

water in Otago streams was consistently colder than down-welling water in both winter and summer. They also noted that interstitial water contained greater dissolved oxygen, ammonium and soluble reactive phosphorus in winter than in summer. Fowler & Scarsbrook (2002) observed lower temperatures and higher conductivity in up-welling stream water in the lower North Island, but no difference in dissolved oxygen levels between up-welling and down-welling water. They also noted variation between the pH of surface water and hyporheic water, although the relationship was not consistent between rivers. Strong gradients in physicochemical factors exist within the hyporheic zone. These are regulated by patterns of up- and down-welling water at the both the reach and pool riffle scale (Collier & Scarsbrook 2000).

3.4 FLOODPLAIN PONDS

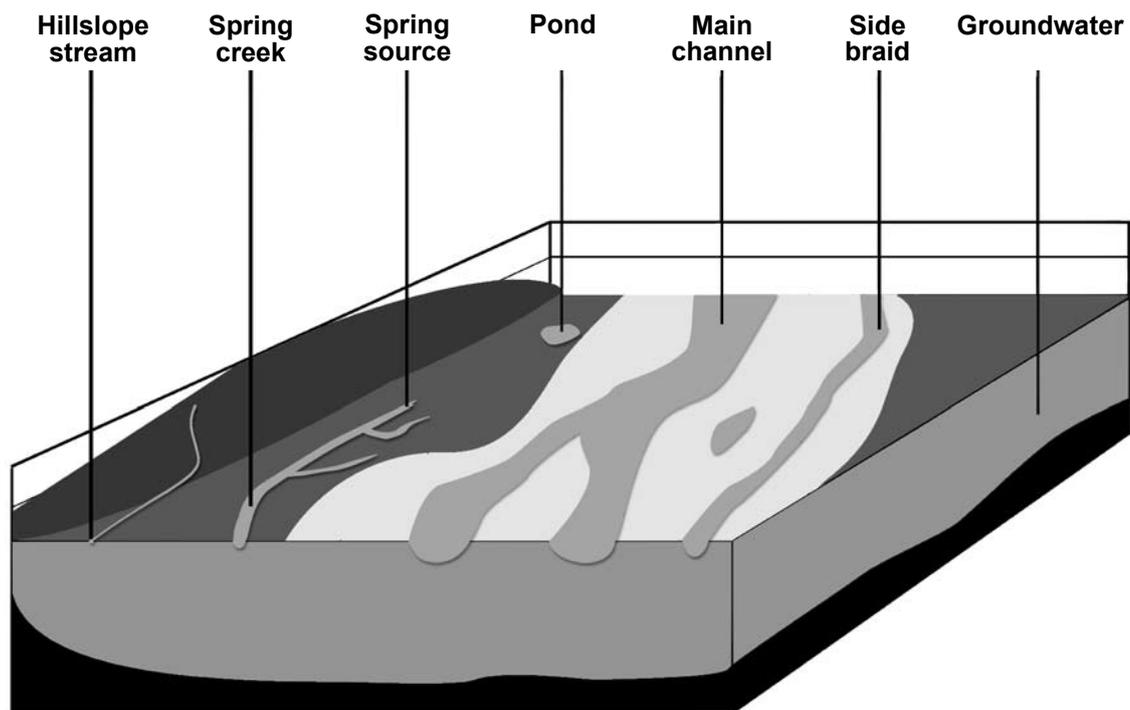
Lentic (standing or slow-moving water) habitats on braided river floodplains may form in two ways (Fig. 7). Firstly, ponds may form where areas of floodplain intersect the water table. Because such areas will be affected by water table height, they may alternate between dry, having ponds of standing water, and having ponds connected to flowing surface water.

Figure 7. A groundwater-fed floodplain pond on the Waimakariri River floodplain.



Alternatively, depressions in the floodplain surface may be perched above the water table but accumulate surface runoff water and form ponds of varying permanence. There is very little specific knowledge about the habitat conditions in New Zealand floodplain ponds, although it is thought that those fed by groundwater are more permanent than those reliant upon rainwater or floods. Mosley (1983b) observed very high temperatures ($> 26^{\circ}\text{C}$) in floodplain ponds of the Ashley River/Rakahuri but did not identify the source of the water.

In the Tagliamento River, Italy, floodplain ponds were numerous in the bar-and-island braided reaches of the river, but were absent from constrained and regulated sections. The number of ponds appeared to be dependent upon sediment grain size, river corridor width, slope of the corridor and degree of river regulation e.g. flood works. Ponds were found to be highly heterogeneous habitats, particularly in terms of temperature and water level fluctuations brought about by groundwater up-welling (Karaus 2004; Karaus et al. 2005). Thus, the physical conditions within each floodplain habitat are broadly predictable and are summarised in Fig. 8.



	Hillslope stream	Spring creek	Spring source	Pond	Main channel	Side braid	Groundwater
Temperature	Seasonally variable	Stable	Very stable	Seasonally	Highly variable	Highly variable	Very stable
Turbidity	Seasonally variable	Low	Very low	–	Highly variable	Variable	Very low
Physical disturbance	Variable	Low	Very low	Very low	Highly variable	Highly variable	Very very low
Permanence	Variable	High	High	Variable	Variable	Very variable	High

Figure 8. A summary of the physical conditions within the habitat types of a braided river floodplain.

3.5 A HOLISTIC VIEW OF FLOODPLAIN HABITATS

Whilst braided river floodplain habitats may be physically and biologically distinct, they are not discrete habitats. A braided river hydrological system consists of a single body of water moving at variable speeds along a valley (Woessner 2000; Poole et al. 2004). Both surface and subterranean habitats are linked, such that the river corridor forms a 3-dimensional mosaic of connected habitats. This dynamic mosaic is characterised by the interrelated themes of ecotones and connectivity between habitats. Ecotones are transition zones between adjacent patches of dissimilar condition (Ward et al. 1999b) and they occur at a range of scales at the boundaries between terrestrial and aquatic environments, groundwater and surface water, and zones within a single habitat 'type'. The importance of ecotones to biodiversity has been a recurrent theme in ecology over recent years (Hansen & di Castri 1992; Lachavanne & Juge 1997). Hydrological connectivity—the transfer of water between patches within the mosaic—has profound implications for a braided river. It regulates the functional and structural attributes of habitat patches and ecotones, giving rise to a diversity of lentic (standing or slow-moving water), lotic (flowing water) and semi-aquatic habitat types (each at various successional stages) that are embedded within the floodplain habitat mosaic. The often extreme heterogeneity in habitat conditions within braided river floodplains is a major contributing factor to the high biodiversity levels found within them. The complex, spatio-temporally dynamic mosaic present within each floodplain provides a physical habitat template that exerts variable degrees of influence upon the biotic communities that inhabit it.

4. Invertebrate communities

Despite the physically unstable nature and high turnover of habitats found on braided river floodplains, their biological communities persist, probably because the relative proportions of each habitat remain roughly constant (Arscott et al. 2002; Hauer & Lorang 2004; Latterell et al. 2006). Consequently, mobile taxa in particular persist within a floodplain, and form part of a meta-population within the river system (Begon et al. 1996). Furthermore, the existence of habitats in different successional stages provides a highly diverse mosaic of floodplain habitats, each with its own distinct biological community.

Braided rivers in New Zealand support diverse communities of plants, invertebrates, fish and birds, both introduced and native (NCCB 1983; O'Donnell & Moore 1983; NCCB 1986; Peat & Patrick 2001). A number of indigenous taxa are recognised as braided river specialists and are restricted to, and dependent upon, braided river habitats. Among braided river birdlife, the wrybill (*Anarhynchus frontalis*), pied and black stilts (*Himantopus* spp.), banded dotterels (*Charadrius bicinctus*), oystercatchers (*Haematopus* spp.), plovers and some gulls (*Larus* spp.) all use braided rivers during some portion of the year and during some stage of their life cycles (Pierce 1979, 1983; Maloney et al. 1997; Caruso 2006). With respect to fish, introduced salmonids, native bullies (*Gobiomorphus* spp.) and

Galaxiidae are relatively common within braided river habitats. Spring-fed streams are particularly important as spawning sites for trout and salmon, and some rare non-migratory galaxiids appear to be restricted to braided rivers (Townsend & Crowl 1991). The longjaw (*Galaxias prognathus*), bignose (*G. macronasus*) and alpine (*G. paucispondylus*) galaxiids have distributions restricted to braided river habitats within several large south and central Canterbury rivers (Peat & Patrick 2001; McDowall 2000; Bowie 2004).

Whilst plant and terrestrial invertebrate communities have been well documented, and include threatened species such as the native forget-me-not (*Myosotis uniflora*) and the robust grasshopper (*Brachaspis robustus*), there is less information on the aquatic invertebrate communities of braided rivers. Percival (1932) referred to the main channels of large braided rivers such as the Waimakariri, Rangitata and Waitaki as 'relative (biological) deserts', owing to the extreme substrate disturbance during floods. Other studies have reported similar views for the main channels of braided rivers, citing low diversity, low abundance and a high degree of domination by well-adapted taxa (Hirsch 1958; Winterbourn et al. 1971; Pierce 1979; Sagar 1986). More recent studies, however, have identified a wide range of braided river floodplain habitats and demonstrated their potential as biodiversity hotspots (Digby 1999; Gray et al. 2006).

4.1 MAIN CHANNEL INVERTEBRATE COMMUNITIES

Various spatio-temporal patterns and drivers of community composition have been recognised within New Zealand braided rivers. For example, physical disturbance has been shown to structure many stream benthic communities (Percival 1932; Death 1991; Winterbourn 1997). In the South Island, despite rivers experiencing aseasonal and unpredictable patterns of rainfall and flooding, consistent seasonal fluctuations in braided river invertebrate communities have been observed. Investigations of faunal densities in Canterbury braided rivers have reported a consistent pattern of high abundance during winter followed by a spring decline, after which density gradually recovers to winter levels (Sagar 1986; Scrimgeour & Winterbourn 1989; Sagar & Glova 1992). However, an inverse seasonal pattern was reported for the Waipawa River (Hawke's Bay) and Timber Creek (Otago); with abundance and taxonomic richness lowest in winter and peaking in summer (Scarsbrook & Townsend 1993; Fowler & Death 2000). These differences may reflect hydrological differences between alpine-sourced and foothill-sourced rivers. In spring, orographic rain, often combined with snow melt, produces major floods in the alpine-fed Canterbury rivers, whilst discharge is most stable during winter when precipitation occurs as snow in the upper catchments. In contrast, the Waipawa River and Timber Creek catchments are situated in the rain shadow of their respective main divides and major floods result from southerly weather fronts, which are more common in winter. Concomitantly, invertebrate abundance responds to the warmer summer temperatures and increased algal biomass that occurs during the stable summer flows of these catchments (Scarsbrook & Townsend 1993; Fowler & Death 2000). In Italy, faunal densities in the Tagliamento River peaked in summer (August), but achieved their lowest levels after autumn floods (Arscott et al. 2003), indicating that they are also structured by discharge events.

Several studies report the overriding influence of discharge variability (discrete flood events in particular) on main channel invertebrate communities. In the lower Rakaia River, invertebrate abundance was inversely related to antecedent discharge, and was lowest following severe floods (Sagar 1986). Similarly, taxonomic diversity and the biomass of invertebrates were greatest during stable flow periods in winter and lowest following spring floods. In the Rakaia River, floods in excess of 400 m³/s caused significant bed-load movement resulting in catastrophic invertebrate drift, physical damage to individuals and a reduction in resource supply (Sagar 1986). Following an extreme flood (454 m³/s) in the Ashley River/Rakahuri, benthic communities were reduced when water velocities reached the threshold needed to move small cobbles (at a discharge > 30 m³/s; Scrimgeour & Winterbourn 1989). However, despite the occurrence of several floods > 30 m³/s over the following 132 days, benthic invertebrate communities rapidly recovered to pre-flood levels (Scrimgeour et al. 1988).

Invertebrate communities can recover rapidly following flood disturbance in braided rivers. For example, Sagar (1986) recorded a doubling of invertebrate abundance in the Rakaia River during a 2-week period of stable flow in winter. Various recolonisation mechanisms have been proposed for post-flood stream invertebrates. Drift downstream, migration upstream within the water column, migration from some flood refuge (e.g. peripheral floodplain habitats) and aerial oviposition (Williams & Hynes 1976; Dole-Olivier et al. 1997; Gayraud et al. 2000; Holomuzki & Biggs 2000) have all been cited as possible recolonisation mechanisms. The persistence and resilience of benthic invertebrate populations has been examined in numerous stream habitats and the varying roles of each recolonisation method assessed for the habitat and its taxa (Scarsbrook 2002). In a spatially heterogeneous environment, the presence of refugia and source patches of colonisers should reduce the effects of disturbance (Townsend 1989). These patches can occur at a range of scales. Stable substrate patches (Biggs et al. 1997; Francoeur et al. 1998; Matthaei et al. 2000) (at the micro-scale), spring creeks and tributaries (Scrimgeour et al. 1998) (at the meso-scale), and the location of a reach (i.e. in a floodplain versus being constrained) (macro-scale) all play a role in the persistence and resilience of stream communities and influence the speed of post-flood recovery in braided rivers (Scarsbrook & Townsend 1993).

In the alpine-sourced Rakaia River, Pierce (1979) reported extremely high post-flood abundances of *Deleatidium* spp. in isolated pools and backwaters that could not be explained by recent oviposition and/or egg hatching. Similarly, Scrimgeour et al. (1988) were unable to provide an adequate explanation for the post-flood abundance of *Deleatidium* larvae in the foothill-sourced Ashley River/Rakahuri. However, immediately after the flood they found high abundances and diversity of taxa in peripheral floodplain habitats, which might have acted as sources of colonisers post-flood. In the foothill-sourced Kye Burn in Otago, benthic invertebrates were observed in the inundated floodplain during a flood (Matthaei & Townsend 2000a). Matthaei & Townsend (2000a) indicate that these individuals probably returned to the main channel, presumably by drifting in the receding flood waters. Another possible flood refugium considered by Matthaei et al. (2000) was the matrix of stable substrates within the streambed. Both taxonomic richness and abundance were higher on stable substrates post-flood, suggesting that some invertebrates actively seek stable substrates. Main channel invertebrates may also use the hyporheic zone as a refuge. In an experimental

flume, *Deleatidium* nymphs were shown to enter deeper sediments with incremental increases in discharge (Holomuzki & Biggs 2000), and in the Kye Burn *Deleatidium* spp. was found to be more abundant in depositional areas than in scour patches (Matthaei & Townsend 2000b), suggesting the use of the shallow hyporheic zone as a flood refuge. However, several conflicting studies about the use of the hyporheic zone by invertebrates as a flood refugium can be found in the literature and any possible role the hyporheic plays as a flood refuge is still unclear.

The wider floodplain also includes other possible flood refugia such as less-disturbed side braids, upstream reaches, springs, hillslope streams and ponds. These habitats may act as sources of new colonisers rather than as potential refugia for inhabitants of main channel braids during floods (Ward et al. 1999a).

A compilation of 18 papers (Appendix 1) recording taxonomic richness and abundance of aquatic macroinvertebrates in the main channels of braided rivers in New Zealand shows a mean taxonomic richness of 25 (SE \pm 4) and a mean density of 2598 individuals/m² (SE \pm 703). Aquatic invertebrate communities were dominated by the leptophlebiid mayfly *Deleatidium* spp., chironomids and elmid beetles. The sandfly *Austrosimulium*, the stonefly *Zelandobius*, Eriopterini (Diptera) and predatory hydrobiosid caddis were all relatively common. Although the highest richness (56 taxa) was recorded in the Waipawa River on the east coast of the North Island, many of the taxa found constituted < 1% of any sample (Fowler & Death 2000). This is probably not surprising, as many taxa might be represented by a few individuals that drift into the mainstem from more stable tributaries and the hyporheic zone (Winterbourn 1997; Kilroy et al. 2004). Collation of the results from six surveys of the main channels of the Tagliamento, Roseg, Brenno and Lesgiuna rivers in Italy showed mean richness of 43 taxa (SE \pm 9) and mean density of 59 179 (SE \pm 36 159) individuals/m², both values being higher than those found in New Zealand (Ward et al. 1999; Brunke 2002; Burgherr et al. 2002; Arscott et al. 2003, 2005). Several issues may affect these comparisons. For example, many workers use variable levels of taxonomic resolution for some of New Zealand's most speciose groups e.g. leptophlebiids, hydrobiosids and chironomids, while a number of New Zealand studies may have also been undertaken prior to more recent advances in taxonomy. In addition, the extremely high macroinvertebrate density in some European braided rivers partly reflects the use of a smaller sampler mesh size (100 μ m), compared with that used in New Zealand (minimum 200 μ m, average 350 μ m). Small chironomids dominated the European results and meiofauna (larger than microfauna, smaller than macrofauna) were included. Furthermore, the high variation in abundance in the European data is exacerbated by the particularly low densities reported for the glacier-fed Roseg River in Switzerland, where faunal densities were more similar to those of New Zealand's braided rivers (Burgherr et al. 2002).

The mean taxonomic richness found in New Zealand braided rivers, both alpine- and foothill-sourced, was 25 \pm 4 (Appendix 1), which is considerably lower than the 61 taxa recorded in forest streams by Rounick & Winterbourn (1982), and the 79 taxa found in springs and 53 taxa found in hillslope tributary streams by Gray et al. (2006). The density of individuals in braided river main channels (2598 \pm 703 individuals/m²) was also considerably lower than that recorded for spring sources (22 982 \pm 3413 individuals/m²), mossy forested streams (218 400 \pm 15 100 individuals/m²) and urban streams (25 000 \pm 8500 individuals/m²) (Suren 1991; Blakely & Harding 2005).

European studies of longitudinal patterns in the invertebrate communities of the main channels of braided rivers have revealed some striking patterns (Arscott et al. 2003, 2005). The composition of headwater benthic communities was more stable over time compared with downstream communities. Faunal diversity, however, was highest at each end of the river continuum. More specifically, Chironomidae and *Baetis* mayflies showed little change in abundance along the river, but stoneflies were mostly restricted to the upper reaches, and Crustacea, nematodes and oligochaetes became more common in the lower reaches. The lowest density recorded in the Tagliamento River in Italy was 433 ± 158 individuals/m², for an island-braided floodplain reach morphologically similar to those in many New Zealand braided rivers.

In a comparison of benthic fauna in the mid-reaches of the Rakaia River with that in the upper reaches of the Waitaki River, Pierce (1979) recorded that both communities were dominated by *Deleatidium* spp. and predatory and cased caddis larvae. Despite low densities in both rivers, the mean density of *Deleatidium* was higher in the upper Waitaki River (176 individuals/m²) than in the middle Rakaia (85 individuals/m²), and the free-living predatory caddis common in the Rakaia River were replaced by case-dwelling Leptoceridae and Conoesucidae in the Waitaki River. Waitaki River invertebrate communities were less temporally variable in composition and abundance than those in the Rakaia. Sagar (1986) investigated invertebrate communities in three longitudinally arranged reaches of the lower Rakaia River and found taxonomic diversity and abundance were greatest in the lower reaches during winter, but showed no significant longitudinal change during summer. The greater diversity in the lower reaches was attributed to longitudinal changes in river morphology leading to greater habitat heterogeneity and reduced substrate movement.

Benthic communities of braided rivers are often dominated by generalist taxa which may exhibit multivoltinism (multiple broods annually), asynchronous lifestyles, refuge-seeking behaviour and the ability to recolonise a denuded substrate. Regular flooding reduces the quantity and quality of epilithic food resources (Scrimgeour & Winterbourn 1989) and the shifting wetted bed of a braided river requires invertebrates to be able to exploit the resulting very thin organic layers on stone surfaces for food (Sagar 1983; Fowler 2004). High fecundity, good dispersal ability and multivoltinism may allow surviving and recolonising invertebrates to rapidly repopulate stream substrates. Coupled with an asynchronous lifestyle, these adaptations ensure that at any time of year there are individuals at various stages of the life cycle, making survival of a disturbance event by some individuals very likely (Winterbourn 1974; Scrimgeour et al. 1988; Scrimgeour & Winterbourn 1989). Specific taxa exhibit different behavioural strategies in response to increases in discharge (Holomuzki & Biggs 2000). Dorsoventrally flattened, clinging but mobile taxa such as *Deleatidium* spp. are rarely dislodged from a stable substrate compared with cased caddis and the hydrobiid snail *Potamopyrgus antipodarum* (Holomuzki & Biggs 2000). However, when substrate particles move, *Deleatidium* spp. may enter the drift voluntarily (Matthaei & Townsend 2000a). In contrast, cased caddis and *P. antipodarum* rely on downward movement within the substrate and the protection offered by their respective case or shell. In a highly disturbed riverbed with highly mobile substrate, drifting downstream into areas of lower current velocity is likely to be a more effective strategy than local-scale movements or reliance on a hardened

covering. Hence, *Potamopyrgus* and cased caddis are not often found in rivers with frequently disturbed beds. Taxa of braided river main channels such as *Deleatidium* spp., *Zelandoperla* spp., Chironomidae, Oligochaeta, Eriopterini and Elmidae all share the trait of effective flood avoidance by drift, which also permits rapid recolonisation of denuded substrates.

A fall in river stage height, or lateral movement of braided river channels, may result in the temporary drying of a section of streambed. The processes by which existing channels become cut off and dry out are described in detail by Digby (1999) and Rundle (1985). The response of invertebrates to the re-wetting of these channels has been described in several studies, which found that they can quickly colonise the newly wetted areas (Sagar 1983; Malmquist 1991; Fowler 2004). However, the rate and mechanism of recolonisation may depend on whether the dry period coincides with the emergence and oviposition of adults, since species whose hatching period overlaps the dewatered period may be slow to recover to post-dewatering levels. Some insect species can also enter diapause to allow eggs to survive dewatering (Storey & Quinn 2007). Recolonisation after dewatering is probably predominantly through drift, though vertical migration and aerial oviposition may all occur (Williams & Hynes 1976). In the Rakaia River, recolonisation of re-watered substrate took 33 days in winter, but only 15 days in summer, and was principally driven by discharge fluctuations and the resulting drift (Sagar 1983; Sagar & Glova 1992). In an analogous study on the east coast of the North Island, species diversity recovered after only 7 days (Fowler 2004). Taxa abundances were slower to recover, especially at sites that had been dry for moderately long periods of time (>6 weeks). The fastest colonisers were chironomids and elmids, and they were also initially dominant at sites that had been dewatered for a longer period of time (Fowler 2004).

Another important driver of benthic invertebrate community structure is in-stream biofilm. Biofilm consists primarily of algae (or periphyton), but also fungi and bacteria, as well as organic and inorganic particles (Rounick & Winterbourn 1983; Biggs & Kilroy 2004a). Biofilm is frequently the basal food resource for invertebrates and, therefore, plays a very important role in structuring communities. The periphytic component of biofilm is influenced primarily by physical and biological factors that operate at a local scale: light, flow regime, wave action, nutrients, temperature and invertebrate grazers (Biggs & Kilroy 2004). Both high and low flows can affect biofilm, by physical abrasion and desiccation respectively. Biggs & Close (1989) and Biggs (2000) found that flooding regimes and nutrient levels explained 63% and 62% of the variance in periphyton communities in two separate studies of braided rivers. The loss of biomass during a flood event depends upon flow velocity, the stability of bed sediments and the ability of algal species to resist 'sloughing' from the substrate. Consequently, in braided river main channels, periphyton and biofilm can be very sparse, although areas with lower water velocities and stable substrates may have relatively high periphyton biomass (Biggs & Close 1989). In the Ashley River/Rakahuri, the organic layer (epilithon) recovered rapidly to post-flood levels despite the occurrence of subsequent minor floods, a pattern which was mirrored by the invertebrate community (Scrimgeour et al. 1988). However, despite the reliance of many invertebrates on highly variable epilithic food resources, many taxa (particularly *Deleatidium*) are able to survive on very low levels of algal biomass and are unlikely to be food limited in streams (Scrimgeour

& Winterbourn 1989). De-watering can also have an effect upon biofilm, depending partly on what species are present, as they show variable abilities to withstand desiccation (Mosisch 2001). In the Waipawa and Tukituki rivers in Hawke's Bay, the recovery of algal biomass was slower in channels that had been subject to longer periods of de-watering, as there was no persistent algal standing crop from which to re-establish algal communities (Fowler 2004).

4.2 SPRING INVERTEBRATE COMMUNITIES

The earliest recorded survey of a spring in a braided river system was of the Glennariffe Stream, a spring-fed tributary of the Rakaia River. Average density of benthic fauna was 2618 individuals/m²; 50% of the community were mayflies and 40% were conoesucid caddis (Boud et al. 1959). Early reports also indicated the presence in springs of some unusual taxa, such as the phreatic flatworm *Prorhynchus putealis* (Percival 1945). There has been little study of the ecology of alluvial springs on braided river floodplains, although this has been rectified (to an extent) by a number of recent studies, especially in the South Island (Death 1991; Death & Winterbourn 1994 and 1995; Digby 1999; Gray 2005; Gray et al. 2006), but also in the North Island (Barquin 2004).

The paucity of studies on the diversity of alluvial springs makes nationwide and international comparisons difficult (Appendix 2). However, five New Zealand studies (all undertaken in the Waimakariri River catchment) found higher invertebrate taxon diversity (mean 66 ± 8) than studies from other countries (mean 33 ± 12). In New Zealand, taxonomic diversity and abundance seem to be higher on average in braided river springs than in adjacent main channels and hillslope streams (Rounick & Winterbourn 1982; Death 1991; Gray et al. 2006) and taxonomic richness and community composition of springs appear to be more stable over time than in more disturbed habitats (Death 1991). Furthermore, Digby (1999) found that secondary production in a perennial seepage stream was an order of magnitude higher than in the main channel of the Rakaia River.

Death (1991) suggested that both density and diversity of invertebrate communities decline downstream from a spring source. However, while Barquín (2004) found an increase in taxonomic richness with distance downstream, Gray (2005) observed a decrease, although the pattern was weak in both studies. Neither study found any longitudinal change in invertebrate abundance, but both reported an increase in filter-feeding taxa away from the source. Both studies concluded that the effect of temperature stability at the source and increased temperature variability downstream were not critical controllers of invertebrate community composition, as had been suggested by studies from the northern hemisphere (Minshall 1968; Ward & Dufford 1979; Glazier 1991). Instead, they suggested that a longitudinal decline in substrate stability, site-specific substrate differences and biological interactions were likely to play more important roles (Barquín 2004; Gray 2005).

Gray (2005) identified two additional factors that affect invertebrates in springs and spring creeks. At spring sources, dense macrophytes supported communities dominated by chironomids and the hydrobiid snail *Potamopyrgus antipodarum*. But, after removal of macrophytes, communities shifted towards dominance

by *Deleatidium* and conoesucid caddis. Successional stage, or time since the last catastrophic disturbance, also influenced spring fauna composition. The inter-montane basin reaches of the Waimakariri River are thought to re-work their entire floodplains approximately every 250 years (Reinfelds & Nanson 1993), implying that their springs may be at different stages along a 250-year successional gradient. In the Waimakariri, Gray (2005) found older springs had a higher proportion of non-insect taxa than younger springs, although there was considerable variation within age categories.

Many of the taxa found in New Zealand springs are widely distributed and not restricted to spring habitats. This differs from findings in the Northern Hemisphere, where obligate spring taxa seem to dominate spring habitats (Death et al. 2004). However, recent surveys across New Zealand have revealed a high diversity of previously undescribed hydrobiid snails in springs and seepages which may yet prove to be crenobionts (spring specialists) (Scarsbrook & Fenwick 2003). Springs are not the only known surface habitats where several groundwater taxa have been collected. The amphipods *Paraleptamphopus* spp. are also common in forested streams on the West Coast, although it is likely that, with an increase in the taxonomic resolution of this group, spring specialist species will be found. However, the amphipod *Phreatogammarus fragilis* and the flatworm *Prorhynchus putealis* have very limited surface habitats outside of springs and spring creeks. More importantly, the presence of springs within the braided river corridor supports a higher number of taxa than exist in the unstable main channels (Gray 2005).

4.3 GROUNDWATER AND HYPORHEIC INVERTEBRATE COMMUNITIES

Studies of groundwater habitats in New Zealand fall into two categories: those of the shallow hyporheic zone and those of the deeper phreatic zone. Studies of the hyporheic zone of braided rivers are most common and include those by Scarsbrook (1995), Fowler (2000), Burrell (2001), Fowler & Scarsbrook (2002), and Olsen & Townsend (2003), although there have been very few investigations that included the deeper aquifer (see Scarsbrook & Fenwick 1993). These deeper groundwater systems may represent the greatest aquatic volume of the river and therefore represent a large, understudied component of the ecosystem (Stanford & Ward 1988, 1993).

The benthic fauna can be classified according to its degree of affinity with groundwater (phreatic) or hyporheic habitats (Gibert et al. 1994; Collier & Scarsbrook 2000; Scarsbrook et al. 2003). A number of terms have been developed to describe taxa that occur in these subterranean zones; in particular, 'stygophiles' are organisms which have an affinity for subsurface zones, and are subdivided into 'occasional', 'amphibitic' and 'permanent' subgroups. 'Occasional' taxa include the caddis *Olinga feredayi*, which has been found at depths of at least 30 cm in several streams and may use the hyporheic zone as a refuge from flood disturbance (Adkins & Winterbourn 1999; Burrell 2001). 'Amphibites' or amphibionts are species that spend their entire larval life within the hyporheos but return to the surface to complete their life cycles (Stanford & Ward 1993). Presently, no amphibionts have been confirmed as occurring in New Zealand, although

Spaniocercoides cowleyi may be one (Cowie 1980; McLellan 1984; Winterbourn et al. 2006). 'Permanent' hyporheos dwellers in New Zealand include some nematodes, oligochaetes, mites, copepods, ostracods and cladocerans (Scarsbrook et al. 2003). Other hyporheic specialists may exist; for example, the unpigmented, eyeless *Namalycastis tiriteae*, a freshwater polychaete, which has been found in the North Island (Winterbourn 1969; Fowler 2000). The final group, the 'stygobites', are true groundwater species that are blind, unpigmented and physiologically and morphologically adapted for groundwater life (Gibert et al. 1994). They are ubiquitous in alluvial and karst aquifers and include 'phreatobites' which are restricted to deep alluvial aquifers, such as those beneath the Canterbury Plains. Phreatobite communities consist primarily of amphipods, isopods, beetles, snails and mites. Although these communities are apparently diverse, little research has been carried out on them in New Zealand, and more taxonomic and ecological studies are needed (Sinton 1984; Fenwick 1987; Scarsbrook et al. 2003; Fenwick et al. 2004). The abundance of fauna within alluvial aquifers is difficult to measure because of sampling difficulties, but abundance may increase where nutrients reach the aquifers (Sinton 1984; Fenwick 1987; Fenwick et al. 2004).

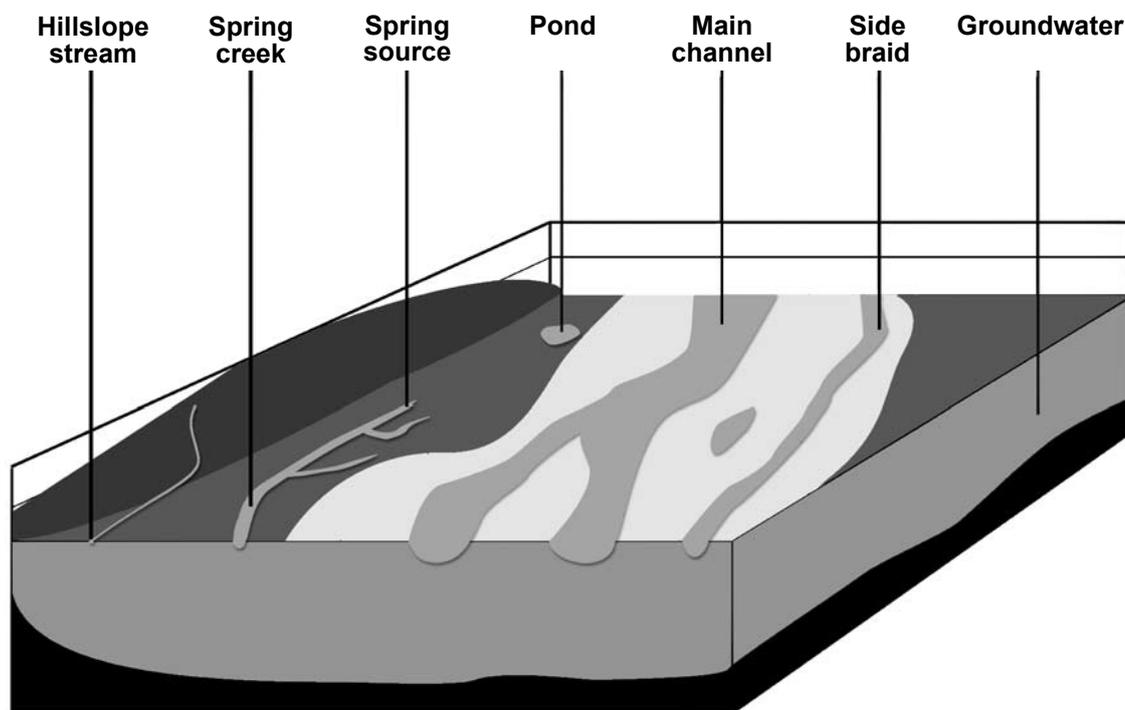
New Zealand's shallow hyporheic zones constitute an interface between surface water and groundwater systems, mediating the movement of energy, matter and individuals between the two zones, and providing habitat for a diverse range of aquatic taxa (Collier & Scarsbrook 2000). The presence of large numbers of aquatic invertebrates in the hyporheic zone has implications for the study of ecosystems, especially large braided rivers with extensive hyporheic zones. Sampling of the surface benthos underestimates the true number of invertebrates in a river (Adkins & Winterbourn 1999; Huryn 1996) and ignores important vertical colonisation pathways (Williams & Hynes 1976). Internationally, most hyporheic research has been carried out in small streams, although significant, large-scale studies have been done in large braided rivers systems such as the Flathead River in Montana (Stanford & Ward 1988). In New Zealand, braided rivers have been the sites of several hyporheic studies. Burrell (2001) conducted hyporheic surveys and experiments in the braided Ashley River/Rakahuri and Waipara River in Canterbury, whilst Olsen et al. (2001) and Olsen & Townsend (2003) worked in the Kye Burn in Otago and Fowler (2000) studied the Makaretu, Tukituki and Waipawa Rivers in the North Island.

The effect of vertical hydrological exchange (VHE), i.e. up-welling versus down-welling of water, on invertebrate community composition has been assessed in the Kye Burn, Waipawa, Tukituki and Makaretu Rivers. In the Kye Burn, taxonomic richness did not differ between up- and down-welling areas (Olsen & Townsend 2003), although species evenness was greater at up-wellings. In the North Island, taxonomic richness was greatest at down-welling sites because of high numbers of epigeal taxa and, possibly, the lower taxonomic resolution of hypogean taxa (Fowler & Scarsbrook 2002). In the Kye Burn, invertebrate density was greatest in the near-surface hyporheic sediment, and sediment composition and VHE was the most influential driver of invertebrate communities, which were dominated by early instar leptophlebiids and asellotan isopods (Olsen et al. 2001; Olsen & Townsend 2003). Hyporheic samples taken from the Ashley River/Rakahuri and Waipara River in Canterbury by Burrell (2001) were also dominated by epigeal taxa, especially harpacticoid copepods, and insect taxa such as Chironomidae

and Polycentropidae. Hyporheic communities increased in abundance where organic matter was more abundant, although the effect declined with increasing depth (Burrell 2001). The information here is summarised in Fig. 9.

4.4 FLOODPLAIN POND COMMUNITIES

The invertebrate communities of floodplain ponds have received little attention. The presence of a dytiscid beetle *Huxelhydrus syntbeticus* and a species of stratiomyid in temporary riverbed ponds in the Waimakariri River catchment has been noted by Winterbourn et al. (2006), while Scrimgeour et al. (1988) observed the larvae of *Aoteapsyche*, *Hydrobiosis* and *Psilochorema* in a stagnant pool 150 m from the main channel of the Ashley River/Rakahuri. These taxa had been absent from the main channel following a large flood, but after a subsequent flood re-connected the pool with a side braid, the taxa were once again present in the braid below the pool. These casual observations suggest that pools created during high flows may act as sources of colonists when they are reconnected to the main channel. In the Tagliamento River floodplain, Italy, more aquatic



	Hillslope stream	Spring creek	Spring source	Pond	Main channel	Side braid	Groundwater
Taxa richness	Medium	Very high	High	Variable	Low	Low–medium	Low (Poor resolution)
Abundance	Medium	High	High	Variable	Low	Low–medium	Unknown
Species evenness	High	High	Medium–high	High	Low	Medium–low	Unknown
Characteristic taxa	<i>Nesameletus</i> <i>Austroclima</i> <i>Oniscigaster</i> <i>Edpercivalia</i>	<i>Pycnocentroides</i> <i>Deleatidium</i> <i>Zelotes</i> <i>Potamopyrgus</i>	<i>Prorhynchus</i> <i>Phreatogammarus</i> <i>Paraleptamphopus</i> Isopoda	<i>Anisops</i> <i>Xanthocnemis</i> <i>Huxelhydrus</i> <i>Rhantus</i>	<i>Deleatidium</i> Elmidae Eriopterini Free-living caddis	<i>Deleatidium</i> Elmidae Chironomidae Eriopterini	Amphipoda Isopoda Ostracoda Acarina

Figure 9. The biological characteristics of braided river floodplain habitat types in New Zealand.

taxa were restricted to parafluvial ponds than in the main river channel, but the similarity between pond communities was quite low, reflecting high between-pond habitat heterogeneity (Karaus 2004; Karaus et al. 2005).

5. A holistic perspective of braided rivers

Braided river floodplains have been identified as hotspots of aquatic biodiversity in the northern hemisphere (Ward et al. 1999b), and although relatively few similar studies have been conducted in New Zealand, this seems likely to be the case here too (Gray et al. 2006). The high biodiversity in braided river floodplains may be attributable in part to high habitat heterogeneity and the large size of many of these river systems. Despite the reputation of braided rivers as harsh physical environments, communities in a confined single-channel river might suffer greater 'disturbance' than those in a braided river when exposed to a flood of equivalent magnitude (Mosley 1982a). Braided river floodplains moderate the physical and biological effects of floods by dispersing the flood water's energy over a greater area, and the presence of an extensive mosaic of habitats provides refugia and sources of recolonists. In contrast, a confined river channel provides fewer refugia for invertebrates or internal sources of colonisers, and the full scouring force of a flood is concentrated within the single channel. Thus, despite the position of a braided river's main channel at the extreme of a disturbance gradient (Scarsbrook & Townsend 1993), braided river floodplain invertebrate communities in total may be more persistent than those within a constrained channel (Fowler & Death 2000). Winterbourn's (1997) suggestion that South Island mountain streams are 'both stable and disturbed' can probably be extended to the braided rivers of the North and South Islands. Whilst disturbance events may spatially re-arrange and temporally reset individual floodplain habitats, the shifting mosaic ensures that representatives of each habitat persist at all times.

6. Threats and pressures

Braided rivers and their associated floodplains provide services and resources to people in a variety of ways beyond their role as conduits of water and gravel to the sea. As New Zealand's population increases, the magnitude of pressures and demands for use of our braided rivers will continue to grow. In this section we briefly review the major pressures on braided rivers in New Zealand.

6.1 IMPOUNDMENT

Both the surface water and groundwater associated with braided floodplains are variably competed for by hydroelectricity generators, irrigators and municipal water suppliers (Young et al. 2004). In New Zealand, a number of major rivers have been impounded for the generation of hydroelectricity; the Clutha, Waitaki,

Waikato, Rangitaiki and Waiau rivers all feature at least one dam, and numerous other rivers are subject to flood harvesting or diversion (Henriques 1987). Further flow diversion takes place to supply irrigation demands, particularly in the water-short eastern regions such as Canterbury. There is a wealth of international and New Zealand literature summarising the general downstream effects of flow regulation by impoundment (e.g. Henriques 1987; Rosenberg et al. 2000; Young et al. 2004; Graf 2006; Poff et al. 2007). Dams and river diversions have major impacts on downstream aquatic habitat, contribute to the loss of fisheries, modify species distributions and reduce ecosystem services (Pringle et al. 2000; Rosenberg et al. 2000). In particular, the negative impact of flow regulation upon the morphological and successional diversity of floodplain habitats has been highlighted by several workers (Ward & Stanford 1995; Gilvear 2004; Hohensinner et al. 2004; Choi et al. 2005; Hauer & Lorang 2004). Impoundments typically reduce channel-forming flows and longitudinal sediment transport which, in turn, reduces the rate of channel migration, and habitat turnover. The effect of flow regulation is similar to that of channelisation, in that it truncates the fluvial system and disconnects the river from its floodplain (Hohensinner et al. 2004). Impounding a river can have marked effects on water chemistry, invertebrates and fish, and on the upstream and downstream transport of organic matter and migratory animals (Pringle et al. 2000; Young et al. 2004). Benthic invertebrate communities are often drastically altered so that former distributions of riverine taxa become discontinuous (Harding 1992a, b). The distribution and abundance of many fish communities are also significantly impacted by impoundments, which create lentic environments unsuited to most river-dwelling fish, and also form barriers to migration of species that spend some of their lives at sea (Young et al. 2004).

6.2 WATER EXTRACTION

Irrigation of farmland, particularly for the dairy industry, requires large volumes of water. The effect of water abstraction, particularly on groundwater invertebrate communities, is poorly understood and no studies have looked at depletion effects on stygofauna (Fenwick et al. 2004). Similarly, the effects of groundwater abstraction on surface habitats and biota that receive aquifer recharge are poorly understood (though see Datry et al. 2007). Surface habitats are supplied by water from the upper levels of aquifers and may be quick to dry out at an early stage of water table lowering. Consequently, springs and wetlands may dry out and seawater intrusion may occur in coastal aquifers (Fenwick et al. 2004). The spring-fed sources of the Avon River/Otakaro in Christchurch have moved several kilometres downstream due to water table lowering associated with urbanisation (Marshall 1973). A compounding effect of irrigation is the leaching of agricultural waste back into the aquifer. The limited biological research done in New Zealand suggests that aquifer ecosystems are likely to be highly sensitive to organic pollution, especially the abundant Crustacea, many of which are sensitive to a range of pollutants (Thomas 1993; Fenwick et al. 2004).

6.3 LOW FLOWS

Low flow conditions are a consequence of natural climatic cycles, and are particularly common in rivers on the east of New Zealand. However, impoundments, diversions and water abstraction have markedly increased the frequency, magnitude and duration of low-flow events. Low flows are exacerbated or prolonged by water extraction for irrigation and other activities and can have serious negative impacts on the in-stream values of braided rivers. Natural fluctuations in flows may result in shifts in depth, velocity, habitat availability, temperature, dissolved oxygen, nutrient concentration and algal communities, while prolonged reductions in flow may have severe effects on them (Suren & Jowett 2006; Dewson et al. 2007). As flow decreases, the amount of habitat available for invertebrates often decreases as well (Suren & Jowett 2006; Dewson et al. 2007). In the short term, this may result in localised increases in invertebrate density as animals are crowded into smaller areas of habitat (Malard et al. 2006). However, if low flows persist, invertebrate densities may decline as a result of mortality (Cowx et al. 1984). Faunal composition also changes as low flows persist, so that midges, snails and Oligochaetes may become dominant where previously mayflies and caddis dominated (Iversen et al. 1978; Extence 1981; Cowx et al. 1984). As discharge declines, some invertebrates may shift their location by drift (Gore 1977), while others may avoid unsuitable conditions by emerging (Greenwood & McIntosh 2004; Harper & Peckarsky 2006). However, if stressful conditions continue, many invertebrates will die (Quinn & Hickey 1990). The trophic effects of increased low flows are also highly likely to be detrimental to fish and bird communities that rely on invertebrates for food. Interestingly, however, invertebrate communities in the Waipara River in north Canterbury responded less strongly to drought than to floods (Suren & Jowett 2006) and the authors concluded that large-scale changes to invertebrate communities were unlikely to occur as a result of low-flow events in New Zealand streams. Nevertheless, over longer time scales, individual river communities may show shifts in species composition as low flows become more extreme and prolonged. The Waipara may be atypical, as it has been subject to extreme low flows for many years and its present fauna may be adapted to low-flow conditions.

6.4 GRAVEL EXTRACTION

There do not appear to be any published records on the effects of gravel extraction on the ecology of New Zealand's braided rivers, although inferences can be made from international studies. In a review of the physical effects of gravel extraction in several European rivers, river incision was noted both up-stream and down-stream of extraction points, along with lateral channel instability and riverbed armouring (Renaldo et al. 2005). Other effects included alteration of the floodplain inundation regime, lowering of the valley water table, and loss or impoverishment of aquatic and riparian habitat. In-stream gravel mining destroyed the heterogeneity of riffles and pools, and may affect the spawning activities of fish (Condole 1994; Cote et al. 1999). Furthermore, the destruction of features such as islands and bars, and the removal of large woody debris, reduce in-stream morphological and hydraulic diversity, leading to the loss of aquatic habitats (Arsine & Green 2000). We might also expect that the cessation of floodplain inundation and lowering of the water table would cause a loss or de-watering of peripheral habitats such as floodplain ponds and springs.

6.5 FLOOD CONTROL

The effects of large flood control projects have received considerable attention in New Zealand and internationally (Brunke 2002; Hancock 2002; Hauer & Lorang 2004; Young et al. 2004; Caruso 2006; Scarsbrook et al. 2007). 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, and can affect the channel's interactions with the aquifer and 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 a river from its floodplain tends to reduce habitat heterogeneity at the landscape scale and alter successional dynamics within existing flood-plain habitats (e.g. springs and floodplain ponds). Following the construction of flood control barriers, extant habitats beyond the barriers are likely to have a reduced probability of disturbance, and tend towards later successional stages, with subsequent implications for biodiversity across the riverscape. Concomitantly, within the flood banks, river constriction means that habitats are likely to experience more regular disturbance and will tend towards earlier successional stages.

Flood retention works may not have universally negative effects on habitat and biotic diversity. In the lower Selwyn River/Waikirikiri, Canterbury, lateral movements of the river during floods are constrained by flood banks and the planting of riparian willows. This channel constriction promotes localised riverbed incision, so that the water table is intersected. The resultant ponds and springs may form refugia for fish and invertebrates during summer low flows, although the hypothesis has yet to be tested (Scarsbrook et al. 2007). Gray (2005) noted spring up-welling complexes formed in the lee of flood retention works in the upper Waimakariri River and Kilroy et al. (2004) collected 42 algal taxa in one of these springs, the highest diversity found in any of the 24 springs they sampled.

Our review highlights a lack of robust studies on the long-term effects of activities such as gravel extraction and flood bank construction on the morphology, habitat heterogeneity and biodiversity of braided river floodplains.

6.6 COMMERCIAL AND RECREATIONAL FISHERIES

In New Zealand, rivers and their floodplains support significant commercial and recreational fisheries. Maori traditionally exploited a number of freshwater fish, including lampreys (*Geotria australis*), eels (*Anguilla* spp.), grayling (*Prototroctes oxyrhynchus*), and whitebait (juvenile migratory galaxiids). The grayling, although once abundant, is now extinct, and Lampreys are only harvested intermittently, and not commercially. Whitebait and eels are subject to on-going commercial and recreational harvest by both Maori and Europeans (McDowall 1990c). Whitebaiting is a seasonal (spring) recreational activity around the mouths and lower reaches of most rivers (McDowall 1984), whereas angling for introduced salmonids is practiced along the entire length of braided rivers throughout much of the country. New Zealand's braided rivers are highly regarded brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) fisheries, although the braided rivers of the east coast of the South Island are better known for their salmon fishery. Runs of chinook salmon (*Oncorhynchus*

tshawytscha) occur from November to March. During this period, anglers queue at the river mouths for a chance to catch them as they return from the sea. The salmon spawn in spring creeks and tributaries of rivers such as the Rakaia and Waimakariri (McDowall 1990b). Major threats to fisheries within braided rivers include instream habitat destruction, loss of spawning areas, lethal and sub-lethal effects of low flow and over-harvesting by recreational and commercial fishers (McDowall 1990a; Geist & Dauble 1998; Hancock 2002).

6.7 POLLUTION

Organic and industrial pollution have been issues affecting braided rivers in the past (Hirsch 1958; Winterbourn et al. 1971), but effects of pollution have latterly been over-shadowed by those associated with impoundment, flood defences and low flows. Pollution is of more concern in smaller, foothill-sourced rivers which are less capable of assimilating/diluting pollutants than the larger, alpine-fed braided rivers. Smaller rivers flowing through areas of intensive agriculture—such as the Canterbury or Southland plains—face increasing organic pollution from livestock and agricultural activities (Davies-Colley & Wilcock 2004).

7. Recreation and landscape values

The recreational, landscape and scenic values of braided rivers are highly valued by many people (Loomis & Walsh 1986). Braided rivers are part of their cultural identity, central to their recreational activities and integral to their cultural landscape. Many large braided rivers are used regularly for kayaking, jet boating, rafting, four-wheel driving and swimming. They also provide access to many mountainous areas and are thus integral to the wilderness experience of people spending time in the mountains. Large river engineering projects, such as hydroelectric power schemes and flood defences, are perceived by many recreational users as having negative effects on the landscape and, thus, diminishing the value of their experience.

8. Management implications and future research

The pressures and threats facing braided rivers have generated a number of management issues which have been outlined above. They have exposed gaps in our understanding of how braided river ecosystems function. The values, functions and uses of braided rivers are variably dependent upon the integrity of their component parts at all scales, including catchment, reach and individual pools or riffles. Future management regimes need to address these issues in order to achieve any efficacy in the conservation of braided river invertebrate fauna.

At the larger catchment scale it is important to maintain the natural flow regime of the river and natural sediment input. Activities such as deforestation, impoundment and extraction of water and gravel can radically alter these factors. At the reach scale, flood prevention works, gravel extraction, floodplain vegetation clearance and low flows can have marked effects on floodplain morphology and dynamics, further influencing the ecology of floodplain habitats. In particular, further research is needed into the effects of gravel extraction, vegetation presence/absence and the role of large woody debris in braided rivers. Impacts operating at the catchment and reach scale combine to regulate the condition and diversity of instream habitats. Anthropogenic activities have severe impacts upon the balance of dynamic riverine systems. Consideration of the biodiversity, economic and recreational values of a river system must take into account habitat diversity and functional integrity of the whole system. The 3-dimensional aspect of floodplains, longitudinal linkages and connectivity between adjacent elements in the landscape mosaic should be central features in our biodiversity management of braided rivers (Pringle 1997; Ward et al. 1999; Pringle 2001; Malard et al. 2002; Wiens 2002). Furthermore, recent research has highlighted the importance of floodplain springs as biodiversity hotspots in braided rivers. This finding provides compelling reasons for more active management and protection of braided river springs and spring creeks.

There are a number of areas where further research is needed to improve our understanding of braided rivers:

- Currently in New Zealand there is no nationally-coordinated effort to assess spatial biodiversity patterns within the country's braided rivers. Braided rivers occur in 11 of New Zealand's 14 regions (Wilson 2001), but no robust comparisons have been conducted on invertebrate communities within braided rivers across regions. Within and between regions, many braided rivers have very different physical conditions, i.e. different sources of flow, geology, catchment vegetation, hydrological regime. A long-standing tenet of freshwater ecology has been the existence of a predictable longitudinal arrangement of physical habitats and invertebrate communities (Vannote et al. 1980; Winterbourn et al. 1981). Does this occur in New Zealand braided rivers? If it does, do taxa and communities vary among braided rivers across differing River Environment Classification (Snelder et al. 2004) classes and eco-regions (Harding & Winterbourn 1997)? Answering these questions should enable us to determine the comparative uniqueness of our braided rivers and place their biodiversity values in a national context.
- Many rivers in New Zealand are subject to either invasion by exotic vegetation or its deliberate planting (Hicks et al. 2004). While the influence of indigenous terrestrial vegetation on floodplain stability has been studied intensively in other countries (Gran & Paola 2001; Mosley 2004, Whited et al. 2007), there is relatively little understanding in New Zealand of the comparative value of indigenous versus exotic vegetation to the morphology of braided river floodplains (but see Miller 2006).
- The role of large woody debris in the formation of in-stream habitats is well known in small, single-channel streams, but in New Zealand there has been very little work on the physical and ecological roles of large woody debris in braided rivers. Presumably, the presence of logs and whole trees within a river reach increases habitat heterogeneity, carbon resources and, potentially,

biodiversity. Research on the role of woody debris should provide new insights into the importance of native vegetation clearance and subsequent invasion by exotic species to the morphology of our riverscapes.

- Although the hydrological links between braided rivers and groundwater have received increasing attention in New Zealand (White et al. 2001), our understanding of the ecology of hyporheic and groundwater systems is less advanced. Given the pressures and values which are placed upon groundwater resources, we need a greater understanding of the ecology of these systems.
- Climate change is liable to affect freshwater ecosystems in New Zealand to varying degrees (MfE 2001, 2000). Greater extremes of precipitation and drought in different areas of the country have the potential to alter hydrological regimes in braided rivers already subjected to water abstraction and flow modification. Studies are needed to determine the likely consequences of global warming and climate change on our braided river ecosystems.
- New Zealand has more relatively un-impacted braided river systems than many other developed nations. These provide us with an opportunity to contribute towards a greater international understanding of the ecological structure and function of braided rivers.

9. Conclusion

Studies of spatial diversity patterns in the braided upper Waimakariri River by Gray (2006) suggested that invertebrate communities reflect the high heterogeneity of floodplain habitats. In contrast to the restricted traditional view of braided rivers as species-depauperate 'ecological deserts', these rivers and their floodplain reaches in fact represent spatially complex, temporally dynamic systems with high landscape- and reach-scale biodiversity values. Living within and around this mosaic of aquatic habitats are a range of often rare and little-understood flora and fauna. A range of spatio-temporal factors appear to be important in regulating braided river invertebrate communities. In order to identify the specific influences of these various factors, it is necessary to consider rivers at the reach scale, where individual floodplain habitats may be important, as well as from a holistic perspective, where river catchments are viewed in their entirety.

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11. References

- Adkins, S.C.; Winterbourn, M.J. 1999: Vertical distribution and abundance of invertebrates in two New Zealand stream beds: a freeze coring study. *Hydrobiologia* 400: 55–62.
- Andrews, E.D. 1984: Bed-material entrainment and hydraulic geometry of gravel-bed rivers in Colorado. *Geological Society of America Bulletin* 95: 371–378.
- 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. 2003: Spatio-temporal patterns of benthic invertebrates along the continuum of a braided alpine river. *Archiv für Hydrobiologie* 158: 431–460.
- Arscott, D.B.; Tockner, K.; Ward, J.V. 2005: Lateral organization of aquatic invertebrates along the corridor of a braided river floodplain river. *Journal of the North American Benthological Society* 24: 934–954.
- Barquin, J. 2004: Spatial patterns of invertebrate communities in spring and run-off fed streams. Unpublished PhD thesis. Massey University, Palmerston North. 181 p.
- Begon, M.; Harper, J.L.; Townsend, C.R. 1996: Ecology, 3rd edition. Blackwell Science, London. 1068p.
- Benke, A.C. 1990: A Perspective on America's vanishing streams. *Journal of the North American Benthological Society* 9: 77–88.
- Biggs, B.J.F.; Close, M.E. 1989: Periphyton biomass dynamics in gravel bed rivers—the relative effects of flows and nutrients. *Freshwater Biology* 22: 209–231.
- Biggs, B.J.F.; Duncan, M.J.; Francoeur, N.; Meyer, W.D. 1997: Physical characterisation of microform bed cluster refugia in 12 headwater streams, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 31: 413–422.
- Biggs, B.J.F. 2000: Eutrophication of streams and rivers: dissolved nutrient-chlorophyll relationships for benthic algae. *Journal of the North American Benthological Society* 19: 17–31.
- Biggs, B.J.F.; Kilroy, C. 2004: Periphyton. Chapter 15 in Harding, J.S.; Mosley, P. M.; Pearson, C.; Sorrell, B. (Eds): Freshwaters of New Zealand. New Zealand Hydrological Society and New Zealand limnological Society, Christchurch.
- Blakely, T.; Harding, J.S. 2005: Longitudinal patterns in benthic communities in an urban stream restoration. *New Zealand Journal of Marine and Freshwater Research* 39: 17–28.
- 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.
- Boud, R.; Eldon, G.A.; Watson, R.C. 1959: Survey of the Glennariffe Stream, Rakaia Gorge. New Zealand Marine Department, Fisheries Advisory Service investigation report, job no. 18.
- Bowie, S. 2004: Bignose galaxias (*Galaxias macronasus*) survey in the Mackenzie Basin, Canterbury, New Zealand. Department of Conservation, Twizel.
- Bravard, J.P.; Gilvear, D.J. 1996: Hydrological and geomorphological structure of hydrosystems. Pp. 98–110 in Petts, G.; Amoros, C. (Eds): Fluvial Hydrosystems. Chapman and Hall, London.
- Brice, J.C. 1964: Channel patterns and terraces of the Loup River in Nebraska. *U.S. Geological Survey Professional Papers* 422-D: Pp. 1–41.
- Bridge, J.S. 1993: The interaction between channel geometry, water flow, sediment transport and deposition in braided rivers. Pp. 13–71 in Best, J.L.; Bristow, C.S. (Eds): Braided rivers. The Geological Society, Oxford.
- Browne, G. 2004: Downstream fining and sorting of gravel clasts in the braided rivers of mid-Canterbury, New Zealand. *New Zealand Geographer* 60: 2–14.

- 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.
- Brunke, M., Gonser, T. 1997: The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology* 37: 1-33.
- 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.
- Burrell, G.P. 2001: Hyporheic ecology of alluvial rivers in Canterbury, New Zealand. Unpublished PhD thesis, University of Canterbury, Christchurch. 109 p.
- Burrows, C.J. 1977: Riverbed Vegetation. Pp. 214-225 in Burrows, C.J. (Ed.): Cass: history and science in the Cass District, Canterbury, New Zealand. Department of Botany, University of Canterbury, Christchurch.
- Burton, J.P.; Fralick, P. 2003: Depositional placer accumulations in coarse-grained alluvial braided river systems. *Economic Geology and the Bulletin of the Society of Economic Geologists* 98: 985-1001.
- Caruso, B.S. 2006: Project river recovery: restoration of braided gravel-bed river habitat in New Zealand's high country. *Environmental Management* 37: 840-861.
- Chilton, C. 1894: The subterranean Crustacea of New Zealand with some general remarks upon the fauna of caves and wells. *Transactions of the Linnean Society of London: Second series (Zoology)* 6: 163-284.
- Collier, K.J.; Scarsbrook, M.R. 2000: Use of riparian and hyporheic habitats. Pp. 179-206 in Collier, K.J.; Winterbourn, M.J. (Eds): New Zealand stream invertebrates: ecology and implications for management. New Zealand Limnological Society, Christchurch.
- Cook, D.R. 1983: Rheophilic and hyporheic water mites of New Zealand. *Contributions of the American Entomological Institute* 21: 1-224.
- Cote, I.M., Vinyoles, D.; Reynolds, J.D.; Doadrio, I.; Perdices, A. 1999: Potential impacts of gravel extraction on Spanish populations of river blennies *Salaria fluviatilis* (Pisces, Blenniidae). *Biological Conservation* 87: 359-367.
- Cowie, B. 1980: Community dynamics of the benthic fauna in a West Coast stream ecosystem. Unpublished PhD thesis, University of Canterbury, Christchurch. 200 p.
- Cowx, I.G.; Young, W.O.; Hellawell, J.M. 1984: The influence of drought on the fish and invertebrate populations of an upland stream in Wales. *Freshwater Biology* 14: 165-177.
- Cullen, L.; Duncan, R.; Wells, A.; Stewart, G. 2003: Floodplain and regional scale variation in earthquake effects on forests, Westland, New Zealand. *Journal of the Royal Society of New Zealand* 33: 693-701.
- Datry, T. F.; Larned, S.T.; Scarsbrook, M.S. 2007: Responses of hyporheic invertebrate assemblages to large scale variation in flow permanence and surface-subsurface exchange. *Freshwater Biology* 52(8): 1452-1462.
- Davies-Colley, R.; Wilcock, B. 2004: Water quality and chemistry in running waters. Chapter 11 in Harding, J.S.; Mosley, P.M.; Pearson, C.; Sorrell, B. (Eds): Freshwaters of New Zealand. The New Zealand Hydrological Society and New Zealand Limnological Society, Christchurch.
- Death, R. 1991: Environmental stability: its effect on stream benthic communities. Unpublished PhD thesis, University of Canterbury, Christchurch. 317 p.
- Death, R.; Barquin, J.; Scarsbrook, M. 2004: Biota of cold water and geothermal springs. Chapter 30 in Harding, J.S.; Mosley, P.; Pearson, C.; Sorrell, B. (Eds): Freshwaters of New Zealand. New Zealand Hydrological Society and New Zealand Limnological Society, Christchurch.
- Death, R.; Winterbourn, M. 1994: Environmental stability and community persistence—a multivariate perspective. *Journal of the North American Benthological Society* 13: 125-139.
- Death, R.G.; Winterbourn, M.J. 1995: Diversity patterns in stream benthic invertebrate communities—the influence of habitat stability. *Ecology* 76: 1446-1460.

- Dewson, Z.S.; James, A.B.W.; Death, R.G. 2007: Invertebrate responses to short-term water abstraction in small New Zealand streams. *Freshwater Biology* 52: 357–369.
- Digby, B. 1999: Invertebrate production within various habitats of a braided river. Unpublished MSc thesis, University of Canterbury, Christchurch. 77 p.
- Dole-Olivier, M.J.; Marmonier, P.; Befly, J.L. 1997: Response of invertebrates to lotic disturbance: is the hyporheic zone a patchy refugium? *Freshwater Biology* 37: 257–276.
- Dynesius, M.; Nilsson, C. 1994: Fragmentation and flow regulation of river systems in the northern third of the World. *Science* 266: 753–762.
- Erskine, M.D., Green, D. 2000: Geomorphic effects of extractive industries and their implications for river management: the case of the Hawkesbury-Mepean River, New South Wales. Pp. 123–149 in Brizga, S.; Finlayson, B. (Eds): River management: the Australian experience. John Wiley and Sons, Chichester.
- Extence, C.A. 1981: The effect of drought on benthic invertebrate communities in a lowland river. *Hydrobiologia* 83: 217–224.
- Fenwick, G.D. 1987: Organic carbon pathways in the Canterbury groundwater ecosystem and the role of phreatic crustaceans. National Water and Soil Conservation Organisation, Ministry of Works and Development, Wellington. 87 p.
- Fenwick, G.D.; Thorpe, H.; White, P. 2004: Groundwater systems. Chapter 29 in Harding, J.S.; Mosley, P.; Pearson, C.; Sorrell, B. (Eds): Freshwaters of New Zealand. New Zealand Hydrological Society and New Zealand Limnological Society, Christchurch.
- Fowler, R.T. 2000: Linking hyporheic and benthic invertebrate communities in New Zealand gravel bed rivers. Unpublished PhD thesis. Massey University, Palmerston North.
- Fowler, R.T. 2004: The recovery of benthic invertebrate communities following dewatering in two braided rivers. *Hydrobiologia* 523: 17–28.
- Fowler, R.T.; Death, R.G. 2000: Effects of channel morphology on temporal variation in invertebrate community structure in two North Island, New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* 34: 231–240.
- Fowler, R.T.; Scarsbrook, M.R. 2002: Influence of hydrologic exchange patterns on water chemistry and hyporheic invertebrate communities in three gravel-bed rivers. *New Zealand Journal of Marine and Freshwater Research* 36: 471–482.
- Francoeur, S.N.; Biggs, B.J.F.; Lowe, R.L. 1998: Microform bed clusters as refugia for periphyton in a flood-prone headwater stream. *New Zealand Journal of Marine and Freshwater Research* 32: 363–374.
- Gage, M. 1977: Glacial geology. Pp. 67–78 in Burrows, C.J. (Ed.): Cass: history and science in the Cass district. Canterbury, New Zealand. Department of Botany, University of Canterbury, Christchurch.
- Garcialozano, L.C. 1990: The floodplains of the middle-lower Magdalena—habitats restoration and conservation. *Interciencia* 15: 396–410.
- Gayraud, S.; Philippe, M.; Maridet, L. 2000: The response of benthic macroinvertebrates to artificial disturbance: drift or vertical movement in the gravel bed of two sub-alpine streams? *Archiv Für Hydrobiologie* 147: 431–446.
- Geist, D.R.; Dauble, D.D. 1998: Redd site selection and spawning habitat use by fall chinook salmon: The importance of geomorphic features in large rivers. *Environmental Management* 22: 655–669.
- Gibbs, G. 2006: Ghosts of Gondwana: the history of life in New Zealand. Craig Potton publishing, Nelson. 232 p.
- Gibert, J.; Stanford, J.A.; Dole-Olivier, M.J.; Ward, J.V. 1994: Basic attributes of groundwater ecosystems and prospects for research. Pp. 1–42 in Gibert, J.; Danielopol, D.L.; Stanford, J.A. (Eds): Groundwater ecology. Academic Press, London.
- Gippel, C.J., Finlayson, B.L.; O’neill, I.C. 1996: Distribution and hydraulic significance of large woody debris in a lowland Australian river. *Hydrobiologia* 318: 179–194.

- Glazier, D. 1991: The fauna of North American temperate cold springs—patterns and hypotheses. *Freshwater Biology* 26: 527-542.
- Goff, J.; McFadgen, B. 2002: Seismic driving of nationwide changes in geomorphology and prehistoric settlement—a 15th century New Zealand example. *Quaternary Science Reviews* 21: 2229-2236.
- Goodwin, C.N. 1996: Channel widening and bank erosion processes on a cobble-bed river. *Geological Society of America Abstracts Programs* 28: 262.
- Gore, J.A. 1977: Reservoir manipulations and benthic macroinvertebrates in a prairie river. *Hydrobiologia* 55: 113-123.
- Gopal, B.; Sah, M. 1993: Conservation and management of rivers in India—case study of the River Yamuna. *Environmental Conservation* 20: 243-254.
- Grant, P.J. 1977: Water temperatures of the Ngaruroro River at three stations. *Journal of Hydrology (New Zealand)* 16: 148-157.
- 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.; 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.
- Graf, W.L. 1978: Fluvial adjustments to spread of tamarisk in Colorado Plateau Region. *Geological Society of America Bulletin* 89: 1491-1501.
- Graf, W.L. 2006: Downstream hydrologic and geomorphic effects of large dams on American rivers. *Geomorphology* 79: 336-360.
- Gran, K.; Paola, C. 2001: Riparian vegetation controls on braided stream dynamics. *Water Resources Research* 37: 3275-3283.
- Greenwood, M.J.; McIntosh, A.R. 2004: Influence of environmental conditions on nymphal development and abundance of *Deleatidium fumosum* mayflies. *New Zealand Natural Sciences* 29: 55-66.
- Griffiths, G.A. 1979: High sediment yields from major rivers of the western Southern Alps, New Zealand. *Nature* 282: 61-63.
- Gurnell, A.M.; Petts, G.E.; Hannah, D.M.; Smith, B.P.G.; Edwards, P.J.; Kollmann, J.; Ward, J.V.; Tockner, K. 2000a: Wood storage within the active zone of a large European gravel-bed river. *Geomorphology* 34: 55-72.
- Gurnell, A.M.; Petts, G.E.; Harris, N.; Ward, J.V.; Tockner, K.; Edwards, P.J.; Kollmann, J. 2000b: Large wood retention in river channels: The case of the Fiume Tagliamento, Italy. *Earth Surface Processes and Landforms* 25: 255-275.
- Gurnell, A.M.; Piegay, H.; Swanson, F.J.; Gregory, S.V. 2002: Large wood and fluvial processes. *Freshwater Biology* 47: 601-619.
- Habit, E.; Belk, M.C.; Tuckfield, R.C.; Parra, O. 2006: Response of the fish community to human-induced changes in the Biobio River in Chile. *Freshwater Biology* 51: 1-11.
- Hancock, P.J. 2002: Human impacts on the stream-groundwater exchange zone. *Environmental Management* 29: 763-781.
- Hansen, A.J.; di Castri, F. 1992: Landscape boundaries. Springer, New York. 432 p.
- Harding, J.S. 1992a: Discontinuities in the distribution of invertebrates in impounded South Island rivers, New Zealand. *Regulated Rivers-Research & Management* 7: 327-335.
- Harding, J.S. 1992b: Physicochemical parameters and invertebrate faunas of three lake inflows and outlets in Westland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 26: 95-102.
- Harding, J.S.; Winterbourn, M.J. 1997: An ecoregion classification of the South Island, New Zealand. *Journal of Environmental Management* 51: 275-287.
- Harper, M.P.; Peckarsky, B.L. 2006: Emergence cues of a mayfly in a high-altitude stream ecosystem: Potential response to climate change. *Ecological Applications* 16: 612-621.

- 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.
- Henriques, P.R. 1987: Aquatic biology and hydroelectric power development in New Zealand. Oxford University Press, Auckland. 280 p.
- Hey, R.D.; Thorne, C.R. 1986: Stable Channels with Mobile Gravel Beds. *Journal of Hydraulic Engineering-Asce* 112: 671–689.
- Hicks, M.D.; Duncan, M.J.; Lane, S.N.; Tal, M.; Westaway, R. in press: Contemporary morphological change in braided gravel-bed rivers: new developments from field and laboratory studies, with particular reference to the influence of riparian vegetation. Chapter 21 in Habersack, H.; Piegay, H.; Rinaldi, M. (Eds): Gravel-bed Rivers VI: from process understanding to river restoration, Elsevier.
- Hicks, D.M.; Quinn, J.; Trustrum, N. 2004: Stream sediment load and organic matter. Chapter 12 in Harding, J.S.; Mosley, P.M.; Pearson, P.; Sorrell, B. (Eds): Freshwaters of New Zealand. New Zealand Hydrological Society and New Zealand Limnological Society, Christchurch.
- Hicks, M.; Westaway, R; Lane, S. 2003: A birds eye view of gravel movement in large braided rivers. *Water and Atmosphere* 11(1): 21–23.
- Hirsch, A. 1958: Biological evaluation of organic pollution in New Zealand streams. *New Zealand Journal of Science* 1: 500–553.
- Hoffsten, P.O.; Malmqvist, B. 2000: The macroinvertebrate fauna and hydrogeology of springs in central Sweden. *Hydrobiologia* 436: 91–104.
- 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.
- Holomuzki, J.; Biggs, B.J.F. 2000: Taxon-specific responses to high-flow disturbance in streams: implications for population persistence. *Journal of the North American Benthological Society* 19: 670–679.
- Huang, H.Q.; Nanson, G.C. 1997: Vegetation and channel variation: a case study of four small streams in south-eastern Australia. *Geomorphology* 18: 237–249.
- Hughey, K.F.D.; Fraser, B.R.; Hudson, L.G. 1989: Aquatic invertebrates in two Canterbury braided rivers related to bird feeding and water development impacts. *Science and Research Series* 12. Department of Conservation, Wellington. 65 p.
- Hurn, A.D. 1996: An appraisal of the Allen paradox in a New Zealand trout stream. *Limnology and Oceanography* 41: 243–252.
- Hynes, H.B.N. 1958: The effect of drought on the fauna of a small mountain stream in Wales. *Internationale vereinigung für theoretische und angewandte limnologie* 13: 826–833.
- Iversen, T.M.; Wilberg-Larsen, P.; Hansen, S.B.; Hansen, F.S. 1978: The effect of partial and total drought on the macroinvertebrate communities of three small Danish streams. *Hydrobiologia* 60: 235–242.
- Kamp, P.J.J. 1992: Tectonic architecture of New Zealand. Pp. 1–30 in Soons, J.M.; Selby, M.J. (Eds): Landforms of New Zealand. 2nd edition. Longman Paul Limited, Auckland.
- Karaus, U. 2004: The ecology of lateral aquatic habitats along river corridors: Unpublished Ph.D thesis, Swiss Federal Institute of Technology, Zurich. 179 p.
- Karaus, U.; Alder, L.; Tockner, K. 2005: 'Concave islands': habitat heterogeneity of parafluvial ponds in a gravel-bed river. *Wetlands* 25: 26–37.
- Kerr, L.C.; Craw, D.; Norris, R.J.; Youngson, J.H.; Wopereis, P. 2000: Structure, geomorphology, and gold concentration in the Nokomai Valley, Southland, New Zealand. *New Zealand Journal of Geology and Geophysics* 43: 425–433.
- Kilroy, C.; Scarsbrook, M.R.; Fenwick, G. 2004: Dimensions in biodiversity of a braided river. *Water and Atmosphere* 12: 10–11.

- Kondolf, G.M. 1994: Environmental planning in regulation and management of in-stream gravel mining in California. *Landscape and Urban Planning* 28: 225-243.
- Korup, O. 2004: Landslide-induced river channel avulsions in mountain catchments of southwest New Zealand. *Geomorphology* 63: 57-80.
- Kownacki, A. 1985: Spring benthic macroinvertebrate communities of selected streams in the High Caucasus (Azerbaijan SSR). *Hydrobiologia* 123: 137-144.
- Lachavanne, J.B.; Juge, R. 1997: Biodiversity in land-inland water ecotones. Parthenon, Pearl River, New York. 326 p.
- Lane, E.W. 1957: A study of the shape of channels formed by natural streams flowing in erodable material. *MRD Sediment Series Report No. 9*. United States Army Engineers Division, Corps of Engineers, Omaha, Nebraska. 38 p.
- Lane, S.N.; Westaway, R.M.; Hicks, D.M. 2003: Estimation of erosion and deposition volumes in a large, gravel-bed, braided river using synoptic remote sensing. *Earth Surface Processes and Landforms* 28: 249-271.
- Laperriere, J.D. 1994: Benthic ecology of a spring-fed river of interior Alaska. *Freshwater Biology* 32: 349-357.
- 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.
- Leopold, L.B.; Wolman, M.G. 1957: River channel patterns: braiding, meandering and straight. *U.S. Geological Survey Professional Papers* 262b: 39-85.
- Loomis, J.B.; Walsh, R.G. 1986: Assessing wildlife and environmental values in cost-benefit analysis: state-of-the-art. *Journal of Environmental Management* 22: 125-131.
- Mackin, J.H. 1956: Cause of braiding by a graded river. *Geological Society of America Bulletin* 67: 1717-1718.
- Malard, F.; Uehlinger, U.; Zah, R.; Tockner, K. 2006: Flood-pulse and riverscape Dynamics in a braided glacial river. *Ecology* 87: 704-716.
- Malmquist, B. 1991: Invertebrate colonization of a new, man made stream in southern Sweden. *Freshwater Biology* 26: 307-324.
- Malmqvist, B.; Rundle, S. 2002: Threats to the running water ecosystems of the world. *Environmental Conservation* 29: 134-153.
- Maloney, R.F.; Rebergen, A.L.; Nilsson, R.J.; Wells, N.J. 1997: Bird density and diversity in braided river beds in the Upper Waitaki Basin, South Island, New Zealand. *Notornis* 44: 219-232.
- Marshall, J.W. 1973: A benthic study of the Avon spring stream, Christchurch. *Mauri Ora* 1: 79-90.
- Matthaei, C.D.; Arbuckle, C.J.; Townsend, C.R. 2000: Stable surface stones as refugia for invertebrates during disturbance in a New Zealand stream. *Journal of the North American Benthological Society* 19: 82-93.
- Matthaei, C.D.; Townsend, C.R. 2000a. Inundated floodplain gravels in a stream with an unstable bed: temporary shelter or true invertebrate refugium? *New Zealand Journal of Marine and Freshwater Research* 34: 147-156.
- Matthaei, C.D.; Townsend, C.R. 2000b: Long-term effects of local disturbance history on mobile stream invertebrates. *Oecologia* 125: 119-126.
- McDowall, R.M. 1984: The New Zealand whitebait book. Reed, Wellington. 210 p.
- McDowall, R.M. 1990a: The human impact. Pp. 472-505 in New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland.
- McDowall, R.M. 1990b: Modern fisheries. Pp. 424-459 in New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland.
- McDowall, R.M. 1990c: Traditional Maori fisheries. Pp. 408-423 in New Zealand freshwater fishes: a natural history and guide Heinemann Reed, Auckland, New Zealand.

- McDowall, R.M. 2000: The Reed field guide to New Zealand freshwater fishes. Reed, Auckland. 224p.
- Meridian Energy 2003: Project Aqua: assessment of effects on the environment.
- McLellan, I.D. 1984: A revision of *Spaniocercooides* Kimmins (Plecoptera: Notonemouridae), and descriptions of new species. *New Zealand Journal of Zoology* 11: 167-178.
- McSaveney, M.J.; Davies, T.R.H. 1998: Natural hazard assessment for the township of Franz Josef Glacier and its environs. Institute of Geological and Nuclear Sciences Limited client report, 44714b.10. Unpublished. 52 p.
- MfE (Ministry for the Environment) 2001: Climate change: impacts on New Zealand. 4 p.
- MfE (Ministry for the Environment) 2000: National science strategy committee for climate change, annual report. 58 p.
- Michaelis, F. 1974: The ecology of Waikoropupu Springs. Unpublished PhD thesis, University of Canterbury, Christchurch. 158 p.
- Miller, C. 2002: Conservation of riparian forest remnants, West Coast, New Zealand. *Landscape Research* 27: 125-140.
- Miller, C.J. 2006: Vegetation on the edge: a gradient analysis of the riparian zone, Poerua River, New Zealand. *New Zealand Journal of Ecology* 30(3): 357-370.
- Millar, R.G. 2000: Influence of bank vegetation on alluvial channel patterns. *Water Resources Research* 36: 1109-1118.
- Minshall, G. 1968: Community dynamics of the benthic fauna in a woodland spring brook. *Hydrobiologia* 32: 305-339.
- Mosisch, T.D. 2001: Effects of desiccation on stream epilithic algae. *New Zealand Journal of Marine and Freshwater Research* 35: 173-179.
- Mosley, P. 1982a: Analysis of the effect of changing discharge on the channel morphology and instream uses in a braided river, Ohau River, New Zealand. *Water Resources Research* 18: 800-812.
- Mosley, P.M. 1982b: New Zealand river temperature regimes. *Water and Soil Miscellaneous Publication* 36. Ministry of Works and Development, Wellington. 37 p.
- Mosley, P. 1983a: Response of braided rivers to changing discharge. *Journal of Hydrology (New Zealand)* 22: 18-67.
- Mosley, P.M. 1983b: Variability of water temperatures in the braided Ashley and Rakaia rivers. *New Zealand Journal of Marine and Freshwater Research* 17: 331-342.
- Mosley, P.M.; Duncan, M.J. 1991: Rivers. Pp. 91-106 in Soons, J.M.; Selby, M.J. (Eds): Landforms of New Zealand, 2nd edition. Longman Paul Limited, Auckland.
- Mosley, P.M. 2001: Gravel-bed rivers V. The New Zealand Hydrological Society, Christchurch.
- Mosley, P.M. 2004: Rivers and the riverscape. Pp. 8.1-8.18 in Harding, J.S.; Mosley, P.M.; Pearson, C.; Sorrell, B. (Eds): Freshwaters of New Zealand. New Zealand Hydrological Society and New Zealand Limnological Society, Christchurch.
- Muhar, S.; Schwarz, M.; Schmutz, S.; Jungwirth, M. 2000: Identification of rivers with high and good habitat quality: methodological approach and applications in Austria. *Hydrobiologia* 422: 343-358.
- Muller, U.C.; Kukla, G.J. 2004: North Atlantic current and European environments during the declining stage of the last interglacial. *Geology* 32: 1009-1012.
- NCCB (North Canterbury Catchment Board) 1983: The Rakaia River and catchment—a resource survey. 4 Volumes.
- NCCB (North Canterbury Catchment Board) 1986: Waimakariri River and catchment resource survey. 4 Volumes.

- NCCB (North Canterbury Catchment Board) 1991: Draft Waimakariri River floodplain management plan. North Canterbury catchment board and regional water board. Christchurch, New Zealand.
- Nevins, T.H.F. 1969: River training—the single thread channel. *New Zealand Engineering*: 367–373.
- Nilsson, C.; Reidy, C.A.; Dynesius, M.; Revenga, C. 2005: Fragmentation and flow regulation of the world's large river systems. *Science* 308: 405–408.
- O'Donnell, C.J.F.; Moore, S.M. 1983: The wildlife and conservation of braided river systems in Canterbury. Fauna Survey Unit Report 33. Wildlife Service, Department of Internal Affairs, Wellington. 73 p.
- Olsen, D.A.; Townsend, C.R. 2003: Hyporheic community composition in a gravel-bed stream: influence of vertical hydrological exchange, sediment structure and physico-chemistry. *Freshwater Biology* 48: 1363–1378.
- Olsen, D.A.; Townsend, C.R.; Matthaei, C.D. 2001: Influence of reach geomorphology on hyporheic communities in a gravel-bed stream. *New Zealand Journal of Marine and Freshwater Research* 35: 181–190.
- Peat, N.; Patrick, B. 2001: Wild rivers: discovering the natural history of the Central South Island. University of Otago Press, Dunedin. 144 p.
- 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*: 48p.
- Percival, E. 1945: The genus *Prorhynchus* in New Zealand. *Transactions of the Royal Society of New Zealand* 75: 33–41.
- Pierce, R.J. 1979: Foods and feeding of the wrybill (*Anarhynchus frontalis*) on its river bed feeding grounds. *Notornis* 26: 1–21.
- Pierce, R.J. 1983: The charadriiforms of a high-country river valley. *Notornis* 30: 169–185.
- Pillans, B.; Pullar, W.A.; Selby, M.J.; Soons, J.M. 1992: The age and development of the New Zealand landscape. Pp. 31–43 in Selby, M.J.; Soons, J.M. (Eds): Landforms of New Zealand. 2nd edition. Longman Paul limited, Auckland.
- Poff, N.L.; Olden, J.D.; Merritt, D.M.; Pepin, D.M. 2007: Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the United States of America* 104: 5732–5737.
- 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 modelling surface and subsurface hydrology in complex flood-plain environments. *Earth Surface Processes and Landforms* 29: 1259–1274.
- Pringle, C.M.; Freeman, M.C.; Freeman, B.J. 2000: Regional effects of hydrologic alterations on riverine macro biota in the New World: tropical-temperate comparisons. *Bioscience* 50: 807–823.
- Quinn, J.M.; Hickey, C.W. 1990: Characterisation and classification of benthic invertebrate communities in 88 New Zealand rivers in relation to environmental factors. *New Zealand Journal of Marine and Freshwater Research* 24: 387–409.
- Raven, P.J.; Holmes, N.T.H.; Dawson, F.H.; Everard, M. 1998: Quality assessment using river habitat survey data. *Aquatic Conservation—Marine and Freshwater Ecosystems* 8: 477–499.
- Reinfelds, I.; Nanson, G. 1993: Formation of braided river floodplains, Waimakariri River, New Zealand. *Sedimentology* 40: 1113–1127.
- Rinaldi, M.; Wyzga, B.; Surian, N. 2005: Sediment mining in alluvial channels: Physical effects and management perspectives. *River Research and Applications* 21: 805–828.

- Rosen, M.R. 2001: Hydrochemistry of New Zealand's aquifers. Pp. 77-110 in Rosen, M.R.; White, O.W. (Eds): Groundwaters of New Zealand. New Zealand Hydrological Society, Christchurch, New Zealand.
- Rosenberg, D.M.; McCully, P.; Pringle, C.M. 2000: Global-scale environmental effects of hydrological alterations: introduction. *Bioscience* 50: 746-751.
- Rounick, J.S.; Winterbourn, M.J. 1982: Benthic faunas of forested streams and suggestions for their management. *New Zealand Journal of Ecology* 5: 140-150.
- Rounick, J.S.; Winterbourn, M.J. 1983: The formation, structure and utilization of stone surface organic layers in two New Zealand streams. *Freshwater Biology* 13: 57-65.
- Rowntree, K.M.; Dollar, E.S.J. 1999: Vegetation controls on channel stability in the Bell River, Eastern Cape, South Africa. *Earth Surface Processes and Landforms* 24: 127-134.
- Rundle, S. 1985: Braid morphology and the formation of multiple channels. *Zeit. Geomorph. N.F. Suppl.-Bd* 55: 15-37.
- Sagar, P.M. 1983: Invertebrate recolonisation of previously dry channels in the Rakaia River. *New Zealand Journal of Marine and Freshwater Research* 17: 377-386.
- 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.; Eldon, G.A. 1983: Food and feeding of small fish in the Rakaia River, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 17: 213-226.
- Sagar, P.M.; Glova, G.J. 1992: Invertebrate drift in a large, braided New Zealand river. *Freshwater Biology* 27: 405-416.
- Sambrook Smith, G.; Best, J.L.; Bristow, C.S.; Petts, G.E. 2006: Braided rivers: process, deposits, ecology and management. Blackwell Publishers. 390 p.
- Scarsbrook, M.R.; Townsend, C.R. 1993: Stream community structure in relation to spatial and temporal variation—a habitat template study of two contrasting New Zealand streams. *Freshwater Biology* 29: 395-410.
- Scarsbrook, M.R. 1995: Disturbance and spatial refugia in stream communities. Unpublished PhD thesis. The University of Otago, Dunedin. 197 p.
- Scarsbrook, M.R. 2002: Persistence and stability of lotic invertebrate communities in New Zealand. *Freshwater Biology* 47: 417-431.
- Scarsbrook, M.R.; Barquin, J.; Gray, D.P. 2007: New Zealand coldwater springs and their biodiversity. *Science for Conservation* 278, Department of Conservation, Wellington. 69 p.
- Scarsbrook, M.R.; Fenwick, G.D. 2003: Preliminary assessment of crustacean distribution patterns in New Zealand groundwater aquifers. *New Zealand Journal of Marine and Freshwater Research* 37: 405-413.
- 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. NIWA, Wellington. 59 p.
- Schumm, S.A. 2005: River variability and complexity. Cambridge University Press, Cambridge. 234 p.
- Scrimgeour, G.J.; Davidson, R.J.; Davidson, J.M. 1988: Recovery of benthic macroinvertebrate and epilithic communities following a large flood, in an unstable, braided New Zealand river. *New Zealand Journal of Marine and Freshwater Research* 22: 337-344.
- 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.
- Sinton, L.W. 1984: The macroinvertebrates in a sewage polluted aquifer. *Hydrobiologia* 119: 161-169.
- Smith, L.N. 2004: Late Pleistocene stratigraphy and implications for de-glaciation and sub-glacial processes of the Flathead Lobe of the Cordilleran Ice Sheet, Flathead Valley, Montana, USA. *Sedimentary Geology* 165: 295-332.

- Snelder, T.; Biggs, B.; Weatherhead, M. 2004: New Zealand river environment classification. National Institute of Water and Atmospheric science. Christchurch, New Zealand.
- 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.
- Stevens, G.R. 1981: New Zealand adrift: the theory of plate tectonics in a New Zealand setting. Reed, Wellington. 442 p.
- Storey, R.; Quinn, J. 2007: When rivers run dry: invertebrate communities in intermittent streams *Water and Atmosphere* 15: 16–17.
- Suren, A. 1991: Bryophytes as invertebrate habitat in two New Zealand alpine streams. *Freshwater Biology* 26: 399–418.
- Suren, A.M.; Jowett, I.G. 2006: Effects of floods versus low flows on invertebrates in a New Zealand gravel-bed river. *Freshwater Biology* 51: 2207–2227.
- Thomas, J.D. 1993: Biological monitoring and tropical diversity in marine environments: a critique with recommendations, and comments on the use of bio-indicators. *Journal of Natural History* 27: 795–806.
- Thoms, M.C.; Southwell, M.; McGinness, H.M. 2005: Floodplain-river ecosystems: fragmentation and water resources development. *Geomorphology* 71: 126–138.
- Tockner, K.; Stanford, J.A. 2002: Riverine flood plains: present state and future trends. *Environmental Conservation* 29: 308–330.
- Tockner, K.; Ward, J.V.; Arscott, D.B.; Edwards, P.J.; Kollmann, J.; Gurnell, A.M.; Petts, G.E.; Maiolini, B. 2003: The Tagliamento River: a model ecosystem of European importance. *Aquatic Sciences* 65: 239–253.
- Townsend, C.R. 1989: The Patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* 8: 36–50.
- Townsend, C.R.; Crowl, T.A. 1991: Fragmented population structure in a native New-Zealand fish—an effect of introduced brown trout. *Oikos* 61: 347–354.
- Van der Nat, D.; Tockner, K.; Edwards, P.J.; Ward, J.V. 2003: Large wood dynamics of complex alpine river floodplains. *Journal of the North American Benthological Society* 22: 35–50.
- 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.
- Wang, S.J.; Chen, Z.Y.; Smith, D.G. 2005: Anastomosing river system along the subsiding middle Yangtze River basin, southern China. *Catena* 60: 147–163.
- Warburton, J.; Davies, T.R.H.; Mandle, M.G.A 1993: Meso-scale field investigation of channel change and floodplain characteristics in an upland braided gravel-bed river, New Zealand. Chapter 15 in Best, J.L.; Bristow, C.S. (Eds): Braided rivers. Geological Society. Special publication No. 75.
- Ward, J.V.; Dufford, R.G. 1979: Longitudinal and seasonal distribution of macro-invertebrates and epilithic algae in a Colorado springbrook-pond system. *Archiv Für Hydrobiologie* 86: 284–321.
- Ward, J.V.; Malard, F.; Tockner, K.; Uehlinger, U. 1999a: Influence of ground water on surface water conditions in a glacial flood plain of the Swiss Alps. *Hydrological Processes* 13: 277–293.
- Ward, J.V.; Stanford, J.A. 1995: Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers—Research and Management* 11: 105–119.
- Ward, J.V.; Tockner, K.; Schiemer, F. 1999b: Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers—Research and Management* 15: 125–139.
- Westaway, R.M.; Lane, S.N.; Hicks, D.M. 2003: Remote survey of large-scale braided, gravel-bed rivers using digital photogrammetry and image analysis. *International Journal of Remote Sensing* 24: 795–815.

- White, D.S. 1993: Perspectives on defining and delineating hyporheic zones. *Journal of the North American Benthological Society* 12: 61–69.
- White, P.A.; Clausen, B.; Hunt, B.; Cameron, S.; Weir, S.J. 2001: Groundwater-surface water interaction. Pp. 133–160 in Rosen, M.R.; White, P.A. (Eds): Groundwaters of New Zealand. New Zealand Hydrological Society, Christchurch, New Zealand.
- Whited, D.C.; Lorang, M.S.; Harner, M.J.; Hauer, F.R.; Kimball, J.S.; Stanford, J.A. 2007: Climate, hydrologic disturbance, and succession: Drivers of floodplain pattern. *Ecology* 88: 940–953.
- Williams, D.D.; Hynes, H.B.N. 1976: The recolonization mechanisms of stream benthos. *Oikos* 27: 265–272.
- Wilson, G. 2001: National distribution of braided rivers and the extent of vegetation colonisation. Landcare Research Contract Report No. LC0001/068 (unpublished). Hamilton.
- 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. 1974: The life histories, trophic relations and production of *Stenoperla prasina* (plecoptera) and *Deleatidium* sp. (Ephemeroptera) in a New Zealand river. *Freshwater Biology* 4: 507–524.
- Winterbourn, M.J. 1997: New Zealand mountain stream communities: stable yet disturbed. Pp. 31–54 in Streit, B.; Stadler, T.; Lively, C.M. (Eds): Evolutionary ecology of freshwater animals: concepts and case studies. Birkhäuser verlag, Basel.
- Winterbourn, M.J.; Alderton, P.; Hunter, G.G. 1971: A biological evaluation of organic pollution in the lower Waimakariri River system 1970–71. *New Zealand Marine Department Fisheries Technical Report No. 67*. Wellington. 69 p.
- Winterbourn, M.J.; Gregson, K.L.D.; Dolphin, C.H. 2006: Guide to the aquatic insects of New Zealand. 4th edition. *Bulletin of the Entomological Society of New Zealand* 14. 108 p.
- Winterbourn, M.J.; Rounick, J.S.; Cowie, B. 1981: Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research* 15: 321–328.
- 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.S.; Mosley, P.; Pearson, C.; Sorrell, B. (Eds): Freshwaters of New Zealand. New Zealand Hydrological Society and New Zealand Limnological Society, Christchurch.
- Zollhoefer, J.M.; Brunke, M.; Gonser, T. 2000: A typology of springs in Switzerland by integrating habitat variables and fauna. *Archiv Für Hydrobiologie* 121: 349–376.

Appendix 1

STUDIES INCLUDED IN THE META ANALYSIS OF BRAIDED RIVER MAIN CHANNEL INVERTEBRATE COMMUNITIES

AUTHOR(S)	SOURCE OF FLOW	RIVER(S)	COUNTRY	SEASON	SAMPLER MESH SIZE (µm)	TAXONOMIC RICHNESS	MEAN ABUNDANCE (INDIVIDUALS/m ²)
Hirsch 1958	Alpine	Lower Waikariri	NZ	winter + autumn		10 total	796
Sagar 1986	Alpine	Lower Rakaia	NZ	winter + autumn	530	33 total	1289
Sagar & Eldon 1983)	Alpine	Lower Rakaia	NZ	winter + summer	530	22 total	2117
Matthaei & Townsend 2000a	Foot hill	Kye Burn	NZ	spring	250	13 mean	4855
Fowler 2004	Foot hill	Tukituki and Waipawa	NZ	summer	300	26 total	5500
Fowler & Scarsbrook 2002	Foot hill	Makaretu	NZ	autumn	300	11 mean	2600
Scrimgeour et al. 1988	Foot hill	Ashley River/Rakahuri	NZ	winter + spring	250	21 max	4070
Matthaei et al. 2000	Foot hill	Kye Burn	NZ	summer	250	12 mean	533
Scarsbrook & Townsend 1993	Foot hill	Timber Creek	NZ		300	16 mean	5330
Fowler & Death 2000	Foot hill	Waipawa	NZ		300	10.4 mean	400
Winterbourn et al. 1971	Alpine	Waikariri	NZ	summer	500	8 max	480
Sagar & Eldon 1983	Alpine	Rakaia	NZ	all year	500	18 max	1798
Sagar & Glova 1992	Alpine	Rakaia	NZ	all year	350	25 total	1630
Pierce 1979	Alpine	Cass	NZ	all year	500	13 total	774
Pierce 1983	Alpine	Rakaia	NZ	all year	500	5	101
Death 1991	Foot hill	Kowai	NZ	all year	250	62 total	
Death 1991	Alpine	Bruce Stream	NZ	all year	250	42 total	
Scrimgeour & Winterbourn 1989	Foot hill	Ashley River/Rakahuri	NZ	all year	250	60	11 000
Digby 1999	Alpine	Rakaia	NZ		200	39	
Burgherr et al. 2002	Alpine	Roseg	Switzerland	all year	100		7575
Brunke 2002	Alpine	Brenno	Switzerland		300	34 max	
Brunke 2002	Alpine	Lesgiuna	Switzerland		300	24 max	
Ward et al. 1999a	Alpine	Roseg	Switzerland				22840
Arcott et al. 2003	Alpine	Tagliamento	Italy	all year	100	51 mean	165 758
Arcott et al. 2005	Alpine	Tagliamento	Italy		100	63 mean	40 543

Appendix 2

STUDIES INCLUDED IN THE ANALYSIS OF BRAIDED RIVER SPRING INVERTEBRATE COMMUNITIES

AUTHOR(S)	CATCHMENT	COUNTRY	SEASON	MESH SIZE (μm)	TOTAL TAXA FOUND	ABUNDANCE (INDIVIDUALS/m ²)
Boud et al. 1959	Glenariffe	NZ	Summer			2618
Barquin 2004	Hawdon valley	NZ	summer	250	50	750
Barquin 2004	Hawdon valley	NZ		250	75	7000
Digby 1999	Rakaia River	NZ				
Death 1991	Waimakariri basin	NZ		250	45	11000
Gray 2005	Waimakariri basin	NZ	All year	250	79	
Gray et al 2006	Waimakariri basin	NZ	All year	251	81	
Burgherr et al. 2002	Roseg River	Switzerland				10000
Ward et al. 1999a	Roseg River	Switzerland				76430
Arscott et al. 2005	Tagliamento River	Italy		100	29	15377
Laperriere 1994	Gerstle, Tanana and Delta Rivers	Alaska		1000	14	1000
Hoffsten & Malmqvist 2000	Various	Sweden	Summer and autumn	500	16	
Kownacki 1985	Various	Azerbaijan			25	
Zollhoefer et al. 2000	Various	Switzerland		600	81	

Ecology of braided rivers—a literature review

This review summarises the New Zealand and international literature on braided rivers, with particular emphasis on our understanding of the diversity and structure of aquatic invertebrate communities in these ecosystems. The introductory section defines braided rivers and describes their location and condition. The review then considers the physical characteristics and ecological patterns of the floodplain habitats typically found within braided rivers. The biotic communities of typical floodplain habitats are presented. Finally, the threats, management issues and research gaps associated with braided rivers in New Zealand are discussed.

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