

# Braided river ecology

A literature review of physical habitats and aquatic invertebrate communities

SCIENCE FOR CONSERVATION 279



Department of Conservation  
*Te Papa Atawhai*

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## A literature review of physical habitats and aquatic invertebrate communities

Duncan Gray and Jon S. Harding

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Cover: The upper Clyde River, Canterbury, during autumnal low flows. Looking southeast towards Erewhon Station, with Watchdog Peak at the right.

*Photo: Duncan Gray.*

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# Braided river ecology

## A literature review of physical habitats and aquatic invertebrate communities

Duncan Gray and Jon S. Harding

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### ABSTRACT

A braided river is one that, over some part of its length, flows in multiple, mobile channels across a gravel floodplain. In New Zealand, many braided rivers remain in a relatively unmodified condition, but increasing demands for hydro-electricity generation, irrigation, gravel extraction and flood protection works are placing pressure on these systems. However, apart from a limited number of studies on the ecology of individual species or reaches, there has been little coordinated ecological research to assess the overall values and function of braided river ecosystems in New Zealand. This review summarises the international and New Zealand literature on braided rivers, with particular emphasis on benthic invertebrate ecology. Braided rivers typically experience short-term channel migration within the active bed and greater lateral channel migration across the entire floodplain in the longer term. Channel migration occurs because steep headwater tributaries supply highly variable discharges and mobile erodible substrates to the mainstem. Braided rivers typically possess extended floodplains, which may contain a mosaic of floodplain habitats ranging from highly unstable main-stem channels to stable spring complexes. Main channel aquatic invertebrate communities are frequently low in diversity and dominated by the leptophlebiid mayfly *Deleatidium* spp., but also chironomids and elmids. In contrast, floodplain springs can have highly diverse communities rich in amphipods, mayflies, caddis, snails and chironomids. Groundwater and floodplain pond habitats also occur frequently and can contain several specialist taxa. Braided rivers and their floodplains are spatially complex, temporally dynamic habitats with high landscape- and reach-scale biodiversity values. The challenge facing managers is to protect this biodiversity within the context of increasing human demands on the rivers. This report highlights the particular threats and management issues associated with braided rivers in New Zealand and identifies areas where future research is required.

Keywords: Braided rivers, benthic invertebrates, geomorphology, springs, diversity, groundwater

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# 1. Introduction

## 1.1 THE SCOPE OF THIS REVIEW

The aim of this review is to summarise the literature available on braided rivers in New Zealand and overseas, 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 the location and condition of braided rivers. The review then considers the habitat template<sup>1</sup> and the physical characteristics of the floodplain habitats typically found within braided rivers, and the ecological patterns generated by this template. 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.

## 1.2 DEFINITION OF A BRAIDED RIVER

A number of definitions have been suggested to describe braided rivers. Most focus on the physical characteristics associated with multiple surface-flowing channels. For example:

‘Braided rivers are characterised by having a number of alluvial channels with bars and islands between meeting and dividing again, and presenting from the air the intertwining effect of a braid.’ (Lane 1957).

‘A braided river is one which flows in two or more channels around alluvial islands.’ (Leopold and & Wolman 1957).’

Historically, braided rivers have been described on the basis of the physical characteristics of the river reach under consideration. Leopold & Wolman (1957) suggested that numerous channel types can be identified within rivers, including braided, meandering and straight channels. One channel type may often be found within another such that further attempts at classification of the entire channel reach become difficult. Reinfelds & Nanson (1993) described a ‘braided river floodplain’ as a generally extensive, vegetated and horizontally bedded alluvial landform, sometimes composed of a mosaic of units at various stages of development, formed by the present regime of the river, occurring within or adjacent to the un-vegetated active river bed and periodically inundated by over-bank flow.

For the purpose of this review we define a braided river as one that at some point in its length flows in multiple, mobile channels across a gravel floodplain. There must be evidence of recent channel migration within the active bed of the river and of historical movements of the active bed across the floodplain. The lateral and vertical limits of the ‘river’ include the entire width of the floodplain and the saturated depths of the alluvial aquifer, within and across which the river moves as a single body of water.

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<sup>1</sup> The habitat template is the physical mosaic of habitats that occur in a river. The term template is used as the physical habitats are generally assumed to define the characteristics of the biological communities within them. Thus the biology sits upon and is defined by the physical template.

### 1.3 WHAT CONDITIONS CREATE BRAIDED RIVERS?

Leopold & Wolman (1957) proposed two primary controlling variables on channel pattern—discharge and slope—for which two rules are apparent. First, for a given discharge and bed material, there are threshold slopes between which channels will braid, and second, that the critical slope decreases with increasing discharge or decreasing sediment size. Both slope and bed material change naturally and predictably down the length of a river. In general, rivers are steeper in their headwaters and bed materials are coarser; however, as rivers flow away from their headwaters, slope decreases and bed materials become finer (Browne 2004). Consequently, channel form changes in a fairly predictable fashion downstream. Nevertheless, smaller-scale changes in slope and bed material, in conjunction with temporally variable changes in discharge, mean that braiding, and other channel patterns, can occur irregularly along the length of the river. A period of time with high discharges may produce a distinctly braided channel pattern, whereas a period of climatic stability, over months or even years, may produce a single, straight channel (Bridge 1993; Whited et al. 2007).

Geomorphologists have developed indices of channel type, which consider surface physical attributes including channel splitting and sinuosity, and the stability of floodplain bars and islands. Increasingly complex attempts at classifying channel types are summarised by Bridge (1993) and Sambrook Smith et al. (2006). However, more recently, research has highlighted the multi-dimensional nature of braided rivers and provides a more complete understanding of the role of the river and its floodplain within the greater catchment (Stanford & Ward 1988; Brunke & Gonser 1997; Woessner 2000). We now understand that braided rivers consist of much more than active surface channels, and that the river flows across an alluvial gravel bed, which may be many metres deep and possibly kilometres wide. Surface water flows over the top of the gravel, but also moves down vertically and horizontally through the gravels as groundwater. This groundwater, which may re-emerge in a spring or wetland, is the vertically connected component of the braided river. Despite most classification systems' preoccupation with surface characteristics, braided rivers are, in fact, three-dimensional ecosystems. They comprise a single body of water moving down the river corridor, and exert an influence far beyond the 'bank' of the active river. It is this multi-dimensional structure which makes braided rivers so important as physical and aesthetic phenomena, as well as diverse and complicated ecosystems.

Morphologically, rivers can be divided into two broad groups: those constrained by narrow valleys and terraces, and those unconstrained and flanked by a flood-plain (Schumm 2005). Braided rivers also depend upon two catchment-scale conditions. The first is a source of highly erodable bedrock, which forms the basis of gravel-dominated highly sinuous channels. This eroded material may be produced by several processes, but is usually the result of glacial activity, erosion of friable bedrock and active mountain building. Many braided rivers are found in areas that experience these erosional forces, notably parts of Canada, Alaska, the Himalayas and the South Island of New Zealand. The second catchment-scale condition is that almost all braided rivers are associated with steep mountain ranges, which have the capacity to create their own weather. For example, the Southern Alps of New Zealand are aligned perpendicular to the prevailing westerly air flow, resulting in orographic rain,



which can occur at any time of year. So, rivers that are not laterally constrained by some geographical feature and that experience a high level of sediment input and high rainfall events may form an alluvial floodplain. Interactions between rainfall, sediment size and slope of the floodplain may create conditions that cause a river to form multiple sinuous channels across its floodplain. However, periods of discharge stability or anthropogenic constriction of the floodplain may shift the channel form away from braiding towards a single channel.

#### 1.4 WHERE ARE BRAIDED RIVERS FOUND?

Braided rivers occur most frequently in arctic and alpine regions that have high precipitation and steep headwaters. However, they also occur in arid and Mediterranean climates subject to torrential rain, and in some tropical regions where there are monsoonal rains (Bravard & Gilvear 1996). Whilst the headwaters of many of the world's braided rivers may be relatively free from direct human modification, their lower reaches are frequently heavily impacted (Tockner & Stanford 2002). In fact, in most developed nations, few examples of non-impacted braided floodplain systems remain (Malmqvist & Rundle 2002; Tockner & Stanford 2002).

Dynesius & Nilsson (1994) estimated that, of the 139 largest rivers in Europe, the former Soviet Union, USA and Canada, 77% were moderately to strongly affected by flow regulation. Human degradation of river systems is a worldwide phenomenon (Benke 1990; Raven et al. 1998; Muhar et al. 2000; Pringle et al. 2000; Rosenberg et al. 2000; Brunke 2002; Young et al. 2004; Nilsson et al. 2005) and flow regulation and channelisation are recognised as particularly important issues in braided floodplain systems (Brunke 2002; Hauer & Lorang 2004; Hohensinner et al. 2004; Thoms et al. 2005). In Europe, human modification of rivers is so common that the Tagliamento River, in north-eastern Italy, is regarded as the only remaining morphologically intact braided river system (Tockner et al. 2003). The majority of extant unmodified systems in the northern hemisphere are concentrated in the extreme north of Alaska, Canada and Eurasia, away from centres of human development (Dynesius & Nilsson 1994). The majority of extant unmodified systems in the southern hemisphere are in New Zealand. Whilst many other alpine regions—such as the Himalayas and Andes—have rivers with braided reaches, the rivers are often severely degraded and published accounts of their ecology are scant (Garcialozano 1990; Gopal & Sah 1993; Wang et al. 2005; Habit et al. 2006).

Despite the paucity of unmodified river systems available for study, both Europe and North America have established centres of intensive research to investigate the function and landscape roles of floodplain systems (Stanford & Ward 1993; Ward & Stanford 1995; Tockner et al. 2003). Insights from these studies have supported a number of rehabilitation and restoration projects, particularly along central Europe's largest rivers (Hohensinner et al. 2004).

In New Zealand, numerous studies on the geomorphology of braided rivers have been published, and our physical braided river research continues to be at the forefront of such research internationally (Mosley 2001; Sambrook Smith et al. 2006). Furthermore, a considerable body of literature has been generated by catchment and regional water boards and regional councils, primarily as resource

reports, draft management plans and water conservation/consent reports (e.g. NCCB 1983, 1986, 1991). However, apart from a limited number of studies on the ecology of individual species or reaches, little coordinated ecological research has taken place to assess the overall values and function of braided river ecosystems (Hughey et al. 1989; Sagar & Glova 1992; Reinfelds & Nanson 1993; Meridian Energy 2003; Gray 2005; but see O'Donnell & Moore 1983). Economic development, particularly demands for hydroelectric power generation and irrigation water are putting increasing pressure on New Zealand river systems (Young et al. 2004).

## 2. The habitat template: physical conditions within a braided river

### 2.1 GEOMORPHIC AND GEOLOGIC TEMPLATE

New Zealand sits atop a geologically active tectonic boundary resulting from the break-up of the ancient Gondwana supercontinent (Kamp 1992). Approximately 80 million years ago (mya), the Tasman Sea began to open, separating New Zealand from what would become Australia and Antarctica. About 60 mya, movement ceased and New Zealand has remained physically isolated ever since (Gibbs 2006). For the first 70 million years of this separation the climate is thought to have been warmer than at present and vegetation was similar to that now found in Australia and New Caledonia (Stevens 1981). At this stage, New Zealand comprised a series of low-lying islands, but about 8 mya the Pacific-Australian plate margin began to move again, lifting the seafloor and beginning the process of mountain building. Subsequent mountain building, volcanic activity, and periods of glacial growth and recession have produced our contemporary landscapes, particularly the major river valleys in the South Island alpine regions. Early Pleistocene (1.8 mya) glaciers were not restricted to the valley systems present today. The broad framework of modern watersheds was developed during the Ross and Porika glaciations (1–2 mya; Pillans et al. 1992). Two major glaciations—the Waimaunga and Otira—further modified these valleys. The brief glacial recessions are particularly well documented in the Waimakariri and Taramakau catchments, and culminated with the end of the second Poulter Advance about 13 000 years ago (Gage 1977). Similarly, the Würm glaciation in Europe and the Wisconsin glaciation in North America ended approximately 10 000 years ago. The most studied braided river systems in other countries are therefore of comparable age to those in New Zealand (Muller & Kukla 2004; Smith 2004).

During the last 10 000 years, New Zealand's braided rivers have been sculpted by fluvial processes augmented by discrete tectonic events. For example, Reinfelds & Nanson (1993) described the three predominant mechanisms in the development of the Waimakariri River's braided river floodplain. First, riverbed abandonment by lateral migration of the active river bed (usually in the lee of tributary fans and bedrock spurs), followed by aggradation during high-magnitude flood events and, finally, localised riverbed incision. In fact, several

authors have described braided rivers as being in a state of ‘dynamic stability’ whereby (despite a high turnover of habitat) the proportions of each habitat type remain relatively constant over time (Arscott et al. 2002; Hauer & Lorang 2004; Latterell et al. 2006). However, over longer time scales (hundreds of years) it would be less accurate to view these rivers as being in a state of balance or equilibrium. For example, Korup (2004) used historical aerial photography and geomorphic, morphostratigraphic and dendrogeomorphic evidence from 250 landslides in south-western New Zealand to describe the channel-altering effects of landslides. At least 6% of landslides caused major avulsions (channel shifting) and it is likely that the characteristic instability of braided rivers is accentuated by sediment pulses (Hicks et al. 2004). The effect of these events upon terrestrial and aquatic floodplain habitats can be very dramatic. In 1967, the Gaunt Creek landslide caused the braided Waitangitona River on the West Coast of the South Island to alter its course, from merging with the Whataroa River to flowing into the Okarito River catchment. The lower reaches of the Waitangitona River are now predominantly fed by groundwater as opposed to surface runoff and, after the landslide, a large portion of the wetlands at the inflow of Lake Wahapo were buried under gravel. Goff & McFadgen (2002), Cullen et al. (2003) and Korup (2004) have documented evidence of several periodic seismic events that have caused river aggradation and driven vegetation destruction and channel instability throughout New Zealand.

## 2.2 CONTEMPORARY GEOLOGY AND GEOGRAPHY

An extensive desk-top mapping exercise by Wilson (2001) identified all the river systems that exhibit braiding within New Zealand. Overall, 163 river systems had braided reaches, with a total of 248 400 ha of braided river habitat occurring in 11 of New Zealand’s 14 regions. Canterbury and the West Coast had the largest areas of braided river habitat, with 60% and 19% of the national total, respectively. Braided rivers occur on both coasts of the South Island but were restricted primarily to the east coast of the North Island (Fig. 1). Wilson (2001) also reported that North Island braided rivers have climatic conditions (temperature, solar radiation and humidity) similar to those in the northern South Island, and unlike those of the more southern regions of the island.

The majority of braided rivers in New Zealand drain lithologically unstable catchments predominantly of greywacke, mudstone or other sedimentary rocks, although some of the rivers in South Westland (such as the Landsborough and Arawata) are dominated by schist and gneiss. In the North Island, highest sediment production occurs in the East Cape region, where high rainfall, natural geologic instability and accelerated erosion (due to deforestation) contribute to high sediment yields (Mosley & Duncan 1991; Hicks et al. 2004). Sediment yields in the South Island are highest on the flanks of the Southern Alps and the yields in some rivers have been estimated to be among the highest in the world (Griffiths 1979).

High precipitation on the flanks of the Southern Alps in the South Island and on the Kaimanawa, Raukumara and Ruahine Ranges in the North Island contributes to the formation of braided rivers. Many of New Zealand’s braided rivers also have glacial sources and snow-laden upper catchments, which also

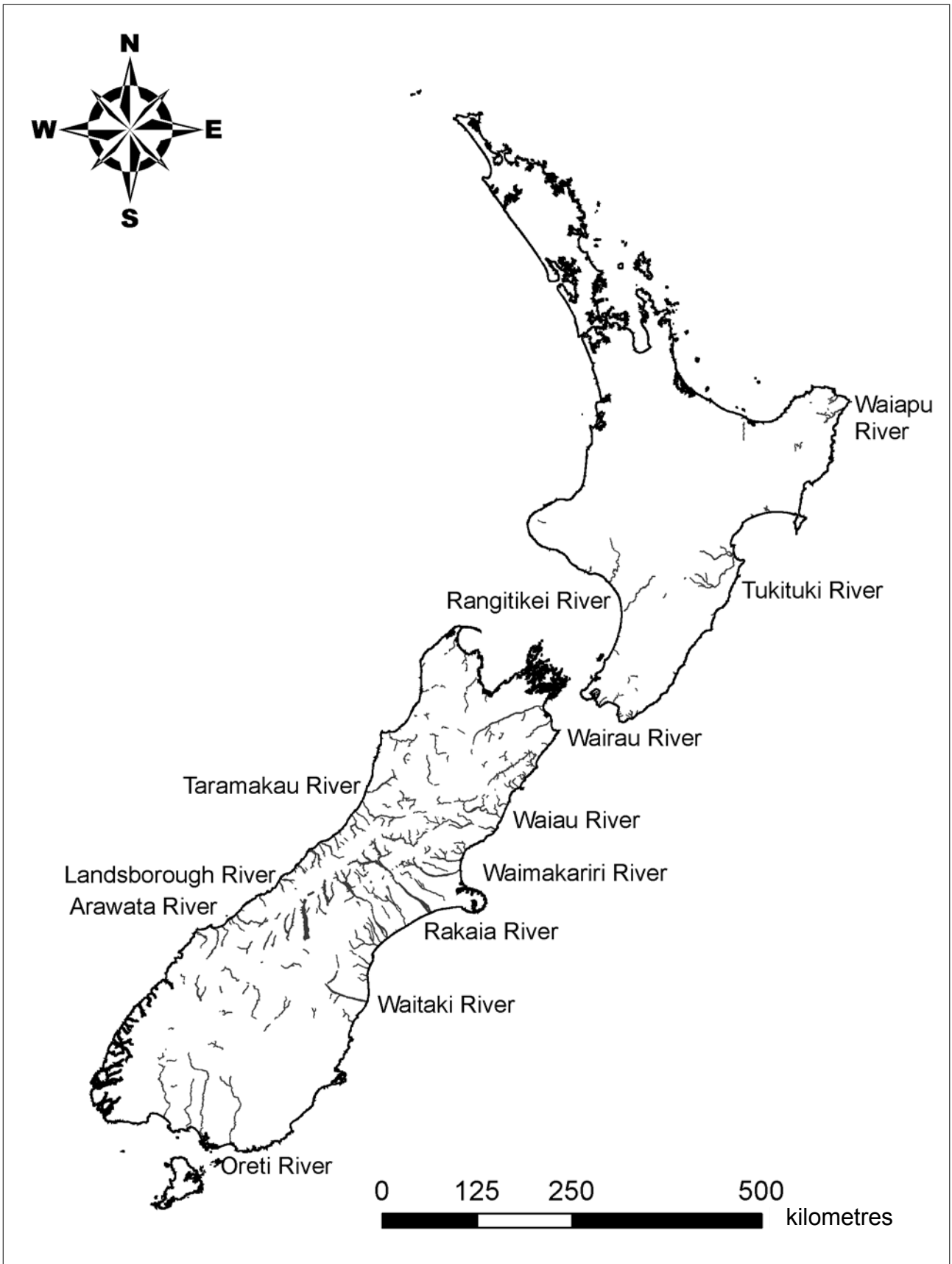


Figure 1. The braided reaches of the 163 braided rivers in New Zealand (New Zealand Land Resource Inventory). The locations of the larger rivers from each region have been labelled.

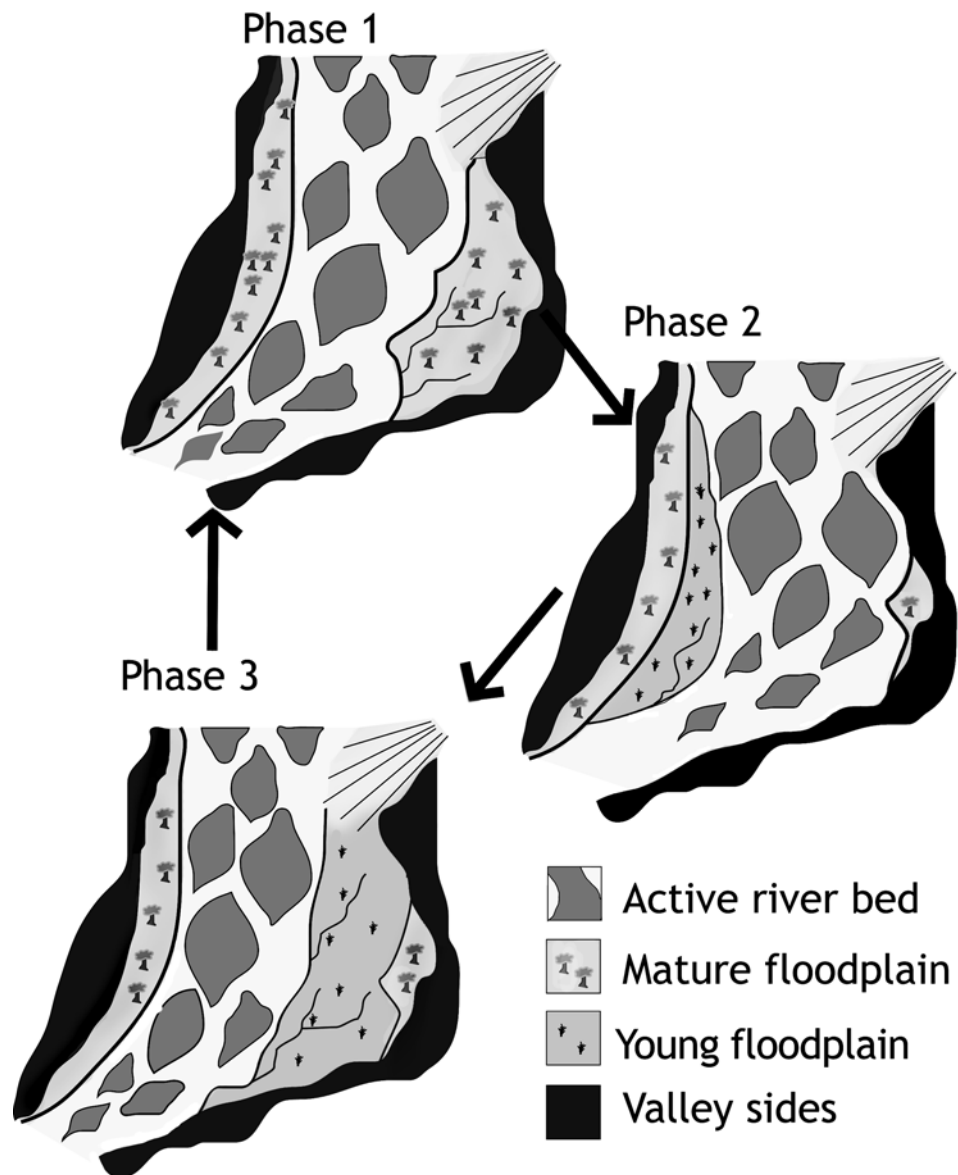
contribute to their volatile hydrologic regimes. The South Island's alpine rivers are characterised by large floods resulting from heavy rain along the Main Divide, often compounded by snow melt. Floods are common in spring and early summer. In contrast, flows are generally low in winter when water is locked in upper catchments as snow and ice, and in high summer and autumn when precipitation levels are low. Many South Island braided rivers experience extreme low flows during late summer and autumn. These seasonally-related water flow trends are common across braided rivers around the world. The Tagliamento in Italy and the Flathead in Montana, USA, have been similarly described as 'flashy pluvio-nival' (i.e. with flow characteristics dominated by rain and snow melt; Tockner et al. 2003; Hauer & Lorang 2004). In Switzerland, the braided Roseg River exhibits a distinct glacial-melt flow regime, which features strong seasonal flow patterns and a marked diel flow pattern during the summer melt period. These diel patterns are generally absent in New Zealand's braided glacial rivers, as any such patterns are usually masked by the high rainfall that also occurs during the melt season (McSaveney & Davies 1998).

### 2.3 CONTEMPORARY FLOODPLAIN HABITATS

Habitats found on braided river floodplains are physically unstable and have high turnovers. Despite this, biological communities survive because the relative proportion of each habitat in any particular floodplain remains roughly constant over time (Arscott et al. 2002; Hauer & Lorang 2004; Latterell et al. 2006). This means that although a particular habitat may be destroyed in one place, it will remain intact or be forming in others. Consequently, mobile taxa will persist within the 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 communities. In New Zealand, Burrows (1977) reviewed the literature on riverbed vegetation of the upper Waimakariri River basin and suggested a time scale for the successional colonisation of riverbed features. Building upon his study, and using aerial photography from 1948 to 1986, Reinfelds & Nanson (1993) proposed that the upper Waimakariri River reworks its entire floodplain every 250 years, predominantly by lateral migration of the most active part of the braid (Fig. 2). Thus, floodplain habitats may be destroyed by high flows and channel movement on one side of the floodplain while other habitats are developing on the other side of the floodplain.

In a similar study in the upper Ashley River/Rakahuri in Canterbury, Warburton et al. (1993) observed the presence of stable bars and islands amongst the unstable materials, and noted that the active channel of the river was steadily migrating northwards. Mosley (1982a) made use of controlled water releases along the braided Ohau River in South Canterbury to estimate the effect of varying discharge from 26.5 m<sup>3</sup>/s to 507 m<sup>3</sup>/s on channel morphology. As discharge increased, the physical characteristics of existing channels changed, and new channels formed that were physically similar to the original channels. Mosley concluded that across the range of discharges the habitat types available remained proportionally relatively constant, and thus braided rivers may, in some respects, be morphologically more stable than single-thread rivers. More recent work has focussed upon riverbed turnover within the lower Waimakariri River. A combination of digital photogrammetry and LiDAR (Light Detection and Ranging

Figure 2. Floodplain re-working by lateral migration of braided channels. Adapted from Reinfelds & Nanson (1993).



or Aerial Laser Scanning) have been used to create 3-D models of the river bed which may be compared over time to investigate the influence of flooding on river morphology (Hicks et al. 2003; Lane et al. 2003; Westaway et al. 2003; Hicks et al. in press). Although it did not specifically focus upon in-stream habitat types, this recent research has shown that the lower Waimakariri River turns over two-thirds of its available floodplain annually ( $> 0.2$  m vertical erosion or deposition) and would probably re-work its entire floodplain within 5 years. The most persistent areas of wetted habitat were those found within the dynamic braids. These were, therefore, the most physically disturbed of the aquatic habitats available. These findings highlight the potential ecological value of spatially minor, but more stable peripheral floodplain habitats. Temporal mapping of habitat types within New Zealand braided rivers has not been done to confirm habitat dynamics and the appropriateness of the shifting mosaic steady state model, although it is considered applicable to unmodified New Zealand systems (M.D. Hicks, pers. comm. 2007).

The role of large woody debris in structuring stream morphology is well documented in New Zealand and elsewhere (Gurnell et al. 2002; Hicks et al. 2004). In small New Zealand streams, large woody debris has been shown to influence channel morphology and pool formation, as well as providing important habitat for invertebrates in streams with otherwise unstable silt or pumice substrates (Hicks et al. 2004). Whilst the role of large woody debris has not been assessed in New Zealand's braided rivers, studies elsewhere indicate that wood may play an important role in large rivers (Gippel et al. 1996; Gurnell et al. 2000a; Van der Nat et al. 2003). In large rivers, wood has been associated with the creation and maintenance of bars and islands and sites for avulsion (channel shifting) and the formation of secondary channels. Pools form around embedded logs in response to flow diversion imposed by the root wad, and fine sediment accumulates downstream along the trunk (Gurnell et al. 2002). Many rivers in Europe suffered major deforestation of their riparian zones prior to the 16th century; however, investigations of woody debris accumulations in the mostly unmodified Tagliamento River, in Italy, have revealed the links between river morphology and riparian forest/woody debris. Wood storage within the active channel of the Tagliamento is spatially variable. Small quantities were found on the open gravel surfaces and intermediate quantities with mature islands, but large quantities were associated with pioneer or developing islands. The majority of this wood accumulated on bar crests, the point of formation for pioneer islands (Gurnell et al. 2000a; Gurnell et al. 2000b). Islands form in the lee of debris jams, as evidenced by the decreasing age of vegetation from upstream to downstream. The process of vegetated island development may also be accelerated if the woody debris is still alive and able to sprout (Gurnell et al. 2002). Furthermore, woody debris appeared to be more abundant in headwaters than in the lower reaches of rivers; thus, under natural vegetation conditions, a debris gradient occurs along the river. How this longitudinal gradient and the movement of wood downstream affects flow, habitat and the availability of carbon to food webs is poorly understood.

The condition and age of vegetation along a river's riparian corridor may substantially influence channel geomorphology, primarily by altering bank strength and flow resistance (Gran & Paola 2001). Numerous studies have linked channel properties such as width, depth and velocity to vegetation density in the riparian corridor (Graf 1978; Andrews 1984; Hey & Thorne 1986; Huang & Nanson 1997; Rowntree & Dollar 1999; Millar 2000), and vegetation type or density to channel form, e.g. braided or meandering (Mackin 1956; Brice 1964; Nevins 1969; Goodwin 1996; Gran & Paola 2001). However, in many developed regions throughout the world, riparian forests have been removed to create farmland. Since people arrived in New Zealand, much indigenous riparian forest has been removed and replaced with tussock grassland and pasture (Miller 2002). Subsequently, thousands of kilometres of stream and river banks have been re-planted with willows in order to prevent floods from damaging adjacent farmland (Miller 2006; Mosley 2004). Mosley (2004) suggested that rivers in New Zealand may be responding to increased riparian re-forestation by narrowing and, for some lowland Canterbury rivers, this may represent a return to the stable anastomosing form they had prior to deforestation by Maori and European colonists.

## 3. Floodplain habitats of braided rivers

### 3.1 MAIN CHANNEL AND SIDE BRAIDS

Most braided reaches will include one or more larger channels which persist between flood and drought events. These larger channels usually have multiple side channels which exemplify the characteristics of a braided river (Fig. 3). Flow regimes in the main channels and side braids can be highly variable.

The substrate of the main channel can be highly unstable. In the upper Waimakariri River, Gray (2005) recorded 99% movement of cobble-size tracer stones over a 6-month period. In the lower reaches of the same river, Hicks et al. (in press) estimated that 88% of the riverbed had undergone significant (> 0.2 m vertical erosion or deposition) change during a 3-year period. Whilst main channels and side braids are part of a continuous surface network, they are not always subject to the same disturbance regime. Side braids may have more stable substrates, as evidenced by algal growths, but also be subject to more regular de-watering with river stage fluctuations. Furthermore, the hydrological source of the river (alpine or foothill) will influence the regularity and intensity of physical disturbance in all channels.

Main and braided channels are major conduits for sediment transport. Estimated sediment yields from New Zealand's braided rivers may be among the highest for rivers anywhere in the world and, despite amounting to only 0.2% of the world's landmass, New Zealand produces 1% of the sediment input to the world's oceans (Griffiths 1979; Hicks et al. 2004).

Temperature regimes in the main channels and side braids are influenced by variations in channel discharge, and the relative contributions of groundwater and surface water runoff (Mosley 1983b). Mosley (1983a) found that during

Figure 3. A typical braided river main channel in the Hopkins River.





autumn and spring, maximum temperatures of the main channels in the Rakaia River and Ashley River/Rakahuri were inversely proportional to discharge. However, Grant (1977) reported that main channel temperatures in the Ngaruroro River in Hawke's Bay were lower when the river was at base flow than at high flow, because of the increased influence of groundwater. Thus, the ground or hyporheic water may buffer the main channel against relatively warmer surface water runoff and atmospheric temperature fluctuations. Under low-flow conditions water temperatures can, however, become very high in the absence of groundwater exfiltration and, in mid-summer, water temperatures in excess of 25°C have been recorded in Canterbury rivers (Mosley 1982b).

### 3.2 SPRINGS

Springs can be common in braided river floodplains, but constitute only a small proportion of the wetted surface area of a braided river. The roles of springs within the braided river landscape are discussed in this review, and put into the larger context of other spring types (e.g. Karst springs) nationally in Scarsbrook et al. 2007. Springs have distinct physical and chemical characteristics (Fig. 4) compared with the main channels of rivers (cf. Fig. 3 and see also section 3.4).

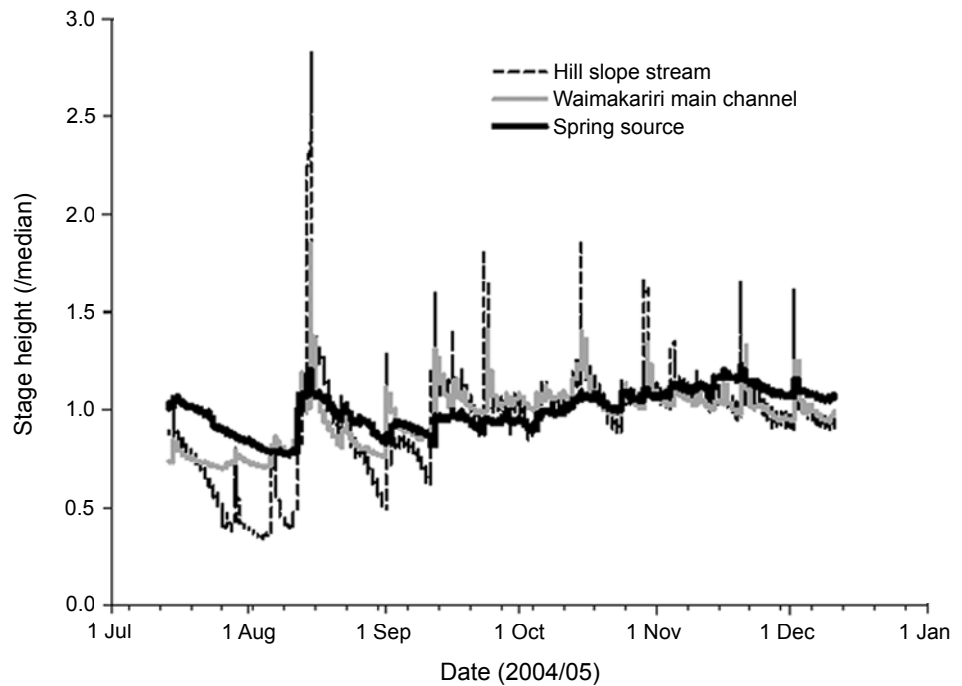
Braided river springs often derive their flow from aquifers. Therefore, although some springs are very stable and permanently wet, others may be subject to drying. Spring permanence appears to be linked to the position of the spring in relation to the main channel and the height of the spring relative to the water table of the floodplain (Poole et al. 2002; Poole et al. 2004). Spring discharge is characteristically stable (Fig. 5) and frequently reflects the broad-scale trends in discharge of the main river, but without the dramatic peak flows characteristic of streams fed by surface run-off (Death 1991; Barquin 2004; Gray 2005).

Consequently, the substrate within spring-fed streams is usually very stable and the water clarity high. Gray (2005) estimated the percentage of substrate movement in floodplain springs in the Waimakariri River to range from 2 to

Figure 4. A floodplain spring in the Hawdon river, Arthur's Pass National Park. Note the abundant macrophytes and mosses.



Figure 5. Stage height (standardised to the median value) of a hillslope stream, a spring-source and the main channel of the Waimakariri River (Gray 2005).



12% per annum. Similarly, Death (1991) detected no substrate movement over 2.5 years in Slip Spring, also in the Waimakariri River basin. The substrate composition of spring creeks is frequently a result of historic deposition and occasional flooding from adjacent surface-fed streams and rivers, rather than in-stream processes. Overbank flooding tends to introduce fine sediment to springs; this input may be augmented by aeolian (windblown) deposits (Reinfelds & Nanson 1993).

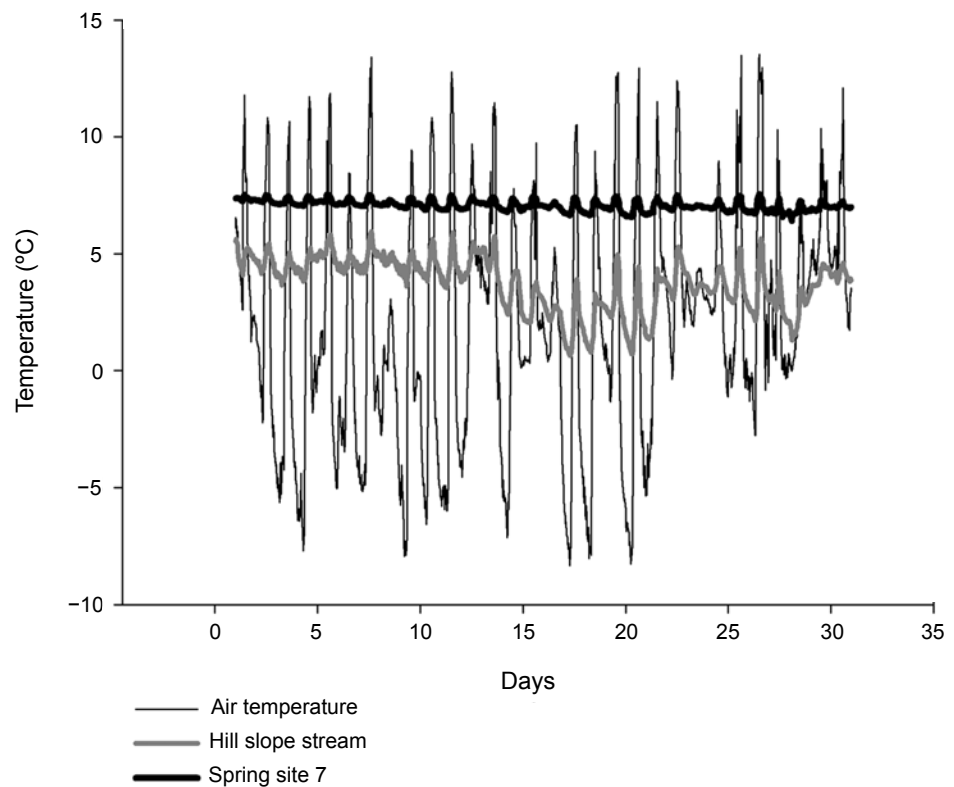
Temperature regimes of floodplain streams in New Zealand that are spring-fed are more stable than those of main channels and approximate the local mean annual air temperature (Death 1991; Gray 2005) (Fig. 6). Thus, spring creeks tend to be warmer in winter and cooler in summer compared with surface-fed streams (Mosley 1983b). However, temperature fluctuations increase with distance from the point of up-welling (Barquin 2004).

### 3.3 GROUNDWATER AND HYPORHEIC ZONES

Groundwaters beneath a braided river are generally subdivided into two intergrading zones—the hyporheic zone and the phreatic zone. The hyporheic zone has been defined by White (1993) as the saturated interstitial areas beneath the streambed, and into the stream banks, that contain some proportion of channel water, or that have been altered by channel water infiltration. Beyond this point the water contained within the interstices is referred to as groundwater within the phreatic zone, where voids are permanently saturated with groundwater. Thus the depth of the hyporheic zone and the points where the hyporheic and phreatic zones merge vary from reach to reach and are unknown in most rivers.

The physico-chemistry of groundwater associated with braided rivers is dictated by a combination of the proximity of the recharge reach of the river from which they are derived and catchment morphology and geology (Rosen 2001; White

Figure 6. Temperature regimes for a spring-fed and a surface runoff stream between the 15th July and 13th August 2004. (Gray 2005).



et al. 2001). With increasing residence time within an aquifer, hydrochemistry becomes more like that of true groundwater. White et al. (2001) made measurements in wells positioned at increasing distances from recharge zones of the Waimakariri River and showed an increase in  $\text{Cl}^-$ ,  $\text{HCO}_3^-$  and nitrate-nitrogen away from the river. Similarly, Scarsbrook & Fenwick (2003) found that dissolved oxygen concentration and temperature were lowest in groundwater samples farthest from the Ngaruroro and Waipawa rivers in Hawkes Bay. Gray et al. (2006) sampled groundwater beneath and adjacent to the lower Waimakariri River and found that temperature and electrical conductivity were highly variable compared with spring sources in the upper river and did not show a predictable correlation with surface water. Temperatures were more similar to those in the main channel, probably reflecting the recent source of groundwater and residence time within the substrate. See also section 3.4 for a summary of this information.

Fenwick et al. (2004) reviewed the general characteristics of groundwater habitats, many of which are probably similar to those of alluvial aquifers of braided rivers. They found that as a consequence of the lack of light and, thus, photosynthetic activity, almost all organic matter is imported. In addition, groundwater habitats are contained within an immovable matrix of alluvial deposits. The size, chemical reactivity and heterogeneity of the matrix pores dictate many of the physico-chemical characteristics of alluvial groundwater. In New Zealand, the generally inert nature of the substrate and the constricted pore space are associated with slow temporal changes in water chemistry.

Several studies have considered the physico-chemistry of the shallower, hyporheic zones of braided rivers (Burrell 2001; Fowler & Scarsbrook 2002; Olsen & Townsend 2003). Olsen & Townsend (2003) found that up-welling

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

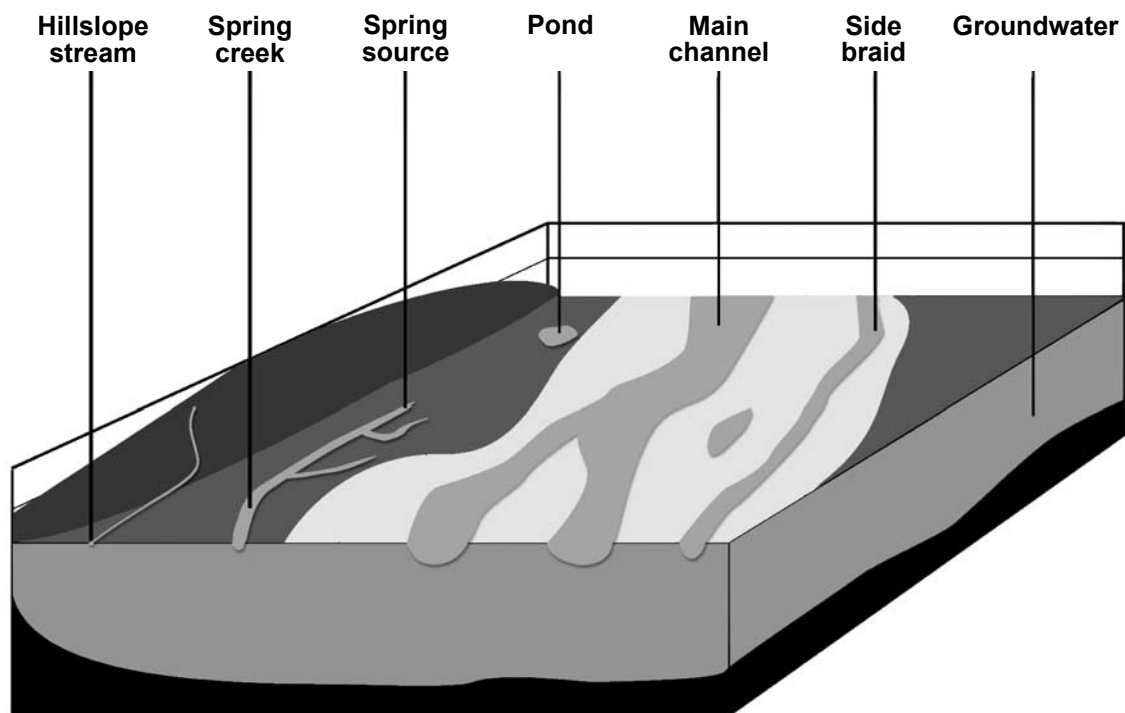
Lentic (standing or slow-moving water) habitats on braided river floodplains may form in two ways (Fig. 7). Firstly, ponds may form where areas of floodplain intersect the water table. Because such areas will be affected by water table height, they may alternate between dry, having ponds of standing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



	<b>Hillslope stream</b>	<b>Spring creek</b>	<b>Spring source</b>	<b>Pond</b>	<b>Main channel</b>	<b>Side braid</b>	<b>Groundwater</b>
<b>Temperature</b>	Seasonally variable	Stable	Very stable	Seasonally	Highly variable	Highly variable	Very stable
<b>Turbidity</b>	Seasonally variable	Low	Very low	–	Highly variable	Variable	Very low
<b>Physical disturbance</b>	Variable	Low	Very low	Very low	Highly variable	Highly variable	Very very low
<b>Permanence</b>	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 m<sup>3</sup>/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 m<sup>3</sup>/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 m<sup>3</sup>/s; Scrimgeour & Winterbourn 1989). However, despite the occurrence of several floods > 30 m<sup>3</sup>/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/m<sup>2</sup> (SE  $\pm$  703). Aquatic invertebrate communities were dominated by the leptophlebiid mayfly *Deleatidium* spp., chironomids and elmids 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/m<sup>2</sup>, 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  $\mu$ m), compared with that used in New Zealand (minimum 200  $\mu$ m, average 350  $\mu$ 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/m<sup>2</sup>) was also considerably lower than that recorded for spring sources (22 982  $\pm$  3413 individuals/m<sup>2</sup>), mossy forested streams (218 400  $\pm$  15 100 individuals/m<sup>2</sup>) and urban streams (25 000  $\pm$  8500 individuals/m<sup>2</sup>) (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  $433 \pm 158$  individuals/m<sup>2</sup>, 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/m<sup>2</sup>) than in the middle Rakaia (85 individuals/m<sup>2</sup>), 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/m<sup>2</sup>; 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  $66 \pm 8$ ) than studies from other countries (mean  $33 \pm 12$ ). 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).

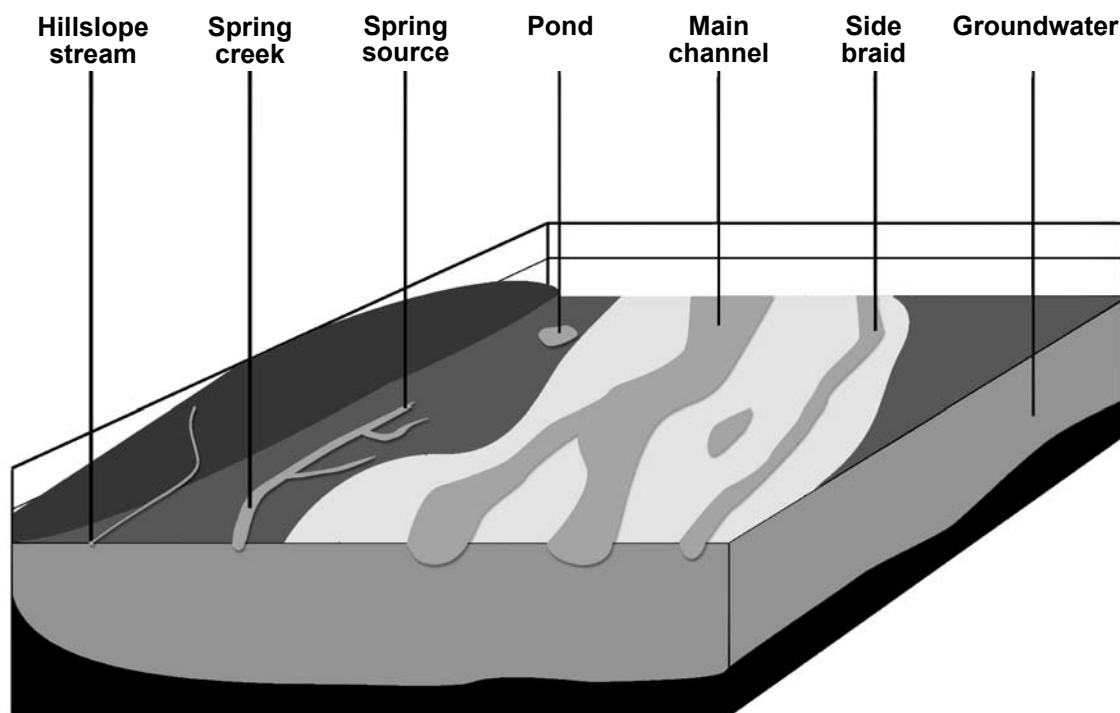
New Zealand's shallow hyporheic zones constitute an interface between surface water and groundwater systems, mediating the movement of energy, matter and individuals between the two zones, and providing habitat for a diverse range of aquatic taxa (Collier & Scarsbrook 2000). The presence of large numbers 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
<b>Taxa richness</b>	Medium	Very high	High	Variable	Low	Low-medium	Low (Poor resolution)
<b>Abundance</b>	Medium	High	High	Variable	Low	Low-medium	Unknown
<b>Species evenness</b>	High	High	Medium-high	High	Low	Medium-low	Unknown
<b>Characteristic taxa</b>	<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/Waikirikiriri, 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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# 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 <sup>2</sup> )
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 ( $\mu\text{m}$ )	TOTAL TAXA FOUND	ABUNDANCE (INDIVIDUALS/m <sup>2</sup> )
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***

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