*. 106 p.

Woessner, W.W. 2000: Stream and fluvial plain ground water interactions: rescaling hydrogeologic thought. *Ground Water 38*: 423–429.

Young, R.; Smart, G.; Harding, J.S. 2004: Impacts of hydro-dams, irrigation schemes and river control works. Chapter 37 in Harding, J.; Mosley, P.; Pearson, C.; Sorrell, B. (Eds): Freshwaters of New Zealand. New Zealand Hydrological Society and New Zealand Limnological Society, Christchurch.

Continue to next file: sfc302b