The physical and biological function of wood in New Zealand's forested stream ecosystems

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Abstract

Since the arrival of humans approximately 1000 years before present (B. P.), New Zealand has lost approximately 80% of its forest cover and along with it, the contribution of wood to our aquatic ecosystems. The aim of this thesis was to undertake a large catchment-scale assessment of LW loadings, spatial distribution and morphological influence in an old-growth indigenous forest to provide some understanding on the natural characteristics of wood that would have been present in many river systems of New Zealand prior to human settlement. The second component of the thesis involved the experimental removal of wood from three small streams in order to provide some insight into what that loss of wood may have meant for fish and aquatic invertebrate communities.

In the first part of the study, a catchment scale survey of large wood (LW) was completed in a 5^{th}order, old-growth forest river system. LW volumes ranged from 59-503 m^3 ha^{-1} and declined down the river system along with the number of LW pieces suspended across the channel and LW influence on channel morphology, whereas piece frequency, number of pieces in debris dams and length increased. Nearly half the pieces were influencing channel morphology, particularly wood accumulation, sediment storage, bank armouring, and pool formation. These key pieces were larger, longer and more stable than average. LW contribution to habitat complexity was highest in the middle to upper sections of the river system. Four key zones of wood distribution and influence were identified in the river system. Zonal boundaries were influenced by changes in transport capacity, fluvial processes and channel morphology.

In the second part of the study, a field trial was established in three small forested streams to measure the influence of wood and its experimental removal on channel morphology, and indigenous fish and aquatic invertebrate communities. Prior to wood removal there were no significant differences in the total density of fish between wood pools (pools with wood cover), open pools and riffles. Total fish

biomass was marginally significant with most of the fish biomass located in wood pools. At the species level, the density and biomass of banded kokopu (*Galaxias fasciatus*) and the weights of longfin eels (*Anguilla dieffenbachii*) were significantly higher in wood pools. Species richness, density and biomass of bluegill bullies (*Gobiomorphus hubbsi*), torrentfish (*Cheimarrichthys fosteri*) and the density of redfin bullies (*Gobiomorphus huttoni*) was highest in riffles. Differences in fish community composition were greatest between riffles and pools, whereas there was considerable overlap between the two pool types.

Total invertebrate density was 70% higher in debris dams than riffles prior to wood removal, but this difference was not significant. Densities of Trichoptera (caddisfly) and Plecoptera (stonefly), and five aquatic invertebrate taxa were significantly higher in debris dams which also contained greater numbers of less common taxa (< 1% total catch) than riffles. Only *Deleatidium* sp. (Ephemeroptera) densities were significantly higher in riffles than in debris dams. Aquatic invertebrate communities in debris dams differed significantly from those in riffles and season had a significant influence on aquatic invertebrate community structure.

Removal of wood and associated debris dams from the treatment sections in each of the three streams resulted in a simplified channel morphology, significantly increasing the length and area in riffles and reducing the area of pools. The impact on the fish community was greatest for the two larger fish, banded kokopu and large longfin eels, whose abundance declined in the treatment sections. At the reach scale, only banded kokopu biomass showed a significant decline following wood removal. Invertebrates were less affected by wood removal and associated loss of debris dams. Invertebrate composition in the remaining riffles in the treatment sections had a higher proportion of Ephemeroptera and lower proportions of Trichoptera, Plecoptera and Diptera with fewer rare species than remaining debris dams in the control sections, but there were no discernable effects on invertebrate densities and functional feeding groups at the reach scale.

Public perception of wood in waterways is mainly negative and wood is managed primarily to reduce flood damage in New Zealand’s streams. With continued research and advocacy on the environmental benefits, careful planning and judicial use, there is the potential to make better use of wood to rehabilitate and enhance New Zealand’s stream environments. This thesis provides some insight into the contribution of wood to forested stream ecosystems in New Zealand and the implicit losses associated with forest removal. It also contributes to our global understanding on the role of wood, its contribution to habitat heterogeneity and influence on biological communities.

Acknowledgements

I would like to thank my supervisors Brendan Hicks and Ian Hogg from the University of Waikato, New Zealand and Mike van den Heuvel from the University of Prince Edward Island, Canada for their guidance, support and sharing of their large wealth of knowledge.

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A part-time PhD is a test of stamina and I wouldn’t have made it without the support of family, friends and work colleagues, thank-you to you all.

To my parents – for a childhood that encouraged me to explore and learn about the natural world around me.

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Preface

This thesis is composed of five chapters. Chapter 1 provides a general overview of wood in stream ecosystems, a review of current knowledge of wood in New Zealand's stream systems and an introduction to the thesis objectives. The next three chapters have been produced as a series of manuscripts, formatted to journal requirements, and have been or are in the process of being published in scientific journals. As a result there is some overlap between these chapters and Chapters 1 and 5. The second chapter examines the spatial distribution, loading and physical influence of wood in a large river system in a catchment of old-growth indigenous forest and has been published in Forest Ecology and Management as:

> Baillie BR, Garrett LG, Evanson AW 2008. Spatial distribution and influence of large woody debris in an old-growth forest river system, New Zealand. Forest Ecology and Management 256: 20-27.

Following on from Chapter 2, Chapters 3 and 4 investigate the effects of wood and its experimental removal from three small streams on channel morphology and indigenous fish and aquatic invertebrate communities. Chapter 5 provides a synthesis of results, conclusions and recommendations.

Chapter One: A global overview of wood in streams

1.1 Wood in forested stream ecosystems

Small streams are basically heterotrophic (Hynes 1975) and forested stream ecosystems in particular, derive a large component of their energy from allochthonous sources of organic matter, although there is an increasing tendency to autotrophy as the stream enlarges (Cummins 1974; Allan & Castillo 2009). Downstream export is a major component of organic matter processing, and opportunities for retention, storage and in-stream biological processing of this material are critically dependent upon the physical structure and retention capacity of the stream channel. Wood is an important component of forested stream ecosystems, influencing stream hydraulics, channel morphology, sediment and organic matter retention, routing and storage, habitat heterogeneity and biological communities (Gregory et al. 2003).

1.1.1 Loss of wood from river systems

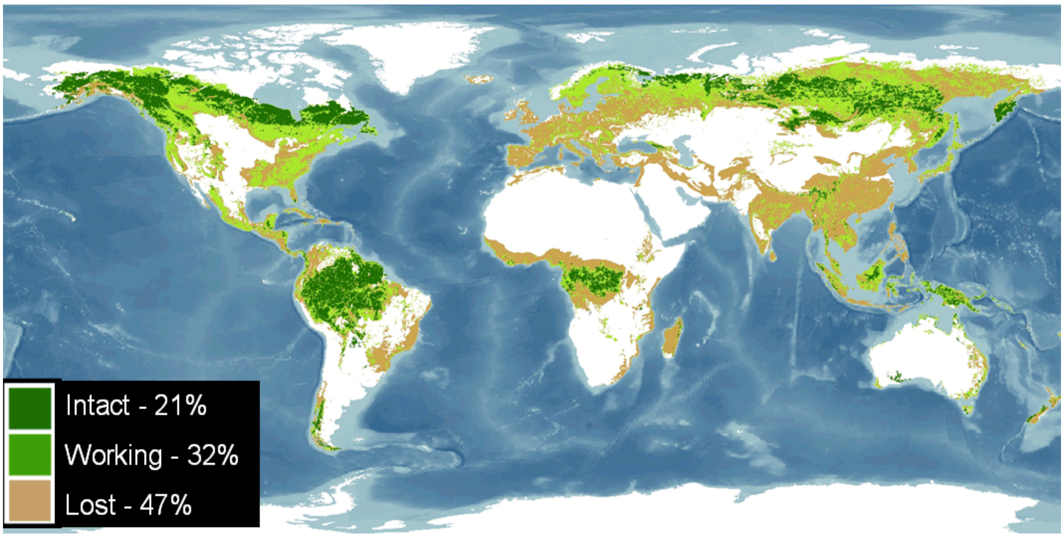

Figure 1.1. State of the World's Forests (World Resources Institute 2009). The white areas do not support forests.

It is estimated that humans have reduced the extent of global forest cover that existed prior to the rise of human civilisation by approximately 50% (Fig. 1.1). Around 20% of remaining forest cover is classified as intact (Fig. 1.1). Forest clearing for agriculture has removed large tracts of riparian forest, particularly in lowland areas. Clear-cutting of riparian forest can leave a paucity of wood that can take decades to centuries to recover. Historical records describe extensive wood accumulations and log rafts in the lower reaches and river mouths of large alluvial river systems in Europe, and America (Triska 1984; Abbe & Montgomery 2003; Montgomery et al. 2003; and references therein). These sites contained vast quantities of sediment, creating extensive floodplains and complex multi-channel networks. Removal of wood from these areas to open up waterways for transportation and other purposes resulted in export of large sediment reservoirs, entrenching and simplifying channel networks and altered floodplain hydrology and ecology (Triska 1984; Abbe & Montgomery 2003).

In smaller streams, loss of wood either through riparian vegetation modification, or harvesting decreases the loading, size and stability of wood in streams, and harvesting in particular increases the frequency of small woody debris (SWD: <10 cm diameter; <1 m length) (Toews & Moore 1982; Smith 1992; Richmond & Fausch 1995). Wood removal typically increases sediment and particulate organic matter transport from streams, with variable effects on pool size and frequency, but commonly resulting in loss of pools and habitat (Bilby 1981; Smith 1992; Dolloff & Warren 2003). Removal of wood from stream channels and floodplains has been shown to reduce the abundance, average size, and biomass of both warm water and coldwater fish species (Dolloff, 1986; Bilby & Bisson 1998; Dolloff & Warren 2003).

1.1.2 Wood source and recruitment

Wood supply to river systems is often sourced from well beyond the immediate stream channel and riparian area (Benda et al. 2003; Reeves et al. 2003; Swanson 2003; Comiti et al. 2008; Fremier et al. 2010). Wood recruited from sources such as upslope landslides, debris flows and avalanches can provide large pulses of wood to stream channels, particularly in steep headwater streams. Debris flows can also transfer wood stored in small headwater streams, and redistribute the material in lower parts of the river system. Chronic large scale disturbances such as widespread mortality from disease, wildfires, large storms, major floods and high wind events provide additional mechanisms for wood recruitment throughout the river system.

Wood recruitment from bank erosion is common throughout channel networks (Fig. 1.2), (Benda et al. 2003; Swanson 2003) and in larger floodplain river systems, wood stored in riparian areas, floodplains and in-channel islands can be sourced some distance from the main channel through channel meandering (Piégay 2003; Latterell & Naiman 2007). Within the stream channel, upstream sources derived from wood fragmentation and fluvial transport, particularly during high flow events, often form a large component of total wood storage in some river systems and flotation is an important process in streams of 3rd - 4th order or larger (Johnson et al. 2000; Swanson 2003; Fremier et al. 2010).

Figure 1.2. Wood delivery via bank erosion, Whirinaki River, New Zealand. Photo by B. R. Baillie.

1.1.3 Large wood (LW) loadings

LW is commonly defined as pieces larger than 10 cm diameter and 1 m in length, although this definition may vary between studies. LW loadings vary markedly in streams around the world (Harmon et al. 1986; Gurnell 2003; Cadol et al. 2009). The first comprehensive review of wood loadings in streams was completed by Harmon et al. in 1986, covering 83 North American sites in natural temperate forests. LW volumes ranged from 2.5 to 4500 m^3 ha^{-1}, with the lowest in-stream wood volumes occurring in *Pinus* forests in Idaho and the highest in *Sequoia sempervirens* forests in California. In the last 10-20 years research on wood in streams has extended beyond North America to include other regions around the world. Gurnell (2003) expanded on Harmon et al.'s (1986) review to include some of these regions, although the dataset still remains biased towards North America. Gurnell's review showed that LW loadings in the western conterminous United States were significantly higher than those in the four other regions included in this review (eastern conterminous United States, Alaska, Australia, and Europe), influenced primarily by the older coniferous forests in this area. Highest variability was in the Australian streams in predominantly *Eucalyptus* forests.

Since Gurnell's review, emerging research on wood in streams in South America (Comiti et al. 2008; Iroumé et al. 2010) showed average LW loadings in three old-growth *Nothofagus* forest catchments and one second-growth evergreen native rainforest catchment, ranging from 109-700 m^3 ha^{-1}. Individual reach loadings peaked at around 4000 m^3 ha^{-1} in one catchment subjected to mass movement and debris flows, following fire disturbance. The highest wood loadings in these catchments are on a par with those in older coniferous stands of the Pacific Northwest (Gurnell 2003). LW loadings in neotropical streams in Costa Rica, Central America ($n = 30$) ranged from 41-612 m^3 ha^{-1}, averaging 189 m^3 ha^{-1} (Cadol et al. 2009). Figure 1.3 compares wood loadings from Cadol et al. (2009) with other sites around the world, including one study from New Zealand.

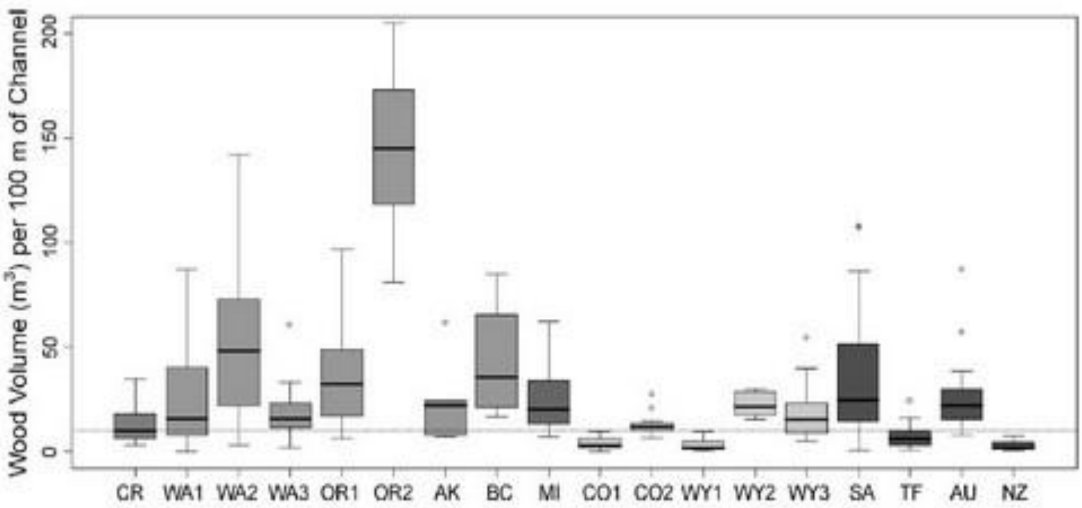

Figure 1.3. Wood volumes from a range of stream sites around the world. CR = La Selva, Costa Rica; WA1, WA2 = western Washington; WA3 = Cascade Range, Washington; OR1 = western Oregon; OR2 = Coast Range, Oregon; AK = southeastern Alaska; BC = southwestern British Columbia; MI = northern Michigan; CO1, CO2 = Colorado Front Range; WY1 = Bighorn Range, Wyoming; WY2 = Absaroka Range, Wyoming; WY3 = Bridger Teton National Forest, Wyoming; SA = southern Andes, Chile; TF = Tierra del Fuego, Argentina; AU = southeastern Australia; NZ = South Island, New Zealand (from Cadol et al. 2009, Figure 8, page 1208).

1.1.4 Spatial distribution

The relative importance of hydrologic processes and geomorphology on LW loadings and spatial distribution, changes along a stream continuum. In small headwater streams (1st and 2nd order), where there is insufficient stream power to transport material, most LW remains *in situ*. As stream size and power increases fewer pieces are retained in the system and LW volumes tend to decrease (Bilby & Ward 1989; Robison & Beschta 1990b; Richmond & Fausch 1995; Gurnell 2003). LW starts to accumulate into debris dams with dam frequency decreasing as dam size and inter-spacing increases along the stream channel (Keller & Swanson 1979; Martin & Benda 2001; Abbe & Montgomery 2003). A study in the Queets river system, Washington, U.S.A., showed basin-wide spatial patterns in the frequency and types of LW accumulations within the river network (Abbe & Montgomery 2003). In larger river systems, geomorphic structure is an important control on LW retention.

Retention sites include the outside of meander bends, the head of point bars, in-channel islands, and secondary channels.

1.1.5 Geomorphic influence of wood

Large stable pieces of wood are primary agents of control on channel morphology in forested streams (Montgomery et al. 2003) and influence a wide range of geomorphic functions (Fig. 1.4) over a wide range of spatial scales. To quote Montgomery (2003, p.1.);

“*No doubt about it, wood complicates fluvial geomorphology. It messes up nice tidy streams, complicates quantitative analysis, invalidates convenient assumptions, and opens new questions about how different contemporary channels are from their pristine state*”.

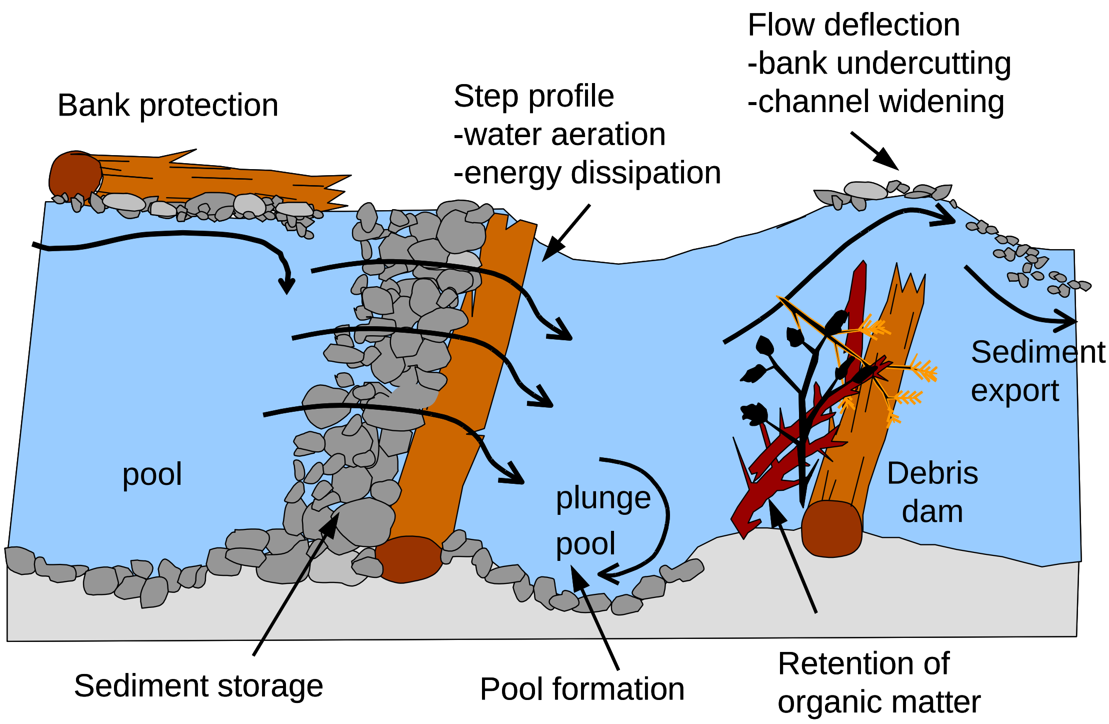

Figure 1.4. Influence of wood on geomorphic processes in streams.

Steps created along the channel profile, by logs or log jams spanning the stream channel, provide sites of energy dissipation and can account for anywhere between 10-80% of elevation loss (Keller & Swanson 1979; Bilby 1981; Abbe & Montgomery 2003; Webb & Erskine 2003; Comiti et al. 2008). Elevation loss from log steps is highest is steep headwater streams, declining in larger, lower gradient river systems.

Large stable wood can exert strong controls on sediment storage and transport, regulating, and reducing the variability of sediment movement through the stream river system (Mosley 1981; Abbe & Montgomery 2003; Montgomery et al. 2003). In small headwater streams, wood accumulations spanning the channel floor, create valley jams that form storage sites for sediment accumulations. In some stream systems, up to 40-50% of LW pieces were storing sediment (Bilby 1981; Webb & Erskine 2003; Cordova et al. 2007). Debris dams stored up to 87% of sediment in a section of a 2nd order stream in New Hampshire, U.S.A., most of which was lost downstream when debris dams were removed (Bilby 1981). In the lower reaches of forested river systems, wood is an integral component in the formation of bars and in-channel islands (Gurnell et al. 2001; Abbe & Montgomery 2003). In some instances, sediment stored by wood can exceed annual sediment yields (Montgomery et al. 2003; Comiti et al. 2008).

Wood is often a primary agent of pool formation, particularly in alluvial river systems. Wood was associated with the formation of 65-70% of all pools in some Pacific Northwest streams (Robison & Beschta 1990a; Montgomery et al. 1995), 76% of pools in sub-alpine old-growth forest in Colorado (Richmond & Fausch 1995), and 82% of pools in an Australian alluvial sand-bed stream (Webb & Erskine 2003). The type and size of pool associated with wood varies with wood position in the channel, spatial arrangement and location in the river network (Bilby & Ward 1989; Abbe & Montgomery 2003; Montgomery 2003; Rosenfeld & Huato 2003). Pool density is generally higher in streams with wood, deeper pools are often associated with wood, and pool frequency generally declines with increasing channel width.

When positioned against or parallel to the bank edge, large wood and wood accumulations can armour banks, increasing channel bank stability and constricting flow. When pieces do not completely span the channel and lie oblique to channel flow, flow deflection and associated bank undercutting, mobilises sediment and widens out the channel. As a result channel width can vary considerably in forested stream channels. In sufficient quantities, wood can significantly increase hydraulic roughness, influencing flow velocity, hyporeic flow patterns, stream power and shear stress in the stream channel (Keller & Swanson 1979; Montgomery 2003; Cordova et al. 2007; Wondzell et al. 2009). In one South American study, wood increased flow resistance by an order of magnitude (Comiti et al. 2008).

1.1.6 Biological roles of wood

The structural diversity and habitat complexity of wood and wood accumulations also provide shelter, refuge, foraging grounds and attachment sites for aquatic and semi-aquatic invertebrate species, at varying stages of their life cycles (i.e. oviposition, pupation and emergence) (Anderson 1982; Hoffmann & Hering 2000; Benke & Wallace 2003). LW can create habitat for certain invertebrates that may be rare elsewhere in the system (Dudley & Anderson 1982; Godfrey & Middlebrook 2007) and enhance invertebrate production by providing a stable substrate in unstable sandy-bottomed streams (Benke et al. 1985; Collier & Halliday 2000). While the nutritional value of wood is low, some invertebrates utilise this material directly as a food source (xylophagous species) or indirectly through ingestion of the epixylic biofilm established on the wood surface. Along with the organic matter trapped by wood, the variety of food available in wood habitat is often greater than that on mineral substrates (Benke & Wallace 2003; Eggert & Wallace 2007). As a result, these sites are often hotspots of aquatic invertebrate production and diversity, enhancing food resources for fish (Benke et al. 1985; Smock et al. 1989; Weigelhofer & Waringer 1999).

LW also provides habitat and refuge for a variety of fish species (Dolloff & Warren 2003). Certain fish species and age groups prefer pool habitat created by LW and will utilize wood cover at various stages of their life-cycle (Murphy et al. 1984; Dolloff & Reeves 1990; Bilby & Bisson 1998; Dolloff & Warren 2003). Wood accumulations provide refuge sites in both high and low flow conditions, concealment from predators and the complexity of habitat facilitates co-existence of competitive species (Sedell et al. 1990; Dolloff & Warren 2003). Consequently, fish diversity and abundance is usually higher in streams with high LW loadings (House & Boehne 1987; Fausch & Northcote 1992; Neumann & Wildman 2002; Wright & Flecker 2004).

While research has commonly focused on salmonid and warm water fish species in North America (Angermeier & Karr 1984; Hicks et al. 1991; Dolloff & Warren 2003), studies elsewhere demonstrate the importance of wood for a range of fish communities around the world. A review by Dolloff & Warren (2003) found more than 80 species of fish associated with wood in southeastern U.S. streams. Woody debris provided cover for juvenile masu salmon (*Oncorhynchus masou*) in Japan and structural habitat for the critically endangered trout cod (*Maccullochella macquarriensis*) in Australia (Inoue & Nakano 1998; Nicol et al. 2007). In the lower reaches of the Danube River in Europe, the structural diversity and shelter provided by LW provided habitat for fish communities dominated by cyprinids (Sindilariu et al. 2006). In tropical forest streams in Venezuela, pools with wood contained a higher abundance and diversity of fish than those without, and in a West African study, the presence of submerged wood influenced habitat use by fish in the River Gambia (Wright & Flecker 2004; Reichard 2008).

1.2 Wood in New Zealand stream ecosystems

1.2.1 Loss of forest cover in New Zealand

New Zealand’s indigenous temperate forests are evergreen, dominated by beech (*Nothofagus* sp.), or beech-conifer-broadleaved forests mainly located along the axial ranges of both the North and South Islands of New Zealand. Conifer-broadleaf forests were the major forest type in lowland areas (Newsome 1987; McGlone 1989). These forests display a general lack of seasonal inputs of organic matter more common in northern hemisphere deciduous forests. Prior to Polynesian settlement (approx. 1000 years B.P.) it is estimated that 85-90% of New Zealand was covered in forest (Fig. 1.5) (Newsome 1987; McGlone 1989). Early Polynesian settlers used fire as a land-clearance tool, particularly around 750-500 years B.P., reducing forest cover by about half at the time of European settlement in the 1840s and 1850s. Land clearance was more extensive in the drier central, eastern and southern areas of New Zealand than in the wetter climates of the northern and western areas (Newsome 1987; McGlone 1989) (Fig. 1.5). Further land clearance by European settlers primarily for agriculture, particularly in the North Island (Fig. 1.5) has reduced present day indigenous forest cover to approximately 24% of New Zealand. The forests most affected by human land clearance were the conifer or conifer-broadleaf forests located in the more fertile lowland and drier areas of New Zealand (McGlone 1989).

The establishment of exotic plantation forests began in the early 1900's with an extensive afforestation programme during the 1920's and 1930's, particularly in the North Island's central plateau (Roche 1990). A second large afforestion programme was initiated in the 1960's through to the 1980's to meet projected demands for timber products. Today, 7% of New Zealand's land area is in plantation forests dominated by *Pinus radiata* (90% of planted forest area). Mature stands are harvested at around 28 years of age, averaging 35-36 m in height and 2.0 m^3 per stem (New Zealand Forest Owners Association 2009).

Today, along with the reduction in forest cover, since the arrival of human settlers, large areas of New Zealand's waterways have lost wood as a natural component of forested stream ecosystems. While New Zealand has lost one known indigenous fish species since human colonisation (McDowall 2000), the impact on aquatic invertebrate is unknown although one study in Banks peninsula highlights the vulnerability of regionally endemic species to deforestation (Hardin 2003).

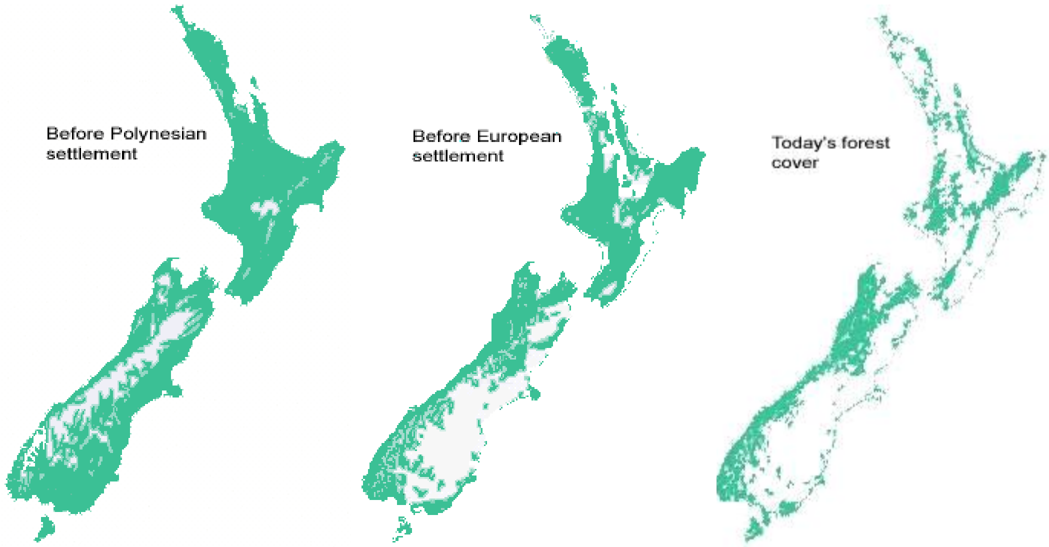

Figure 1.5. Human impact on forest and shrubland cover in New Zealand (McGlone 1989; Department of Survey and Land Information n.d.).

1.2.2 Characteristics of wood in New Zealand's forested streams

LW loadings in New Zealand's remaining indigenous forest streams range from 6-470 m^3 ha^1 (Evans et al. 1993; Baillie & Davies 2002; Meleason et al. 2005). These figures are comparable with international figures for LW volumes in streams of deciduous softwood and mixed conifer and hardwood forests (Gurnell 2003) in other regions around the world (Section 1.1.3.) but lower than the large amounts of wood stored in the older *Sequoia* and *Pseudotsuga* forested streams of the Pacific Northwest. LW in New Zealand's indigenous forest streams contribute to a range of morphological functions (Fig. 1.6), including storage and retention of sediment and organic matter, formation of debris dams, pool formation and bank armouring (Mosley 1981; Evans et al. 1993; Quinn et al. 1997; Baillie & Davies 2002).

LW volumes in New Zealand's mature pine plantation streams are similar to those in indigenous forest streams ranging from 2-327 m^3 ha^{-1} (Baillie et al. 1999b; Baillie & Davies 2002). Remnant indigenous timber comprised some of the LW at a few of those sites. LW in mature plantation forest streams contributed to a similar range of morphological functions as LW in indigenous forests streams. However, a high percentage of the LW in mature pine plantation streams was composed of recent wind-thrown stems suspended across the stream channel (Baillie et al. 1999b; Baillie & Davies 2002). Also piece length was on average lower in mature pine plantation streams than indigenous forest streams (1.9 m in Baillie & Davis 2002 c.f. 3.4 m in Meleason et al., 2005). As a result, the proportion of LW pieces influencing channel morphology tended to be lower than that in indigenous forest streams (Baillie & Davies 2002; Meleason et al 2005).

Harvesting operations in plantation forests can potentially contribute large pulses of wood to stream channels, particularly when extracting timber across waterways. A large proportion of this material is composed of SWD, often referred to as logging slash (branches, twigs, tops, needles etc.) (Baillie et al. 1999a). However, some of this material is composed of LW. If retained, and not removed during post-harvest stream-cleaning operations this source of LW can potentially last in streams for up to 20 years (Collier & Baillie 1999; Collier & Smith 2003).

There is no information on in-stream decay rates for New Zealand’s indigenous timbers but terrestrial decay rates (Clifton 1994; Stewart & Burrows 1994) vary widely and indicate that many indigenous species are likely to decay more slowly and last much longer in a stream system than *Pinus radiata* (Collier & Smith 2003). These differing decay rates along with hydrological and climatic variation will likely influence the strength and duration of debris dams in streams of different forest types across New Zealand.

Figure 1.6. Geomorphic influence of large wood in a New Zealand old-growth forest river system. Photo by B.R. Baillie.

1.2.3 Biological influence of wood in New Zealand's streams

Wood provides habitat for a range of organisms in New Zealand's waterways. The stable nature and rough surface of wood provides an organic substrate for the development of biofilms. Biofilms are a gelatinous matrix found on organic and inorganic surfaces in streams and contain complex communities of micro-organisms including algae, cyanobacteria, fungi, bacteria, protozoa and micro-invertebrates such as rotifers. Biofilms are an important component of stream food webs providing sites for primary production, carbon and nitrogen fixation, nutrient processing and accumulating detritus (Allan & Castillo 2009). In New Zealand, biofilm communities on wood often differ in composition to those found on inorganic substrates such as stones (Tank & Winterbourn 1996). Biofilm communities on wood blocks placed in some forested streams in the South Island were dominated by filamentous micro-organisms such as fungi and actinomycetes (bacteria), unicellular bacteria rods, and occasional algal cells (Tank & Winterbourn 1995, 1996). Colonisation of micro-organisms on wood was generally higher than on leaves. In contrast diatoms were more common in biofilms on stones and fungi were absent in biofilms on this substrate (Tank & Winterbourn 1996). Diverse microbial communities were also observed in biofilms that developed on exotic and indigenous blocks of wood placed into in a pine plantation spring-fed central North Island stream, including diatoms, filamentous algae, bacteria, fungi and/or actinomycetes (Collier et al. 2004). These findings contrasted however with the low diversity in microbial communities observed in biofilm on wood blocks in a pine plantation stream in Otago, a result the authors thought may have been affected by the chemical characteristics of the stream as wood in more open tussock streams supported higher densities of both bacteria and fungi (Thompson & Townsend 2004).

Wood is also used by a wide range of New Zealand's aquatic and semi-aquatic invertebrates. Most invertebrates are opportunists utilizing wood for habitat, pupation and oviposition sites, and as an additional food resource (wood biofilm, associated fine particulate organic matter, and detritus) (Anderson 1982; Tank & Winterbourn 1995; Collier & Halliday 2000; Collier & Smith 2003). Few species in New Zealand are xylophagous although three species, a Tipulidae larvae (*Limonia nigrescens*), a caddisfly larvae (*Pycnocentria funerea)* and a stonefly larvae (*Austroperla cyrene*) all preferring wood at more advanced stages of decay (Anderson 1982; Collier & Halliday 2000; Collier & Smith 2003). Wood is associated with high invertebrate taxa richness, density and total abundance. This is particularly notable in sandy or soft-bottomed streams that lack inorganic stable substrates (Collier & Halliday 2000; Maxted et al. 2003). Collier and Halliday (2000) found 81 taxa on wood compared with 64 taxa in a pumice-bed substrate, significantly higher densities of invertebrates on wood compared with the pumice stream bed and differences in community composition between the two substrates. Decay rate influenced the density of some species found on wood. In one North Island study, there was no significant difference in aquatic invertebrate community composition between *Pinus radiata* wood blocks and four other native wood species also indicating that decay rates and hence surface texture may be more important than wood type in influencing biofilm development and utilisation by invertebrates (Collier et al. 2004).

Wood is very effective at capturing and accumulating organic matter such as branches, twigs, leaves and finer particulate organic matter, and retaining this material for in-stream processing (Bilby 1981). This organic material provides additional habitat for aquatic invertebrates and in New Zealand, aquatic invertebrates in organic detritus often form distinct communities from those on inorganic substrates (Winterbourn 1978; Collier & Smith 2003). Part of this is attributable to the habitat heterogeneity provided by organic accumulations but also to the range of potential food sources available. A comparison of respiration rates and invertebrate colonisation of differing *Pinus radiata* organic substrates (wood blocks, cones, twigs and needles) indicated that the variability in habitat, decay rates and food source provide by this material were influencing aquatic invertebrate community composition (Collier & Smith 2003). Shifts in community composition, in particular shredder biomass, in association with leaf decay rates were also observed by Linklater (1995) in pools of three forested Canterbury, South Island streams. The role of wood in retaining organic matter and its influence on invertebrate community composition forms the basis of Chapter 5 and further information on this topic can be found in this chapter.

Wood provides overhead cover and pool habitat for a range of native fish, particularly species such as longfin eels (*Anguilla dieffenbachii*), inanga (*Galaxias maculatus*), giant kokopu (*Galaxias argenteus*), and banded kokopu (*Galaxias fasciatus*) and has a contributing influence on fish community structure (Hanchet 1990; Jowett et al. 1998; Chadderton & Allibone 2000; Bonnett & Sykes 2002; Baker & Smith 2007). Chadderton & Allibone (2000) reported that on Stewart Island, New Zealand, woody debris provided pool and backwater habitat particularly for banded kokopu. Banded kokopu's strong preference for cover was also observed by Rowe & Smith (2003) in some Coromandel, North Island streams, although undercut banks and large boulders were often preferred over woody debris. Larger sized longfin eels also showed a preference for in-stream debris in three New Zealand lowland streams (Glova et al. 1998). The role of wood in providing pool habitat and cover for fish is the focus of Chapter 3 and this topic is expanded in that chapter.

The diversity of habitat provided by wood also benefits other aquatic fauna in New Zealand's streams. The habitat heterogeneity provided by wood, increased available habitat for a freshwater crayfish (*Paranephrops planifrons*) in a central North Island stream (Parkyn et al. 2009). Although crayfish were abundant in undercut banks, sub-reaches containing stable embedded pieces of wood supported high densities and biomass of crayfish and higher numbers of larger sized crayfish than sub-reaches without wood. Similarly for the endangered blue duck (*Hymenolaimus malacorhynchos*), a species that lives year-round on rivers, the presence of LW increased the availability of roost habitat in a river system in the Bay of Plenty region of New Zealand (Baillie & Glaser 2005). Blue duck prefer roost habitat that provides cover and concealment and in this study, stable undercut banks were most commonly used as roost habitat followed by log jams. LW contributed solely, or in conjunction with other factors such as undercut banks and rocks toward 50% of roost sites utilised by blue duck.

1.3 Thesis Structure

1.3.1 Background

While numerous overseas studies have demonstrated the importance of wood in stream ecosystems (e.g. Harmon et al. 1986; Gregory et al. 2003; and chapters 1-4 in this thesis), much of the research has been focused at the reach scale, using a range of methodologies (Gregory et al. 2003 and references therein). New Zealand is similar in this regard (e.g. Mosley 1981; Evans et al. 1993; Baillie & Davies 2002; Meleason et al. 2005). Few studies have examined the spatial distribution and influence of wood within large river networks in old-growth undisturbed forests, using consistent sampling methods (Martin & Benda 2001; Reeves et al. 2003), and our knowledge on the role of wood at this scale is limited. Many western or industrialised countries have limited opportunities for this scale of research due to the heavy modification or removal of forests by humans (Montgomery et al. 2003). While New Zealand has also lost a large portion of its original indigenous forest cover, large areas of relatively undisturbed old-growth forest still remain. One such area provided an opportunity to undertake a study on the role of wood in a large forested river network and forms the first part of this thesis.

Most of the research on wood and the effects of wood removal on biological communities, has limited applicability to New Zealand's indigenous aquatic fauna. Research has focused on salmonid species, particularly in North America (Dolloff & Warren 2003), but no members of this group are a part of New Zealand's indigenous fish fauna. Most of New Zealand's freshwater fishes are endemic, and show a high degree of diadromy, with both species richness and abundance declining markedly with increasing altitude and distance inland (McDowall 2000; McIntosh & McDowall 2004). A high number of New Zealand's aquatic invertebrate species are also endemic, with no known obligate xylophages. New Zealand has few obligate shredders owing to the lack of strong synchrony with leaf fall patterns, commonly associated with northern hemisphere deciduous forests (Winterbourn et al. 1981; Boothroyd 2000; Thompson & Townsend 2000).

Implicit in the loss of forest cover since humans settled in New Zealand, is the loss of wood from water ways. While some studies in New Zealand have examined the effects of wood removal on stream ecosystems (Collier & Bowman 2003; Baillie et al. 2005), confounding factors associated with harvesting and riparian vegetation removal, such as changes in light, temperature and sediment regimes, have made it difficult to isolate the contribution of wood removal to ecosystem response. The direct effects of wood removal on New Zealand's indigenous aquatic invertebrate and fish communities are largely unknown and this topic forms the second part of this thesis.

1.3.2 Objectives

The overall aim of this thesis is to enhance knowledge on the functional and ecological role of wood in New Zealand's forested stream ecosystems. The specific objectives are to:

1) understand the role of wood at the catchment-scale by undertaking a field survey to classify and quantify the spatial variation in the source, volume, location and morphological influence of LW in a large river catchment of old-growth forest; and
2) determine the biological influence of wood by;
    a. assessing the influence of habitat provided by wood on indigenous fish and aquatic invertebrates and
    b. experimentally removing wood and associated debris dams from three stream sections to assess the effects on channel morphology, stream habitat, and aquatic invertebrate and native fish community characteristics.

The outcome is to provide information on the spatial distribution, function and ecological role of wood, and the effects of its removal, in New Zealand's freshwater systems in order to enhance its potential use as a tool in stream restoration. In plantation forests, results from this study will assist forest managers in the development of effective intervention strategies for post-harvest management of woody debris.

The hypotheses tested in this thesis and the rationale for predicting these hypotheses can be found in the core chapters of the thesis, Chapters 2-4.

1.3.4 Thesis outline

The next three chapters (Chapters 2-4) have been produced as a series of manuscripts for publication. As a result there is some overlap between chapters. The second chapter examines the spatial distribution, loading and physical influence of wood in a river system at the catchment scale. Following on from Chapter Two, Chapters Three and Four investigate the effects of experimental removal of wood from three small streams on channel morphology and indigenous fish and aquatic invertebrate communities. Chapter Five summarises the results of the thesis and provides recommendations for research and management.

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Chapter Two: Spatial distribution and influence of large woody debris in an old-growth forest river system, New Zealand

2.1 Abstract

A field survey was undertaken to determine the quantity, spatial distribution and influence of large wood (LW) in a fifth-order river system in old-growth forest in New Zealand. LW attributes were assessed at 25 sites distributed in the headwaters and along the main stem of the Whirinaki River system (73 km^2). LW volume, number of pieces, piece length and piece size, were positively correlated with bankfull width, whereas the number of pieces/unit area, LW/unit area, number of pieces suspended across the channel and LW influence on channel morphology, were negatively correlated. Pieces influencing channel morphology were larger, longer and more stable than average. We identified four key zones in the river system based on LW spatial distribution patterns and influence on habitat complexity. Zonal boundaries occurred where there were changes in the transport capacity, fluvial processes, channel width and geomorphic structure of the channel. The results of this study highlight the need to understand the characteristics, spatial distribution patterns and influence of LW at the catchment level when undertaking protective, management or rehabilitation programmes in forested river ecosystems.

2.2 Introduction

Large wood (LW) is an important component of forested stream ecosystems, influencing stream hydraulics, channel morphology, sediment and organic matter routing and storage, habitat heterogeneity and biological communities (Harmon et al. 1986; Bilby & Ward 1989; Bilby & Bisson 1998; Benke & Wallace 2003; Dolloff &

Warren 2003; Swanson 2003). LW enters stream systems via a range of chronic and episodic processes (Keller & Swanson 1979; Bilby & Bisson 1998; Reeves et al. 2003). The source area and amount of contributing LW to stream systems varies according to the species, composition and age of riparian forests, local topography, channel characteristics and disturbance history.

The relative importance of geomorphic and hydrologic processes that control input, loadings, redistribution and morphological influence of LW vary with position in the stream network (Keller & Swanson 1979; Bilby & Bisson 1998; Gurnell 2003; Swanson 2003; Chen et al. 2006). In steep forested headwaters, input processes such as avalanches, landslides, and debris torrents can deliver large quantities of debris to the stream system, often from distances well beyond the immediate stream channel (Keller & Swanson 1979; Bilby & Bisson 1998; Reeves et al. 2003; Chen et al. 2006). Where there is insufficient discharge and stream power in these small streams, LW pieces remain relatively immobile (Bilby & Ward 1989; Robison & Beschta 1990; Gurnell 2003; Swanson 2003). In medium sized streams, there is an increase in LW recruitment from tree mortality and bank undercutting (Keller & Swanson 1979; Robison & Beschta 1990; Martin & Benda 2001). Hydraulic processes dominate, as stream size and depth increases; LW pieces are less likely to span the channel, and are more likely to mobilise with increasing discharges. The number of LW pieces tends to decrease down the stream system with a corresponding increase in piece diameter, length, and volume, (Bilby & Ward 1989; Robison & Beschta 1990; Richmond & Fausch 1995; Gurnell 2003; Chen et al. 2006). Dam frequency and channel-spanning dams also decrease as dam size and inter-spacing increases down the stream channel (Keller & Swanson 1979; Martin & Benda 2001; Abbe & Montgomery 2003). In-channel inputs of LW operate throughout the river system, and are mainly derived from downstream movement of LW. In wider channels of larger rivers where LW no longer spans the channel and discharge regime can move most pieces in high flows, flotation is a significant process and the rivers geomorphic structure is an important control on LW retention and debris dam structure (Keller & Swanson 1979; Harmon et al. 1986; Abbe & Montgomery 2003; Gurnell 2003).

Morphological function of LW also exhibits trends within a catchment. LW is often a primary agent in step and pool formation and controls the movement and storage of sediment, particulate organic matter and nutrients through channel networks (Mosley 1981; Harmon et al. 1986; Bilby & Ward 1989; Richmond & Fausch 1995; Bilby & Bisson 1998; Rosenfeld & Huato 2003). Its influence on all these factors tends to decline along the stream system as LW loadings decrease and channels widen. Key factors influencing the stability and retention of LW pieces throughout a river network include the ratio of piece length and diameter to bankfull width and depth, wood density, and degree of anchoring, with rootwads greatly increasing piece stability (Martin & Benda 2001; Abbe & Montgomery 2003; Gurnell 2003).

Our knowledge and understanding of LW dynamics within a river network has been derived by integrating information from a large number of studies, over a wide range of stream types and sizes, in varying forest types, using a range of sampling methods. Few studies have examined spatial distribution of LW over a range of stream sizes within a large catchment using consistent sampling methods (Swanson 2003). Martin and Benda (2001) and Reeves et al. (2003) are two examples, although neither study sampled the steeper headwater streams.

In New Zealand, reach-scale studies to date have examined LW loadings and influence on stream channel morphology in a number of stream systems, focusing on smaller sized streams in both indigenous and exotic pine plantation forests (Mosley 1981; Evans et al. 1993; Baillie et al. 1999; Baillie & Davies 2002; Meleason et al. 2005), but distribution patterns of LW and morphological influence have not been studied at the catchment level. The objectives of this study were to a) describe and quantify the amount and spatial distribution of LW in a large catchment of old-growth forest, and b) determine the influence of LW on channel morphology and habitat complexity.

2.3 Study Area

The Whirinaki River is located in the Whirinaki Forest Park in the central North Island of New Zealand (Fig. 2.1). This catchment was chosen for the study as it provided a large 5th order river system in old-growth forest, representative of the dominant indigenous forest type in New Zealand. The catchment area is 73 km^2 and altitude ranged from 580 to 1180 m.a.s.l. Hillslopes are steep, >35° in the headwaters, and 26-35° throughout most of the catchment, except for a plateau area in the south-western corner (slope 0-3°), (Ministry of Works and Development 1979). Geology is predominantly greywacke in the southern section of the study area with overlying Podzolised Orthic Pumice Soil, and predominantly ignimbrite in the remaining northern and eastern areas with associated Humose Orthic Podzol Soil (Grindley 1960; Ministry of Works and Development 1979; Hewitt 1998). Mean annual rainfall in the area is 1523 mm (New Zealand Meteorological Service (n.d.)).

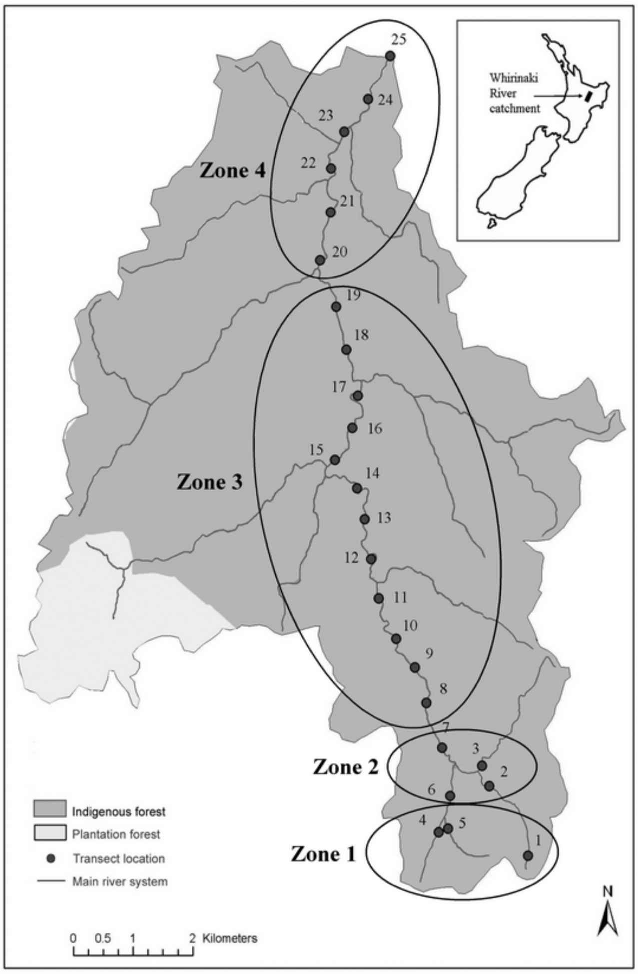

Figure 2.1. Forest type, transect location and zones (sections with similar LW distribution patterns and influence on channel morphology) in the Whirinaki catchment. Descriptions of each Zone are in Section 2.6.3. Zonal patterns of LW distribution and influence.

The indigenous forest (Fig. 2.1) is primarily beech (*Nothofagus* sp.) or beech-rimu (*Dacrydium cupressinum*) forest (Nicholls 1974), which developed following the Taupo eruption 1850 BP (Wilmhurst & McGlone 1996). Beech or mixed beech forests comprise approximately 68% of New Zealand's indigenous forests (Wardle 1984). Silver and red beech (*Nothofagus menziesii*, *Nothofagus fusca*) were the dominant riparian tree species throughout the river system, additional species included tawari (*Ixerba brexiodes*), kamahi (*Weinmannia racemosa*) and tree ferns (mainly *Cyathea smithii*). The plateau area in *Pinus radiata* plantation forest (Fig. 2.1) was outside the main study area.

Catchment areas upstream from transects ranged from 0.2 km^2 in the headwaters to 73 km^2 at the downstream end of the study area. Bankfull width ranged from 1.5 m in the headwaters to 18.0 m in the lower part of the river system. Channel gradients ranged from 1.5–15.5° in the headwaters and were ≤2° along the remainder of the channel system (Fig. 2.2). Riffles were the dominant channel unit in the Whirinaki River system, followed by runs, pools and rapids (Fig. 2.2). Waterfalls, cascades and steps were confined to the steeper headwater sites or where mean gradient was ≥2º.

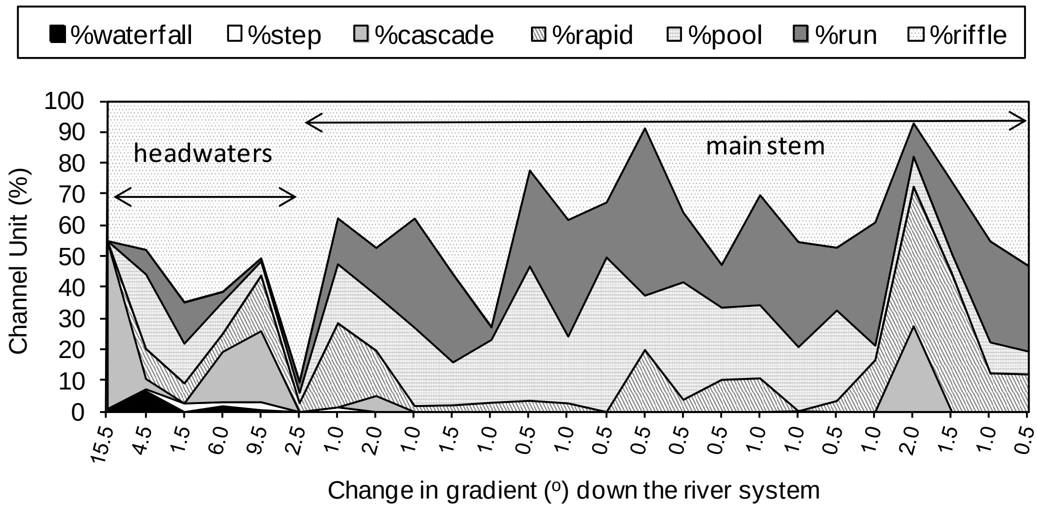

Figure 2.2. Changes in average gradient and channel unit composition in the head waters and along the main stem of Whirinaki River system. The x axis shows the average gradient of each of the 25 transects.

2.4 Methods

The field survey was undertaken in autumn (March/April) in baseflow conditions. Twenty-five transects, 200 m in length, and extending across the bankfull width (the horizontal distance between the tops of the channel banks) of the stream channel were spaced at approximately 1 km intervals in the headwaters and along the main stem of the channel of the Whirinaki River (Fig. 2.1). Several transects were relocated from their original position because of access and safety issues. Bankfull width was measured to the nearest 0.1 m at 10 m intervals along each transect and averaged. Channel gradient was measured to the nearest 0.5 degree using a clinometer. Gradients less than 0.5 degree were recorded as 0.1 for calculation purposes. Several gradient readings were taken to capture as much of the transect length as possible, averaging 10 readings per transect (range 5-20). An average gradient weighted by distance was calculated for each site. Channel units (i.e. pool, riffle, run) were defined using the hierarchical classification system of Hawkins et al. (1993) and the length of each unit along the 200 m transect was measured to the nearest 0.1 m. Pool type (Hawkins et al. 1993) and pool-forming factors were recorded for each pool.

For each transect, we measured the length of transect where only one channel unit spanned the channel width (simple habitat) and the length where 2 or more units spanned the channel width (complex habitat). The factors creating the complex habitat were recorded for each section of complex habitat, i.e. LW, gravel bar etc.

All LW ≥ 10 cm in diameter and 1 m length, within the bankfull channel was measured for small-end diameter, mid-stem diameter and large-end diameter. The three diameters were averaged to calculate mean diameter for each piece. The length submerged or above the water column was recorded. The volume of each piece was calculated using Newton’s formula (Harmon & Sexton 1996):

$$V_{piece} = \frac{L(A_b+4A_m+A_t)/6}{10,000}$$

where V_{piece} = volume of piece (m^3); L = length of piece (m); A_b = area at the base of the piece (cm^2); A_m = area at the mid-point of the piece (cm^2); and A_t = area at the top of the piece (cm^2). The width, height, and depth of rootwads were summed to give an approximate volume and were excluded from LW diameter and length statistical analysis. LW volumes in each transect were expressed as m^3 ha^{-1} using bankfull width and transect length to calculate streambed area.

Each piece was classified according to orientation (1: parallel to stream flow; 2: 90° to stream flow; 3: 45/225° to stream flow and 4: 135/315° to stream flow) and position in the channel (suspended across channel; partly suspended across channel; on the channel floor; along bank edge; in a debris dam). Each piece was classified as stable if it had one or more of the following characteristics; a rootwad, length extended outside the channel, or the piece was partially buried. Where possible, the source of each piece was recorded under the following categories; bank undercutting, upslope wind-throw, bank edge windthrow, landslide/slip and unknown. LW influence on channel morphology was described as follows; no influence, sediment storage, step formation, flow deflection, bank armouring, wood storage, organic matter (twigs, leaves, fine organic matter) storage and pool formation. Key riparian species most likely to supply LW to the stream system were recorded at each site (see study area), along with descriptive notes on LW and debris dam distribution patterns in the stream channel.

2.5 Analysis

Correlation analysis was used to examine the relationships between bankfull width, gradient and catchment area. Descriptive statistics were used to analyse channel unit composition and LW characteristics. Linear regression was used to examine relationships between bankfull width and a range of LW characteristics. Paired t-tests were used to determine whether LW orientation and position in the channel differed from a random distribution pattern and linear regression was used to examine longitudinal distribution patterns using bankfull width as the dependant variable. T-tests using SAS statistical software (Version 9) were performed on log-transformed (geometric) mean diameter and (geometric) mean length to test for significant differences in the dimension of LW pieces influencing versus those LW pieces not influencing channel morphology. Paired t-tests were used to compare LW piece stability and piece length to bankfull width ratios, between pieces influencing versus those not influencing channel morphology. Based on these results and field notes, we identified 4 zones of LW distribution and influence. One-way ANOVA was used to test for significant differences in key LW and pool attributes between zones. Log transformations were used where appropriate. Angular transformation was used for all percentage variables. Results were considered significant if $P \leq 0.05$.

2.6 Results

The three catchment variables of catchment area, bankfull width and gradient were highly correlated ($r = 0.82\text{-}0.98$). Initial analysis of a range of LW dependant variables with the three catchment variables showed that in most instances, strongest correlations were with bankfull width, followed by catchment area and gradient. Therefore results are presented for bankfull width only, with reference to the other catchment variables where appropriate.

2.6.1 LW characteristics

A total of 2799 pieces of LW were measured in the 25 transects. Details of LW characteristics are in Table 2.1. The majority of pieces were ≤10 m in length and the majority of piece diameters were ≤ 40 cm. There was a significant increase in the number of pieces and a significant decrease in pieces/unit area with increasing bankfull width (Fig. 2.3a). Geometric mean piece length increased significantly down the river system (Fig 2.3b). However, LW geometric diameters showed a weak and slightly negative downstream trend. As a result, mean piece size (m^3) showed a weakly positive, but non-significant relationship, with bankfull width. LW volume/unit length (m^3/200m) showed a significant increase in a downstream direction, whereas LW volume/unit area showed a significant negative trend (Fig

2.3c). Most of the LW volume was above the surface of the water, averaging 80% (range 57 – 97%), with 20% on average (range 3 – 43%) submerged in the water.

Table 2.1. LW characteristics in the Whirinaki River.

	Mean	Range	R^2 values bankfull width
Abundance (pieces 200 m^{-1})	112	23-228	0.43**
Density (pieces/unit area (m^2))	0.06	0.02-0.19	0.47**
Diameter (cm) ^{A}	22.5	18.5-28.9	0.18*
Length (m) ^{A}	2.1	1.5-2.5	0.55**
Mean piece size (m^3)	0.35	0.16-0.93	0.07
Vol (m^3 200 m^{-1})	39	9-78	0.45*
Vol/unit area (m^3 ha^{-1})	212	59-503	0.37*
Piece length (m) to bankfull width (m) ratio	0.29	0.12-1.21	0.98**

* $P \leq 0.05$; ** $P \leq 0.01$; n = 25.
^{A} geometric mean

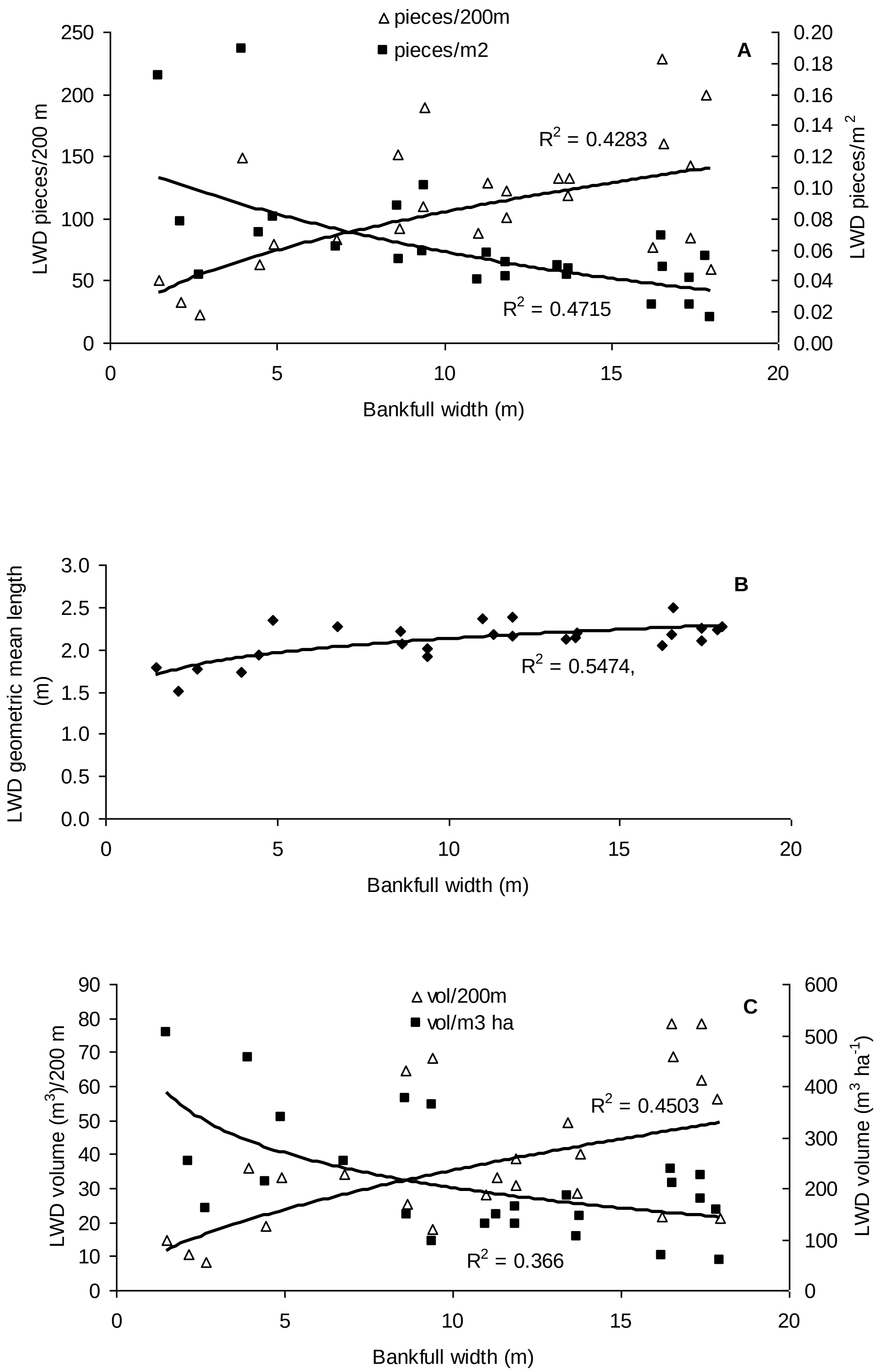

Figure 2.3. Relationships between bankfull width and a) LW piece frequency and LW piece density; b) LW piece length; c) LW volume/unit length and LW volume/unit area. $P \leq 0.01$ for all trend lines.

The percentage of pieces orientated parallel or perpendicular to stream flow (class 1 and 2) were significantly higher than if the pieces had been randomly orientated whereas the percentage of pieces in orientation classes 3 and 4 were lower (Table 2.2). Downstream trends in the 4 orientation classes were in most cases either weak or absent. The percentage of pieces in position 1 and position 4 (Table 2.2) were significantly lower and higher respectively than if the pieces had been randomly positioned. Sixty percent of pieces suspended across the stream channel were located in the 6 headwater sites and decreased significantly down the river system with increasing bankfull width (R^2 = 0.80; P<0.01). The percentage of pieces in position 2 showed a weaker but significant decrease down the river system (R^2 = 0.24; P<0.01 for bankfull width) whereas the percentage of pieces in position 5 increased (R^2 = 0.55; P<0.01 for bankfull width).

Table 2.2. LW source and location.

Orientation	**1**	**2**	**3**	**4**	
%	33	29	19	18	
Position	**1**	**2**	**3**	**4**	**5**
%	5	21	19	32	23
Source*	**bank undercutting**	**upslope windthrow**	**bank edge windthrow**	**landslide/ slip**	**unknown**
%	41	25	17	2	15

* *in situ* pieces only, n = 247. Orientation - 1: parallel to stream flow; 2: 90° to stream flow; 3: 45/225° to stream flow and 4: 135/315° to stream flow. Position in the channel - 1: suspended across channel; 2: partly suspended across channel; 3: on the channel floor; 4: along bank edge; 5: in a debris dam.

Forty percent of the pieces were classified as stable. The main stability factor was partial burial in the bank or substrate (65%), followed by the piece length extending outside the channel (16%) or possessing a rootwad (13%). Five percent of pieces had a combination of stability factors. We identified 9% of LW pieces as *in situ*, and the majority were sourced from bank undercutting (Table 2.2). There were no identifiable downstream trends in *in situ* LW sources.

2.6.2 LW influence on channel morphology and habitat diversity

Of the 2799 LW pieces measured, 1351 pieces (48%) were influencing channel morphology, and 468 (35%) of those pieces were influencing more than one aspect of channel morphology. Wood storage, bank armouring and sediment storage were key morphological functions of LW in the Whirinaki River system (Fig. 2.4). The proportion of pieces influencing wood storage was positively correlated with bankfull width (R^2 = 0.42; P<0.01); bank armouring was negatively correlated with bankfull width (R^2 = 0.32; P<0.01), whereas sediment storage showed no trends at all. LW influenced pool formation in 43% of all pools (n = 219) and the density of pools influenced by LW was positively correlated with LW volume (R^2 = 0.35; P <0.01). LW influence was highest for debris pools, backwater pools and plunge pools (93%, 76% and 45% of all pools respectively).

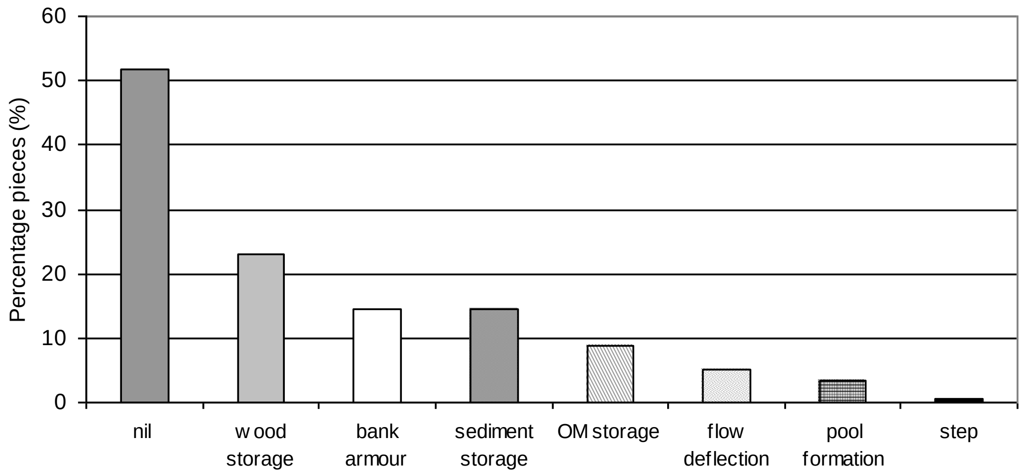

Figure 2.4. Morphological function of LW in the Whirinaki river system. OM = organic matter (twigs, leaves, fine organic matter). NB: total % >100 as some pieces provided multiple functions.

The pieces influencing channel morphology had significantly larger diameters and lengths, higher piece length to bankfull width ratios, and a higher proportion of stable pieces than pieces with no influence. There were eighty-three key LW pieces forming debris dams and they were longer (mean length 4.5 m), larger (mean diameter 36 cm) and more stable (75% of key pieces) than average (Fig 2.5). Sixty-two percent of the key pieces were orientated across the stream channel.

Figure 2.5. An example of a key piece of stable wood forming a debris dam in the Whirinaki River.

Habitat complexity (where 2 or more channel units spanned the channel width) was 0% in the three smallest headwater sites and low in the three remaining headwater sites (3-8% of channel length). Habitat complexity varied along the remainder of the river channel (Fig 2.6) but showed a significant increase with increasing bankfull width (R^2 = 0.47; P<0.01). LW, gravel bars and variations in substrate influenced habitat complexity in the upper to middle sections of the river system (Fig. 2.6). In the lower section, mid-channel islands were the key contributors to habitat complexity, with an exception in a steeper section of rapids and cascades (transect 22) where the influence of LW dominated. The length of sections of complex habitat averaged 6.7 m and was significantly shorter than the average length of simple habitat (where only one channel unit spanned the channel width) at 9.7 m (paired t-test, P = 0.01, n = 22).

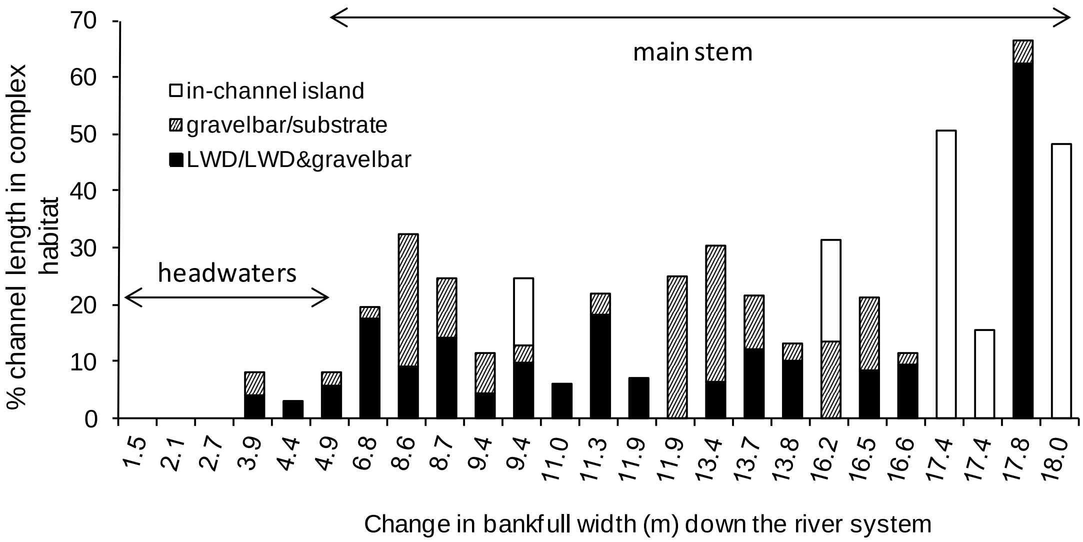

Figure 2.6. The influence of LW and other factors on habitat complexity in the headwaters and along the main stem of the Whirinaki River system. The x axis shows the average bankfull width of each of the 25 transects.

2.6.3 Zonal patterns of LW distribution and influence

We identified 4 main zones of LW distribution patterns in the Whirinaki River system (Table 2.3). In Zone 1, the three small headwater sites (Fig. 2.1), wood loadings were lower than the three remaining zones (Table 2.3). The majority of pieces were *in situ*, and high proportions were suspended across the channel. Debris dams were absent and influence of LW on channel morphology and habitat complexity was low (Table 2.3). The majority of plunge pools were located in the headwater sites (Zones 1 and 2) and pools were absent at one site.

In Zone 2 (Fig. 2.1), wood loadings increased along with influence on channel morphology and habitat complexity. The proportion of pieces spanning the channel width was significantly lower than Zone 1 but higher than the two downstream zones (Table 2.3). Debris dams spanned the channel and there was an increase in the proportion of pieces stored in debris dams. The average number of pools and influence of LW on pool formation was highest in this zone. Lateral pools increased significantly in this and the remaining 2 downstream zones and were rarely found where mean gradient was $\geq 3°$.

Table 2.3. Zonal characteristics of LW in the Whirinaki River system.

	Zone 1	Zone 2	Zone 3	Zone 4
No. of transects	3	4	12	6
Bankfull width (m)	1.5-2.7	3.9-8.6	9-18	16-18
Mean LW vol. (m^3 200 m^{-1} transect)	11b	38ab	40a	50a
Mean no. pieces	36b	111a	133a	109a
Mean % suspended pieces	27a	9b	1c	0.2c
Mean % pieces in debris dam	0c	16b	26ab	31a
Piece influence on habitat complexity (mean %)	0b	6ab	15a	3b
Piece influence on channel morphology (mean %)	34a	44a	37a	42a
Piece influence on pool formation (mean %)	4b	51a	47a	36ab
Mean no. of pools 200 m^{-1} transect	8ab	13a	10a	4b

* Figures with the same letters are not significantly different ($P \geq 0.05$).

Zone 3 (Fig. 2.1) was characterised by a pool/riffle/run morphology (Fig 2.2). Wood loadings, and influence on channel morphology and pool formation were similar to Zones 2 and 4 but LW influence on habitat complexity was highest in this zone (Table 2.3). As bankfull width increased beyond 9 m, there were fewer channel spanning LW pieces. There was a significant increase in the proportion of pieces in debris dams (Table 2.3), wood storage sites were predominantly along the outer bends (Fig 2.7) or at the head of gravel bars and debris dam inter-spacing increased.

While wood loadings in Zone 4 were similar to Zones 2 and 3, LW influence on habitat complexity was lower (Table 2.3). Instead in-channel islands were the main contributor to habitat complexity for Zone 4 and provided additional storage sites for wood. Channel spanning pieces were rare and pools were scarce in Zone 4.

Figure 2.7. Wood storage along an outer bend in Zone 3 of the Whirinaki River.

2.7 Discussion

There were distinct catchment-scale distribution patterns of channel units and LW in the Whirinaki River system. Longitudinal trends in LW frequency, volume, length, piece size and position were obvious along the river system and most strongly related with bankfull width. The influence of LW on channel morphology decreased along the river system as LW loadings declined. Most of these trends are similar to other catchment studies (Bilby & Ward 1989; Robison & Beschta 1990; Abbe & Montgomery 2003; Chen et al. 2006), in spite of the smaller piece dimensions compared to the Pacific Northwest. As stream size and power increases, piece retention and stability decreases and only the larger more stable pieces which are more resistant to movement downstream are likely to remain in place, and influence channel morphology. However we did not find an increase in piece diameter down the river system. This is in contrast to some other studies (Bilby & Ward 1989; Robison & Beschta 1990; Chen et al. 2006) but similar to Beechie and Sibley (1997) who also found no correlation between LW diameter and channel width. The non-random orientation of pieces in the channel indicated that angle of tree entry and fluvial processes were influencing piece orientation. LW was a key pool-forming factor in the Whirinaki River system, influencing pool formation in 43% of the pools. This figure is similar to Beechie and Sibley (1997) and Baillie and Davies (2002); but lower than Richmond and Fausch (1995).

There were no obvious longitudinal trends in sources of LW to the stream channel. Bank undercutting and wind throw were the principle wood delivery processes to the channel along the Whirinaki River system, similar to some other studies (Keller & Swanson 1979; Bilby & Bisson 1998; Martin & Benda 2001). Only a quarter of *in situ* pieces were from upslope sources. The low contribution of upslope sources of LW to the headwater streams of the Whirinaki River, even in the steeper headwater streams, may indicate relatively stable hill slopes, or timing of sampling during a relatively stable period in the disturbance regime of the catchment. In steep headwater sites, upslope processes such as landslides and avalanches can deliver large amounts of LW to streams (Keller & Swanson 1979; Lienkaemper & Swanson 1987). However, in Reeves et al. (2003) upslope sourcing of LW was highest in middle stream reaches and in the U shaped valleys and in lower gradients observed by Martin and Benda's (2001) study, landslides were a minor source of LW for streams. This shows that the contribution of upslope sources to in-stream LW does vary between sites depending on factors such as topographical features, hill slope stability and vegetation composition.

Piece length, diameter, stability and geometric mean length to bankfull width ratios were important factors in determining which pieces were likely to influence channel morphology and debris dam formation in the Whirinaki. These features were consistently higher in pieces influencing channel morphology throughout the river system. Rootwads, degree of burial, piece length and diameter and associated ratios with bankfull width and depth, are critical factors in determining piece stability and influence on channel morphology and debris dam formation in river systems, as previously reported by other studies (Martin & Benda 2001; Abbe & Montgomery 2003; Gurnell 2003; Rosenfeld & Huato 2003).

Changes in transport capacity, fluvial processes and geomorphic characteristics in the Whirinaki River system, defined the transitional boundaries between zones of LW distribution patterns. We found similar zonal patterns of LW distribution and influence to those in Gurnell's (2003) review paper, which were derived from a variety of studies, when tested in a single large river system with consistent methodology. In Zone 1 (Fig. 1), there was insufficient stream power to move LW pieces and in one site, pools were absent, indicating insufficient stream power during high flows to initiate scouring processes. Small colluvial reaches such as these have a limited transport capacity (Montgomery & Buffington 1997) and are unlikely to provide a source of LW and sediment to the lower river system, except in extreme hydrological events or debris flows.

In Zone 2, the increase in channel width and stream power increased the capacity of fluvial processes to shift wood down the river system, redistributing pieces into distinct accumulations. However, channel width constrained movement of larger pieces and a high proportion of individual pieces and debris dams still spanned the channel width, typical of streams this size (Keller & Swanson 1979; Robison & Beschta 1990; Bilby & Bisson 1998; Chen et al. 2006).

In Zone 3 where bankfull widths increased beyond 9 m, the influence of channel width on piece retention diminished and there was a shift to fluvial processes and the geomorphic structure of the river system dominating wood distribution. Fluvial processes redistributed LW pieces into debris dams predominantly located along the outside of meander bends although in-channel obstructions to wood movement such as heads of gravel bars also provided wood storage sites. Presence of sediment deposits such as gravel bars indicated that in this section of the river system, sediment supply exceeded the transport capacity of the river system.

Similar processes operated in Zone 4, with in-channel islands providing additional wood storage sites and a major contribution to habitat complexity. The exception was one transect in a higher gradient bedrock controlled section of river. In spite of the high transport capacity usually associated with this type of morphology (Montgomery & Buffington 1997), LW levels were comparable with adjacent transects and LW was the key influence on habitat complexity.

2.8 Conclusion

This study demonstrates the importance of sampling both the headwaters and the main stem of a river system to capture catchment-wide LW distribution patterns. Distribution patterns can change rapidly in headwater sites where there are considerable changes in bankfull width, gradient and stream power over comparatively short distances. While most LW studies have focused solely on the role of LW in providing habitat diversity we have been able to quantify the impact of LW on habitat diversity in relation to other contributing factors in the wider river network.

The characteristics and location of pieces likely to be retained in a river system and their contribution to habitat diversity varies throughout the river network. This information can provide guidance to managers when manipulating, enhancing or protecting LW sources in large river systems. For example the retention of appropriate pieces following harvest can assist in minimising harvest impacts on aquatic ecosystems and accelerating post-harvest recovery. Judicial use of LW can also enhance habitat for a variety of in-stream and riparian species and provides a management tool in the conservation of endangered species (Benke and Wallace, 2003; Dollof and Warren, 2003; Steel et al., 2003; Baillie and Glaser, 2005; Nicol et al., 2007).

This study, contributes to our global understanding of the role of LW in old-growth forested stream ecosystems and shows similar results to other large catchment scale studies in the northern hemisphere forests, primarily in the Pacific North-west region of the United States of America (Bilby and Ward 1989; Martin and Benda 2001; Abbe and Montgomery 2003; Chen et al., 2006). However, this study has focused on a single catchment and requires replication in other forest types (natural and man-made), with differing levels of natural and human disturbance. These results highlight the need to understand river systems and associated LW patterns at the catchment level when undertaking protective, management or rehabilitation programmes in forested river ecosystems.

To determine whether or not the habitat diversity provided by wood results in increased biological diversity a wood manipulation experiment was carried out which examined the effects of wood and its removal on indigenous fish (Chapter 3) and aquatic invertebrate communities (Chapter 4).

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Chapter Three: The effects of wood and wood removal on channel morphology and indigenous fish communities in New Zealand forest streams

3.1 Abstract

The influence of wood on the structure and function of stream ecosystems and associated fish communities has been extensively studied overseas, particularly in North America. Little is known on the effects of wood and its removal on New Zealand's indigenous fish communities. To study this, we conducted a field trial to a) examine differences in fish communities between wood pools (where wood provided cover), open pools and riffles in three small forested streams prior to wood removal and b) measure the effects of wood removal on channel morphology and fish communities.

Prior to wood removal, there were no significant differences in total fish density between the three habitats. Total fish biomass was marginally significant with most of the fish biomass located in wood pools. Species richness was highest in the riffles and torrent fish, bluegill bullies and redfin bullies were the main species differentiating fish communities in riffles from wood and open pools. The density and biomass of banded kokopu (*Galaxias fasciatus*) and the weights of longfin eels (*Anguilla dieffenbachii*) were highest in the wood pools. While habitat partitioning was evident for a few specialist species such as torrentfish (*Cheimarrichthys fosteri*), bluegill bullies (*Gobiomorphus hubbsi*), and banded kokopu, a core of generalist species contributed to the spatial overlap in community composition between the three habitats.

Wood removal had a marked effect on channel morphology, significantly reducing the area of pools and increasing the length and area of riffles. After wood removal most of the fish biomass was located in the remaining wood pools in the

control sections. Banded kokopu densities were highest in the wood pools and open pools in the control sections and large longfin eel densities were highest in the wood pools in the control sections. At the reach scale, banded kokopu biomass was significantly lower in the sections where wood was removed.

Although wood pools were a small portion of total habitat, they provided important habitat for two of New Zealand's larger indigenous fish species. These two fish constituted most of the fish biomass and were key determinants of fish community structure in these streams.

3.2 Introduction

Large wood (LW) provides a significant structural and functional role in streams by increasing hydrological and geomorphological complexity and controlling the retention and movement of organic matter and sediment through the stream system (Bilby 1981; Mosley 1981; Montgomery et al. 2003; Mutz 2003; Rosenfield & Huato 2003; Andreoli et al. 2007; Wondzell 2009). LW influences ecological and biological processes in stream systems by increasing habitat heterogeneity, and providing food resources, refuge and habitat for aquatic biota (Anderson 1982; Benke & Wallace 2003; Dolloff & Warren 2003; Rowe & Smith 2003; Nicol et al 2007).

One of the more important functions of LW for fish is the creation of pool habitat and overhead cover. The diversity and complexity of habitat created by LW also provides refuge in extreme hydrological conditions, protection from predators, isolation from competitors, and facilitates co-existence of competitive species (Sedell et al. 1990; Fausch & Northcote 1992; Dolloff & Warren 2003). LW has a secondary effect on fish populations by influencing the underlying food web that supports fish communities (Benke & Wallace 2003). LWD facilitates primary production by providing an alternate substrate for algae and biofilms and storages site for the retention of nutrients and organic matter for in-stream processing. This enhances secondary production by providing additional food sources and an alternate stable substrate for aquatic invertebrates, a primary food source for fish (Bilby & Bisson

1992; Tank & Winterbourn 1995, 1996; Collier & Halliday 2000; Benke & Wallace 2003; Bilby 2003; Dolloff & Warren 2003). As a result, fish species and abundance is usually higher and fish populations are typically larger in streams with high LW loadings (House & Boehne 1987; Fausch & Northcote 1992; Inoue & Nakano 1998).

Clear-cut logging to the stream edge, followed by stream cleaning (removal of logging slash i.e. stems, branches, twigs, and needles, from the stream channel) can affect channel morphology, water chemistry, light, temperature, fluvial, sediment and organic regimes, and primary and secondary production. The interaction of these physical, chemical and biological changes can adversely affect stream biota such as invertebrates and fishes (Campbell & Doeg 1989; Hicks et al. 1991; Collier & Bowman 2003; Baillie et al. 2005). In these circumstances, it can be difficult to isolate the effects of wood removal on the stream environment.

Wood removal experiments undertaken in mature or second-growth forest typically increase sediment export from stream systems due to the immediate loss of material stored behind debris dams. Marked changes in channel morphology often occur as sediment is mobilised and redistributed throughout the system (MacDonald & Keller 1987; Smith et al. 1993a; Diez et al. 2000). The most significant effect of wood removal on fishes is the degradation of aquatic habitat, through the loss of wood cover and undercut banks, and reduction of low energy refuge sites such as pools. While the effects of LW on stream hydrology and habitat have been well demonstrated (Montgomery et al. 2003), the modification of fish communities is less consistent as it is dependent on the life-history of the species present. In some cases, loss of LW resulted in a decrease in the abundance, size and biomass of both warm water and coldwater fish species, particularly in smaller sized streams (Angermeier & Karr 1984; Fausch & Northcote 1992; Dolloff & Warren 2003), while in other cases fish response varied both spatially and temporally with some species showing little or no response to wood removal (Lestelle 1978; Warren & Kraft 2003).

Most of the research on wood and fish interactions has focused on pelagic salmonid and warmwater fish species in North America (Dolloff & Warren 2003), which are not part of New Zealand's indigenous freshwater fish fauna. Stream dwelling species in New Zealand tend to be endemic, benthic, nocturnal, and show a high degree of diadromy (McDowall 2000; McIntosh & McDowall 2004). A number of these fish species exploit the pool habitat and overhead cover provided by wood and associated vegetation. Galaxiid species such as banded kokopu, giant kokopu and inanga all show a preference for cover provided by overhanging or submerged wood and vegetation, undercut banks, and low velocity habitat such as pools and backwaters (Main 1988; Taylor 1988; Jowett et al. 1998; Chadderton & Allibone 2000; Bonnett & Sykes 2002; Baker & Smith 2007). Longfin eels are more ubiquitous, exploiting a wide range of habitats, but their preference for in-stream cover and slow-flowing waters has been noted in a number of studies (Taylor 1988; Glover et al 1988; McDowall 2000), particularly the larger sized eels. Other fish species such common bullies (*Gobiomorphus cotidianus*) are more closely associated with open habitats whereas bluegill bullies, torrentfish and koaro (*Galaxias brevipinnis*) are more commonly associated with faster flowing habitats such as riffles and torrents where cover is mainly provided by cobbles and boulders (Taylor 1988; McDowall 2000).

The direct effects of wood removal on New Zealand's indigenous fish communities are unknown. However as wood removal usually results in the loss of cover and low velocity habitats such as pools, it is likely that the greatest effect will be on those species where cover and low velocity areas are important components of their habitat requirements.

The objective of this study was to evaluate the role of wood in small forested stream ecosystems by artificially removing wood from the stream channel and measuring the effect on channel habitat and indigenous fish communities. I hypothesised that: (1) prior to wood removal, fish communities in pools with wood would differ from pools without wood (open pools) and riffles; (2) wood removal would alter channel morphology reducing the number, size and type of pools; and (3) wood removal would reduce fish abundance and alter fish communities.

3.3 Materials and methods

3.3.1 Study area

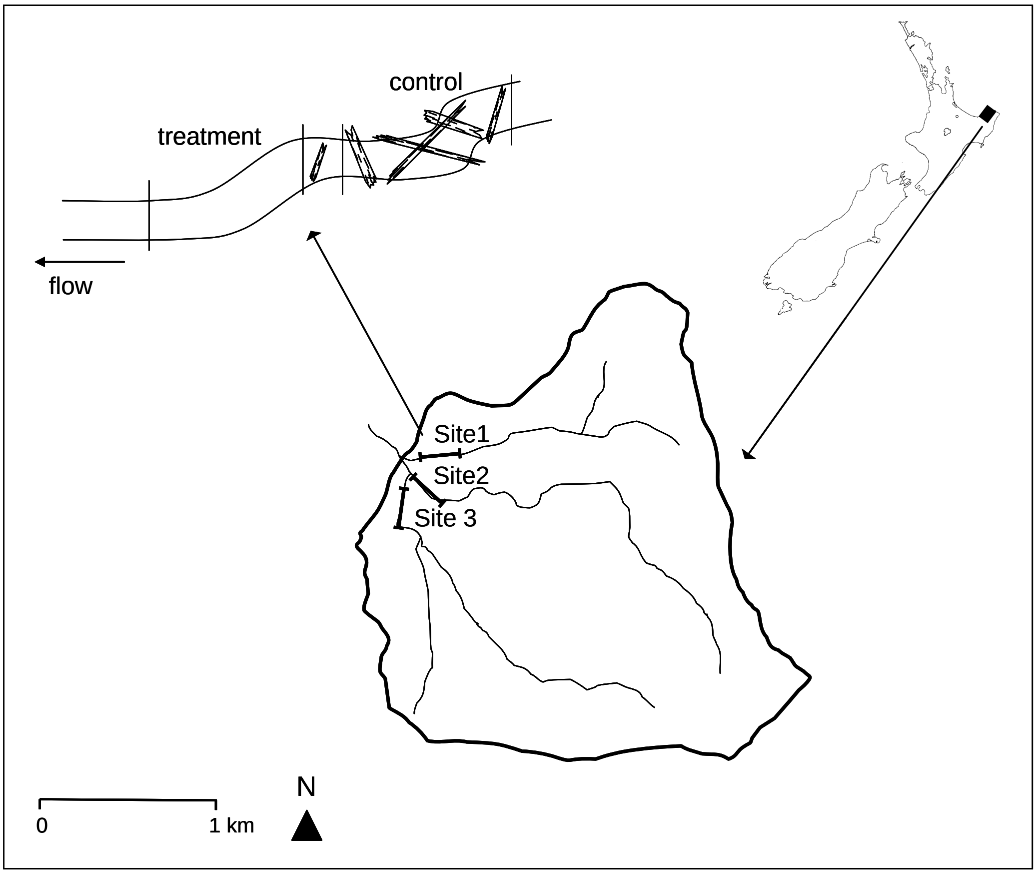

Figure 3.1. Location of the study area in the Bay of Plenty Region of New Zealand showing the layout of the study design.

The study area was located in three small tributaries of the Waiopoahu Stream in the Bay of Plenty region of New Zealand (Figure 3.1, Table 3.1). Mean annual rainfall for the area is 1400 mm (Quayle 1984). The area is in steep (20-35°) hill country underlain by greywacke, with remnant Pleistocene marginal marine lacustrine gravels, silt and peat beds up to 200 m above sea level overlain by loess and rhyolitic ash (Ministry of Works and Development 1975; Hewitt 1998; R. Black pers. comm., Hancock Forest Management (NZ) Limited). The catchment was previously a mix of indigenous scrub and low productivity pasture land (Ministry of Works and Development 1975), and at the time of the study was in mature first-rotation *Pinus radiata* forest (age 24-25 years) with riparian buffers of predominantly indigenous vegetation of varying width (approximately 5 – 50 m) along the stream margins.

3.3.2 Study design

Sites were selected to maximise the likelihood of capturing a full range of diadramous indigenous fish species. For this reason they were within 6 km of the coast, at low altitude (50 m a.s.l.), with no downstream obstructions or exotic fish species. The three sites were in close proximity to each other (Figure 3.1) to minimise background variation in climate, hydrology, geology and soils. First rotation, mature pine plantations removed any possible confounding effects of recent harvesting on the stream and riparian environments. At each of the three sites, an upstream 200 m control (C) and a downstream 200 m treatment (T) section (Figure 3.1) was selected with similar channel morphology characteristics. The literature suggests a section of 12-15 times or 20 times the bankfull width to ensure adequate sampling of channel bed units (Gordon et al. 1992); around 100 m for the streams in this study. I doubled the length to provide a longer reach to assess the morphological response of wood removal and the effects on fish communities and to ensure sufficient pools for my sampling strategy. Two hundred meters is at the upper end of reach lengths used in similar studies. A 10 m buffer was left between each upstream and downstream section. The range of variables in Sections 3.3.3.to 3.2.5. were measured at each of the three sites in autumn (March/April) and spring (October) 2006 before wood removal. The wood was removed from the treatment sections in December 2006, and the sites were re-measured the following year in autumn and spring after wood removal. Measurements were carried out in low flow conditions.

Table 3.1. Characteristics of the three stream sites in the Waiopoahu catchment.

			Mean water temperature (°C)				Mean bankfull width (m)				Gradient (%)				Wood volume (m^3 ha^{-1})			
Site and treatment	Catchment area (ha)	Discharge (L s^{-1})	Pre Autumn	Pre Spring	Post Autumn	Post Spring	Pre Autumn	Pre Spring	Post Autumn	Post Spring	Pre Autumn	Pre Spring	Post Autumn	Post Spring	Pre Autumn	Pre Spring	Post Autumn	Post Spring
Site 1																		
Control	91	6.5	13.3	9.9	13.9	12.4	4.8	4.7	4.4	4.5	3.3	ND	3.8	3.7	58	76	72	73
Treatment							3.9	3.9	3.7	3.6	3.2	ND	4.0	3.3	69	52	5	2
Site 2																		
Control	178	14.6	13.9	10.3	14.6	12.3	4.8	4.9	5.0	5.4	2.2	ND	2.4	2.4	55	60	67	50
Treatment							4.6	4.8	4.6	4.8	2.2	ND	2.5	2.8	60	46	20	27
Site 3																		
Control	179	13.8	13.5	10.1	14.2	ND	4.0	4.2	4.2	4.4	2.4	ND	2.6	2.9	53	41	45	36
Treatment							4.1	4.4	4.2	4.3	2.6	ND	2.3	2.3	76	54	12	6

Pre refers to the two measurements prior to wood removal, and Post to the two measurements after wood removal; ND = no data.

3.3.3 Wood characteristics

All large pieces of wood (≥ 10 cm diameter and ≥ 1 m length) within the bankfull width (the horizontal distance between the tops of the channel banks) of the stream channel, along each 200 m section were measured for length, small-end, mid-stem and large-end diameter. Each piece was classified according to position in the channel (partly suspended across channel; on the channel floor; along bank edge; in a debris dam), and whether the piece was influencing pool formation. The volume of each piece was calculated using Newton's formula (Harmon & Sexton 1996):

$$V_{piece} = \frac{(L(A_b+4A_m+A_t)/6)}{10{,}000} \qquad (1)$$

where V_{piece} = volume of piece (m^3); L = length of piece (m); A_b = area at the base of the piece (cm^2); A_m = area at the mid-point of the piece (cm^2); and A_t = area at the top of the piece (cm^2). The width, height, and depth of rootwads were summed to give an approximate volume. Wood volumes in each section were expressed as m^3 ha^{-1} using bankfull channel width and transect length to calculate streambed area.

Data on the debris accumulations stored by LW was also collected; details on the methodology, analysis and results are in Chapter 4.

After the first year of measurements, chainsaws were used to cut up the larger pieces of wood and all wood, branches and associated accumulations of organic matter were manually removed from the stream channel in the three treatment sections (Fig. 3.2 a & b). Pieces suspended above the channel and not influencing channel morphology were retained. Pieces embedded in the banks were cut flush with the bank edge. Treatment sections were regularly maintained in the year following wood removal and any additional pieces or large accumulations of organic matter entering the system or exposed by channel down-cutting were removed.

Figure 3.2. a. Wood removal operation in one of the treatment sections.

Figure 3.2. b. A section of channel after stream-cleaning. Photos by B. R. Baillie.

3.3.4 Channel characteristics

Channel gradient (%) was measured using a clinometer and an average gradient, weighted by distance, calculated for each section. Water temperature was logged at 15 minute intervals over a four-day period during each measurement period using StowAway Tidbit temperature loggers deployed at the downstream end of each site to calculate average temperature (Table 3.1). Single discharge measurements were taken at the downstream end of each site using a Marsh McBirney Inc. Flo-Mate water velocity meter, Model 2000 (Table 3.1). Bankfull width was measured to the nearest 0.1 m at 10 m intervals along each of the six 200 m sections. Surficial substrate was systematically sampled at the same locations using Leopold’s (1970) pebble count procedure (200 samples per 200 m section) and classified into nine inorganic classes based on Gordon et al. (1992) and two organic substrate classes (LW and small wood (< 10 cm diameter; < 1 m length)). The channel habitat in each section was classified as pool, riffle or run using the definitions in Hawkins et al. (1993) and measured for length and width (m) to determine the percentage length and percentage area of stream channel in each type of habitat for each section. These physical measurements were repeated at each of the 4 assessment periods, twice before and twice after wood removal. The exceptions were that a single assessment of stream baseflow was conducted and the gradient wasn't assessed in the second measurement prior to wood removal (Table 3.1).

3.3.5 Fish

Figure 3.3. Example of a wood pool (left) and open pool (right). Photos by B. R. Baillie.

Three wood pools (where wood and associated debris provided cover), three open pools (minimal or no wood cover) (Fig. 3.3) and three riffles were randomly selected from each of the control and treatment sections at each site to assess the effects of wood removal on fish populations. However, with the loss of wood pools and pools generally in the treatment sections following wood removal only open pools could be sampled. Pool sample size in the treatment sections after wood removal ranged from two to six. Runs were omitted as they formed a small percentage of habitat in these streams.

To determine the number of passes to be used in the study, three riffles, open pools and wood pools were electro-fished using multipass electric fishing, up to a maximum of six passes. Working in an upstream direction, each habitat was blocked off at the down-stream end with a 10 mm mesh net and fished using a battery powered backpack electric fishing machine (Kainga EFM 300). Each fish captured was identified in the field, measured for length to the nearest millimetre, and weighed to the nearest 0.1 gram. Each habitat fished was measured for length, width and depth. Results showed that 58% of the total number of fish, similar to Jowett and Richardson (1996) and 75% of the fish biomass was captured in the first pass. One-pass electric fishing was used for the remainder of the trial in order to sample a larger number of habitats to capture the range of fish communities present in these streams, rather than multi-pass fishing of fewer habitat units.

3.3.6 Data analysis

Data were examined using Proc Univariate (SAS statistical software version 9.0) and where necessary, transformed using log (x) in order to achieve assumptions of normality. For datasets which contained zeros, I used log (x+1). Fish data collected prior to wood removal were tested for differences in species richness, fish density, biomass and physiology (length and weight) between the three habitats (wood pools, open pools and riffles) using analysis of variance (ANOVA) (SAS Proc Mixed) with habitat included as a fixed effect and site and site x habitat as random effects. Tukey's test was use to test for significant differences in pair-wise comparisons of fish variables between the three habitats.

Nonmetric multidimensional scaling (NMS; PC-ORD Version 4.41) was used to examine differences in fish community composition between wood pools, open pools and riffles. NMS is an ordination technique that arranges samples in multidimensional space so that the distance between samples reflects the difference in community structure (McCune & Grace 2002). NMS is a flexible technique that caters for non-normal data, arbitrary or discontinuous scales, and avoids the assumption of linear relationships among variables. NMS is often considered more suitable for ecological community analysis than principal components analysis and detrended correspondence analysis, because of the underlying assumptions, techniques and performance of both these methods compared with the NMS (Minchin 1987; Clarke 1993; McCune & Grace 2002).

In this NMS analysis, I used Sørenson distance to measure dissimilarity between samples (McCune & Grace 2002) based on log transformed mean fish abundance data, including rare species. The preliminary 50 runs identified 3 dimensions, as the optimal solution and 500 iterations were used in the final run giving a final stress of 12.64 and a final instability of 0.00044.

The coefficients of determination (r^2) were then used to determine the proportion of variation represented by each axis. ANOVA followed by Tukey's test was then used to compare axis scores in relation to habitat, season (autumn and spring) and site and Pearson correlations (r) were used to examine relationships between transformed abundance of fish species, a range of environmental variables, and the ordination axes.

To assess the effects of wood removal on channel morphology, ANOVA were used to test for homogeneity in channel characteristics between the control and treatment sections at each site prior to wood removal and to examine the effects of wood removal on bankfull width, substrate and habitat, with period (before and after) and treatment (control versus treatment) as the experimental factors to test the treatment x period interaction.

ANOVA was also used to assess the effects of wood removal on fish populations, with treatment (control versus treatment), period (before and after) and treatment x period as fixed effects, and site, site x treatment and site x treatment x period as random effects. The interaction of treatment x period provided the BACI (before-after-control-impact) test of whether wood removal significantly influenced fish density and biomass. To achieve this, as there were no wood pools in the treatment sections after wood removal, data from the fished sections of wood pools, open pools and riffles were weighted by the actual area in each control and treatment section to estimate fish density and biomass. Results of data analyses were considered statistically significant if $P < 0.05$.

3.4 Results

3.4.1 Fish Capture

A total of 2183 fish comprising 11 indigenous species were caught over the study period. Bullies comprised the largest component of total fish captured; common bullies (*Gobiomorphus cotidianus*) 27%, redfin bullies (*Gobiomorphus huttoni*) 21%, and bluegill bullies (*Gobiomorphus hubbsi*) 19%. The remaining species caught included longfin eels, banded kokopu, shortfin eels (*Anguilla australis*), torrentfish (*Cheimarrichthys fosteri*) and common smelt (*Retropinna retropinna*). Inanga, koaro (*Galaxias brevipinnis*), and shortjaw kokopu (*Galaxias postvectis*) were rarely caught.

3.4.2 Influence of habitat type on fish community characteristics

The 779 fish caught prior to wood removal were used to analyse fish community characteristics between wood pools, open pools and riffles. There was no significant difference in total fish density (fish 100 m^{-2}) between the three habitats (Table 3.2), and a marginally significant difference in total fish biomass (g 100 m^{-2}) ($P = 0.048$). This difference was driven by the higher fish biomass in wood pools compared with open pools and riffles (Table 3.2). However, this difference was not significant in pair-wise comparisons of log transformed data (Tukey-Kramer test, $P = 0.06$ & 0.07 respectively).

Species richness was higher in riffles (average, 3.5 species) than open pools (average, 2.2 species) ($P = 0.006$) but was not different between riffles and wood pools (average, 2.8 species) or between the two pool types. Banded kokopu density and biomass were higher in wood pools than riffles ($P = 0.020$ & 0.016 respectively) (Table 3.2) but not significantly different between the two pool types. Bluegill bully density and biomass were higher in riffles than open or wood pools (density: $P = 0.029$ & 0.031; biomass: $P = 0.026$ & 0.028 for open and wood pools respectively). Torrentfish density and biomass were also higher in riffles than open or wood pools (density: $P = 0.014$ & 0.029; biomass: $P = 0.012$

& 0.026 for open and wood pools respectively).Redfin bully density was higher in riffles than open pools (P = 0.039). Neither the density nor biomass of common bullies, nor longfin eels (total, large (≥ 300 mm in length) and small (< 300 mm in length)) differed significantly among the three habitats (Table 3.2). Small sample sizes precluded analysis of other fish species.

Of all the species caught, only longfin eels showed differences in size among the three habitats (Table 3.2). Longfin eel lengths and weights were greater in wood pools compared with riffles but only marginally significant for weights (lengths, P = 0.051; weights, P = 0.049).

Table 3.2. Density, biomass and size of key fish species in wood pools, open pools and riffles before wood removal (± represent one standard error; for fish density and biomass, means with the same letters are not significantly different).

	Bluegill bully	Banded kokopu	Common bully	Longfin eel	Redfin bully	Torrentfish	Total
Mean fish density (no 100 m^{-2})							
Wood pool	5.2 ± 2.1b	11.7 ± 2.7a	13.9a ± 2.6a	23.7 ± 3.6a	19.3 ± 4.3ab	3.1 ± 1.7b	79.5 ± 10.0a
Open pool	4.7 ± 2.5b	4.1 ± 1.4ab	22.9a ± 6.3a	11.6 ± 2.7a	12.3 ± 2.6b	1.2 ± 1.2#b	60.9 ± 7.2a
Riffle	48.1 ± 8.0a	0.2*b	7.1a ± 1.9a	18.6 ± 3.7a	28.4 ± 4.2a	8.6 ± 1.9a	111.9 ± 10.0a
Mean fish biomass (g 100 m^{-2})							
Wood pool	5.7 ± 2.5b	432.3 ± 136.7a	61.0 ± 12.8a	1817.1 ± 450.9a	53.6 ± 12.8a	15.1 ± 8.1b	2574.4 ± 495.3a
Open pool	4.1 ± 1.9b	56.3 ± 24.7ab	81.6 ± 19.6a	597.8 ± 275.5a	34.1 ± 9.1a	3.5 ± 3.5#b	875.3 ± 289.9a
Riffle	46.2 ± 7.7a	2.1*b	21.3 ± 6.0a	183.7 ± 58.7a	60.5 ± 10.9a	39.2 ± 9.8a	356.2 ± 59.7a
Fish geometric mean length (mm) ± SE							
Wood pool	51 ± 2	120 ± 19	68 ± 3	194 ± 13	60 ± 2	72 ± 5	
Open pool	49 ± 2	90 ± 17	63 ± 2	164 ± 16	60 ± 2	61 ± 8#	
Riffle	49 ± 0.4	90*	62 ± 3	140 ± 9	56 ± 1	71 ± 3	
Fish geometric mean weight (g) ± SE							
Wood pool	1.1 ± 0.1	18.1 ± 11.0	3.5 ± 0.5	12.2 ± 2.8	2.2 ± 0.2	4.3 ± 1.0	
Open pool	0.9 ± 0.1	6.4 ± 4.8	2.9 ± 0.4	6.8 ± 2.3	2.0 ± 0.3	3.0 ± 1.3#	
Riffle	0.9 ± 0.1	7.0*	2.5 ± 0.4	4.0 ± 0.8	1.7 ± 0.1	3.9 ± 0.5	

*n = 1; #n = 2.

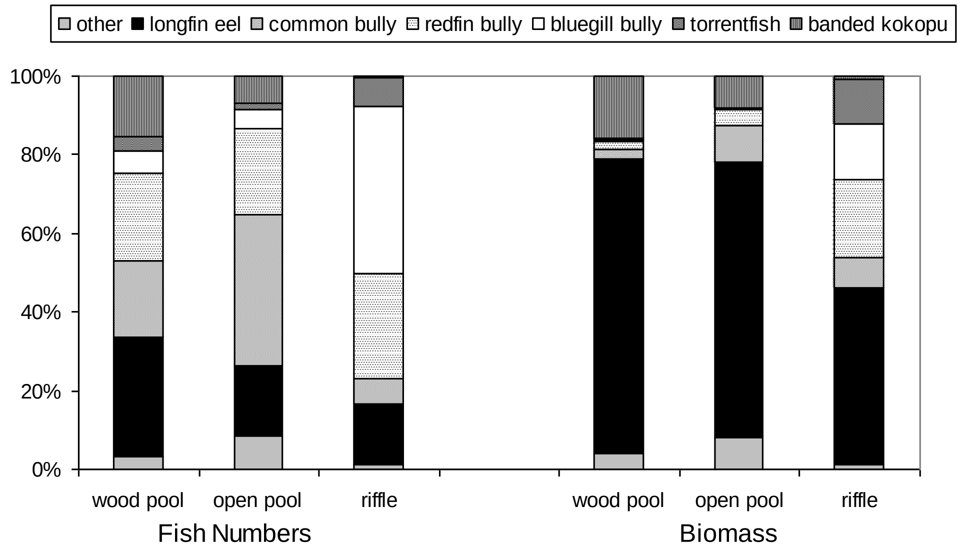

Figure 3.4. Comparison of fish community composition and biomass distribution between wood pools, open pools and riffles before wood removal. Other = inanga, koaro, shortfin eel, shortjaw kokopu and smelt. N = 191, 144 and 444 fish for wood pools, open pools and riffles respectively. Sample size is the same for fish numbers and biomass.

Fish community composition was similar between the two pool types (Fig. 3.4). Both were dominated by common and redfin bullies and longfin eels with wood pools containing a higher proportion of banded kokopu and longfin eels and open pools a higher proportion of common bullies. Although included in Figure 3.4 under ‘Other’, a high proportion of common smelt were also found in open pools. Common smelt were caught in the autumn sampling period only. Riffle community composition was dominated by bluegill and redfin bullies followed by longfin eels and torrentfish. Longfin eels comprised most of the biomass in all three habitat types (Fig. 3.4).

The total variation in fish community explained by all three axes in NMS ordination was 88% (axis 1, 21%; axis 2, 51%; axis 3, 16%) (Fig. 3.5). Analysis of NMS scores in relation to habitat, season and site showed that season had a significant influence on Axis 1 (P = 0.03). The main fish species influencing this result were common smelt which were negatively correlated with Axis 2, having higher abundances in autumn (r = -0.55) and common bullies, longfin eels and redfin bullies having higher abundances in spring (r = 0.56, 0.47 and 0.39 respectively). Habitat had a significant influence on axis 2 with fish community composition in riffles differing significantly from wood and open pools (P = 0.004

& 0.002 respectively). The main fish species differentiating fish communities in riffles from pools were bluegill bullies, redfin bullies, torrentfish and longfin eels which were significantly and negatively correlated with axis 2 (r = -0.81, -0.75, -0.73 and -0.42 respectively), all having higher abundances in riffles compared with pools. Common bullies, banded kokopu and smelt were significantly and positively correlated with axis 2 (r = 0.42, 0.37 and 0.33 respectively), all having higher abundances in pools compared with riffles. Neither habitat, season, nor site was influencing Axis 3.

To examine the effect of other environmental variables on fish communities I correlated mean habitat length, depth, area and volume with the axes scores. Average habitat depth was positively correlated and average habitat length and area were negatively correlated with Axis 2 scores.

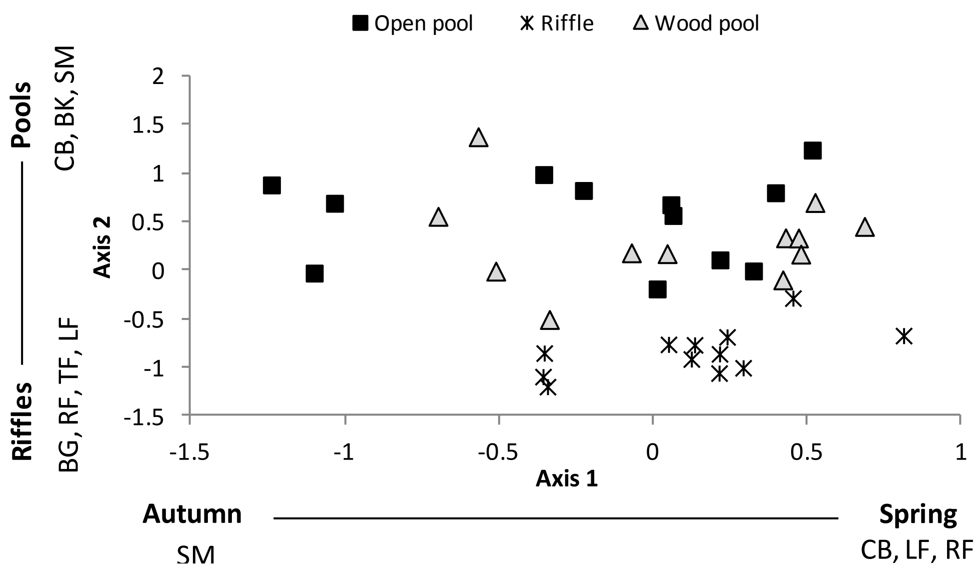

Figure 3.5. The first two axes of three-dimensional ordination of fish communities from nonmetric multidimensional scaling to determine differences between riffles, open pools and wood pools before wood removal, based on log transformed average abundance data (stress value = 12.64; instability = 0.00044). BG = bluegill bully, RF = redfin bully, TF = torrentfish, CB = common bully, LF = longfin eel, SM = common smelt, BK = banded kokopu.

3.4.3 Effects of wood removal on channel morphology

Prior to wood removal, wood loadings in the control and treatment sections of the three study sites ranged from 41 to 76 m^3 ha^{-1} (Table 3.1). On average 65% of pieces were located in debris dams (range 55-74%). After wood removal from the stream channel, wood volumes in the control sections were similar to pre-treatment volumes (Table 3.1). Any remaining wood in the treatment sections was mainly attributable to pieces embedded in the bank or substrate and in the case of Site 2, several large tree fern root wads embedded in the bank contributed to the remaining wood volumes in the treatment section at that site.

There were no significant differences in bankfull width between the control and treatment sections at each site, prior to and after wood removal (Table 3.1). Channel gradients remained similar between the control and treatment section at each site throughout the trial period (Table 3.1). Gravels dominated substrate composition in all three sites throughout the trial period, ranging from 50-84% of substrate composition, followed by fines (10-28%) and cobbles (5-21%). Medium-large gravels comprised the median substrate size at most sites. Prior to wood removal, the percentage of substrates in most classes were not significantly different between the control and treatment sections at the three sites. After wood removal, the percentage of large gravels increased significantly in all three treatment sections ($P = 0.004$).

Figure 3.6. Treatment section before (left), immediately after (middle), and one year after (right) wood removal. Photos by B. R. Baillie.

The streams in this study were composed of a pool-riffle-run morphology, dominated by riffles (Fig. 3.6 & 3.7). Prior to wood removal, there were no significant differences in the proportion of channel area in pools, riffles and runs between the control and treatment sections. The number of pools declined ($P = 0.053$) and proportion of channel area in pools significantly declined ($P = 0.037$) in the treatment sections at all three sites after wood removal (Fig. 3.7). Pool numbers and area recovered to pre-wood removal levels at Site 3 only by the time of the second assessment after wood removal. Wood removal had no significant effect on mean pool length (Fig. 3.8) and maximum pool depth. Wood contributed to formation of 59-67% of pools before wood removal and wood pools comprised 13-14% of the channel area. Wood influence on pools was similar after wood removal in the control sections. In the treatment sections, remaining wood pieces embedded in the bank influenced 8-21% of pool formation. However, none of these pieces provided wood cover.

Wood removal caused an overall reduction in the number of riffles in the treatment sections with a corresponding significant increase in the proportion of length ($P = 0.012$) and channel area in riffles ($P = 0.009$) (Fig. 3.6 - 3.8). The largest decline occurred at Sites 1 and 2 immediately after wood removal. By the second assessment after wood removal the number and average length of riffles at Sites 1 and 3 and the proportional area in riffles at Site 3 had recovered to pre-wood removal levels. Runs formed a minor component of channel composition and were least effected by wood removal, showing no significant responses.

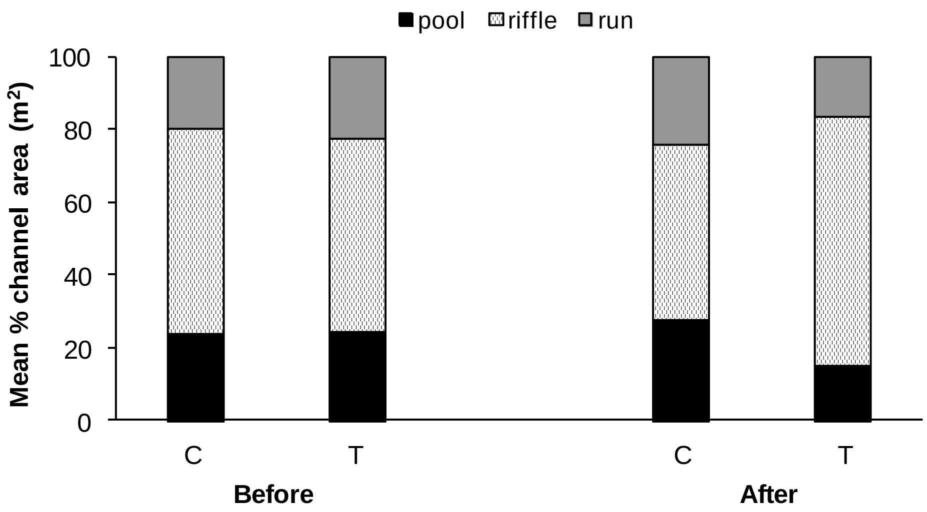

Figure 3.7. The proportional average of the control (C) and treatment (T) sections in pools, riffles and runs before and after wood removal (n = 3 sites).

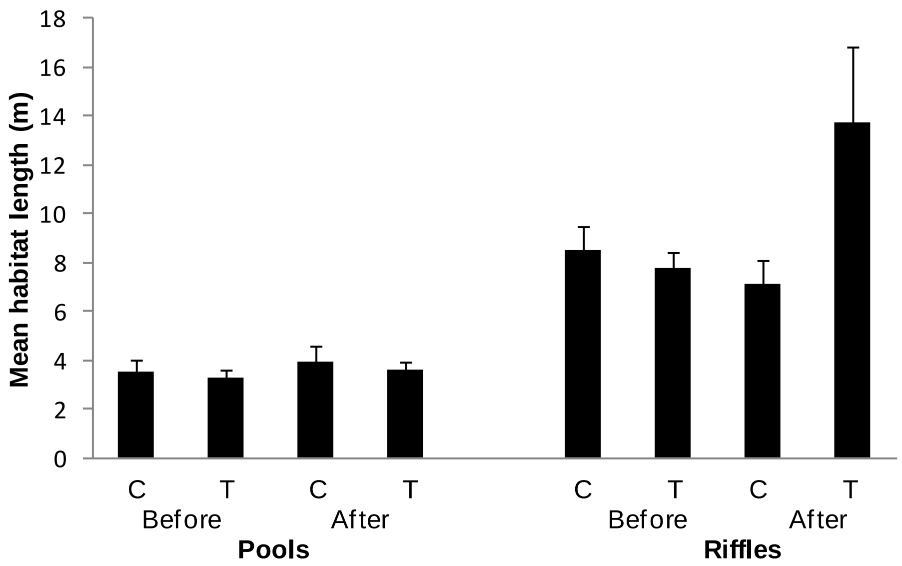

Figure 3.8. The average lengths of pools and riffles in the control (C) and treatment (T) sections before and after wood removal (n = 3 sites). Runs were excluded as they were a minor component of channel morphology. Error bars indicate SE.

3.4.4 Effects of wood removal on fish communities

Although the total area of stream channel fished before (976 m^2), and after (910 m^2) wood removal was similar, total catch increased by approximately 80%, with approximately 800 fish caught prior to wood removal and approximately 1400 fish caught after wood removal. About half the increase was common bullies (450 fish); the remainder was attributable to increases in longfin eels, redfin bullies, shortfin eels and banded kokopu. Although there was a large increase in shortfin eels (3 before to 61 after wood removal) only small eels were caught (<300 mm). Similar to pre-wood removal, common smelt were caught in the autumn sampling period only. The influx of fish increased fish density mainly in the pools (Fig. 3.9 a).

Prior to wood removal, most of the fish biomass was in wood pools (Fig. 3.9 b). After wood removal total biomass increased by 14% and common bullies accounted for 68% of the increase. However, longfin eel still comprised most of the total biomass at 58%. Most of the fish biomass was located in the remaining wood pools in the control sections with a smaller increase in biomass in the open pools and riffles in the control and treatment sections (Fig. 3.9 b).

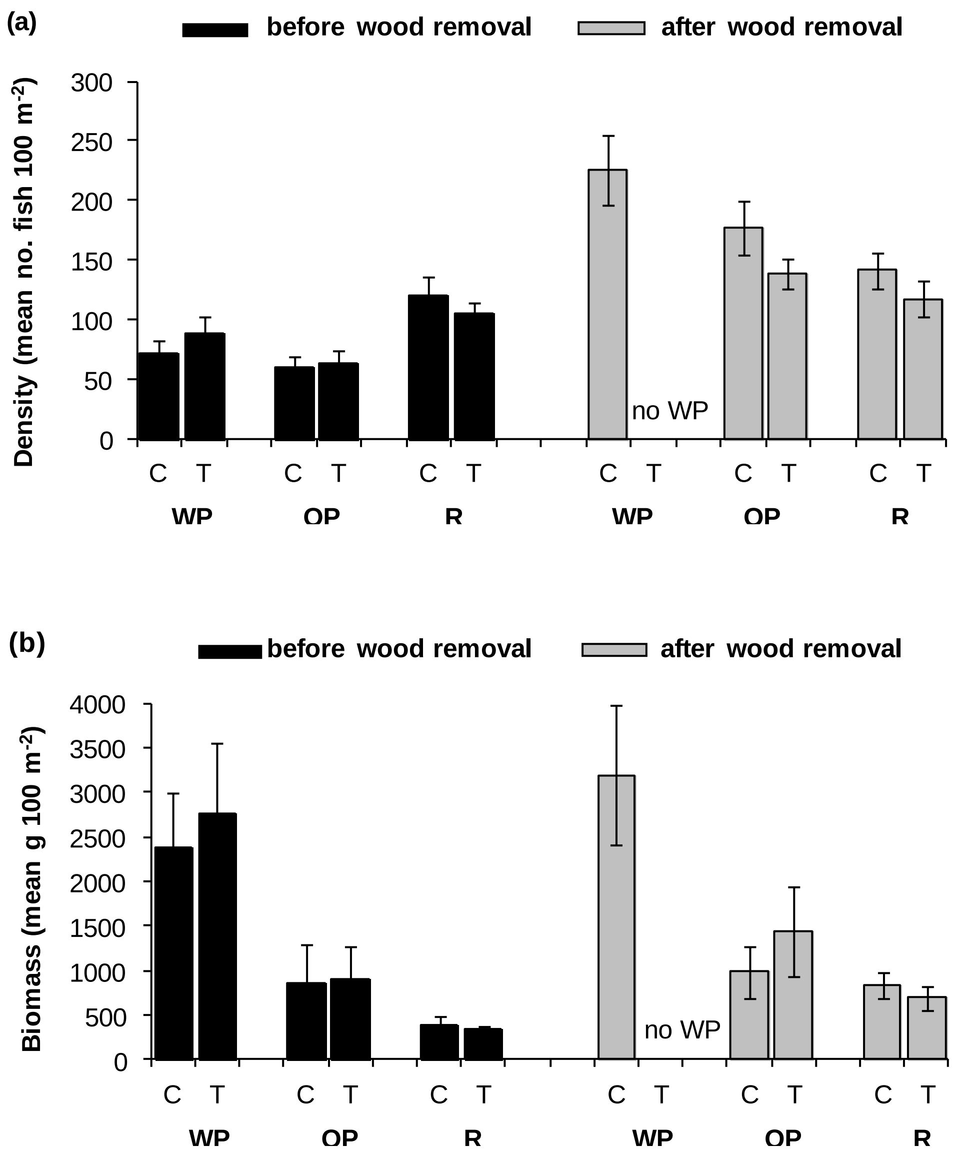

Figure 3.9. Average fish density (a) and biomass (b) in the control (C) and treatment (T) sections, and between the three habitats (WP = wood pool, OP = open pool, R = riffle) before and after wood removal. Error bars indicate SE.

Prior to wood removal, banded kokopu densities were highest in wood pools in both the control and treatment sections (Fig. 3.10 a) (73% of all banded kokopu caught). After wood removal, although the number of banded kokopu doubled (Fig. 3.10 a), most of the fish (84%) were caught in pools the control sections. Highest average banded kokopu densities were in the wood pools in the control sections (47% of all banded kokopu caught), followed by open pools in the control sections (31% of all banded kokopu caught). Similar to banded kokopu, large longfin eel (≥ 300 mm in length) densities were highest in wood pools in both the control and treatment sections prior to wood removal (Fig. 3.9b)

(70% of all large longfin eels caught). After wood removal large longfin eel densities were highest in the wood pools in the control sections (50% of all large longfin eels caught) (Fig. 3.10 b).

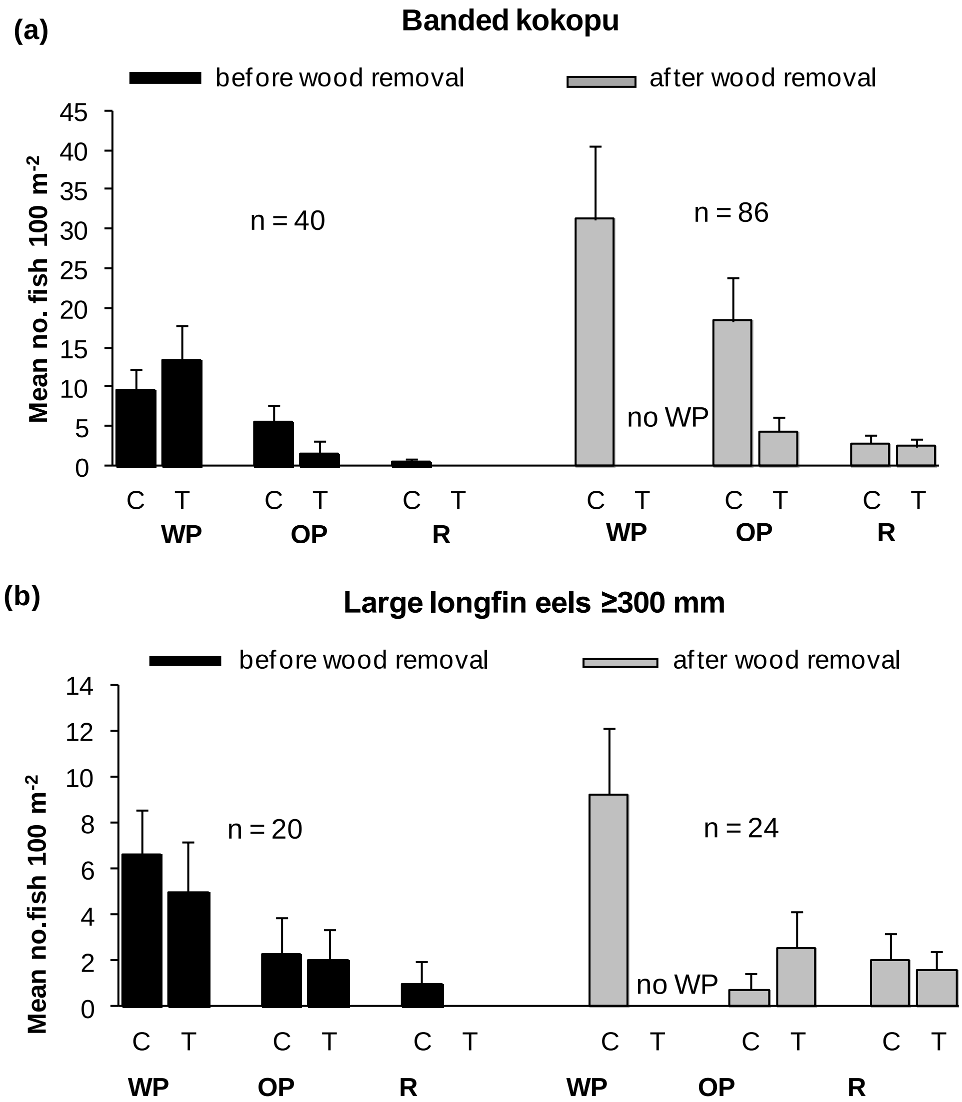

Figure 3.10. Average density of (a) banded kokopu and (b) large longfin eels in the control (C) and treatment (T) sections, and between the three habitats (WP = wood pool, OP = open pool, R = riffle) before and after wood removal. Error bars indicate SE.

The density and biomass of fish in the sampled wood pools, open pools and riffles was converted to an estimate of total fish density (fish 100 m^{-2}) and biomass (g 100 m^{-2}) (Table 3.4), based on the proportional area of each 200 m reach in each habitat, to determine any changes associated with wood removal at the reach scale. Although there was an 80% increase in fish catch after wood removal, most of the increase was attributable to inter-annual variation in recruitment and occurred mainly in the pools (Fig. 3.9) which formed a small proportion of the total habitat which was dominated by riffles (Fig. 3.7). Therefore, there were no significant changes in total fish density or biomass attributable to wood removal at the reach scale. Nor were any significant changes observed for the key fish species with the exception of banded kokopu. Even though the density of banded kokopu increased slightly in the treatment sections following wood removal (Table 3.3), fish were smaller than prior to wood removal resulting in a significant decrease in banded kokopu biomass (Table 3.3).

Table 3.3. Estimated mean fish density and biomass in the treatment and control sections, before and after wood removal (± 1 S.E). N.B. the total fish densities and biomass do not equal the sum of the individual species as only the results of the key species are shown.

		Estimated fish density (no 100 m^{-2})		Estimated fish biomass (g 100 m^{-2})	
Species		Control	Treatment	Control	Treatment
Bluegill bully	Before	39.8 ± 14.2	27.1 ± 10.9	40.8 ± 14.4	24.9 ± 9.1
	After	30.2 ± 14.2	27.2 ± 10.1	37.3 ± 14.6	34.0 ± 10.8
Banded kokopu	Before	2.4 ± 0.2	1.9 ± 0.2	60.0 ± 14.3	69.0 ± 30.3
	After	9.7±1.6	2.3 ± 1.4	199.8 ± 21.1	28.3 ± 24.5
Common bully	Before	10.6 ± 4.4	8.6 ± 2.5	36.4 ± 14.3	34.1 ± 1.7
	After	38.7 ± 8.5	22.7 ± 5.5	124.5 ± 47.8	71.0 ± 22.2
Longfin eel	Before	15.4 ± 5.6	18.3 ± 1.2	423.1 ± 117.9	441.0 ± 99.7
	After	30.9 ± 6.6	32.5 ± 6.9	588.8 ± 82.3	523.1 ± 51.0
Redfin bully	Before	26.4 ± 5.9	24.6 ± 9.3	60.5 ± 13.5	56.8 ± 27.3
	After	34.2 ± 6.7	19.9 ± 3.6	79.9 ± 23.9	51.1 ± 10.3
Torrentfish	Before	3.4 ± 1.6	8.3 ± 2.5	17.1 ± 8.0	35.3 ± 9.5
	After	4.5 ± 2.3	3.7 ± 1.8	32.5 ± 16.4	21.9 ± 11.1
Total	Before	99.4 ± 11.5	90.5 ± 3.4	643.4 ± 140.1	713.5 ± 68.9
	After	156.4 ± 13.3	116.8 ± 24.3	1142.1 ± 76.3	749.0 ± 118.7

3.5 Discussion

3.5.1 Fish communities before wood removal

The first hypothesis that fish communities in wood pools would differ from open pools and riffles was partly supported by the results of this study. Wood pools, although a small proportion of total habitat, were the main habitat provider for the two largest fish species (banded kokopu and large longfin eels) and supported most of the fish biomass. Given the inherent difficulties in electro-fishing wood pools compared with open pools and riffles, it is likely that density and biomass were underestimated in this habitat. Fish communities in open pools contained higher proportions of both common bullies and smelt than wood pools and riffles. Higher species richness, higher densities and biomass of bluegill bullies and torrent fish, and higher densities of redfin bullies were the key factors differentiating fish communities in riffles from both wood and open pools.

However there were commonalities in fish community characteristics between the three habitats and there were a number of factors contributing to this. A core group of species including common bullies, longfin eels (all sizes) and redfin bullies were numerically dominant in these streams (Table 3.2) and utilised all three habitats. The ubiquitous nature of these fish and longfin eels in particular, has been observed in a number of other studies (Taylor 1988, Hanchett 1990, Jowett & Richardson 1995, Glova et al. 1998), although Taylor (1988) observed a significant association between common bullies and slow flowing waters and a high proportion of these fish in habitats with little cover which concurs with the higher proportion of common bullies found in open pools in this study.

Pools are generally defined as areas of relatively deeper and still or slower flowing water (Hawkins et al. 1993). However, some pool types such as plunge pools contain areas of high turbulence and where these areas were located adjacent to downstream riffles, species such as bluegill bullies and torrentfish, commonly associated with higher energy habitats such as riffles (Taylor 1988, Jowett & Richardson 1995; McDowall 2000) were occasionally found in pools. In addition, while the majority of banded kokopu and large longfin eels were found in pools with wood cover they also occurred in open pools where they exploited alternative sources of cover such as large cobbles or rock crevices (author's personal observations). Consequently, fish communities associated with the three habitats showed some spatial overlap, particularly between the two pool types.

Factors underpinning fish community structure are varied and complex and habitat isn't always the strongest driver. While wood provides important habitat structure and cover for many fish species (Dolloff & Warren 2003; Wright & Flecker 2004; Nicol et al. 2007), and contributes to higher fish diversity and abundance (House & Boehne 1987; Hicks et al 1991, Fausch & Northcote 1992; Inoue & Nakano 1998), hydrological variables, substrate composition, food resources, competition and predation pressures and temporal variability in habitat requirements, all influence fish community composition. Stressors such as low flows, poor water quality and high fish densities tend to result in more structured habitat partitioning and fish assemblages (Greenberg 1991; Prenda et al. 1997; Braaten & Berry Jr. 1997; Reichard 2008; Crow et al. 2010). Hydrologically unstable stream systems often contain a wide range of generalist fish species occupying a variety of habitats, with considerable habitat overlap, whereas more distinct fish guilds are identified in stable stream systems (Mathews & Hill 1980; Braaten & Berry Jr. 1997; Prenda et al. 1997).

Similar complexities influence fish communities in New Zealand (McIntosh & McDowall 2004), and diadromy in particular is a strong driver behind declining fish diversity and abundance with increasing altitude and distance from the sea (Joy et al. 2000, McIntosh & McDowall 2004). In the case of this study, seasonal influences on fish community structure were also apparent. However, many of New Zealand's small streams are hydrologically and morphologically unstable (Winterbourn 1995; Duncan & Woods 2004) and this may be a contributing factor to the core of generalist species, and fewer habitat specialists (i.e. torrent fish, bluegill bullies and banded kokopu) encountered in this study. In South Westland, Taylor (1988) identified a similar range of generalist fish species (longfin and shortfin eels, redfin bullies, common bullies and inanga) occupying a diverse range of habitats. While Taylor (1988) identified three major fish community groupings, he also found considerable species overlap between the three groups and fewer habitat specialists, such as the bluegill bullies and torrentfish preference for faster flowing waters and the banded kokopu preference for small streams with cover. West Coast streams are hydrologically unstable and have some of the highest flood frequency rates in New Zealand (Duncan & Woods 2004). Chadderton & Allibone (2000) also found galaxiids occupying a diverse range of habitats in a Stewart Island stream. The ability to exploit a wide range of habitats is thought to be an adaptive strategy to cope with the large changes in environmental conditions associated with hydrologically unstable streams (Matthews & Hill 1980). Matthews & Hill (1980) also theorised that in this type of environment, the most successful fish species will have this trait and fish distribution patterns in New Zealand (McDowall 2000) indicate that those native fish species with broad habitat adaptability are more widely distributed across New Zealand's waterways.

3.5.2 Effect of wood removal on channel morphology

The second hypothesis that removal of wood would affect channel morphology, and pools in particular, was supported by the results of this study. Wood removal instigated downstream movement of sediment and organic matter stored behind debris dams, in-filling pools (Fig. 3.6). This resulted in a simplified morphology with longer sections of riffles, increased riffle area, and a reduction in the number and area of pools. The paucity of large wood in the treatment sections resulted in reduced pool habitat with limited cover provided primarily by undercut banks and to a lesser extent by cobbles and boulders on the channel bed and overhanging vegetation. Some coarsening of gravels occurred following wood removal, as the sediment stored behind debris dams often in-filled pools further downstream, but I did not measure significant changes in fine sediment. Coarser substrates can result as finer sediments stored in debris dams are lost from the system following wood removal (MacDonald & Keller 1987; Diez et al. 2000).

Pools often disappear after wood removal. For example, in a Spanish stream, some pools disappeared after wood was removed from the stream channel and new, smaller pools were created (Diez et al. 2000). Similarly in North American old-growth forest stream in Washington, the large pools disappeared after wood removal (Lestelle 1978). However, new pools were created within a year as new wood sources from undercutting of the banks and bank collapse re-established pre-wood removal stream conditions. Numerous scour pools around debris dams in a Californian stream were replaced with new pools and pre-existing pools deepened at bends above and below the debris removal sites (MacDonald & Keller 1987). In contrast, although experimental removal of wood in an Alaska stream had marked effects on sediment distribution and channel morphology, there were no obvious changes in pool characteristics (Smith et al. 1993b).

3.5.3 Fish response to wood removal

Wood removal had the least effect on fish communities in riffles, whose habitat actually expanded as a result of wood removal. Greatest impacts were on large fish associated with wood pools; banded kokopu and large longfin eels. The reduction in banded kokopu and longfin eel abundance in the treatment sections after wood removal and the significant reduction in banded kokopu biomass in the treatment sections at the reach scale indicated sub-optimal habitat for these fish. Banded kokopu are most often found in small forested streams containing small pools with cover (Main 1988, Taylor 1988, McDowall 2000, Rowe & Smith 2003; Baker & Smith 2007), and availability of suitable microhabitat is considered an important constraint on banded kokopu distribution (Main 1988). As wood removal reduced not only the number of pools but eliminated the cover provided by wood it is not entirely surprising that these fish were most affected by wood removal. Longfin eels however, can exploit a wide range of habitats (Taylor 1988; Glova et al. 1998) and may be more adaptable to the loss of wood pools than banded kokopu which are more constrained in habitat requirements (Main 1988, Taylor 1988, McDowall 2000). Even so, wood pools were the preferred habitat of large longfin eels in this study and the decrease in large longfin eels in the treatment sections after wood removal is most likely the result of the loss of wood pools. The preference of banded kokopu and large eels for deeper slower moving habitat with cover such as woody debris, undercut banks, boulders and macrophytes has been observed elsewhere in New Zealand (Glova et al. 1998; Jowett et al. 1998; Chadderton & Allibone 2000; Rowe & Smith 2003; Baker & Smith 2007).

Variable fish responses have characterised studies of wood removal. Wood removal has resulted in a decrease in the abundance, size and biomass of both warm water and coldwater fish species and a reduction in fish production (Angermeier & Karr 1984; Dolloff 1986, Zalewski et al. 2003) sometimes lasting decades (Fausch & Northcote 1992). However, fish response to wood removal varies both spatially and temporally. In high gradient streams of the Adironack Mountains in U.S.A. there was no obvious response of brook trout one month after debris dam removal. One year later while there were no significant changes in fish abundance in 1st order streams, abundance decreased in 2nd order and increased in 3rd order streams (Warren & Kraft 2003). Pre-existing habitat conditions other than woody debris such as high gradient, boulders and undercut banks were likely confounding factors. Lestelle (1978) found that wood removal did not significantly affect cutthroat trout populations until the following winter when numbers and biomass of significantly declined. Populations returned to normal within a year as new wood sources entered the system from slips and undercut banks. The fish communities in this study had low diversity, included a number of habitat generalists and most species were benthic although similar to salmonids, banded kokopu are predominantly pelagic (McCullough & Hicks 2002). Fish response to wood removal was immediate for the two larger species, in spite of one species (large longfin eel) being ubiquitous in habitat requirements.

Long-term impacts can result from wood removal (Hicks et al. 1991). In a fourth-order river system in California, wood removal reduced sediment storage capacity more than 10 years after wood removal (Klein et al. 1987). Historical stream cleaning from WWII to 1965 in some coastal Oregon streams still impacted the stream systems in the early 1980s. Stream cleaned reaches had lower pool numbers and salmonid use than uncleaned reaches (House & Boehne 1987). Twenty to thirty years on, stream cleaned sections in a small British Columbia stream still retained a simplified channel morphology, with fewer pools, less overhead cover and lower salmonid densities than undisturbed sections (Fausch & Northcote 1992). Recovery time for the treatment sections in the streams in this trial is unknown and will depend on the available wood supply both upstream and in the riparian area, delivery mechanisms providing wood to the stream and fluvial processes within the stream system.

3.5.4 Study design

Although this study was designed to minimise variation between sites, and remove confounding factors associated with riparian removal, harvesting and exotic fish species, there are spatial and temporal factors associated with climate variation, diadromy and life cycle patterns which would have been outside the control of this study. By using a BACI design that included spatial and temporal replication, I was able to capture the natural variation that occurs between sites and the strong inter-annual variation in fish abundance, although time constraints limited this study to two measurements over the course of one year after wood removal. While this has added complexity to the interpretation of the results it also shows the importance of site and temporal replication to assess the natural geomorphic and biological variation that occurs in stream ecosystems. It also highlights the importance of isolating the effects of wood removal from other disturbances associated with land-use change and harvesting that can affect New Zealand fish communities such as riparian removal and changes in light, temperature, sediment and organic regimes (Graynoth 1979, Ryan 1991, Rowe et al. 2002).

Selection of scale needs to be considered in studies of this nature. As this study showed, changes in fish community composition from wood removal at the habitat scale may not be evident at the reach scale. This is particularly true where the greatest effects were on wood pools which comprised a small portion of the total habitat yet contained most of the large fish and biomass.

3.5.5 Management implications

Longfin eels in New Zealand are generally widespread and present across a range of habitats (Glova et al. 1998; Chadderton & Allibone 2000) yet longfin eels, along with eels globally, are declining from commercial and customary fishing and loss of habitat (Doole 2005; Jellyman 2009). Retention of wood in stream systems is recommended as a tool to improve the productive potential of salmonid species in the Pacific Northwest (House & Boehne 1987; Fausch & Northcote 1992). Wood is currently undervalued as a resource and rehabilitation tool for eel habitat globally and could play a part in a recovery strategy for these species. In New Zealand in particular, judicial use of wood to improve habitat for longfin eels in stream networks not subject to fishing pressure could provide potential refuge sites for these fish.

Prior to the arrival of humans, forests covered approximately 80% of New Zealand. Land clearing and land management practices have altered and reduced that to 25% indigenous and 7% plantation forest cover (McGlone 1989; New Zealand Forest Owners Association 2009). This has seriously reduced recruitment of wood to New Zealand streams, particularly larger trees that are critical in forming complex, longer-lasting habitat. The repercussions of historical wood loss on trophic structure, food webs, productivity and carrying capacity in New Zealand's small streams are largely unknown. This study indicates that densities of at least two species, banded kokopu and longfin eels are likely to be negatively effected by the paucity of wood in New Zealand's small streams, as well as species such as inanga, and giant kokopu (*Galaxias argenteus*), which prefer pool habitat and overhead cover (Jowett et al. 1998; Chadderton & Allibone 2000, Bonnett & Sykes 2002; Baker & Smith 2007). These larger fish are at the top of the food chain, constitute most of the fish biomass, and are important determinants of community structure.

Chapter 4 describes the second component of this experimental study; the effects of wood removal and associated debris dams on aquatic invertebrate communities.

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Chapter Four: Aquatic invertebrate communities in debris dams and riffles and their response to the removal of wood and associated debris dams from New Zealand forest streams

4.1 Abstract

To determine whether debris dams were influencing aquatic invertebrate communities, the characteristics of aquatic invertebrate communities associated with organic matter in debris dams were compared with aquatic invertebrate communities in substrates in riffles in three small forested streams in New Zealand. Wood and associated debris dams were subsequently removed from three treatment sections in each of the three streams to assess the effects on aquatic invertebrate communities.

Prior to wood removal debris dam cover ranged from 8-19% of the channel area and were formed mainly by large pieces of dead wood. Total invertebrate densities in debris dams were 70% higher than in riffles but this difference was not significant. Plecoptera and Trichoptera densities, densities of five aquatic invertebrate taxa, and Plecoptera taxa richness were all significantly higher in debris dams than riffles. Debris dams contained a higher number of less common taxa. One Ephemeroptera taxa (*Deleatidium* spp.) had significantly higher densities in riffles. There were no significant differences in functional feeding groups between the two habitats. Plecoptera and Trichoptera comprised a larger proportion of community composition in debris dams and Ephemeroptera comprised a larger proportion of community composition in riffles. Nonmetric multidimensional scaling analysis found significant differences in aquatic invertebrate community composition between debris dams and riffles. Season had a significant effect on both invertebrate densities and community composition. There were no significant effects of wood and debris dam removal on the densities and functional feeding groups of aquatic invertebrates in the riffles in the

treatment sections of the three streams. The aquatic invertebrate communities still present in the debris dams in the control sections, were absent from the treatment sections.

Historical loss of forest cover in New Zealand has deprived many small streams of their natural forested riparian environment and associated sources of large wood and allochthonous organic matter, limiting the contribution of wood to the retention of organic matter for in-stream processing and the habitat heterogeneity for aquatic invertebrate communities provided by debris dams.

4.2 Introduction

Wood contributes to a wide range of structural, functional and ecological processes in riverine ecosystems (Gregory et al. 2003). Wood can exert considerable control on the storage, retention, and transport of organic and inorganic material (Beschta 1979; Mosley 1981; Bilby 1981; Montgomery et al. 2003). In particular, wood can play an important role in trapping leaf litter, especially in small forested streams where wood is generally more abundant (Benke & Wallace 2003; Bilby 2003) and allochthonous inputs provide a major source of organic matter to stream ecosystems (Kaushik & Hynes 1971; Cummins 1974; Jones 1997). Freshly fallen leaf litter has a high C:N ratio and consequently is generally unpalatable to aquatic invertebrates. However, if retained in the stream system long enough, leaching, conditioning by microbes, and mechanical breakdown processes can improve the palatability of this resource for some aquatic invertebrates (Kaushik & Hynes 1971; Linklater 1995; Parkyn & Winterbourn 1997; Hicks & Laboyrie 1999, Webster et al. 1999; Quinn et al. 2000).

The architecture of wood increases its effectiveness at retaining and slowing the movement of organic matter through the stream system, compared with inorganic substrates such as boulders. As a result, while often covering a small percentage of the stream bed, debris dams (wood accumulations and their associated sediment and organic matter) often contain a high proportion of the total organic material in the stream system, either in the dam itself or in the sediments stored directly upstream (Smock et al. 1989; Weigelhofer & Waringer 1999). The structural complexity of debris dams also increases habitat diversity for aquatic invertebrates (Fig. 4.1). Consequently, aquatic invertebrate density and diversity is typically higher in organic matter in debris dams than in the surrounding inorganic substrate, particularly in sites with fine, mobile substrates (Smock et al. 1989; Friberg & Larsen 1998; Weigelhofer & Waringer 1999; Benke & Wallace 2003).

Figure 4.1. Example of aquatic invertebrate fauna associated with organic material in a debris dam in a New Zealand stream. Photo by B. R. Baillie.

The removal of debris dams in a number of experimental studies resulted in the export of most of the coarse and fine particulate matter from the stream system (Beschta 1979; Bilby & Likens 1980; Diez et al. 2000). However, few studies have examined the response of aquatic invertebrates to debris dam removal. Results of two North American studies showed a reduction in the high aquatic invertebrate densities and biomass associated with debris dams along with changes in functional feeding-group composition although at the reach scale differences were variable and sometimes minor (Smock et al. 1989; Warren & Kraft 2006). Another large-scale study that excluded allochthonous inputs into a forest stream for three years resulted in significant changes to aquatic invertebrate abundance, biomass and productivity (Wallace et al. 1997).

New Zealand's aquatic invertebrates differ from those in North America and may provide useful insights into the influence of debris dams on aquatic invertebrate communities. New Zealand's biogeographical history of separation and isolation from continental land masses has resulted in an aquatic invertebrate community with a high degree of endemism and speciation within some groups, and a number of primitive taxa, with poor representation of some groups common elsewhere in the world (Boothroyd 2000). New Zealand's aquatic invertebrate fauna contain a core group of widely distributed taxa, a high number of generalist browsers, few obligate shredders and is characterised by poorly synchronised life histories. This has been attributed to the instability, poor retentive capabilities and relatively aseasonal food supply of New Zealand's waterways, compared with North American (Winterbourn et al. 1981; Thompson & Townsend 2000).

Several studies have examined aquatic invertebrate assemblages associated with wood and organic matter in New Zealand streams (Anderson 1982; Linklater 1995; Tank & Winterbourn 1996; Parkyn & Winterbourn 1997; Hicks & Laboyrie 1999; Collier & Halliday 2000). My contribution to this area of research was to evaluate the role of debris dams in providing habitat for aquatic invertebrates by conducting a debris dam removal experiment. I hypothesized that (1) prior to debris dam removal, aquatic invertebrate density would be higher in debris dams and community composition would differ from benthic substrates in riffles; and (2) removal of debris dams would reduce aquatic invertebrate density and alter invertebrate community composition in the remaining riffles. This trial contributes to a larger project examining the effects of wood and its removal on small stream ecosystems (Chapter 3).

4.3 Material and Methods

4.3.1 Study area and design

The trial was located in three small headwater streams in the Bay of Plenty region of New Zealand. The streams were in close proximity to minimise background geological, hydrological and climatic variation. The catchment was in first rotation mature (24 – 25 years old) *Pinus radiata* plantation forest with riparian margins (approximately 5 – 50 m in width) of predominantly indigenous vegetation. Stream substrate was dominated by gravel, mean bankfull width ranged from 3.7 – 5.4 m, channel gradient ranged from 2.2 – 4.0°, and channel morphology was dominated by riffles (refer to Chapter 3, sections 3.3.1 & 3.3.2 for further site details).

At each of the three stream sites, an upstream 200 m section was retained as the control (C) and a 200 m downstream section as the treatment (T) area. The three sites were assessed in 2006 in autumn (March/April) and spring (October) prior to wood removal and again in autumn and spring in 2007 after wood removal.

4.3.2 Debris dams

Definitions of debris dams, debris jams and debris accumulations vary in the literature (Máčka et al. 2011) and are often used interchangeably. For the purposes of this study, debris dams were defined as one or more large pieces of wood (≥ 10 cm diameter and ≥ 1 m length) accumulating organic material and sediment and either partially or fully spanning the streambed. In each 200 m section, the width and breadth of each debris dam was measured to determine the area of streambed covered by debris dams. The main debris dam forming factor was also recorded i.e. large wood, boulder, live tree etc. Pieces of large wood were classified as stable if they had one or more of the following characteristics: a mass of tree roots (rootwad), the piece extended outside the channel or the piece was embedded in the bank or substrate. Bankfull width measurements taken at 10 m intervals along each transect and along with transect length were used to calculate channel area. At the end of the first year, all the wood and associated large organic matter (fronds, twigs, branches, leaf and needle accumulations) were manually removed from the three treatment sections (see Chapter 3, Section 3.3.3). These sections were regularly maintained during the second year by removing any additional large wood and organic matter accumulations that entered the site (Fig. 4.2.), hereafter referred to as ‘wood removal’.

Figure 4.2. Treatment section before (left), and after (right) debris dam removal. Photos by B. R. Baillie.

4.3.3 Aquatic invertebrate sampling

Prior to wood removal, five random Surber samples (0.1 m^2, 500 µm mesh) were taken from riffles, along with another five samples from the organic matter within debris dams, in the control and treatment sections in each of the three sites in autumn and in spring (120 samples). Samples were taken from debris dams in locations suitable for Surber sampling. Care was taken to ensure a seal was maintained around the Surber when sampling organic matter. Three water depths were measured to calculate mean depth and the substrate composition was visually assessed for each Surber sample. After wood removal, the same sampling regime continued in the control sections and 10 Surber samples were randomly taken from riffles in the treatment sections (120 samples). All the organic matter and invertebrates collected in each sample were preserved in 80% ethanol. In the laboratory, each sample was washed through a 500 µm sieve, emptied into a tray and aquatic invertebrates were picked out by eye and preserved in 80% ethanol (Fig. 4.3).

Figure 4.3. Surber sample collected from a riffle (left) and debris dam (right). Photos by B.R. Baillie.

Invertebrates were counted and identified under a binocular microscope using the guides of Winterbourn et al. (2006), Winterbourn (1973), Chapman & Lewis (1976) and Moore (2010). Invertebrates were identified to the levels indicated in Appendix 1 of Stark and Maxted (2007) (see Appendix A) and key taxa (see list in Table 4.1) were classified into one of four functional feeding groups; collector-gatherer (CG), collector-filterer (CF), shredder (S) and predator (P). To determine the classification of *Olinga* spp., a facultative shredder, gut contents were examined from five samples in debris dams, five samples from riffles before wood removal and five samples from riffles after wood removal. Based on these samples, *Olinga* spp. were classified as shredders.

4.3.4 Data Analysis

Data were examined using Proc Univariate (SAS statistical software version 9.0) and where necessary, log transformed to meet requirements for normal distribution. Angular transformation (arcsine) was used for percentage data. Prior to wood removal, analysis of variance (ANOVA) (SAS Proc Mixed) was used to test for differences in invertebrate community characteristics between habitats (debris dams and riffles) and season (autumn and spring). These factors were included in the model as fixed effects while site (3 sites), site x habitat and site x season were included as random effects. Tukey's test was used to test for significant differences in pair-wise comparisons of aquatic invertebrate variables between the three habitats. The variables analysed were total density, order and taxa density, functional feeding groups, along with the following biotic indices; taxa richness (no. of taxa), %EPT (Ephemeroptera, Trichoptera, Plecoptera) taxa, and %EPT abundance.

Patterns in invertebrate community composition in debris dams and riffles prior to wood removal were examined using nonmetric multidimensional scaling (NMS; PC-ORD Version 4.41) with Sørenson's distance to measure dissimilarity between samples (McCune & Grace 2002) (see Chapter 3, Section 3.3.6. for further explanation on NMS). The preliminary run on log transformed mean invertebrate abundance data, including rare species, identified 3 dimensions as the optimal solution for the final run which resulted in a final stress of 7.67 and final instability of 0.00003. The coefficient of determination (r^2) was then used to determine the proportion of variation represented by each axis. ANOVA followed by Turkey's test was then used to compare axis scores in relation to habitat, season and site and Pearson correlations (r) were used to examine relationships between mean invertebrate abundance and the ordination axes. Pearsons correlations were also used to examine relationships between the environmental variables of water depth and substrate composition and the ordination axes.

ANOVA was used to test the effects of wood removal on invertebrate communities with treatment (control versus treatment), period (before and after) and treatment x period as fixed effects and site, site x treatment and site x treatment x period as random effects. The interaction of treatment x period provided the BACI (before-after-control-impact) test of whether wood removal significantly affected invertebrate density. As there were no debris dams in the treatment sections after wood removal, invertebrate data from the debris dams and riffles were weighted by the actual area in each control and treatment section to estimate invertebrate densities. All analyses were considered statistically significant if $P < 0.05$.

4.4 Results

4.4.1 Characteristics of invertebrate communities

A total of 90 taxa were recorded during the study period (Appendix A), 83 taxa were found in debris dams, 69 taxa in the riffles. Overall, Diptera and Trichoptera recorded the highest number of taxa (25 and 22 respectively) and Ephemeroptera and Trichoptera, the highest percentage of individuals (53 and 24% respectively). *Deleatidium* spp., *Coloburiscus humeralis* and *Olinga* spp. accounted for just under 60% of the total count with a further 6 taxa (*Zephlebia* spp., *Potamopyrgus antipodarum*, *Pycnocentria* spp., *Austroperla cyrene*, Tanytarsini spp., *Helicopsyche* spp.) accounting for just under 80% of all individuals caught. Most taxa (71) comprised less than 1% of total catch. The main predator caught was New Zealand's only dobsonfly (Megaloptera) *Archichauliodes diversus* (2% of total catch).

4.4.2 Influence of habitat type on aquatic invertebrates

Prior to wood removal, total invertebrate density was 70% higher in debris dams than in riffles (Table 4.1) although this difference was not statistically significant. Plecoptera and Trichoptera densities were higher in debris dams ($P = 0.017$ & 0.034 respectively) than riffles. *Austroclima* spp., *Zephlebia* spp. (Ephemeroptera), *Olinga* spp., *Pycnocentria* spp. (Trichoptera), and *Polypedilum* spp (Diptera) were all higher in debris dams ($P < 0.05$) (Table 4.1). The only taxon with significantly higher densities in riffles prior to wood removal was *Deleatidium* spp. (Ephemeroptera). Some seasonal variation was evident (Table 4.1); Coleoptera, *Pycnocentrodes* spp. (Trichoptera), and *Austrosimulium* spp. (Diptera) densities were all higher in autumn, and *Acroperla* spp. (Plecoptera) densities were higher in spring ($P < 0.05$). While densities of all four functional feeding groups were higher in debris dams than riffles, none of these differences were significant (Fig. 4.4).

Table 4.1. Mean densities (no. m^{-2}) and standard error (± SE) of key invertebrate orders and taxa in debris dams and riffles and by season prior to wood removal, control and treatment data combined (n = 3 sites).$^{*}P < 0.05$ for habitat and seasonal paired comparisons.

Taxon	Debris dam	Riffle	Autumn	Spring
Total density	1463 ± 139.6	859 ± 78.8	1076 ± 93.8	1245 ± 140.5
INSECTA				
Ephemeroptera	**749 ± 95.4**	**555 ± 53.3**	**481 ± 51**	**823 ± 93.1**
Acanthophlebia	16 ± 3.7	21 ± 5.3	34 ± 5.8	3 ± 0.8
Austroclima	27* ± 6.9	2 ± 0.8	7 ± 2	22 ± 6.9
Coloburiscus	353 ± 58.6	190 ± 31.5	242 ± 39.7	301 ± 55.2
Deleatidium	122 ± 16.1	315* ± 37.6	147 ± 14.4	290 ± 40
Neozephlebia	37 ± 14.4	10 ± 2.1	11 ± 2.1	36 ± 14.4
Zephlebia	190* ± 33.4	13 ± 2.9	33 ± 8.1	170 ± 34.2
Plecoptera	**174* ± 27.5**	**17 ± 3.5**	**44 ± 8.6**	**146 ± 28.5**
Acroperla	59 ± 16.9	7 ± 2	5 ± 1.5	62* ± 16.8
Austroperla	102 ± 17.8	7 ± 2.3	32 ± 7.8	77 ± 17.9
Trichoptera	**322* ± 46.5**	**162 ± 33.5**	**327 ± 51.6**	**158 ± 24.3**
Helicopsyche	20 ± 7.4	63 ± 24.9	71 ± 25.2	12 ± 5.1
Olinga	205* ± 36.3	58 ± 10.2	170 ± 35.8	94 ± 16.6
Pycnocentria	49* ± 7.1	6 ± 2.1	34 ± 7.2	21 ± 4.3
Pycnocentrodes	1 ± 0.7	20 ± 7.5	21* ± 7.5	0
Coleoptera	**41 ± 6.1**	**64 ± 9**	**83* ± 8.9**	**22 ± 3.4**
Elmidae	12 ± 3.5	30 ± 6.6	35 ± 7.1	7 ± 1.4
Hydraenidae	8 ± 1.9	8 ± 2.1	14 ± 2.5	2 ± 1
Ptilodactylidae	21 ± 3.7	26 ± 4.6	34 ± 4.9	13 ± 2.7
Diptera	**75 ± 14.5**	**21 ± 5.1**	**58 ± 9**	**38 ± 13.3**
Austrosimulium	23 ± 6.2	9 ± 4.3	30* ± 7.2	2 ± 0.8
Polypedilum	36* ± 13.1	1 ± 0.6	8 ± 2.8	29 ± 13
Tanytarsini	11 ± 2.9	7 ± 1.6	15 ± 3.1	3 ± 0.7
Megaloptera				
Archichauliodes	32 ± 4.2	23 ± 3	33 ± 3.8	22 ± 3.5
MOLLUSCA				
Gastropoda	**56 ± 13.7**	**15 ± 5**	**43 ± 12.5**	**28 ± 8.2**
Potamopyrgus	56 ± 13.7	15 ± 5	43 ± 12.5	27 ± 8.2

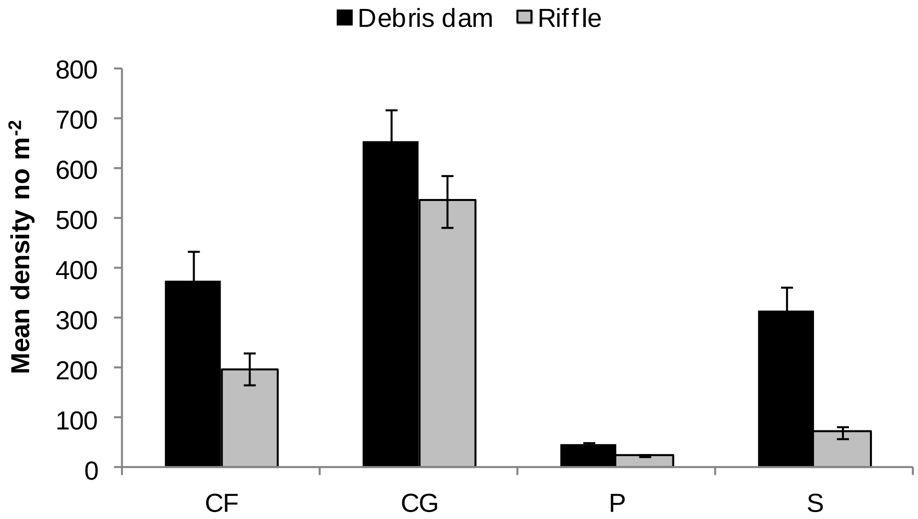

Figure 4.4. Mean density of functional feeding groups (for key invertebrate taxa) in debris dams and riffles prior to wood removal, control and treatment data combined (n = 3 sites). CF = collector-filterer, CG = collector-gatherer, P = predator, S = shredder. Error bars indicate SE.

Total taxa and Plecoptera taxa richness were higher in debris dams than riffles prior to wood removal (Table 4.2), but only significant for Plecoptera (P = 0.024). Coleoptera taxa richness was higher in autumn than spring (P = 0.023) (Table 4.2). The percentage of both EPT abundance and taxa was high in both habitats, indicative of high water quality in these streams. A total of 64 less common taxa (<1% total catch) were found in debris dams, 18 of which were exclusive to debris dams, compared with 50 less common taxa in riffles, one of which was exclusive to riffles.

Ephemeroptera, Plecoptera and Trichoptera dominated invertebrate community composition in debris dams and riffles prior to wood removal (Fig. 4.5) ranging from 79-94% of total community composition across habitats and seasons. Ephemeroptera comprised a larger proportion of community composition in riffles compared with debris dams in both autumn and spring, whereas Plecoptera and Trichoptera formed a larger proportion of community composition in debris dams. Community composition varied seasonally. Ephemeroptera were proportionally higher in spring, whereas Trichoptera, Coleoptera and Diptera were proportionally higher in autumn across both habitats.

Table 4.2. Comparison of biological indices (mean ± SE) between debris dams and riffles and by season before wood removal. *P < 0.05.

Index	Debris dam	Riffle	Autumn	Spring
Taxa richness:				
All taxa	16.8 ± 0.6	11.4 ± 0.6	15.9 ± 0.5	12.3 ± 0.7
Ephemeroptera taxa	4.8 ± 0.1	3.8 ± 0.2	4.5 ± 0.2	4.1 ± 0.2
Plecoptera taxa	2.3* ± 0.1	0.8 ± 0.1	1.4 ± 0.1	1.7 ± 0.2
Trichoptera taxa	4.2 ± 0.2	2.7 ± 0.2	4.1 ± 0.2	2.9 ± 0.3
Coleoptera taxa	1.4 ± 0.1	1.6 ± 0.1	2.0* ± 0.1	1.0 ± 0.1
Diptera taxa	1.9 ± 0.2	1.0 ± 0.1	1.9 ± 0.2	1.0 ± 0.2
Gastropoda taxa	0.6 ± 0.1	0.4 ± 0.1	0.6 ± 0.1	0.5 ± 0.1
Other taxa	1.6 ± 0.1	1.1 ± 0.1	1.5 ± 0.1	1.3 ± 0.1
% EPT taxa	68.9 ± 1.2	64.7 ± 1.8	63.0 ± 1.1	70.6 ± 1.8
%EPT no.	80.7 ± 2.3	83.0 ± 1.7	74.8 ± 2.0	88.9 ± 1.6

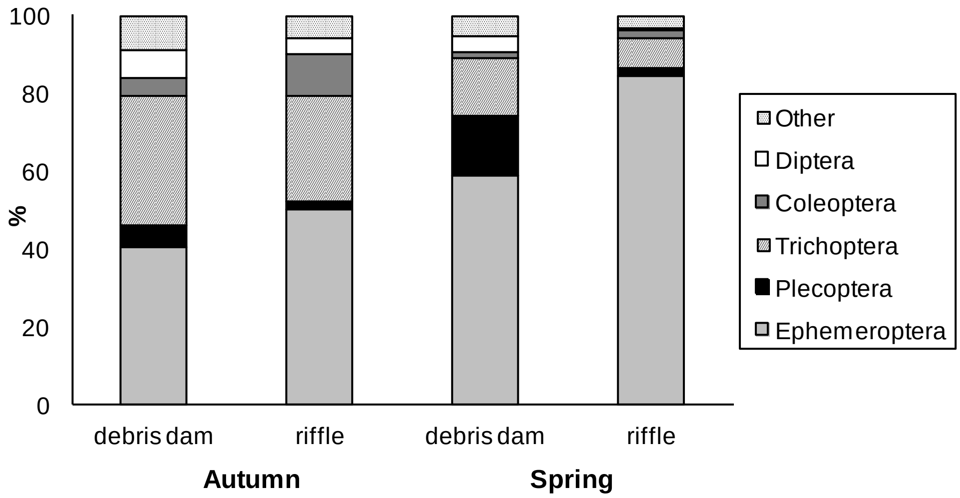

Figure 4.5. Aquatic invertebrate community composition in debris dams and riffles in autumn and spring prior to wood removal, all sites combined.

NMS analysis showed that 94% of the variation in invertebrate community composition was explained by the first three axes. Twenty percent of the variation was explained by Axis 1, 23% by Axis 2 and 51% by Axis 3. Habitat had a significant effect on Axis 2 (P = 0.011) and season had a significant effect on Axis 1 and 2 (P = 0.0001 & 0.025 respectively). Neither habitat nor site had a significant effect on Axis 3. Invertebrate communities in debris dams were spatially separated from invertebrate communities in riffles and invertebrates community composition was also spatially separated by season (Fig. 4.6). Table

4.3 shows the key taxa correlated with Axes 1 and 2. Nine key taxa were significantly and negatively correlated with Axis 1 (Fig. 4.6, Table 4.3), having higher average abundances in autumn than spring. One taxa (*Acroperla*) was significantly and positively correlated with Axis 1 with higher average abundance in spring. Seven key taxa were significantly and negatively correlated with Axis 2 with higher average abundances in debris dams and three taxa were significantly and positively correlated with Axis 2 having higher average abundances in riffles (Fig. 4.6; Table 4.3). Although Pearson's correlations for *Deleatidum* spp. (r = 0.38 and 0.35 for axes 1 and 2 respectively) were below the 5% confidence level, as *Deleatidium* was one of the most abundant taxa present in these streams (Section 4.4.1., Table 4.1), it is likely that this taxa was also influencing invertebrate community composition in riffles and in spring.

To examine the effects of other environmental variables on invertebrate communities, mean water depth, and the mean percentage of fines, gravels, cobbles and small wood were correlated with the axis scores of axes 1 and 2. There was insufficient data to analyse large wood. The mean percentage of fines and small wood were positively correlated with the Axis 1 scores. The mean percentage of gravels was positively correlated and the mean percentage of small wood was negatively correlated with Axis 2 scores ($P < 0.05$). There were no significant correlations between the remaining environmental factors and Axes 1 and 2.

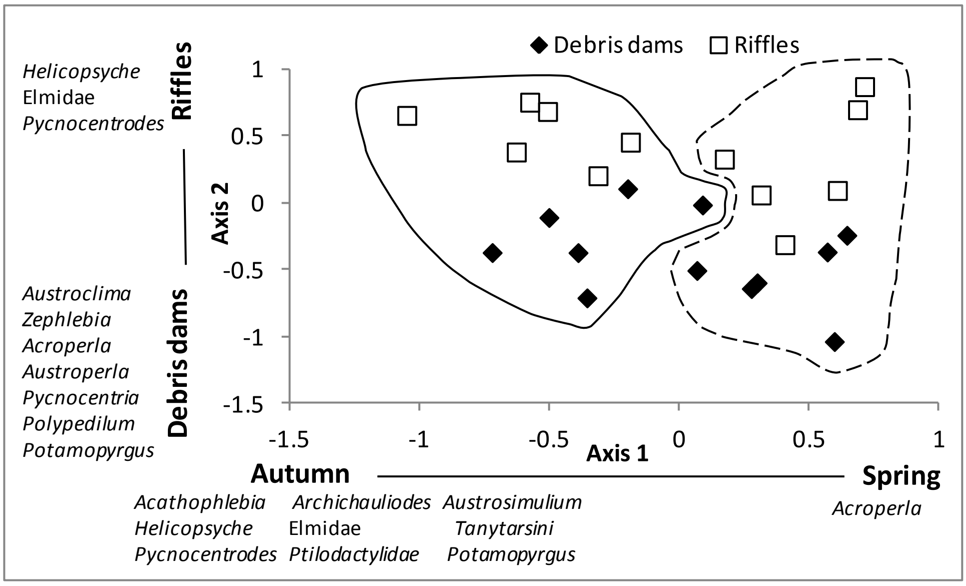

Figure 4.6. The first two axes of the three-dimensional ordination of invertebrate communities from nonmetric multidimensional scaling showing differences between habitat (debris dams and riffles) and season (autumn and spring) before wood removal, based on log transformed average abundance data (stress value, 7.67; instability, 0.00003). Autumn samples are enclosed in a solid line; spring samples in a dashed line.

Table 4.3. Pearson correlation (*r*) of aquatic invertebrate taxa with nonmetric multidimensional scaling ordination axes scores for axes one and two, where $r > 0.404$ or $r < -0.404$; $P < 0.05$; based on average abundance data prior to wood removal.

Taxa	Axis 1	Axis 2
Ephemeroptera		
Acanthophlebia	-0.47	
Austroclima		-0.59
Coloburiscus		
Deleatidium		
Neozephlebia		
Zephlebia		-0.82
Plecoptera		
Acroperla	0.55	-0.55
Austroperla		-0.55
Trichoptera		
Helicopsyche	-0.72	0.49
Olinga		
Pycnocentria		-0.52
Pycnocentrodes	-0.64	0.52
Coleoptera		
Elmidae	-0.49	0.70
Hydraenidae		
Ptilodactylidae	-0.63	
Diptera		
Austrosimulium	-0.58	
Polypedilum		-0.68
Tanytarsini	-0.48	
Megaloptera		
Archichauliodes	-0.55	
Gastropoda		
Potamopyrgus	-0.49	-0.41

4.4.3 Effects of wood removal on the physical stream environment

After removal of wood from the three treatment sections, there was a significant decline in the proportion of channel area in pools. Both the proportion of length and area of stream channel in riffles increased significantly and there was a significant increase in the percentage of large gravels. Further details on the results of the effects of wood removal on wood volumes, substrate and channel morphology are in Chapter 3, Section 3.4.3.

The number of debris dams in the control and treatment sections ranged from 5 – 18 (average 12) prior to wood removal, and from 7 -19 (average 12) in the control sections after wood removal. Debris dams covered 8 – 19% of the channel area before wood removal and 6 – 20% of the channel area in the control sections after wood removal. No debris dams remained in the treatment sections after wood removal. Large pieces of dead wood were the main contributor to debris dam formation, comprising 69-87% of all debris dam forming factors across the four measurement periods (autumn and spring, before and after wood removal). Of those pieces, 67-88% were classified as stable. Dead wood was a mix of indigenous and exotic *Pinus radiata* pieces. Tree ferns (*Cyathea* and *Dicksonia* sp.) comprised 20 – 29% of all dead pieces. Live wood comprised 10-25% of all debris dam forming factors and tree ferns were the main component (67-89%).

Gravels dominated mean substrate composition in the Surber samples from debris dams and riffles in both the control and treatment sections before and after wood removal (Fig. 4.7). Fines and gravels comprised similar proportions of Surber substrate composition across all sites but small wood was rarely sampled in the riffle Surber samples. Mean water depth in Surber samples ranged from 55-75 mm (Fig. 4.8) and showed little variation between the control and treatment sections in the debris and riffles both before and after wood removal.

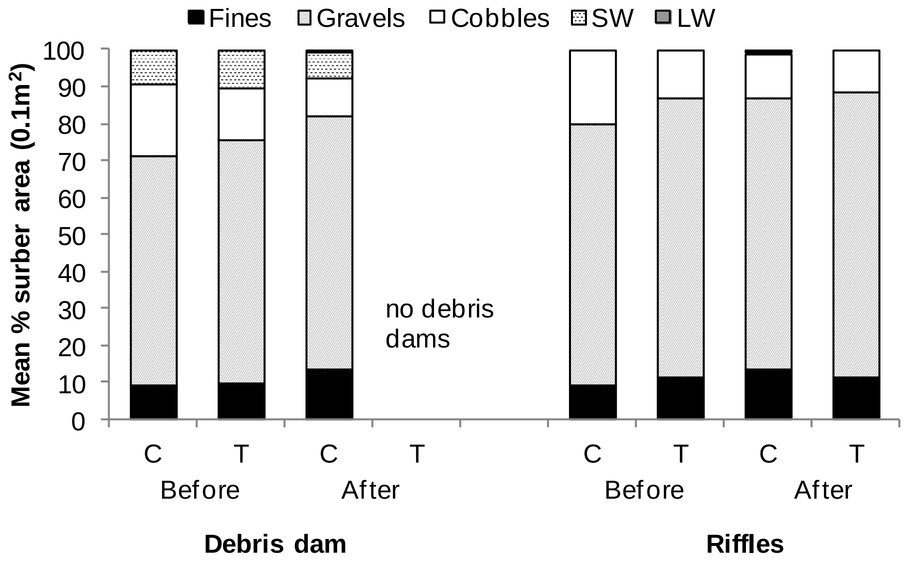

Figure 4.7. Mean substrate composition in Surber samples from debris dams and riffles in the control (C) and treatment (T) sections before and after wood removal. Fines (≤ 2 mm); gravels (2-64 mm); cobbles (64-256 mm); SW (small wood < 10cm diameter); LW (large wood ≥ 10 cm diameter).

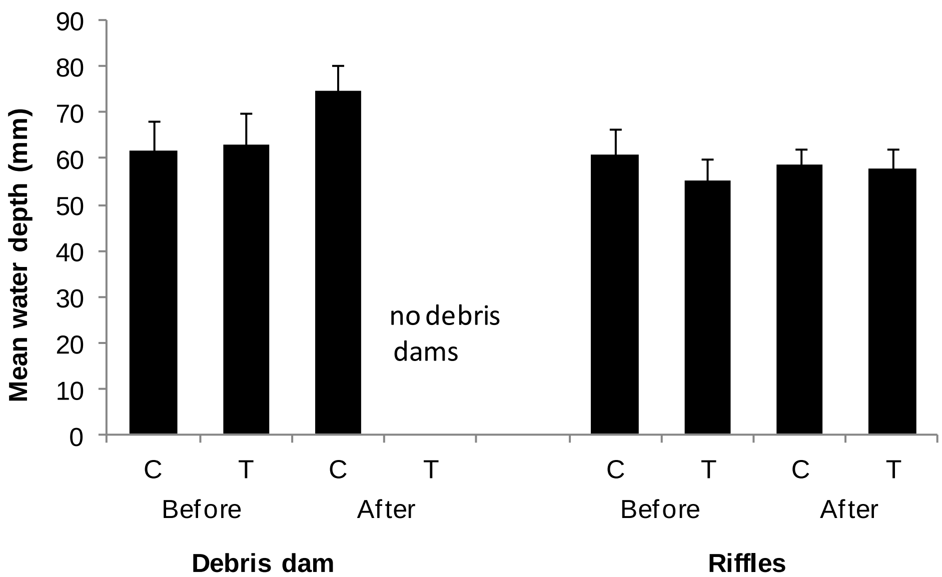

Figure 4.8. Mean water depth in Surber samples from debris dams and riffles in the control (C) and treatment (T) sections before and after wood removal. Error bars indicate SE.

4.4.4 Effects of wood removal on aquatic invertebrate communities

Similar to the fish (Chapter 3, section 3.4.4), there were more invertebrates caught in Year 2 than in Year 1. The total invertebrate abundance increased 2.5-fold in Year 2 (approximately 35 000) compared with Year 1 (approximately 13 900). The increase was consistent for Ephemeroptera which comprised approximately half the total catch in both years, whereas Diptera and Mollusca showed a 4-fold increase between Years 1 and 2. Although Plecoptera increased numerically after wood removal, they declined from 8% to 1% of total catch between Year 1 and 2.

As there were no debris dams in the treatment sections after wood removal, invertebrate data from the debris dams and riffles were weighted by the actual area in each control and treatment section to estimate invertebrate densities. Pool and run area was excluded as these habitats were not sampled for invertebrates. There were no significant effects of wood removal on any of the key aquatic invertebrate order or taxa densities after wood removal (Table 4.4). Neither were there any significant changes in densities in any of the four functional feeding groups after wood removal.

After wood removal, Ephemeroptera, Plecoptera and Trichoptera continued to dominate community composition (Fig. 4.9) in the remaining debris dams in the control sections and in the riffles. Community composition in the riffles in the control and treatment sections after wood removal was very similar to that prior to wood removal, containing higher proportions of Ephemeroptera than invertebrate communities in debris dams. Invertebrate community composition in the remaining debris dams in the control sections was similar to that prior to wood removal contained a higher proportion of Plecoptera and Trichoptera and Diptera than the riffles. Fifty less common taxa, 13 of which were exclusive, were found in the debris dams in the control sections after wood removal. Thirty-five and 42 less common taxa respectively, were found in the riffles in the control and treatment sections. Three were exclusive to riffles in the control sections and seven to the riffles in the treatments sections.

Table 4.4. Mean densities (no. m^{-2}) and standard error of key invertebrate orders and taxa in the control and treatment sections before and after wood removal. The estimated treatment effect was calculated by subtracting the difference between the control and treatment density before wood removal, from the difference between the control and treatment density after wood removal. SE = standard error.

	Control		**Treatment**		**Treatment Effect**	
Taxon	before	after	before	after	Estimate	SE of the estimate
Total density	918	2559	799	2063	-376.8	339.7
INSECTA						
Ephemeroptera	**586**	**1504**	**523**	**1276**	**-165.3**	**235.4**
Coloburiscus	213	445	167	294	-105.7	108.0
Deleatidium	326	869	303	903	57.0	185.3
Neozephlebia	8	59	11	24	-37.8	22.4
Zephlebia	13	81	13	24	-57.7	32.8
Plecoptera	**16**	**53**	**17**	**49**	**-4.5**	**14.7**
Acroperla	5	26	9	29	-1.7	10.7
Austroperla	8	16	5	13	0.3	9.5
Trichoptera	**187**	**542**	**137**	**421**	**-71.2**	**106.1**
Helicopsyche	57	80	69	40	-53.0	44.8
Olinga	65	302	51	247	-40.3	83.7
Pycnocentria	9	66	3	18	-41.2	19.0
Coleoptera	**73**	**149**	**54**	**101**	**-28.5**	**24.6**
Elmidae	37	49	22	41	5.8	15.8
Hydraenidae	6	56	10	35	-25.2	23.9
Ptilodactylidae	31	44	21	25	-9.7	14.8
Diptera	**14**	**126**	**27**	**130**	**-9.5**	**33.9**
Austrosimulium	4	12	14	25	2.8	12.5
Polypedilum	1	2	2	15	11.7	7.6
Tanytarsini	6	82	8	66	-18.2	26.5
Megaloptera						
Archichauliodes	29	66	17	27	-27.2	15.2
MOLLUSCA						
Gastropoda	9	108	20	47	-72.8	51.8
Potamopyrgus	9	106	20	46	-71.5	50.5

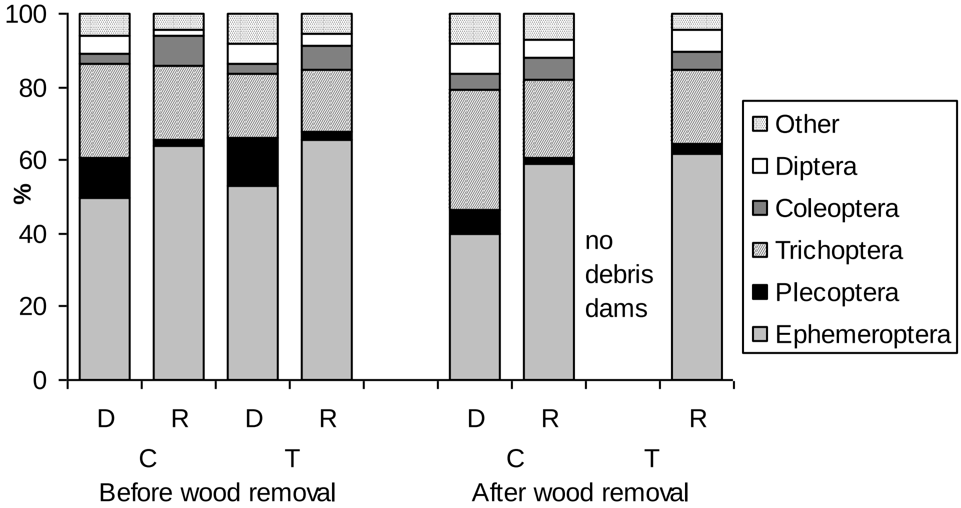

Figure 4.9. Comparison of aquatic invertebrate community composition between debris dams (D) and riffles (R) in the control (C) and treatment (T) sections before and after wood removal.

4.5. Discussion

4.5.1 Invertebrate communities before wood removal

The first hypothesis that invertebrate density would be higher in debris dams and invertebrate community composition would differ from that in riffles, was partly upheld by the results of this study. While this study observed higher densities of invertebrates in debris dams compared with riffles, these differences were not significant. The structural and hydrological complexity of debris dams usually support higher densities of aquatic invertebrates compared with inorganic substrates (Smock et al. 1989; Friberg & Larsen 1998; Weigelhofer & Waringer 1999). However, the high percentage of EPT taxa and abundance in my study indicated streams of high quality and the predominantly gravel substrate provided ideal habitat for aquatic invertebrates. Therefore the difference in total invertebrate densities between debris dams and inorganic substrates may not be as extreme as in other studies with sub-optimal substrates of sand, silt or clay (Angermeier & Karr 1984; Smock et al. 1989). Nevertheless, in these streams, aquatic biodiversity was higher in debris dams, which contained a wider diversity of taxa, higher taxa richness and a larger portion of less common taxa than in riffles, resulting in community composition with characteristics that differed from those in riffles (Fig 4.6). While wood provides a direct contribution to aquatic biodiversity (Wondzell & Bisson 2003), its efficiency in trapping organic material and increasing habitat heterogeneity provided an additional indirect contribution to aquatic invertebrate biodiversity in these streams.

The community composition of invertebrates in debris dams differed significantly from riffles (Fig. 4.6) and was dominated numerically by Ephemeroptera taxa (mainly *Coloburiscus humeralis*), *Zephlebia* spp. and *Deleatidium* spp., (all collector- gatherers) along with two predominantly shredder taxa, *Olinga* spp. (Trichoptera) and *Austroperla cyrene* (Plecoptera) (Table 4.1). Community composition of invertebrate communities in organic accumulations varies considerably in New Zealand, although some commonalities exist. Plecoptera taxa and *Deleatidium* spp. were the most abundant taxa in organic accumulations in a small South Island *Nothofagus* forest stream (Winterbourn 1978). Mesh bags containing leaves of exotic and indigenous species introduced into the same stream contained higher abundances of Chironomidae and Oligochaeta taxa than natural organic accumulations (Winterbourn 1978; Parkyn & Winterbourn 1997). Linklater (1995) found fewer differences in invertebrate community composition between indigenous leaf packs and natural leaf litter accumulations in pools of three streams in Banks Peninsula. Shredders were a large component of community composition in Linklater's (1995) streams dominated by *Oeconesus maori*, and Ephemeroptera and Coleoptera taxa were the most abundance collectors. In two leaf pack experiments in a North Island stream, invertebrate community composition was dominated Trichoptera (*Pycnocentria evecta* and *Olinga feredayi*) and Ephemeroptera taxa (Hicks & Laboyrie 1999; Quinn et al. 2000), and in the case of Quinn et al. (2000), Naididae (Oliochaete) were the most abundant taxa in their leaf packs. Quinn et al. (2000) found higher densities of aquatic invertebrates, a greater proportion of collector-browsers and shredders and fewer filters in leaf packs, compared with the natural stream bed.

Natural organic accumulations vary widely in composition. For example, the debris dams in my study were a composite of large and small wood, leaves, fronds, needles and finer organic matter at varying levels of decay, along with varying levels of sediment (author's pers. obs.) and would have contributed to the variety of taxa found in these habitats. Some of the variability in invertebrate community composition in organic accumulations is also likely to be an artefact of leaf packs and mesh bags. They can provide a more stable environment for leaf material than natural accumulations, and create internal physical and chemical environments that differ from natural accumulations, while both the type and size of leaf pack or mesh bag can also influence leaf breakdown rates (Webster and Benfield 1986). These factors may be contributing to the higher abundances of Oligochaetes and Chironomids found in some leaf breakdown studies (Parkyn & Winterbourn 1997; Quinn et al. 2000). There were indications that invertebrate biomass peaked in the intermediate and latter stages of leaf decay (Linklater 1995; Hicks & Laboyrie 1999). Wood is very effective at trapping organic matter (Benke & Wallace 2003; Bilby 2003) and the trapping capability of large wood in my streams would have contributed to the retention time of organic matter in the stream system, facilitating the breakdown and decay of organic material into a more palatable form for aquatic invertebrates.

Although habitat had a significant influence on invertebrate community composition, seasonality was another factor influencing invertebrate community composition in my study (Fig. 4.6). Aquatic invertebrates in New Zealand generally have poorly synchronised, weakly seasonal or non-seasonal life histories (Winterbourn 1978; Towns 1981; Scarsbrook 2000) with few taxa showing seasonal life cycle patterns (Scarsbrook 2000). This has been attributed to a combination of factors including New Zealand's generally mild climate muting seasonal cues, aseasonal allochthonous inputs (although individual species show varying degrees of seasonality i.e. Winterbourn 1976; Cowan et al. 1985; Linklater & Winterbourn 1993), and unstable stream environments (Winterbourn 1981; Scarsbrook 2000). Towns (1985) found low seasonality in aquatic invertebrate communities which he attributed to the poorly synchronised life cycles of New Zealand's aquatic invertebrates. However, seasonal abundance does not necessarily always align with seasonal life histories as a high abundance of a given taxa may contain a wide range of size classes. In my sites, the abundance of a number of taxa was influencing seasonal variation in invertebrate communities and these seasonal differences were much stronger in autumn than in spring (Table 4.1; Fig. 4.6).

Although direct sampling of wood was not part of the sampling strategy in this trial, community characteristics of invertebrates in debris dams showed some similarities with those directly associated with wood (Anderson 1982; Collier & Halliday 2000). *Zephlebia* spp., *Deleatidium* spp., *Austroclima* spp., *Coloburiscus humeralis, Pycnocentria* spp., and *Olinga* spp. were the most abundant Ephemeroptera and Trichoptera taxa associated with wood, similar to the results in this study. The diversity of diptera taxa associated with wood was also similar to my results. Notable differences were the lack of *Olinga* spp. and low abundance of *Austroperla cyrene* in Collier & Halliday's (2000) study, both facultative shredders (Winterbourn & Rounick 1985; McLellan 1997; Parkyn & Winterbourn 1997). The latter is also a facultative xylophage and was the most abundant Plecoptera associated with wood in Anderson's (1982) study. Anderson (1982) and others (Hoffmann & Hering 2000; Benke & Wallace 2003) have found that most taxa were opportunistically associated with wood, utilising this substrate for various stages of their life cycles and accessing the additional allochthonous and autochthonous food resources associated with wood. Few species directly utilise wood as a food resource. Most of the main invertebrate taxa identified in this study and associated with debris dams, were generalist feeders (collector-gatherers), typical of aquatic invertebrate communities in New Zealand (Winterbourn et al. 1981; Thompson & Townsend 2000). However the higher densities of *Olinga* spp., and *Austroperla cyrene* and total shredders associated with debris dams (Table 4.1; Fig. 4.4), and were probably a result of these and other facultative shredders exploiting the additional organic food resources present in this habitat (Smock et al. 1989; Friberg & Larsen 1998).

4.5.2 Invertebrate response to wood removal

Removal of wood in Year 2 resulted in a pulse of sediment and organic matter stored in debris dams moving down through the treatment sections, simplifying channel morphology (Chapter 3, Section 3.3.3.). The hypothesis that this would result in a reduction in aquatic invertebrate density in the remaining riffles was not upheld by the results of this study and the hypothesised change in the remaining invertebrate communities in the treatment sections was only partly upheld by the results of this study. There are a number of factors that likely contributed to this result. Invertebrates appear to have some degree of resilience to this type of pulse disturbance associated with wood removal, which left no significant residual amounts of fine sediment in the system (Chapter 3, Section 3.3.3.). Prolonged inputs of sediment, particularly fine sediment from land-use change or land-use activities sustained over an extended period of time, appear to be more damaging to invertebrate communities (Fahey et al. 2004; Parkyn & Wilcock 2004).

Similar to other studies (Friberg & Larsen 1998; Weigelhofer & Waringer 1999), debris dams supported aquatic invertebrate communities that differed from those in riffles. However, debris dams comprised a small component of total habitat for aquatic invertebrates in the streams in my study. Therefore, at the reach scale, there were no significant effects on aquatic invertebrate density or community composition in the treatment sections even though the habitat heterogeneity and more diverse community composition associated with debris dams had been lost and riffles in the treatment sections supported fewer less common taxa. These results are similar to other experimental studies that manipulated wood and debris dams in streams (Friberg & Larsen 1998; Warren & Kraft 2006). This is in contrast to the results of a North American trial that excluded terrestrial litter inputs from a forested stream for several years, resulting in a far greater impacts on invertebrate community composition than in my streams (Wallace et al. 1997).

Other factors likely influencing the limited response of aquatic invertebrates to the removal of wood and associated debris dams, are the generalist feeding behaviours of many aquatic invertebrate fauna and the limited number of specialised feeders, particularly obligate shredders in New Zealand’s aquatic invertebrate communities(Winterbourn et al. 1981; Boothroyd 2000; Thompson & Townsend 2000). In North American streams seasonal leaf fall patterns are strong determinants of invertebrate community structure and shredder life cycles (Cummins et al. 1989) compared with the weaker temporal relationships between invertebrate communities and organic matter that exist in association with the relatively aseasonal allochthonous inputs New Zealand’s waterways (Friberg et al. 1997; Winterbourn 1978; Linklater 1995; Thompson & Townsend 2000).

My results highlight the degree of inter-annual variation that can occur in small stream systems and the flexibility in the carrying capacity of small stream ecosystems which concurrently experienced a corresponding increase in fish density that same year (Chapter 3, section 3.4.4). In Agüera, Spain Elosegi et al. (2002) also observed small seasonal but large inter-annual variation in aquatic communities and emphasised the need both for caution in interpreting data from a single sampling season and the importance of long-term studies to capture and understand inter- annual variation in carrying capacity in streams. The BACI design used in this study was essential in separating inter-annual and seasonal variation from treatment effects.

4.5.3 Management implications

Although debris dams comprised a small portion of the channel area, as this study showed, they were important storage sites for organic matter and invertebrate biodiversity, even in streams with optimal benthic substrates for aquatic invertebrates. Depending on debris dam attributes, they also provide sites of refuge for invertebrates during flood events (Palmer et al. 1996). Large stable pieces of wood play an important role in the formation, duration and resilience of debris dams, particularly in small streams (Bilby & Likens 1980; Weigelhofer & Waringer 1999) and can provide sites of high invertebrate productivity (Benke & Wallace 2003).

Not only has the loss of forest cover depleted the source of allochthonous material to many of New Zealand's small streams, the associated reduction in loadings of large stable structural pieces of wood has removed a key structural component for retention of organic matter for in-stream processing. While the first part of this project examined the direct benefit of wood to fish (Chapter 3), this study shows a secondary benefit of wood to aquatic invertebrates via the efficiency of wood in retaining organic matter in a stream ecosystem and providing additional habitat in associated debris dams. Post-harvest practices that require the removal of all logging slash, including large pieces, will not only reduce habitat heterogeneity, but also the retentive capacity of stream ecosystems. The information from this study highlights the ecological importance of large structural pieces of wood in small streams and its potential contribution to aquatic systems within managed forests and degraded stream ecosystems.

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4.7 Appendix A. Taxa collected in debris dams and riffles

(+ present; - absent)

Taxa	Debris dams	Riffles
INSECTA		
Ephemeroptera		
Acanthophlebia	+	+
Ameletopsis	+	+
Arachnocolus	+	-
Austroclima	+	+
Coloburiscus	+	+
Deleatidium	+	+
Ichthybotus	+	+
Neozephlebia	+	+
Oniscigaster	+	+
Tepakia	+	-
Zephlebia	+	+
Plecoptera		
Acroperla	+	+
Austroperla	+	+
Nesoperla	+	-
Spaniocerca	+	+
Spaniocercoides	+	-
Stenoperla	+	+
Zelandobius	+	+
Zelandoperla	+	+
Trichoptera		
Aoteapsyche	+	+
Beraeoptera	+	+
Costachorema	+	+
Ecnomidae	+	-
Helicopsyche	+	+
Hudsonema	+	-
Hydrobiosella	+	+
Hydrobiosis	+	+
Hydrochorema	-	+
Neurochorema	-	+
Oeconesidae	+	+
Olinga	+	+
Orthopsyche	+	+
Plectrocnemia	-	+
Polyplectropus	+	+
Psilochorema	+	+
Pycnocentria	+	+
Pycnocentrodes	+	+
Triplectides	+	+
Triplectidina	+	-
Zelandoptila	+	-
Zelolessica	-	+
Odonata		
Anisoptera	+	+
Antipodochlora	+	+

Hemicordulia	-	+
Procordulia	-	+
Hemiptera		
Microvelia	-	+
Megaloptera		
Archichauliodes	+	+
Neuroptera		
Kempynus	+	-
Coleoptera		
Elmidae	+	+
Hydraenidae	+	+
Hydrophilidae	+	+
Ptilodactylidae	+	+
Scirtidae	+	+
Diptera		
Austrosimulium	+	+
Ceratopogonidae	+	+
Dolichopodid	+	-
Empididae	+	+
Ephydridae	+	-
Eriopterini	+	+
Harrisius	+	-
Hexatomini	+	+
Limonia	+	-
Mischoderus	+	+
Molophilus	+	+
Muscidae	+	+
Nothodixa	+	+
Orthocladiinae	+	+
Paradixa	+	+
Paralimnophila	-	-
Podominae	+	-
Polypedilum	+	+
Psychodidae	+	+
Sciomyzidae	+	-
Tabanidae	+	+
Tanypodinae	+	+
Tanytarsini	+	+
Tipulidae	+	-
Zelandotipula	+	-
COLLEMBOLA	+	+
CRUSTACEA		
Amphipoda	+	+
Isopoda	+	+
Ostracoda	+	-
Paratya	+	+
ACARINA	+	-
MOLLUSCA		
Latia	+	+
Potamopyrgus	+	+
OLIGOCHAETA	+	+
POLYCHAETA	+	+
PLATYHELMINTHES	+	+
NEMATOMORPHA	+	-

Chapter Five: Wood in streams – conclusions and recommendations

5.1 Synthesis and conclusions

Since the arrival of humans in New Zealand, a large percentage of the natural forest cover that extended across most of New Zealand has disappeared. Many of New Zealand's streams no longer have forested streams margins and have been deprived of their natural wood loadings. The aim of the first part of this thesis was to undertake a large catchment-scale assessment of LW loadings, spatial distribution and morphological influence in an old-growth indigenous forest to provide some understanding on the natural characteristics of wood that would have been present in many river systems of New Zealand prior to human settlement. The second component of the thesis involved the experimental removal of wood from three small streams in order to provide some insight into what that loss of wood may have meant for fish and aquatic invertebrate communities.

The results of the catchment-scale assessment of wood in an old-growth forest river system showed that LW loadings, spatial distribution and functional role varied greatly within a stream network. However, longitudinal patterns were evident. LW attributes such as piece frequency and length were positively correlated with bankfull width whereas LW volume (m^3 ha^{-1}) and number of pieces suspended across the channel were negatively correlated. In the Whirinaki River system, LW was a major contributor to habitat complexity. Along with other geomorphic structures such as gravel bars and in-channel islands, LW broke up long section of runs and riffles into smaller and more varied habitats. Around half of all LW pieces provided a functional role in the river system. In particular LW influenced wood, organic matter and sediment storage, bank armouring and pool formation. LW contributed to the formation of 43% of pools and pool density was positively correlated with LW volume. The influence of LW in the river channel was negatively correlated with bankfull width. Large stable pieces of wood were key pieces influencing channel morphology. The volumes of wood in the Whirinaki River system (range 6-500 m^3 ha^{-1}) and were similar to wood volumes in overseas studies, although wood volumes are well below those in Douglas Fir and Redwood forested streams of the Pacific Northwest (Gurnell 2003; Cadol et al. 2009).

Gurnell (2003) identified three broad zones of change in wood storage characteristics in response to changes in hydrology and geomorphology down a river system; (1) small headwater streams containing relatively immobile, randomly distributed pieces of wood where stream discharge was insufficient to move wood; (2) channel width and hydrological regime were the main controls on wood storage patterns, there was sufficient stream discharge to move wood but channel width constrained larger pieces of wood, pieces mobilised into accumulations or debris dams which increased in spacing down the stream channel and; (3) channel width no longer constrained pieces, hydrological regime shifted most pieces and geomorphic structure was the main factor determining wood storage sites.

A comparison of the data from the Whirinaki River showed very similar patterns in wood distribution to Gurnell's (2003) review. Four zones of wood distribution and influence were proposed based on wood loadings, piece size, location and frequency, and influence on channel morphology and habitat diversity. Zone 1 included small headwater streams where wood was mainly *in-situ*, suspended above the stream channel, there was insufficient stream power to move pieces and LW had no influence on the channel. In Zone 2 as the channel widened and stream power increased, pieces shifted into debris dams which frequently spanned the channel width. Some pieces remained *in situ* and suspended above the stream channel. In Zone 3 as the channel widened beyond 9-10 m few pieces or debris dams spanned the channel, the distance between debris dams increased and channel morphology controlled storage sites, primarily on outer bends in the channel. A fourth zone was identified where in-channel islands were a key morphological feature influencing wood storage. Transitional boundaries between these zones occurred as catchment area and channel bankfull width increased and where changes occurred in transport capacity, fluvial processes and geomorphic structure of the channel. This study demonstrated the importance of including headwater sites in sampling designs, where distribution patterns of LW changed rapidly over short distances in response to changing underlying environmental variables.

The experimental component of the thesis examined the role of wood in providing habitat for fish and aquatic invertebrates. Pools with wood cover contained most of the fish biomass and provided habitat for two of the larger fish species in these streams; banded kokopu and the larger longfin eels. There was some overlap in fish community composition between the two pool types (wood pools and open pools), particularly where fish exploited alternate sources of cover in the open pools such as boulders and crevices in bedrock. Fish communities in riffles differed from those in the two pool types, influenced by species such as bluegill bullies and torrentfish that prefer the shallower, faster flowing environment in riffles. The presence of a number of species across all three habitats (longfin eels, common bullies, redfin bullies) was a contributing factor to the degree of overlap in fish community composition between the three habitats.

Debris dams formed by wood created localised habitat for aquatic invertebrates resulting in a community structure that differed significantly from aquatic invertebrate communities in the benthic substrate in riffles. Aquatic invertebrate communities in debris dams contained higher total densities of aquatic invertebrates (although the difference was not significant), higher densities of Plecoptera and Trichoptera and a number of invertebrate taxa and contained a larger proportion of the less common taxa present in these streams. *Deleatidium* spp. (Ephemeroptera) was the only taxa with significantly higher densities in riffles than debris dams. For both fish and aquatic invertebrates season was an additional factor influencing community composition with season variation a stronger influence on aquatic invertebrate communities than fish.

The removal of wood from the treatment sections in each of the three streams had a significant effect on the stream channel, reducing the area of pools and the number and area of stream channel in riffles, simplifying channel morphology. Wood removal eliminated pools with wood cover, although some pools still remained, resulting in fewer banded kokopu and large longfin eels in the treatment sections. Once the wood and associated debris dams were removed, this habitat disappeared entirely for the aquatic invertebrates in the treatment sections along with the community structure associated with this habitat. For both fish and invertebrates, wood provided localised areas of habitat diversity that comprised a small proportion of total habitat in the stream reach. As a result, at the reach scale the only significant effect on fish was a reduction in banded kokopu biomass in the treatment sections and no significant effects were evident in the remaining aquatic invertebrate communities or invertebrate functional feeding groups in the riffles. The generalist feeding strategies and habitat requirements of a wide number of aquatic invertebrate taxa would have contributed to this response.

The additional habitat complexity provided by wood in the form of wood pools for fish and debris dams for aquatic invertebrates, had the strongest influence on biological communities at the habitat scale, results at the reach scale were less discernable indicating that reach-scale studies are less likely to capture this information and that scale is an important consideration in study design. It is likely, based on other studies (Angermeier & Karr 1984; Benke et al. 1985; Collier & Halliday 2000), that the morphological and biological influence of wood will be greater in degraded streams, with fine unstable bed substrates and lacking riparian and in-stream cover. Sampling wood and associated debris dams will be necessary to capture the full range of aquatic biodiversity in these types of streams (Maxted et al. 2003).

LW provides an additional organic structural layer to river networks that affects the physical, hydrological and biological functions at multiple spatial and temporal scales (Gregory et al. 2003). The ecological status of many river systems in New Zealand is likely to differ from their original natural state, not only because of the wide spread removal of forests but also the associated loss of the structural component of wood. While the influence of wood extends throughout a river network, smaller stream are mainly heterotrophic, deriving a large component of their energy from allochthonous sources of organic matter. These are the streams where LW and associated debris dams interacted across the full width of the channel, are likely to be most impacted by the loss of wood from waterways.

The River Continuum Concept (RCC) is a prevalent synthetic view of fluvial systems as a continuously integrated series of physical gradients coupled with the hydrological cycle. This forms a template for biological responses, resulting in consistent patterns of community structure and function, organic matter loading, transport, utilization, and storage along the length of the river (Vannote et al. 1980). The authors hypothesize that in forested headwater streams with high allochthonous inputs, the stream system will be heterotrophic changing along a continuum gradient to autotrophic in mid reaches with a gradual return to a heterotrophic system downstream as increasing water depth and turbidity limits primary production. As wood is a component of organic matter, the spatial patterns of wood (such as those identified in the Whirinaki River system and other studies), along a river continuum contribute to the RCC, although LW patterns deviate from the RCC in larger, braided river systems (Piégay & Gurnell 1997; Gurnell 2003).

The concept of disruptions or discontinuities to the longitudinal patterns advocated by the RCC have been promoted by a number of authors who have highlighted the importance of over-riding factors such as stream hydraulics, tributaries and the anthropogenic influence of dams on the stream continuum (Ward & Stanford 1983; Bruns et al. 1984; Statzner & Higler 1986). The development of the patch dynamics theory (Pringle et al. 1988; Townsend 1989) viewed streams as mosaics of patches (i.e. nutrient patches, debris dams, riparian vegetation patches) creating localized disruptions along the stream continuum, increasing spatial heterogeneity. Wood provides an additional overlay of complexity to existing stream systems, and is a contributing influence, both directly and indirectly to discontinuities and disruptions within river networks over a wide range of spatial scales (Montgomery 2003).

5.2 Recommendations

5.2.1 Research

New Zealand has built up a recognisable body of research on wood in waterways (Chapter 1.2.3 & 1.2.4). However, when compared to the extensive international body of research, particularly in North America (Gregory et al. 2003), many gaps still exist including the following:

- Research in New Zealand has focused mainly on small streams; there is very little information on the role of LW in larger river systems;
- There has been only one large catchment scale study in old-growth forest, completed as part of this thesis. New Zealand still has large tracts of relatively unmodified forest, with vegetation ranging from sub-tropical to sub-Antarctic and can provide further contributions to our global understanding on the role of wood in forested river systems;
- Many wood studies are short-term and lack the spatial and temporal replication needed to capture the variation across the hydrological and ecological regions of New Zealand;
- There is no information on decay rates of New Zealand's indigenous and exotic timbers in aquatic environments;
- There is limited information on the role of wood in providing refuge sites in extreme hydrological events such as droughts and floods and its potential to improve ecosystem resilience (Evans et al. 1993);
- The experimental wood removal component of the thesis was undertaken in forested stream catchments with forested riparian vegetation, in-stream cover and benthic substrates dominated by gravel. It would be useful to repeat this experiment in degraded sites with fine unstable substrates, that are deficient in forested riparian margins and lacking in-stream cover for fish;
- The use of wood as a rehabilitation tool has received very little attention in New Zealand (Aldridge 2008).

5.2.2 Wood as a restoration tool

An obvious recommendation is to promote the use wood as a rehabilitation tool in New Zealand streams. Wood is increasing used around the world to rehabilitate aquatic habitat, particularly for fish (Reich et al. 2003; Nagayama & Nakamura 2010). However, complexities associated with geomorphology, hydrology, and sediment regimes along with the variable responses of target fish species often results in the failure of the project to achieve the desired ecological outcome. In spite of its widespread use as a rehabilitation tool for fish, Nagayama and Nakamura (2010) found only 35 studies in academic journals. These studies focussed predominantly on salmonids, although one Australian study targeted a galaxiid species. Rigorous scientific evaluation and long-term monitoring of rehabilitation projects was also lacking. A review by Palmer et al. (2010) that evaluated the effectiveness of restoration activities in enhancing habitat heterogeneity in order to increase aquatic invertebrate diversity also found little robust scientific evidence that increasing habitat heterogeneity leads to increased biodiversity.

Introduction of wood into streams to enhance or restore aquatic habitat usually initiates a rapid geomorphic response, increasing habitat heterogeneity in the form of increased pool variety and pool area, channel narrowing or widening, creation of undercut banks, cover and development of spawning gravels (Kail et al. 2007; Floyd et al. 2009). Response of biological communities is varied and often confounded by the inherent environmental variability in river systems. Some trials have recorded increases in overall aquatic invertebrate abundance or taxa groups, or changes in community composition, following the introduction of wood to streams, although differences are not always significant, whereas other studies show no significant invertebrate responses to wood addition (Hilderbrand et al. 1997; Lester et al. 2007; Testa et al. 2010; Flores et al 2011). Response of fishes to wood addition projects have focused primarily on salmonids. While responses vary, positive results are often recorded in the initial years after wood introduction including increases in fish abundance and biomass across a range of age classes, higher spawning densities or improved carrying capacity in seasonal extremes such as summer low flows and winter conditions (Cederholm et al. 1997; Kail et al. 2007; Floyd et al. 2009;

Nagayama et al. 2009; Antón et al. 2011). Restoration projects that use natural sources of wood to minimally modify the existing channel, and integrate restoration efforts within a wider geomorphic and hydrological context of the catchment appear to be factors that assist in increasing the longevity and functionally of wood structures in streams (Wendell et al. 1998; Frissell & Nawa 1992; Kail et al. 2007).

There is enough information currently in the literature to serve as a word of caution when entering into restoration projects. Any rehabilitation projects using wood require careful consideration and planning using a combination of ecological and fluvial engineering skills. Judicial use of LW has the potential to enhance habitat for a variety of in-stream and riparian species and is a potential management tool in the conservation of some endangered aquatic species (Benke & Wallace 2003; Dolloff & Warren 2003; Baillie & Glaser 2005; Nicol et al. 2007).

Public perception of wood is also an issue both globally (Piégay et al. 2005) and in New Zealand where wood in streams is managed primarily for flood damage to downstream infrastructure, property and receiving environments. Media attention on intense rainfall events, which have triggering landslides, debris flow and movement of woody debris and logging slash off-site, with subsequent damage to downstream properties have contributed to the negative perception of wood. Minimal consideration is given to the potential disruption to fundamental functions and processes in small stream ecosystems through widespread removal of wood. However, any management of wood in NZ streams for ecological benefit needs to take into account the hydrology of many New Zealand's small streams which are often short, high-gradient and subject to frequent flooding (Winterbourn 1995). Restoration efforts using wood should form part of an integrated catchment-scale approach, and be considered as an interim measure until the natural processes and linkages between riparian areas and waterways are restored (Dolloff 1994; Kail et al. 2007).

5.2.3 Management of wood in plantation forest streams

Approximately one-third of the remaining forests in the world are managed (World Resources Institute n.d.) and in New Zealand around 22% of forest cover is in plantation forests (New Zealand Forest Owners Association 2009). These figures highlight the importance of managing the integrity of the aquatic ecosystems within these forests.

In plantation forests, streams are subjected to varying degrees of disturbance from harvesting activities approximately every 28 years. Although some streams have unplanted riparian margins, historical plantings were frequently to the stream edge and these areas are still in the process of being harvested. The amount of wood and logging slash (stems, branches, twigs, needles) that enters waterways during harvesting activities varies considerably depending on factors such as the harvesting system used, topography, stand characteristics, species, and the extent of riparian buffers (Baillie et al. 1999). Post-harvest management of logging slash also varies depending on regional and district council regulations and forest company rules. Logging slash is managed primarily for risk, stream-cleaning (removing logging slash from waterways) is common practice and as mentioned in Section 5.2.2., recent debris flow events have reinforced the negative perceptions of wood in waterways (Baillie 1999; Bay of Plenty Regional Council 2011). However, the ecological benefit of wood is recognised by some forest companies in their logging slash management strategies (Hancock Forest Management (NZ) Limited 2010). Plantation forests have the advantage of a readily available supple of LW including wind-thrown stems that enter waterways as the stand matures, and additional non-merchantable pieces at harvest. Retention of appropriate large stable pieces following harvest could assist in minimising harvest impacts on aquatic ecosystems, provide habitat and refuge sites for aquatic biota and contribute to post-harvest recovery.

When considering the enhancement and sustainability of waterways in New Zealand, the role of wood is often overlooked, mainly because of a lack of knowledge and understanding of its role in New Zealand’s streams or concerns over risks associated with movement of wood in streams. It needs better recognition as a natural component of stream ecosystems and managed accordingly. Understanding wood dynamics (sources, modes of entry, spatial and temporal distribution, stability and movement, functional and biological roles) in New Zealand’s climatic, geological and hydrological conditions is necessary if wood is to be incorporated in the future protection and management of streams.

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