

The effects of forest fragmentation on stream invertebrate communities on Banks Peninsula

A thesis

submitted for partial fulfilment for the degree of

Master of Science in Zoology

at the

University of Canterbury

By

Iain A. Fraser

University of Canterbury

2006

Table of contents

Abstract	1
-----------------	----------

Chapter 1: Forest fragmentation: a review of the effects on stream invertebrate communities

Introduction	2
Influence of shade	3
Effects on stream biota - light	5
Effects on stream biota -- temperature	5
Effects on adult insects	6
Allochthonous inputs	8
Sediment	10
Forest fragment location within the catchment	11
Implications for riparian management	13

Chapter 2: Study sites

Site selection	16
Physiochemical sampling	18
Sites descriptions	19
Fragmented forest catchments	19
Continuous forest catchments	25
Physiochemical properties	29

Chapter 3: The effects of forest fragmentation on stream invertebrate communities

Introduction	31
Methods	32
Analysis	32
Results	33
Functional Feeding Groups	38
Stream health	42
Discussion	47

Chapter 4: Adult stream invertebrate dispersal between forest fragments

Introduction	53
Methods	54
Malaise trapping	54
Sticky trapping	54
Identification	55
Analysis	55
Results	56
Malaise trapping	56
Sticky trapping	58
Longitudinal stratification	61
Comparisons between benthic and adult catch	65
Discussion	68

Chapter 5: Conclusions

Concluding comments	75
Implications for managment	76
References	79
Acknowledgements	85
Appendices	86

Abstract

The removal of indigenous forest and associated fragmentation of habitats has probably had significant impacts on the diversity of stream communities in New Zealand. In this study I investigated the effects of forest fragmentation on stream invertebrate communities on Banks Peninsula. Six catchments were investigated, three with continuous indigenous forest in the riparian zone and three with fragmented indigenous riparian forest. An extensive benthic survey was conducted at three sites in each river catchment, one downstream on the mainstem of the river and two sites in different headwater tributaries. Adult sampling, consisting of malaise and sticky trapping, was also conducted at a sub-set of sites. Taxonomic richness of both the benthic and adult communities was significantly higher in continuous forest than in fragmented forest, and the composition of benthic communities also differed between continuous and forest fragments. Furthermore, benthic invertebrate densities were higher in fragments than continuous forest sites. The fragments in the headwaters were more likely to support forest specialist taxa (e.g. the stonefly *Zelandobius wardi*, and the caddisfly *Costachorema peninsulae*), than the downstream fragments. My results indicate that forest fragmentation has resulted in marked changes in benthic communities on Banks Peninsula, and that location of the fragment within the catchment also is important in influencing the diversity and composition of benthic communities. The maintenance of indigenous forest in the headwaters of streams may be essential for the persistence of endemic and forest specialist taxa on Banks Peninsula.

Chapter 1: Forest fragmentation: a review of the effects on stream invertebrate communities

Introduction

Human induced deforestation is a globally prevalent phenomenon and is a major component of global land use change (Benstead et al. 2003, Foley et al. 2005). In third world countries forests are being felled for lumber and cleared to make way for agriculture and urban development, while in developed nations urban expansion continues to infringe on remnant forest and riparian zones (Naiman and Turner 2000, Wissmar 2004, Giller 2005). Deforestation of pristine indigenous forest is prevalent in many developing or underdeveloped countries as well as several developed nations (Benstead and Pringle 2004). In some developing nations deforestation of riparian zones is legally encouraged. For example, Chilean law promotes the removal of riparian vegetation under the irrigation law, *Ley para el fomento del riego y drenaje*, passed in 1986 (Medina-Vogel et al. 2003). Within New Zealand since human colonisation roughly two thirds of the original native forest cover has been removed (McGlone 1989, Quinn et al. 1997a). Regionally even greater forest losses have occurred. On Banks Peninsula between 1860 and 1900 >98% of the indigenous forest was cleared (Harding 2003).

Consequently remnant and regenerating forest fragments are common and frequently patchily distributed throughout river systems. Murcia (1995) defines forest fragmentation as “the replacement of large areas of native forest by other ecosystems leaving isolated forest patches, with deleterious consequences for most of the native forest biota (p58)”. Forest fragmentation may be one of the most important causes of habitat loss and is regarded as one of the major causes of global biodiversity loss (Fahrig 2003, Hanski 2005, Pichancourt et al. 2006). Fragmentation threatens the persistence of

metapopulations reliant on continuous habitat by isolating populations into remnant patches (Moilanen and Hanski 1998, Goodsell and Connell 2002, Shirley 2006, Zartman and Shaw 2006). The fragmentation of riparian forests can lead to dramatic changes in stream ecosystem functioning (Giller 2005), as riparian vegetation has been shown to reduce sediment input from the surrounding treeless watershed, improve bank stability and reduce pollutants and agricultural runoff leaching into streams (Vuori and Joensuu 1996, Quinn et al. 1997a, Perry et al. 1999, Boothroyd et al. 2004). Riparian forests also exert influence over light levels and microclimatic conditions such as water, air and ground temperatures, humidity and wind speed (Sinokrot and Stefan 1993, Rutherford et al. 1997, Davies-Colley et al. 2000, Malcolm et al. 2004). The vegetation in the riparian zone also dictates the terrestrial subsidies available to the stream in the form of the allochthonous inputs such as Coarse Particulate Organic Matter (CPOM), woody debris and terrestrial invertebrates (Cummins 1974, Winterbourn 1976, Nakano et al. 1999, Gomi et al. 2002, Lepori et al. 2005). This review will focus on the impacts of riparian forest fragmentation and its effects on stream macroinvertebrates.

The influence of shade

One of the most immediately apparent effects of riparian forests is the shading it provides to the stream. Stream light levels are strongly influenced by the presence and composition of riparian vegetation (Boothroyd et al. 2004, Malcolm et al. 2004). Quinn et al. (1997a) found that streams with native forest or introduced pine forest cover received 1-3% of incident light compared to 30% incident light in nearby pastoral streams. Given that solar (shortwave) radiation is the most important contributor to stream water surface temperature in small streams (Sinokrot and Stefan 1993). The presence or absence of riparian forest also has a great effect on stream temperatures. The

removal of riparian vegetation leading to an increase in mean stream temperature and maximum daily temperatures in summer has been well documented (Quinn et al. 1994, Rutherford et al. 1997, Gomi et al. 2002, Benstead et al. 2003, Kiffney et al. 2003, Wissmar 2004). In the upper Midwest of the United States in shallow streams with little shading Sinokrot and Stefan (1993) noticed diurnal fluctuations of up to 5°C in water temperature.

Riparian vegetation can also affect the valley and stream channel microclimate, affecting local air temperature, humidity and wind speed, which in turn affect evaporation rates, conduction, and ground temperatures, all of which have some influence on stream water temperatures (Rutherford et al. 1997, Davies-Colley et al. 2000, Meleason and Quinn 2004, Wissmar 2004). Davies-Colley et al. (2000) found that 80m into forest wind speed had dropped to c. 20% of that in open pasture. They also found that ground temperature changed markedly over a distance of only 10m into the forest. Thus removal of forests exposes ecosystems to the stresses of temperature fluctuations and desiccation due to increased exposure to sunlight and wind (Davies-Colley et al. 2000).

Riparian forest has been shown to reduce diel variability in thermal regimes as well as reducing temperature extremes in both air and stream temperature (Malcolm et al. 2004). Long wave radiation emitted from riparian vegetation has the ability to raise the daily minimum stream temperature by partially offsetting the outgoing radiation emitted by the stream (Sinokrot and Stefan 1993, Rutherford et al. 1997). Air temperatures in forests are frequently cooler during the day and warmer at night than open pasture sites (Meleason and Quinn 2004). Given that low order streams running through forest tend to have wider channels than those running through pasture there is greater surface area of stream for evaporative and heat transfer allowing air temperature to have a greater influence on stream temperature than in narrower banked open pasture sites (Scarsbrook

and Halliday 1999, Broadmeadow and Nisbet 2004). Research in New Zealand into the effects of forest's effect on air temperature have pointed toward a buffer of 50m being required to maintain forest interior conditions, irrespective of fragment size (Young and Mitchell 1994, Davies-Colley et al. 2000).

Effects on stream biota - light

The major driver of periphyton production and biomass appears to be light, as increases in light increase the photosynthetic rate (Quinn et al. 1997b, Kiffney et al. 2003, Boothroyd et al. 2004, Death and Zimmermann 2005). Shading by riparian vegetation decreases light, which reduces net photosynthesis, and at the same time decreases water temperature, which reduces the metabolic rate of the periphyton, resulting in an overall decrease in primary production and total periphyton biomass. For example, in open canopy streams Boothroyd et al. (2004) found that periphyton biomass was 100 times greater than in closed canopy forested streams.

Large changes in stream primary production have direct effects on stream invertebrate community composition and abundance. Nyström et al. (2003) found lower abundances of invertebrates at forested sites compared to open sites and implied that the presence of canopy cover constrained the size of the benthic community. Shading limited primary production and in turn limited the food available to primary consumers, resulting in strong bottom-up effects on the stream community (Nyström et al. 2003). Greater primary production can lead to primary consumers, such as chironomids and gastropods, forming a greater proportion of the community (Quinn et al. 1997b).

Effects on stream biota - temperature

Water temperature is a major factor influencing the functioning and biota of stream ecosystems controlling the metabolic rate of periphyton, microbes, invertebrates and fish (Cummins 1974, Sinokrot and Stefan 1993, Quinn et al. 1994, Boothroyd et al. 2004, Malcolm et al. 2004). Stream temperatures can also have a direct effect on mortality. Plecoptera, Ephemeroptera and several species fish are regarded as being sensitive to temperature (Townsend et al. 1983, Rutherford et al. 1997). Research on the upper thermal tolerances of 12 New Zealand stream invertebrate taxa found that LT₅₀ (lethal temperature for 50% of individuals) after 96 hours exposure ranged from 22.6 to 32.6°C (Quinn et al. 1994). Two Ephemeroptera taxa (*Zephlebia dentata* and *Deleatidium* spp.) and a Plecopteran (*Zelandobius furcillatus*) were the most sensitive and an Elmidae beetle larvae the most tolerant insect (Quinn et al. 1994). Using these findings Rutherford et al. (1997) estimated the thermal tolerance for sensitive New Zealand benthic invertebrates was about 20°C and calculated that c. 70% shade should be sufficient to maintain headwater stream temperatures beneath 20°C. However the water temperature in open streams in New Zealand during summer has been shown to frequently exceed 20°C and in small streams to even exceed 30°C (Rutherford et al. 1997). Even during Spring, Quinn et al (1997) found that pasture streams exceeded 20°C on a daily basis while forest streams rarely exceeded 15°C. Quinn and Hickey (1990) noted that Plecopteran biomass was very low at sites that had mean average temperatures greater than 13°C and suggested that New Zealand Plecopteran taxa may be reliant on heavy riparian shading to maintain stream temperatures beneath sub optimal or lethal temperatures.

Effects on adult insects

Shading caused by riparian vegetation also has an influence on the survival of the adult stage of many stream insects (Davies-Colley et al. 2000). Flying adults frequently traverse intervening terrestrial habitat to disperse to neighbouring sites (Briers et al. 2004), and their survival is dependant on air temperatures and humidity (Collier and Smith 2000). The presence of the moderating effects of riparian forest may therefore prolong the survival of dispersing adults (Collier and Smith 2000, Davies-Colley et al. 2000). Collier and Smith (2000) found that survival of three species of gripopterygid stonefly adults decreased with increasing air temperature and decreasing mean relative humidity. The LT_{50} for the female gripopterygid stoneflies averaged 22-23°C. These temperatures were exceeded 25% of the time in pasture and <0.1% of the time in native forest (Collier and Smith 2000, Davies-Colley et al. 2000). Hence riparian forest may allow adults to live long enough to reach distant sites for oviposition. The removal of riparian forest may create areas where adult insects are unable to disperse, preventing their recruitment to areas. These effects may be greater in taxa with longer adult lives, such as Plecoptera which often require time in the adult phase for ovarian maturation and egg production (Smith and Collier 2000), rather than taxa with short adult lives, such as conoesucid caddisflies (Winterbourn and Crowe 2001).

The availability of food in the riparian zone can also affect the life span of some adult insects (Beer-Stiller and Zwick 1995, Smith and Collier 2000). Several taxa need to feed as adults to successfully complete their development (Beer-Stiller and Zwick 1995). In Germany several species of Nemourid stoneflies were found to double and triple in biomass during their adult phase due to terrestrial feeding (Beer-Stiller and Zwick 1995). In New Zealand the adults of two stonefly species, *Acroperla trivacuata* and *Zelandoperla decorata*, collected from riparian vegetation had more food in their

stomachs than those collected away from riparian vegetation (Smith and Collier 2000), suggesting that after emergence adults move to the riparian vegetation to feed (Smith and Collier 2000). Therefore the presence of riparian forest may be doubly important to the survivorship of adult insects, and also to the dispersal and abundance of the next generation. Not only is the surrounding riparian vegetation important to the adult stages as a source of food, but is also important to the in-stream community as well through terrestrial subsidies.

Allochthonous inputs

Cummins (1974) stated that communities in small woodland streams in temperate zones are heterotrophic, in that they depend on allochthonous inputs from the surrounding catchment. Allochthonous inputs provided by riparian forest include terrestrial arthropods (Nakano et al. 1999, Broadmeadow and Nisbet 2004), CPOM, leaf litter (Winterbourn 1976, Wallace et al. 1997), Fine Particulate Organic Matter (FPOM) (Cummins 1974, Winterbourn et al. 1981) and coarse woody debris (Quinn et al. 1997a).

Terrestrial arthropod inputs have been shown to have an indirect effect on stream food webs and therefore community structure (Nakano et al. 1999). Nakano et al. (1999) found that in the presence of allochthonous inputs, the fish Dolly Varden (*Salvelinus malma*) consumed mainly terrestrial arthropods that had fallen into the stream. When allochthonous inputs were prevented from reaching the stream by greenhouse-type covers, *S. malma* switched to eating benthic invertebrates (Nakano et al. 1999). The change in diet of *S. malma* had a cascade effect on the stream's biota, with the decrease in herbivorous invertebrates causing an increase in periphyton biomass as it was released from grazing pressure (Nakano et al. 1999). Therefore the presence and composition of

riparian vegetation can be important to the quantity and type of terrestrial arthropods that fall into the stream.

The composition of riparian vegetation also influences the quantity and quality of leaf litter and wood received by the stream (Wallace et al. 1997). Standing stocks of wood, leaves and other CPOM enables streams to support greater abundances of facultative shredders (Harding and Winterbourn 1995, Benstead et al. 2003). CPOM is also converted to FPOM through physical abrasion with substrate within the stream channel, animal feeding and microbial metabolism (Cummins 1974). Shredders assimilate only c. 40% of CPOM ingested, and the rest is egested as faeces (Cummins 1974). These faeces are then available to filterers and collector/browsers as FPOM. A fundamental component of the River Continuum Concept (Vannote et al. 1980) is that downstream communities rely on energy exported from upstream. The generation of FPOM by upstream shredder communities is one component of this exported subsidy. The importance of CPOM may vary globally. In forested streams in New Zealand, Winterbourn et al. (1981) has suggested that shredders do not play a fundamental roll in the processing of CPOM and that the majority of FPOM consumed by browsers is from allochthonous sources.

Dissolved Organic Matter (DOM) is another important product of terrestrial processes, where soluble organic matter leaches from submerged leaves (Cummins et al. 1972, Cummins 1974). The majority of the leaching occurs within the first 24 hours, when 5 – 30% of the dry weight of leaf litter can be lost depending on the leaf species (Cummins et al. 1972). Dissolved organic matter is then used by the algal and microbial communities, which in turn make the nutrients available to the browsers and grazers, and through them to the rest of the food web.

Coarse particulate organic matter and woody debris also provide substrate that can be colonised by stream biota (Cummins 1974, Winterbourn 1976, Collier 2004). The surface of CPOM is usually rapidly colonised by microorganisms, bacteria, fungi and protozoans (Cummins 1974, Winterbourn 1976). Microbial communities on CPOM have been likened to the 'peanut butter on the cracker' – the nutritious layer on a rather innutritious substrate consumed by shredding invertebrates (Cummins 1974). Much of the energy gained by invertebrates from eating CPOM probably comes from consuming the microbial flora and fauna growing on it (Cummins 1974). The role of CPOM as a habitat may be one of its more important functions.

Larger woody debris also forms microhabitats for macroinvertebrates and fish (Collier 2004), but the importance of woody debris as habitat may vary. Collier (2004) found that woody debris was more important as a habitat in soft bottomed streams than in stony bottomed streams. Woody debris within the stream creates diversity in channel form and water depth, raising the potential retentiveness and productivity of the stream (Broadmeadow and Nisbet 2004). Coarse woody debris submerged in the stream channel is also instrumental to the retention of CPOM (Lepori et al. 2005). Studies have also shown that woody debris may be important to the distribution of vertebrate predators (Medina-Vogel et al. 2003). The presence or absence of vertebrate predators can alter the benthic community by affecting the food-web through top down effects (Nyström et al. 2003).

Sediment

Human activities such as agriculture (Harding et al. 1998, Scarsbrook and Halliday 1999, Broadmeadow and Nisbet 2004), logging (Boothroyd et al. 2004), road building and land drainage (Vuori and Joensuu 1996) often lead to increases in

sedimentation in streams. Pasture streams generally have higher levels of suspended inorganic solids than undisturbed forest streams (Quinn et al. 1997a). Harding et al. (1998) found that sediment levels in streams in western North Carolina were higher with current or even past agricultural land use in the adjacent watershed. However, in Madagascar Benstead et al. (2003) found no evidence for higher sedimentation rates in agricultural streams compared to forested streams. Clearly there is some variation in land use practises that can have different impacts on nearby streams.

Riparian vegetation encourages sheet flow rather than channelled flow which reduces surface runoff by increasing the infiltration rate, leading to increased deposition of sediment before it reaches the stream (Broadmeadow and Nisbet 2004). However excessive shading may reduce ground plants along the immediate riparian zone and can lead to increased sedimentation through erosion (Broadmeadow and Nisbet 2004).

In extreme circumstances sedimentation can smother the substrate, changing the stream bottom from a stony-bottomed stream to a soft-bottomed stream. Clogging of the interstitial spaces and reduction in substrate complexity can negatively affect invertebrate communities, and soft-bottomed streams typically have different invertebrate communities from cobble streams (Quinn and Hickey 1990). New Zealand benthic taxa are probably adapted to coarser substrate (Collier 2004). In a study done in 88 rivers throughout New Zealand, invertebrate abundance and taxonomic richness was lowest in soft bottomed rivers and rivers with cobbles overlaid with sand (Quinn and Hickey 1990). A study of 12 common benthic invertebrate taxa found that taxa generally prefer coarse substrate and that none of the taxa studied showed a clear preference for fine substrates (Jowett et al. 1991).

Forest fragment location within the catchment

Given the continuum nature of streams and rivers, where headwaters are connected to the downstream reaches by the unidirectional flow of water, conditions upstream directly influence downstream conditions (Vannote et al. 1980, Gomi et al. 2002, Eikaas et al. 2005).

If the stream passes through open land, solar energy will raise the water temperature of the stream (Sinokrot and Stefan 1993). This warmed water moves downstream and even if the stream then passed into a reach with riparian shading the temperature would remain high despite the riparian vegetation limiting further heating. The stream would have to be shaded by riparian vegetation for some distance before the water temperature would return to what would be expected in a forest stream; perhaps for several hundred metres (Rutherford et al. 1997, Scarsbrook and Halliday 1999). In wider, higher-order rivers the riparian vegetation provides less shading, allowing more light to reach the stream, limiting the potential of riparian forest to moderate water temperature.

Headwater streams in forest fragments will have more stable temperatures. As long as the stream is surrounded by a riparian buffer of c. 50m it should experience temperature and microclimatic conditions similar to that of continuous forest (Davies-Colley et al. 2000). However when the stream passes into the open, it will be exposed to the heating effects of solar radiation. Rutherford et al. (1997) calculated that in the New Zealand summer a stream passing from forest to pasture will be heated to 20°C within 250m for a first order stream, 500m for a second order stream and within 1.5km for a 3rd order stream.

Elevated water temperatures within streams passing through forest fragments may be beneficial as long as temperatures remain beneath the tolerance levels of the local taxa. Given that the rate of conversion of CPOM to FPOM by microbial activities is

dependent on temperature (Cummins 1974, Lepori et al. 2005), and that downstream fragments may have elevated stream temperatures due to heating, greater amounts of FPOM may be created in downstream fragments, than in similar reaches of forested streams.

The presence of riparian forest in the headwaters of a stream may not lead to a local abundance of CPOM for shredders. Local availability of CPOM is dependent on the retentiveness of the stream and discharge rates (Winterbourn 1976, Lepori et al. 2005). As headwater streams tend to have steeper gradients and more variable flow, potentially flushing the CPOM downstream especially during periods of high flow (Winterbourn 1976).

Sediment is also transported from upstream sources to lower reaches. In downstream reaches with riparian forest fragments, even if the riparian buffer is wide enough to prevent local influxes of sediment, sediment levels can be elevated due to sediment imported from open land upstream. Scarsbrook and Halliday (1999) found that 300m within forest, suspended sediment levels were still elevated due to upstream agriculture. Suspended sediment may be carried rapidly downstream, however deposited sediment moves more slowly and can remain in streams long after the cause of its input has been removed. Harding et al. (1998) found that large scale and long-term agricultural disturbances in a catchment may affect the stream for many decades.

Headwater streams are potentially at greater risk from sedimentation as they are smaller and influxes of sediment will have a greater impact in smaller streams.

Headwater streams are also liable to be located in land where the slope is greater, and this typically decreases the effectiveness of riparian vegetation in entraining sediment. In a study in the UK, a 60-70m wide riparian buffer reduced the amount of suspended sediment by 50%, however this effect was reduced on slopes greater than 4° due to

surface runoff flattening the vegetation during periods of high rain fall (Broadmeadow and Nisbet 2004).

Implications for riparian management

There have been many suggestions on appropriate riparian buffer widths for the protection of stream ecosystems. Broadmeadow and Nisbet (2004) suggest that riparian buffers of 5-30m should ideally be expected to provide between 50% - 75% effectiveness at preserving the functions of forest streams. However, the riparian buffer may need to extend to at least 50m from the stream to maintain climatic conditions (wind, air temperature, humidity) typical of undisturbed forest (Young and Mitchell 1994, Davies-Colley et al. 2000). Research into litter inputs from riparian buffers suggests that even a 50m buffer may not adequately replace continuous forest (Oelbermann and Gordon 2000). Oelbermann and Gordon (2000) found that leaf litter inputs into a stream with a 50-100m riparian buffer was c.50% of that of a stream with mature riparian forest. Therefore, it would be prudent to implement riparian buffers >50m around streams and rivers in an attempt to retain forest-like conditions.

However, it would be uneconomical to maintain or reforest a >50m buffer around all the streams and rivers in a catchment. Therefore, if money is an issue, the riparian forest is often going to end up fragmented. Headwater streams would benefit the most from riparian buffers as they are smaller and more easily impacted by land use changes. Also placing riparian forest in the headwaters prevents the stream within the forest fragment from being affected by impacted reaches upstream. However low order headwater streams are more numerous than larger streams within a catchment and a greater area of forest may be required to protect all of them rather than the downstream reaches.

Riparian forest fragments in higher order streams in lower reaches would have to contest with land use effects from upstream. Therefore they may need to be larger than buffers in the headwaters to have a similar effect. In order to attain in-stream conditions similar to those in forest streams, the riparian buffer would have to cover a c.300m reach of the stream (Rutherford et al. 1997, Scarsbrook and Halliday 1999).

If the goal of the restoration or protection of the riparian forest was to preserve the stream biodiversity then forest fragments in the headwaters would be advisable if a limited area of forest could be preserved. If presented with a catchment with fragmented riparian forests, a thin strip of riparian trees joining the fragments may mitigate the most extreme effects of stream exposure and maximise the buffering effect of the forest fragment. If the riparian trees can keep the shading level above 70%, stream temperatures should remain within the tolerance levels of sensitive taxa (Rutherford et al. 1997). The small strip of trees may limit primary production, but this would be compensated for by increased inputs of CPOM. A 2-5m buffer can supply around 22% of the leaf litter expected from a mature riparian forest (Oelbermann and Gordon 2000). The addition of CPOM will add to the diversity of food resources, which should in turn support a greater diversity of taxa.

By restricting the light inputs, and therefore temperature, to the stream, conditions within downstream forest fragments approach those of a forested stream over a shorter distance. This may allow the fragments to support more sensitive taxa that may have previously been affected by high summer temperatures. Less harsh conditions within the riparian channel may also aid in the survival of dispersing winged adults (Collier and Smith 2000, Smith and Collier 2000). As the stream channel is seen as the main 'highway' for adult dispersal (Petersen et al. 2004). This may lead to increased rates of migration between fragments and aid in the persistence of metapopulations.

Chapter 2: Study sites

Site selection

This study was conducted on Banks Peninsula which adjoins the Canterbury Plains on the east coast of the South Island of New Zealand. Banks Peninsula provided an ideal location for this research for several reasons. Prior to human colonisation much of the peninsula was covered in forest, 98% of which was removed between 1860 and 1900 (Porteous 1987). This deforestation coupled with a reduction in farming on the peninsula has led to the creation of numerous forest fragments as the forest regenerates. The uniform geomorphology of the peninsula also creates an ideal natural experimental region with replicated valleys, streams and landforms. The peninsula consists of two extinct shield volcanoes ‘mantled by wind-deposited loess from the Southern Alps to the west’, with over 60 valleys and streams (Harding 2003, Eikaas et al. 2005). The peninsula also exhibits a high level of endemism in its stream invertebrate fauna presenting an opportunity to investigate the influence of habitat fragmentation on endemic taxa (Harding 2003).

Initially all catchments with either complete indigenous riparian forest cover (from headwaters to the lowest reaches) or catchments with significant fragments of indigenous riparian forest were identified from topographical maps (NZNS 260 series) and local knowledge. From these a subset of catchments were chosen and investigated for suitability based on physical accessibility and the willingness of landowners to allow access.

Six catchments were finally selected, three catchments with continuous riparian forest and three with fragmented riparian forest (Fig 2.1). The three continuous riparian

forest catchments were; Narbey stream within the Hinewai reserve in Otanerito Bay, Long Bay Stream within Long Bay, and the Okuti River in Okuti Valley (Fig 2.1CD).

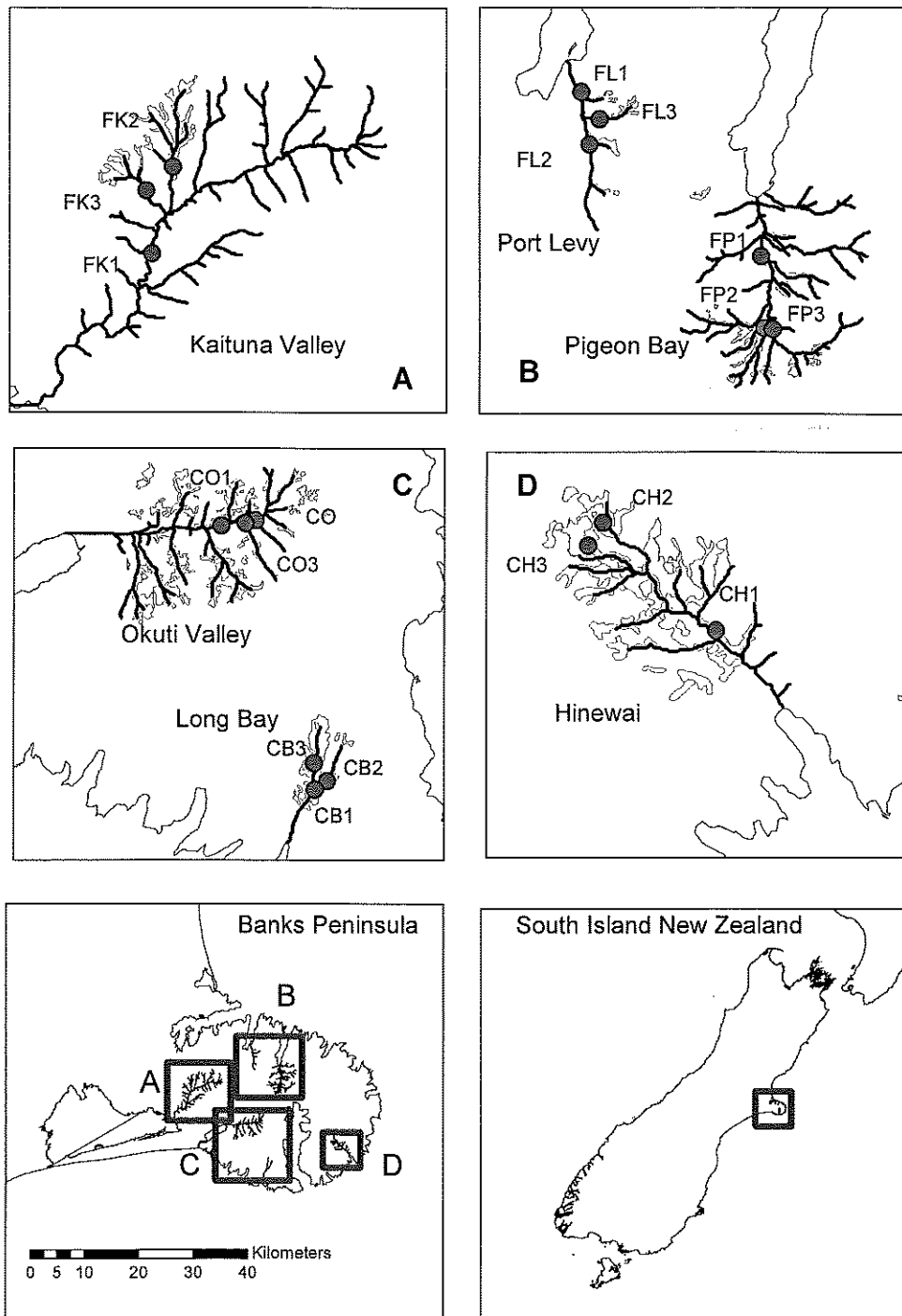


Figure 2.1: Banks Peninsula and the catchments and reaches used during the study.

The three catchments with fragmented riparian forest cover were; Pigeon Bay Stream in Pigeon Bay, Kaituna River in Kaituna Valley, and Koukourarata Stream in Port Levy. Within each of the catchments three sampling reaches were chosen, two in 1st or 2nd order headwater tributaries and one site further downstream (Fig 2.1AB).

All sites were located within riparian forest. Riparian forest was defined as having native forest cover for at least 5m on both sides of the stream. All sites were at least 50m, along the stream, from a forest pasture boundary.

Physiochemical sampling

Within each sampling location a 30m reach was selected and a suite of physical and chemical variables were measured. Stream width and depth was measured, across three random transects within each reach. While surface velocity was estimated by timing the speed of a polystyrene float over a set distance three times. Stream stability was estimated using the method described by Pfankuch (1975). Substrate composition was visually estimated within the 30m reach area and recorded as percentage of; bedrock, boulders, cobbles, pebbles, and silt using the Wentworth scale (Wentworth 1922). Conductivity, pH and temperature were measured, mid channel in riffle zones, using an Y5163 meter, dissolved oxygen (D.O.) using an Y51550 meter and light using a licor LI-250 light meter.

Percent riparian overhead cover was estimated by visually determining the percentage of visible sky above the stream. The proportions of indigenous and exotic vegetation present was also recorded within each reach.

Coarse Particulate Organic Matter (CPOM) was collected from the invertebrate Surber samples (0.25m x 0.25m Surber, 250µm mesh, see invertebrate sampling in chapter 3 for the collection method). CPOM was sieved and picked from the invertebrate samples, placed in a drying oven at 40°C for at least 24 hours and weighed.

Algal biomass was assessed by randomly selecting 5 or 10 small cobbles and estimating chlorophyll *a* v surface area. Cobbles were returned to the laboratory, placed in 100ml of 90% ethanol overnight in a fridge. Chlorophyll *a* was then estimated with a spectrophotometer and the following equation.

$$\frac{12 \times (665\text{nm} - 750\text{nm}) \times 100 \text{ ml ethanol}}{\text{Stone area cm}^2 \times 2.6\text{cm path length}}$$

Sites descriptions

Table 2.1: Catchment stream lengths and forest cover

Catchment	Stream	Total stream length (km)	Stream length in Native forest
Port Levy	Koukourarata stream	8.8	34%
Pigeon Bay	Pigeon Bay stream	46.8	26%
Kaitnua Valley	Kaituna river	63.0	48%
Hinewai	Narbey stream	15.6	87%
Long Bay	Long bay stream	6.2	80%
Okuti Valley	Okuti river	38.5	60%

Fragmented forest catchments

Port Levy: (Fig 2.1B)

The forest fragments within Port Levy were comprised of broadleaf natives such as mahoe (*Melicytus raniflorus*), and karanui (*Coprosma robusta*). Manuka

(*Leptospermum scoparium*) and kanuka (*Kunzea ericoides*) were present on the margins of the fragments and along the border of the stream riparian zone where they provided intermittent shading. Exotic flora was also spread throughout the catchment, primarily evergreen conifers.

FL1: The downstream site in Port Levy lies on the floor of the valley where the stream begins to meander to the sea. Dense indigenous forest covers the hillside to the east and extends across the stream, providing c.70% cover (Table 2.2). Downstream of the fragment is open farmland until the sea. The stream bed comprised of boulder, cobble, and pebble sized substrate. Within the reach there was evidence of past bank erosion but the stream channel is relatively stable, as indicated by a good stability score (Table 2.2).

FL2: A headwater site in Port Levy, on the main branch of the Koukourarata stream. Canopy cover shaded c. 70% of the stream (Table 2.2). The bed substrate was dominated by cobbles and pebbles with relatively few boulders and within this reach the stream was fast flowing and moderately deep (Table 2.2).

FL3: Located on the eastern tributary of the mainstream, this stream is in a small forested gully. Canopy cover was shaded only c.45% of the stream (Table 2.2). The stream bed was dominated by boulders with pebble and cobbles common. The forest cover thinned to pasture 5m out on the southern side of the stream and about 15m out on the northern side. The reach sits in a steep sided valley and the stream slope was steep, though surface water velocity was low (Table 2.2).

Pigeon Bay: (Fig 2.1B)

Native forest in the catchment was mixed including broadleaf (*Griselinia littoralis*), mahoe, karanui, tree fuchsia (*Fuchsia exorticata*), five finger (*Psuedopanex arboreus*), and tutu (*Coriaria arborea*). Plantations of exotic *pinus radiata* and Australian blue gum were present in the upper reaches of some tributaries.



Figure 2.2: Section of the reach in FP1 site within the Hay Reserve.

FP1: The downstream site in Pigeon Bay lies within the Hay Reserve which is a 7 hectare fragment of native forest. The reserve also contains a few old growth podocarp trees; totara (*Podocarpus totara*), matai (*Prumnopitys taxifolia*) and kahikatea (*Dacrycarpus*

dacrydioides). Transition from the surrounding pasture to the forest was very abrupt due to the managed nature of this fragment. The stream bed was dominated by cobbles and fine sediment covered most of the substrate. The stream bed and channel was stable with riparian trees growing right to the banks in most places (Table 2.2). The stream itself was wide and shallow in this reach and canopy cover provided c. 85% shading (Table 2.2).

FP2: Located on a stream draining the south-western region of the catchment. The reach was within a steep gully where riparian vegetation provided c.90% canopy cover. The stream bed was dominated by boulders and substantial beds of silt (Table 2.2). The stream was stable with little erosion or bed movement evident (Table 2.2). Fish were noticed at this site during sampling. The bottom edge of the fragment stopped abruptly at a road bridge under which the natural substrate was replaced by concrete.

FP3: Located on the tributary that drains the south-eastern part of the catchment this reach was in a band of native trees mixed in with some exotics that covered c.60% of the stream (Table 2.2). Further up the valley the forest became an exotic pine plantation. Beneath the fragment the stream comes into the open for a hundred metres before merging with the other tributary. The substratum within the reach was roughly equal measures of boulders and cobbles with small amounts of pebbles (Table 2.2).

Kaituna Valley: (Fig 2.1A)

Forest within the catchment was comprised of natives and exotics. The native species included broadleaf, mahoe, marbleleaf/putaputaweta (*Carpodetus serratus*) and some

manuka and kanuka in the tributaries. Plantations of exotic *pinus radiata* were present in the riparian zones of some tributaries. Willow trees (*Salix spp.*) were also present, scattered throughout the riparian zone.



Figure 2.3: Kaituna reserve as seen from the hillside to the East.

FK1: Located in the Kaituna Reserve, a 5 hectare fragment of predominately native forest, including some old growth podocarps as was the case in the Hay reserve. The Kaituna River entered the fragment slightly off centre on the northern side and then ran down the western margin. The canopy cover above the stream was c. 60% within the sampled reach (Table 2.2). The substrate within the reach was constituted almost entirely of pebbles. Eels and small fish were sighted during the sampling of this site. Upstream and downstream of the fragment was pasture land grazed by beef cattle.



Figure 2.4: Part of the reach within FK1 site in Kaituna reserve.

FK2: Located on one of the northern tributaries accessed from the packhorse trail. The forest fragment was infiltrated multiple times along its southern edge by the walking trail and around the reach the forest thinned 12m to the east where the walking trail was, though it extended further to the west. Within the reach there was c.85% canopy cover. The stream bed was c.45% pebbles, c.30% boulders and c.25% cobbles.

FK3: Located on the closest tributary to the east of the one containing FK2. Stream within the reach was very narrow and shallow (Table 2.2). The trees in the riparian zone provided c.60% cover to the stream and ceded to exotics, primarily pines, c.30m away from the stream. The benthos was half boulders and half cobbles and pebbles (Table 2.2).

The stream channel was stable with boulders and riparian vegetation stabilising the banks (Table 2.2).

Continuous forest catchments

Hinewai - Otanerito Bay: (Fig 2.1D)

The Hinewai Reserve in Otanerito Bay is a forest restoration project, native forest covers 40% of the 1050 hectare reserve (Wilson 2005). The native flora contains kanuka, mahoe, fuchsia, five finger, lacebark (*Hoheria sexstylosa*), red beech (*Nothofagus fusca*), and scattered podocarps (totara, matai and kahikatea) (Wilson 2005). The majority of the catchment is exotic gorse (*Ulex europaeus*) and broom being used as a nursery for native seedlings.

CH1: Located on the main branch of Narbey Stream just above the southern edge of the Hinewai Reserve. The stream channel was wide and there were islands in the stream within the reach (Table 2.2). Due to the width of the stream the surrounding trees only provided c.30% cover (Table 2.2). The streambed was dominated by boulders, with small patches of cobbles and pebbles. Riparian vegetation was present right to the stream bank within the reach, contributing to the good stability score (Table 2.2).

CH2: Located on a small 1st order tributary of Narbey Stream with a shallow, narrow channel and low flow (Table 2.2). The substrate was dominated by silt, cobbles and pebbles. The riparian trees achieve complete canopy cover above this reach (Table 2.2).

CH3: Located on another 1st order tributary the Narbey Stream catchment this reach also had little flow (Table 2.2). The native riparian vegetation provided c.95% canopy cover and very little light made it to the stream (Table 2.2, 2.3). The stream bed was dominated by boulders with small amounts of cobbles and silt.

Long Bay: (Fig 2.1C)

The forest within this catchment was dominated by natives including kanuka, fuchsia, five finger, tutu, lacebark, broadleaf, karanui and red beech. The forest covered c.80% of the total length of the stream opening up in the lower reaches before entering the sea (Table 2.1).



Figure 2.5: CB1 site reach, with sticky trapping line set up in background

CB1: The downstream site in the Long Bay catchment, located just below the junction of the two tributaries. Above the stream the riparian trees provided c.90% canopy cover (Table 2.2). Within the reach the substrate comprised of boulders, cobbles, pebbles and bedrock. Directly above the reach the majority of the stream bed on both tributaries was bedrock. The D.O reading at this site was low, potentially due to deoxygenated water coming from the eastern headwater tributary which had lower levels (Table 2.3). A large eel was sighted within the site reach.

CB2: Located on the western of the two tributaries, situated just upstream of a c. 40m high waterfall. The riparian vegetation covered c.90% of the stream (Table 2.2). The substrate in the stream was composed of bedrock, cobbles and pebbles with the occasional boulder (Table 2.2). A juvenile eel was caught during sampling at this site.

CB3: Located on the eastern of two tributaries in a steep walled rocky gully. Due to the steep gully walls and the c.85% canopy cover very little light reached this reach (Table 2.2, 3). Very low levels of D.O. were recorded at this site (Table 2.3). The stream bed was 50% cobbles, 30% boulders and 20% pebbles.

Okuti Valley: (Fig 2.1C)

Okuti Valley has around 88 hectares of native forest (Harding 2003), concentrated in the riparian corridor of the Okuti river and its tributaries, covering c.60% of the length of the river (Table 2.1). The native trees within the catchment included kanuka, fuchsia, five finger, tutu, broadleaf, karanui, and mahoe.



Figure 2.6: Upstream of CO1 reach, with cord for sticky traps in foreground

CO1: Located in the Okuti Valley scenic reserve on a 3rd order stream with high flow (Table 2.2). The riparian vegetation provided c.90% canopy cover within the reach. The substrate was comprised of 50% boulders, 30% cobbles and 20% pebbles.

CO2: One of the headwater sites in Okuti Valley located just above the last bridge on the public road, while heading up the valley. Within the reach the riparian trees gave c. 95% cover (Table 2.2). The stream bed is composed of about 40% boulders, 30% cobbles and 30% pebbles.

CO3: Located just above the penultimate bridge on the public road, while heading up the valley, just after a major fork in the river. To the north of the site the forest is bisected by

the road c.15m from the stream, though above the stream the riparian trees provided c. 90% cover (Table 2.2). The stream bed within the reach was composed of 50% boulders, 30% cobbles and 20% pebbles.

Table 2.2: Stream channel variables, flow and riparian characteristics of the sites

Site	Velocity (m/s)	Depth (m)	Width (m)	Flow/discharge (m ³ /s)	% Native Riparian veg	Canopy Cover %	Pfankuch score
FL1	0.35	0.25	2.47	0.216	100	70	56=Good
FL2	0.49	0.21	1.89	0.185	100	70	50=Good
FL3	0.25	0.11	1.64	0.045	80	45	51=Good
FP1	0.37	0.17	5.5	0.346	100	85	51=Good
FP2	0.27	0.1	2.07	0.056	100	90	52=Good
FP3	0.38	0.09	2.97	0.102	70	60	50=Good
FK1	0.5	0.1	4.34	0.217	65	60	56=Good
FK2	0.08	0.15	1.74	0.021	100	85	48=Good
FK3	0.31	0.04	1.09	0.014	100	60	47=Good
CH1	0.2	0.26	5.76	0.300	100	30	47=Good
CH2	0.25	0.04	0.98	0.010	100	100	69=Good
CH3	0.17	0.12	0.77	0.016	100	95	60=Good
CB1	0.69	0.22	3.06	0.465	100	90	39=Good
CB2	0.2	0.1	1.52	0.030	100	90	50=Good
CB3	0.4	0.16	3.89	0.249	100	85	50=Good
CO1	0.47	0.27	4.06	0.515	100	95	58=Good
CO2	0.51	0.23	3.2	0.375	100	95	49=Good
CO3	0.39	0.19	4.1	0.304	90	90	55=Good

Physiochemical properties

There were no significant differences in pH, D.O., temperature, light, CPOM and chlorophyll a concentration (Table 3). There was a significant (Two-way ANOVA $F_{1,17}$ $p=0.001$) difference in conductivity between fragmented and continuous forest sites, with the fragmented forest sites exhibiting higher conductivities (Table 2.3).

Table 2.3: Chemical variables, allochthonous and autochthonous inputs for each site

Site	pH	D.O. (mg/l)	Conductivity (μ S)	Temperature ($^{\circ}$ C)	Light (μ mol)	CPOM (g/m ²)	Chlorophyll a (ml/cm ³)
FL1	7.9	10.1	182	8.5	0.26	43.1 \pm 24.4	0.95 \pm 0.034
FL2	7.8	10.2	150.9	8.2	0.01	26.4 \pm 9.1	1.54 \pm 0.23
FL3	7.7	10	184.3	7.5	0.14	43.0 \pm 24.0	1.95 \pm 0.51
FP1	7.8	5.6	178	10.6	0.03	135.4 \pm 65.5	2.94 \pm 1.00
FP2	7.9	4.1	182.8	12	0.06	22.3 \pm 8.4	1.77 \pm 0.39
FP3	8.3	7.7	197.2	9.8	0.13	12.5 \pm 3.9	2.00 \pm 0.39
FK1	7.7	4.7	170.5	15.4	0.21	41.0 \pm 19.6	0.32 \pm 0.13
FK2	8.1	9.6	292	8.9	0.16	36.5 \pm 7.1	4.91 \pm 1.44
FK3	8	6.3	193	10	0.05	29.4 \pm 17.8	1.63 \pm 0.037
CH1	7.6	8.7	110	14.5	0.48	27.4 \pm 20.0	3.54 \pm 0.77
CH2	7.5	11.7	82.4	10.4	0.4	21.1 \pm 4.8	*
CH3	7.4	*	82	13.3	0.01	93.9 \pm 54.7	2.34 \pm 0.95
CB1	7.8	3.2	140.6	13.2	*	42.8 \pm 15.9	3.03 \pm 0.13
CB2	7.6	6.4	132.8	16.3	0.1	37.7 \pm 22.1	2.75 \pm 1.02
CB3	7.8	1	143.6	8.4	0.01	45.1 \pm 25.2	2.07 \pm 0.27
CO1	8	*	127.7	9.7	0	24.6 \pm 7.7	0.29 \pm 0.07
CO2	7.9	10.2	122.8	9	0.07	37.4 \pm 3.2	3.41 \pm 0.82
CO3	7.9	10	127.5	9.2	0.01	38.3 \pm 1.4	1.25 \pm 0.49

* = missing

Chapter 3: The effects of forest fragmentation on stream invertebrate communities

Introduction

The greatest threat to stream macroinvertebrates has been the loss and reduction in quality of habitat caused by anthropogenic modifications, including alterations to riparian and channel environments (Collier 1993). The importance of riparian vegetation and the role of forests in influencing stream ecosystems is a major theme in stream ecology (Cummins 1974, Vannote et al. 1980). However, while the effects of forest fragmentation of terrestrial ecosystems is relatively well explored little has been done on the effects of forest fragmentation on stream ecosystems (Didham et al. 1998, Scarsbrook and Halliday 1999, Shirley 2006, Zartman and Shaw 2006). Forest fragmentation would be expected to lead to changes to benthic invertebrate communities in particular the loss of forest specialist taxa due to influences from the surrounding land.

Another major theme in stream ecology is the continuous gradient of physical conditions from headwaters and downstream and the influence this gradient exerts upon the stream community (Vannote et al. 1980, Winterbourn et al. 1981). Therefore the presence or absence of riparian forest may have different effects depending on the location of the forest along river continuum. For example, we might expect that forest fragments located in the headwaters should have higher water quality and more healthy and diverse stream communities than those in fragments in the lower catchment.

This study compared benthic macroinvertebrate communities between fragmented and continuous riparian forest. The effects of the location of riparian forest fragments were also examined.

Methods

I investigated 18 sites in six catchments which are described in Chapter 2. At each site a 30m reach was selected and benthic invertebrates were sampled by collecting three random Surber samples (250 μ m mesh; 0.0625 m²) from riffles. Within each Surber the substrate was vigorously disturbed and larger substrate rubbed clean. A further composite kick-net (500 μ m mesh) sample was also collected. This sample was an amalgamation of approximately 5 kicks within the reach, covering a range of microhabitats (ie. silt, leaf packs, wood). All samples were preserved in c. 90% ethanol and returned to the laboratory for processing.

In the laboratory, benthic samples were rinsed through a 250 μ m mesh sieve. Samples containing large amounts of CPOM were separated by using multiple sieves to make the sorting easier. In the Surber samples, all invertebrates were identified and counted under a microscope (40x magnification), while kick-net samples were processed to find any additional taxa not present in the Surbers. Taxa were identified to the lowest taxonomic level used in calculation of the MCI (Boothroyd and Stark 2000). Keys used were Winterbourn et al.(2000) and Smith (2001, 2003).

Analysis

To test the differences between fragmented and continuous forest and the headwaters or downstream location of forest a series of two-way ANOVAs were performed on the data, using SigmaStat 9.0 (Systat Software 2004). Significance was accepted at $P < 0.05$. Pairwise multiple comparisons were also carried out using the

Holm-Sidak method to isolate where the differences occurred. Ordinations and cluster analysis of species presence/ absence, and abundance were performed using PCOrd (McCune and Mefford 1999).

MCI and QMCI scores were also calculated (Boothroyd and Stark 2000). The MCI score is gained using this formula $20\sum a_i/S$ and the formula for QMCI is

$\sum(n_i a_i)/N$. Where

a_i = MCI tolerance score for the i^{th} taxon.

n_i = the number of individuals in the i^{th} taxon.

S = the total number of taxa.

N = the total number of individuals.

MCI tolerance scores for taxon were acquired from the literature (Boothroyd and Stark 2000, Smith 2003) and through personal communication with Jon Harding.

Results

A total of 71 taxa were collected from the 18 sites. Insect taxa dominated all sites particularly Ephemeroptera and Trichoptera. Taxonomic richness was high at all sites with approximately 30 taxa present among the sites, however richness was significantly higher at the continuous forest sites than it was at the fragmented forest sites (two-way ANOVA $F_{1,17}=4.907$ $P=0.044$) (Fig 3.1A). When comparing location, the downstream sites had lower diversity than the headwater sites although there was no significant difference in diversity between forest types and location. In general, the downstream sites in the fragmented catchments tended to have the lowest taxonomic richness (Fig 3.1B).

The number of EPT taxa present showed a similar trend with the continuous forest sites having greater diversity than the fragmented forest sites (Fig 3.1C). Again,

the sites with the poorest representation of EPT taxa were the downstream sites within catchments with fragmented riparian forest, though these differences were not significant (Fig 3.1D).

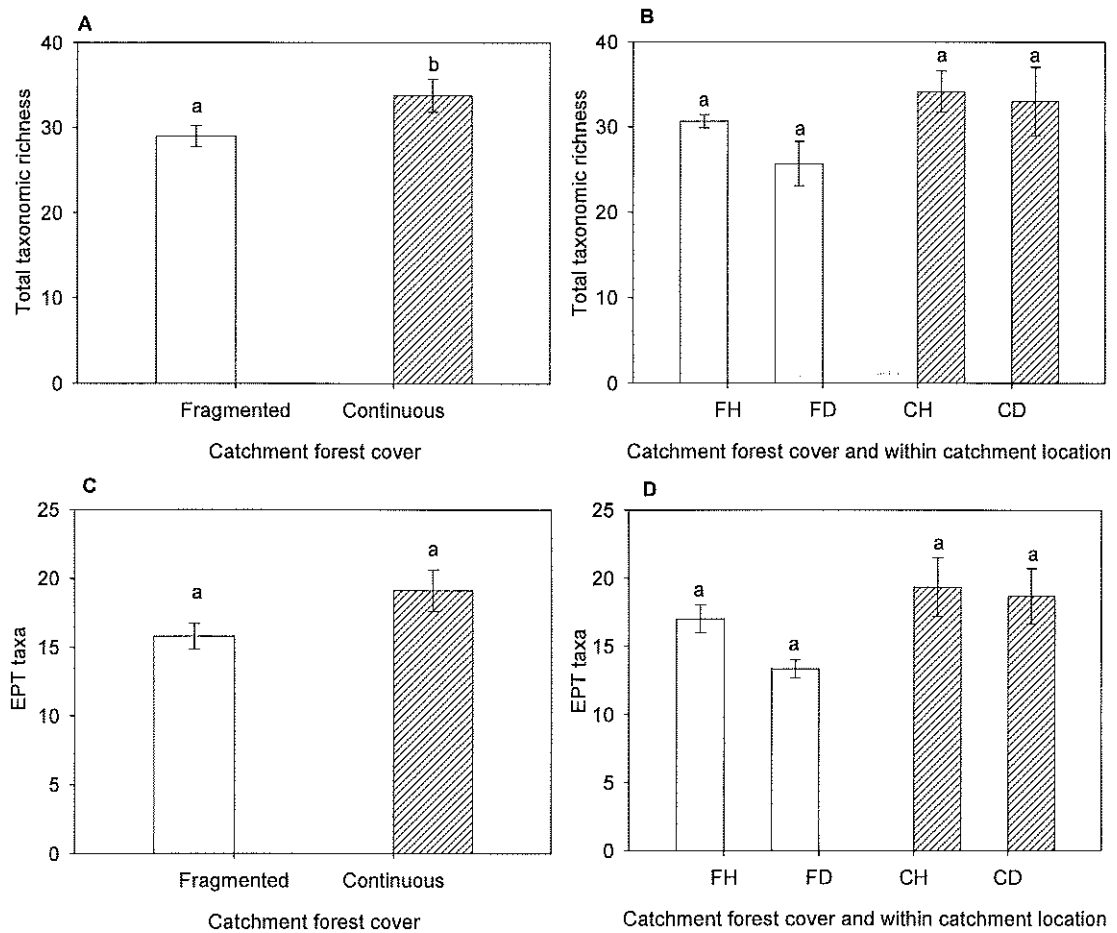


Figure 3.1: Comparisons of total taxonomic richness (mean \pm 1 SE) and EPT richness (mean \pm 1 SE) between catchments with fragmented and continuous riparian forest. FH = fragmented headwaters (n=6), FD = fragmented downstream (n=3), CH= continuous headwaters (n=6), CD= continuous downstream (n=3). Letters show the results of two-way ANOVA and Holm-sidak pairwise comparisons where means with the same letter are not significantly different, $p > 0.05$.

Invertebrate densities were on average higher in the fragmented forest sites, with abundance about 150% greater than in continuous forest sites (Fig 3.2A). The invertebrate abundance in the fragmented forest sites is significantly greater than that of the continuous forest sites (two-way ANOVA $F_{1,17}=5.475$, $p=0.035$). This was

mainly an artifact of high densities in the downstream fragmented sites which were about 250% higher densities of invertebrates than at the other sites (Fig 3.2B).

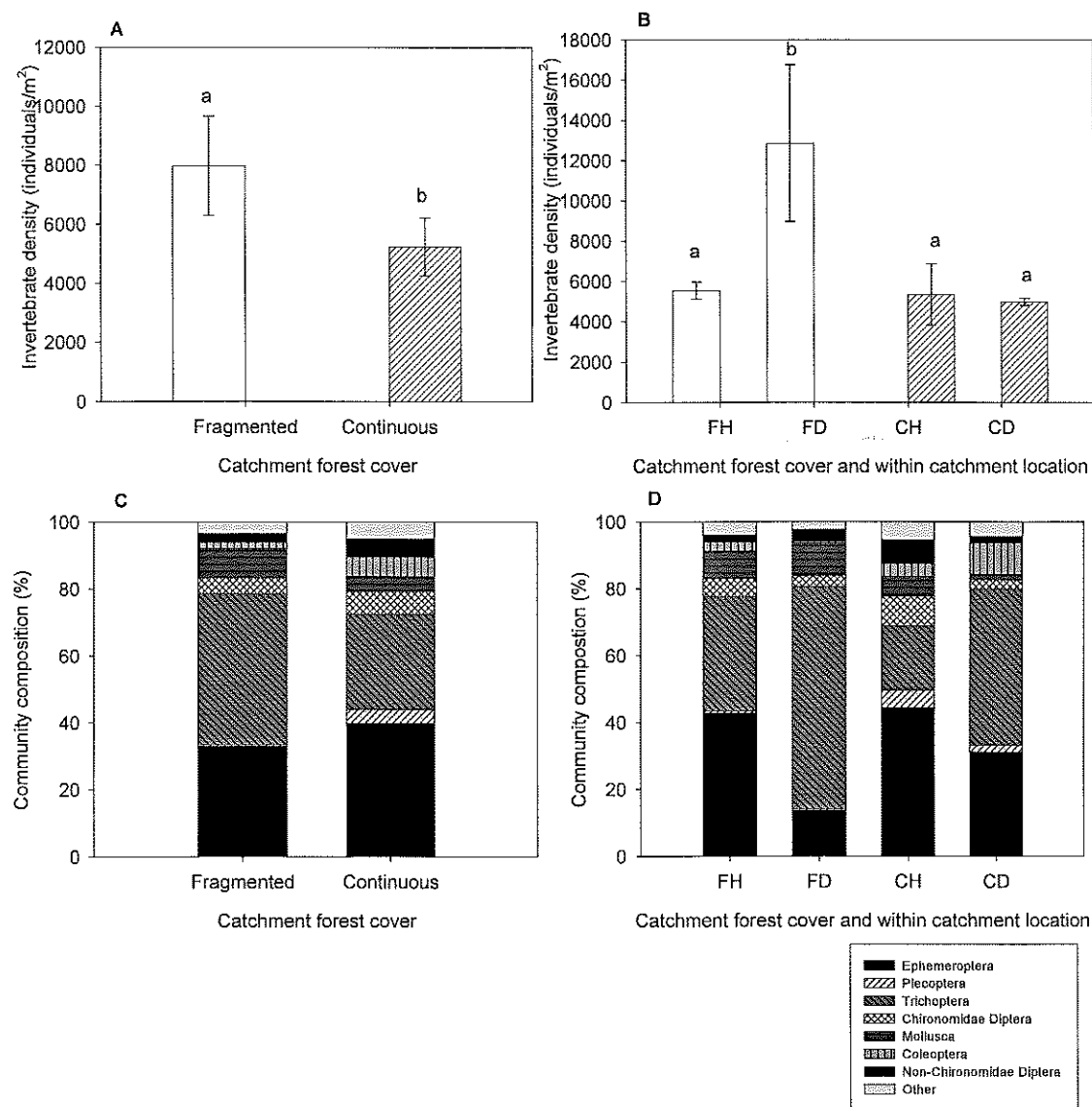


Figure 3.2: Mean invertebrate densities (± 1 SE) and community composition in abundance by taxonomic group between catchments with fragmented and continuous riparian forest. FH = fragmented headwaters (n=6), FD = fragmented downstream (n=3), CH= continuous headwaters (n=6), CD= continuous downstream (n=3). Letters show the results of two-way ANOVA and Holm-sidak pairwise comparisons where means with the same letter are not significantly different, $p > 0.05$.

Location within the catchment did not differ significantly between forest types as the downstream sites in the continuous forest catchments had very similar densities to the headwater sites in the continuous forest catchments (two-way ANOVA $F_{1,17}=4.096$ $p=0.063$) (Fig 3.2B). However, the interaction between catchment forest type and catchment location is significant and driven by high densities in the downstream fragmented sites (two-way ANOVA $F_{1,17}=5.002$, $p=0.042$).

The community composition of benthic communities in these stream types differed slightly (Fig 3.2CD). Trichoptera made a greater contribution to the overall community in the fragmented riparian forest sites and in downstream sites compared to the headwater sites (Fig 3.2D, 3.3C). While Ephemeroptera constituted a greater percentage of the community in the continuous riparian forest and headwater sites (Fig 3.2CD, 3.3A). In the fragmented riparian forest Plecoptera were rare (Fig 3.2CD), but were more highly represented in the headwaters of the continuous riparian forest sites (Fig 3.3B). Coleopterans also were more common in the continuous riparian forest, than the fragmented sites (Fig 3.2C, 3.3F). Whereas, molluscs comprised a greater percentage of the population in the fragmented forest sites (Fig 3.2C, 3.3E).

However, there was no significant difference in community composition across the catchment forest types for Ephemeroptera, but there was a significant difference in their representation in the headwaters as opposed to the downstream reaches (two-way ANOVA $F_{1,17}=10.253$ $p=0.006$). This was primarily influenced by the fragmented sites which gave an unadjusted P value of 0.008 while the within the continuous sites the unadjusted P value was 0.178. However, there was no significant interaction between catchment forest type and within catchment location for Ephemeroptera.

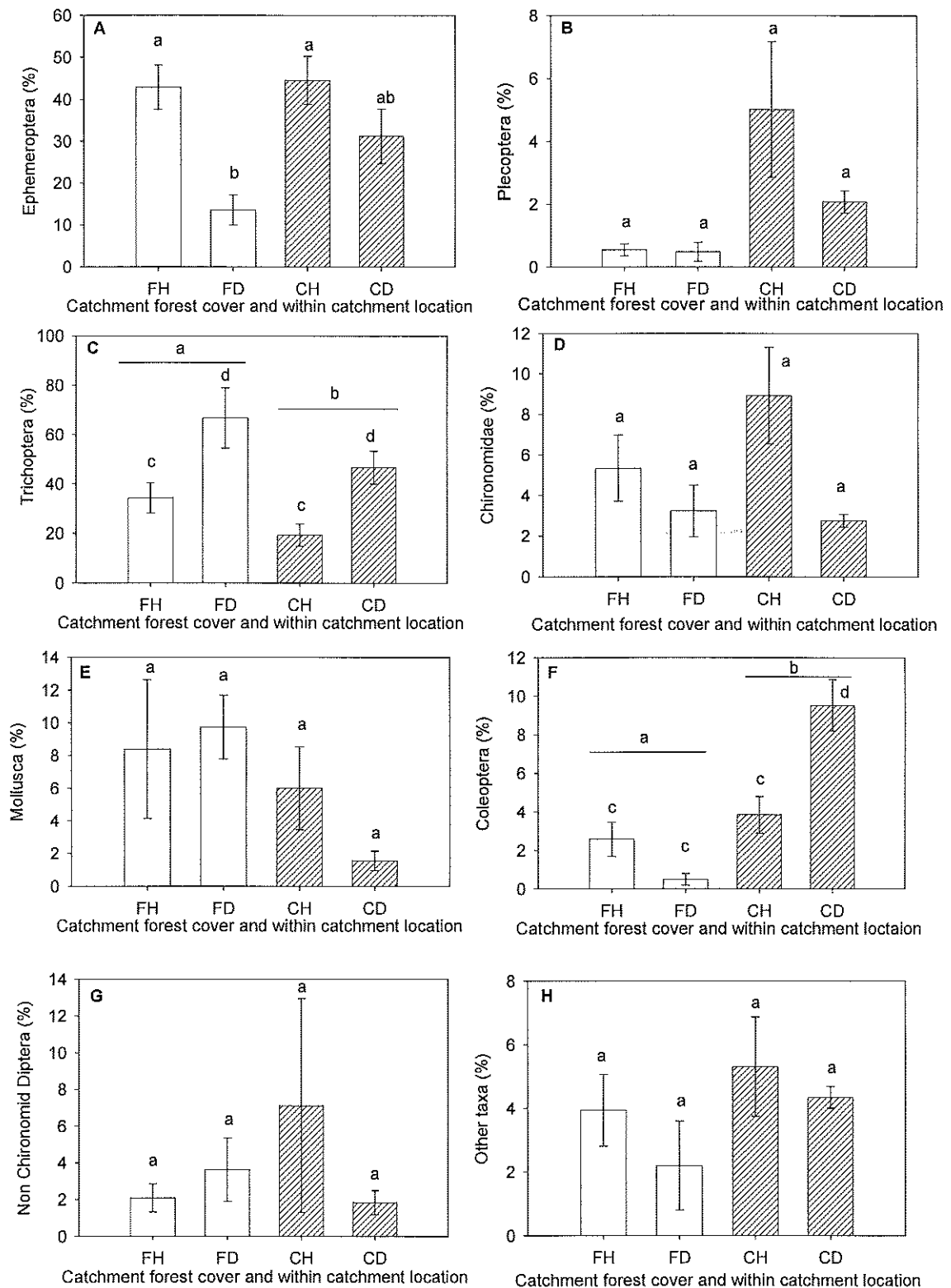


Figure 3.3: Community composition (mean \pm 1 SE) for all the groups, at the within and between catchments levels. FH = fragmented headwaters (n=6), FD = fragmented downstream (n=3), CH= continuous headwaters (n=6), CD= continuous downstream (n=3). Letters show the results of two-way ANOVA and Holm-sidak comparisons where means with the same letter are not significantly different, $p > 0.05$.

Trichopterans made up a significantly greater proportion of the community in fragmented riparian forest sites than in the continuous riparian forest sites (two-way ANOVA $F_{1,17} = 5.880$ $p = 0.029$) (Fig 3.3C), and also in the sites from the lower reaches opposed to the headwaters (two-way ANOVA $F_{1,17} = 17.177$ $p < 0.001$) (Fig 3.3C). There was no significant interaction between the catchment forest cover types and within catchment location.

Coleoptera showed significant differences between fragmented and continuous forest, contributing a greater percentage of the community in the continuous riparian forest catchments than the fragmented riparian forest catchments (two-way ANOVA $F_{1,17} = 20.228$ $p < 0.001$) (Fig 3.3F). However, there was no significant trend for within catchment location, as they were less well represented in the fragmented downstream sites than in the fragmented headwaters. In the continuous forest catchments this pattern was reversed (Fig 3.3F). Resulting in a significant interaction between the catchment forest cover type and within catchment location (two-way ANOVA $F_{1,17} = 11.338$ $p = 0.005$) (Fig 3.3F).

There were no significant differences between catchment riparian forest cover type for any of the other groups.

Functional Feeding Groups

Collector browsers were the largest functional feeding group in both the fragmented and continuous forest streams (Fig 3.4A). The proportion of the community comprised of collector-browsers was marginally higher in the downstream fragmented forest sites, though this was not significantly different (Fig 3.4BE).

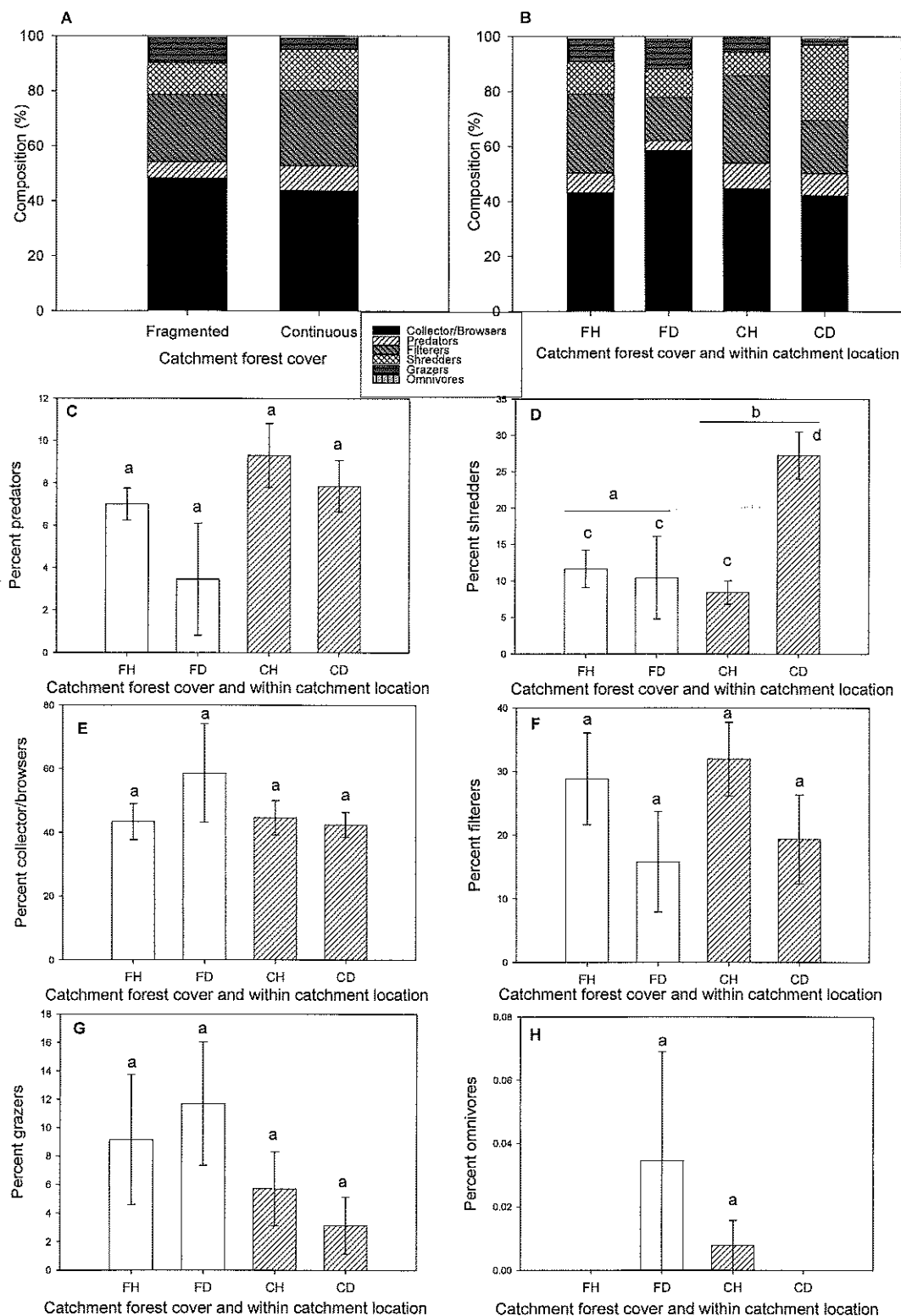


Figure 3.4: Community composition as functional feeding groups shown between fragmented and continuous riparian forest and location (mean \pm 1 SE). FH = fragmented headwaters (n=6), FD = fragmented downstream (n=3), CH= continuous headwaters (n=6), CD= continuous downstream (n=3). Letters show the results of two-way ANOVA and Holm-sidak comparisons where means with the same letter are not significantly different, $p>0.05$.

Grazers made up a larger, but not significantly greater, percentage of the community in fragmented riparian forest than in continuous riparian forest (Fig 3.4A). In the fragmented forest catchments the percentage of grazers was greater in the downstream sites than the headwater sites, while in the continuous forest sites the percentage of grazers was lower in the downstream sites than the headwater sites (Fig 3.4BG). However none of these variances were great enough to be significant.

Shredders were also significantly more important in the continuous forest than in the fragmented forest (two-way ANOVA $F_{1,17} = 4.885$ $p = 0.044$) and there was also a significant difference between the headwaters and the downstream sites (two-way ANOVA $F_{1,17} = 8.202$ $p = 0.013$) (Fig 3.4ABD). There were also significant interactions within the catchment forest type sites and within catchment location (two-way ANOVA $F_{1,17} = 10.716$ $p = 0.006$) with shredders in the downstream continuous forest sites being more important than in the continuous forest headwater communities (Holm-Sidak comparison $t = 4.340$ $p = 0.001$) and the downstream fragmented forest sites (Holm-Sidak comparison $t = 3.358$ $p = 0.005$) (Fig 3.4D).

The proportion of predators was marginally higher in the continuous forest and than in the downstream sites in the fragmented forest catchments (Fig 3.4BC). However, there was no significant difference between predators in continuous forest and fragmented forest (two-way ANOVA $F_{1,17} = 4.564$ $P = 0.051$) (Fig 3.4C).

Filter feeders were also in similar proportions in the communities of both the fragmented and continuous forest sites, but made a larger contribution, though not significantly so, to the community composition in the headwater sites than in the downstream sites (Fig 3.4ABF). Omnivores were rare and did not contribute a great enough percentage of the population to appear on the figure (Fig 3.4ABH), and discrepancies in normality and variance prevented analysis.

Stream health

There was little difference in MCI scores between forest types and locations (Fig 3.5AB), and this was confirmed by a lack of statistical significance. However there was a difference in interpretation of the MCI scores between the sites. The fragmented headwaters, continuous headwaters and continuous downstream all scored >120 and were defined as 'clean water' (Boothroyd and Stark 2000) (Fig 3.5B). Whereas the fragmented downstream sites score between 100-119 which are categorised as 'Doubtful quality or possible mild pollution' (Boothroyd and Stark 2000) (Fig 3.5B).

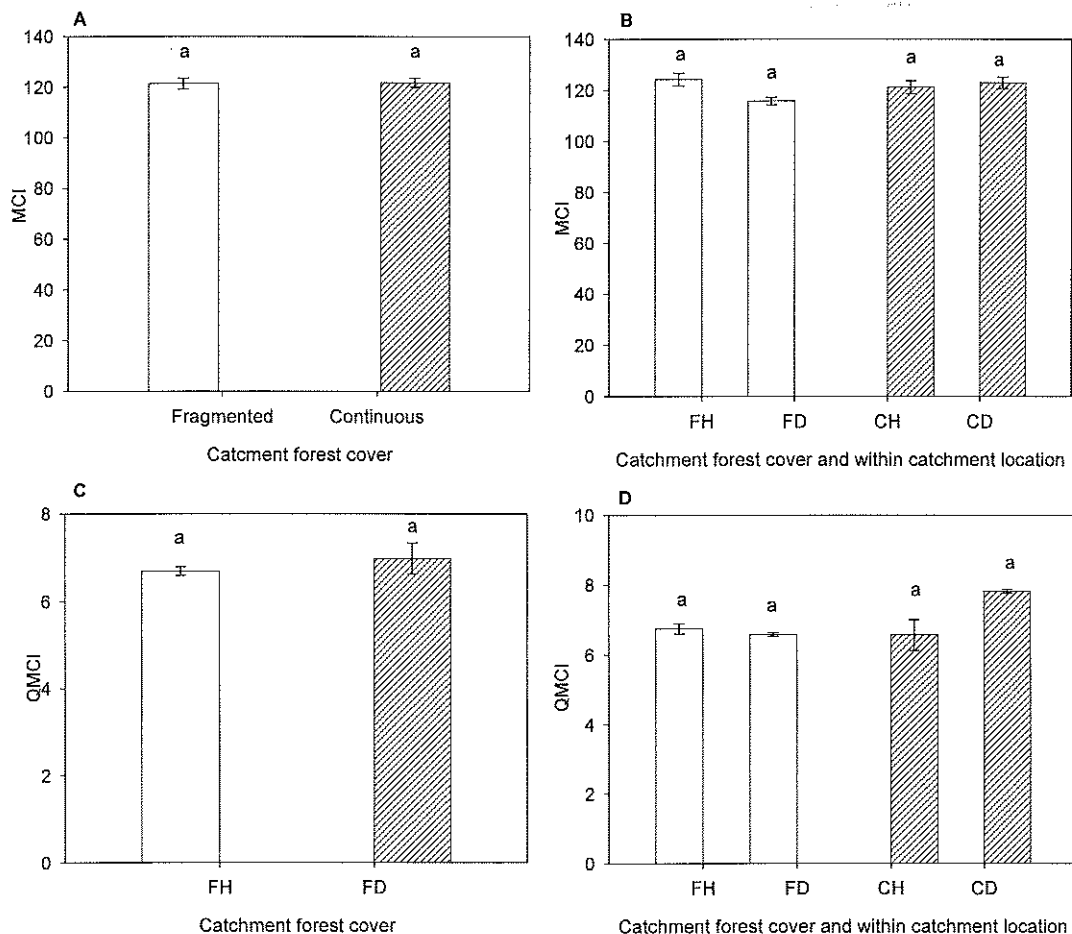


Figure 3.5: MCI and QMCI scores (mean \pm 1 SE) for fragmented and continuous riparian forest. FH = fragmented headwaters (n=6), FD = fragmented downstream (n=3), CH= continuous headwaters (n=6), CD= continuous downstream (n=3). Letters show the results of two-way ANOVA where means with the same letter are not significantly different, $p > 0.05$.

The QMCI also showed little difference between treatments with only the downstream sites in the continuous forest being slightly higher than the others (Fig 3.5CD). However this difference was also not statistically significant (two-way ANOVA $F_{1,17} = 4.371$ $P = 0.055$). All sites were classified as ‘clean water’ according to Boothroyd and Stark (2000).

An ordination of species presence/absence data showed a distinct trend with headwater sites generally located to the left of Axis 1 compared to downstream sites within the same catchment (Fig 3.6). However one continuous and one fragmented catchment differ with all sites closely clustered along axis 1, with the downstream site to the right of the headwater sites (Fig 3.6). The majority of the continuous forest sites are also located to the left of the fragmented forest sites along Axis 1 (Fig 3.6).

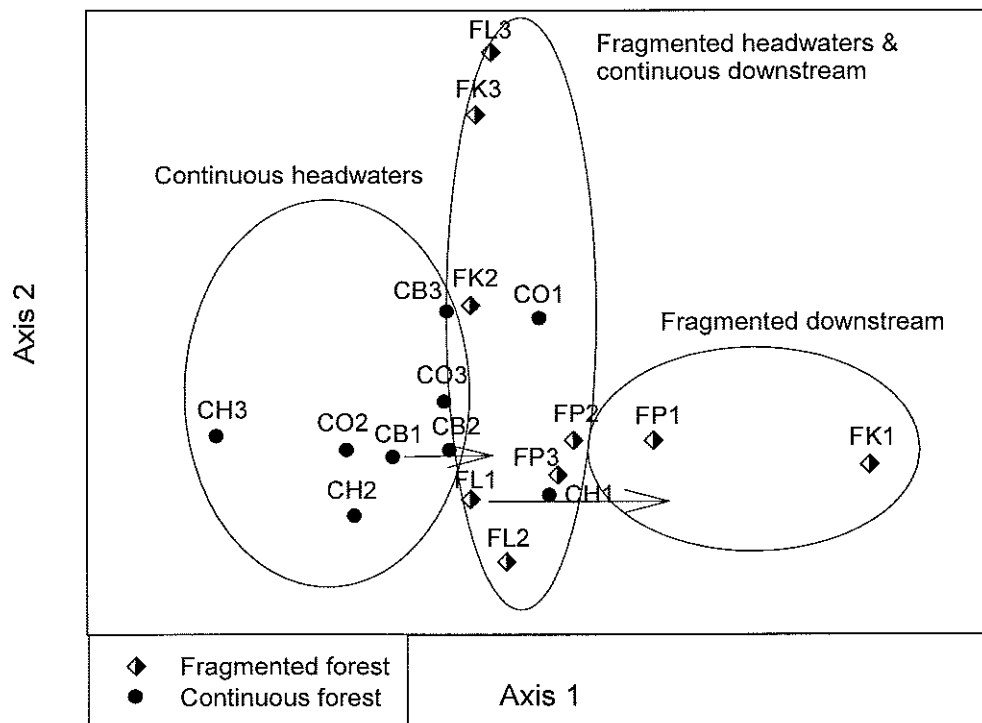


Figure 3.6: Ordination graph of species presence/absence across the 18 study sites. First letter signifies forest cover; F= fragmented, C= Continuous. 2nd letter signifies catchment; K= Kaituna Valley, P=Pigeon Bay, L= Port Levy, O= Okuti Valley, B= Long Bay, H= Hinewai. The number 1 signifies downstream sites and 2 and 3 are headwater sites.

The sites group along axis 1 into a continuous headwater group a fragmented headwater group and a fragmented downstream group (Fig 3.6). The downstream sites that were to the left of their headwater sites are the only ones to fall outside of my assigned groupings (Fig 3.6).

Several taxa were common across my sites and three were present in all sites sampled (Table 1). The majority of these common taxa have winged adult phases however one of the species present at all site was the mollusc *Potamopyrgus antipodarum*, which has no terrestrial phase. All the major functional feeding groups are represented in the top ten most widespread taxa (Table 3.1).

Table 3.1: The 10 commonest taxa, showing percentages of presence within fragmented and continuous forest catchments.

Taxa	# sites present	% of fragmented sites present in	% of continuous sites present in
<i>Deleatidium</i>	18	100	100
Orthocladinae	18	100	100
<i>Potamopyrgus antipodarum</i>	18	100	100
<i>Coloburiscus humeralis</i>	17	100	89
<i>Aoteaphsyche</i>	17	100	89
<i>Olinga</i>	16	100	78
<i>Archichauliodes diversus</i>	16	100	78
Tanypodinae	16	89	89
<i>Philoreithrus agilis</i>	15	78	89
Hydraenidae	15	78	89

Several of the most widespread taxa were also amongst the most abundant taxa. For example, the mayfly *Coloburiscus humeralis* had the greatest densities within the headwaters of the continuous forest fragments and followed the pattern of higher proportions of Ephemeroptera in the headwaters than downstream reaches (Fig 3.3A, 3.7A). One of the taxa that did not feature among the most widespread but was among the most abundant was the conoesucid caddisfly *Pycnocentria evecta*. *P. evecta* was found in significantly greater densities in the downstream sites in the

fragmented riparian forest catchments (Fig 3.7B). *Deleatidium* showed no significant differences in density between fragmented or continuous riparian forest or within catchment location with very similar average densities between the site types, except for in the headwater sites in fragmented forest catchments which had slightly greater densities (Fig 3.7C).

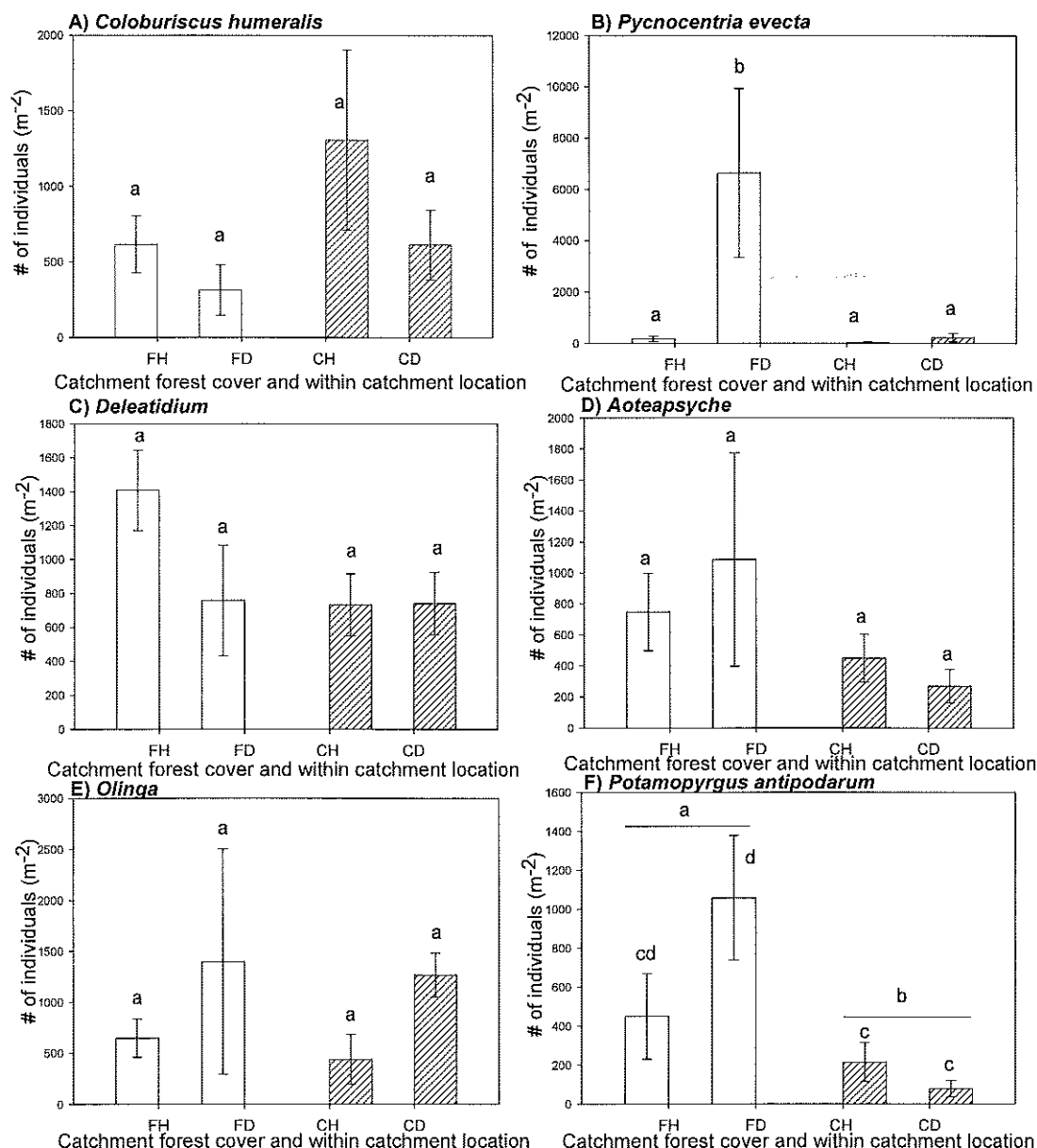


Figure 3.7: Densities of six of the most abundant taxa shown for the different catchment forest covers and within catchment locations. FH = fragmented headwaters (n=6), FD = fragmented downstream (n=3), CH= continuous headwaters (n=6), CD= continuous downstream (n=3). Letters show the results of two-way ANOVA and Holm-sidak pairwise comparisons where means with the same letter are not significantly different, $p > 0.05$.

The density of the net spinning caddisfly *Aoteapsyche* was abundant but showed no real pattern or significant differences (Fig 3.7D). The downstream sites within the fragmented catchments had the greatest densities of *Aoteapsyche*, but also had the greatest variance between sites (Fig 3.7D). Similarly the conoesucid *Olinga* followed a similar pattern to the proportion of Trichoptera, with greater densities in downstream reaches compared to headwater reaches (Fig 3.3C, 3.7E). The abundance of the hydrobiid snail *P. antipodarum* varied between fragmented and continuous sites with significantly greater densities found in the fragmented catchments than continuous catchments (two-way ANOVA $F_{1,17} = 8.708$ $p=0.011$) (Fig 3.7F). *P. antipodarum* appeared to increase from headwaters to downstream in fragmented catchments whereas in the continuous forest catchments the reverse occurred and densities decreased from headwaters to downstream (Fig 3.7F).

Some taxa were found more often in the continuous forest catchments than riparian forest catchments (Table 3.2, Fig 3.8). *Hydrobiosis gollanis* and *Nannochorista philpotti*, were found in only a limited number of sites but of these they were only collected in the continuous forest catchments (Table 3.2). *N. philpotti* also was only found in the headwaters of the continuous forest catchments (Fig 3.8).

Table 3.2: Taxa with ≥ 3 more occurrences in continuous forest than fragmented

Taxa	# sites present	% of fragmented sites present in	% of continuous sites present in
<i>Austroclima jollyae</i>	13	56	89
<i>Costachorema peninsulae</i>	12	44	89
<i>Hydrobiosis gollanis</i>	3	0	33
<i>Nannochorista philpotti</i>	5	0	56
<i>Neozephlebia scita</i>	12	44	89
<i>Nesameletus vulcanus</i>	5	11	44
<i>Oeconesus maori</i>	7	22	56
<i>Pycnocentria sylvestris</i>	5	11	44
<i>Triplectides obsoletus</i>	8	11	78
<i>Zelandobius wardi</i>	7	11	67

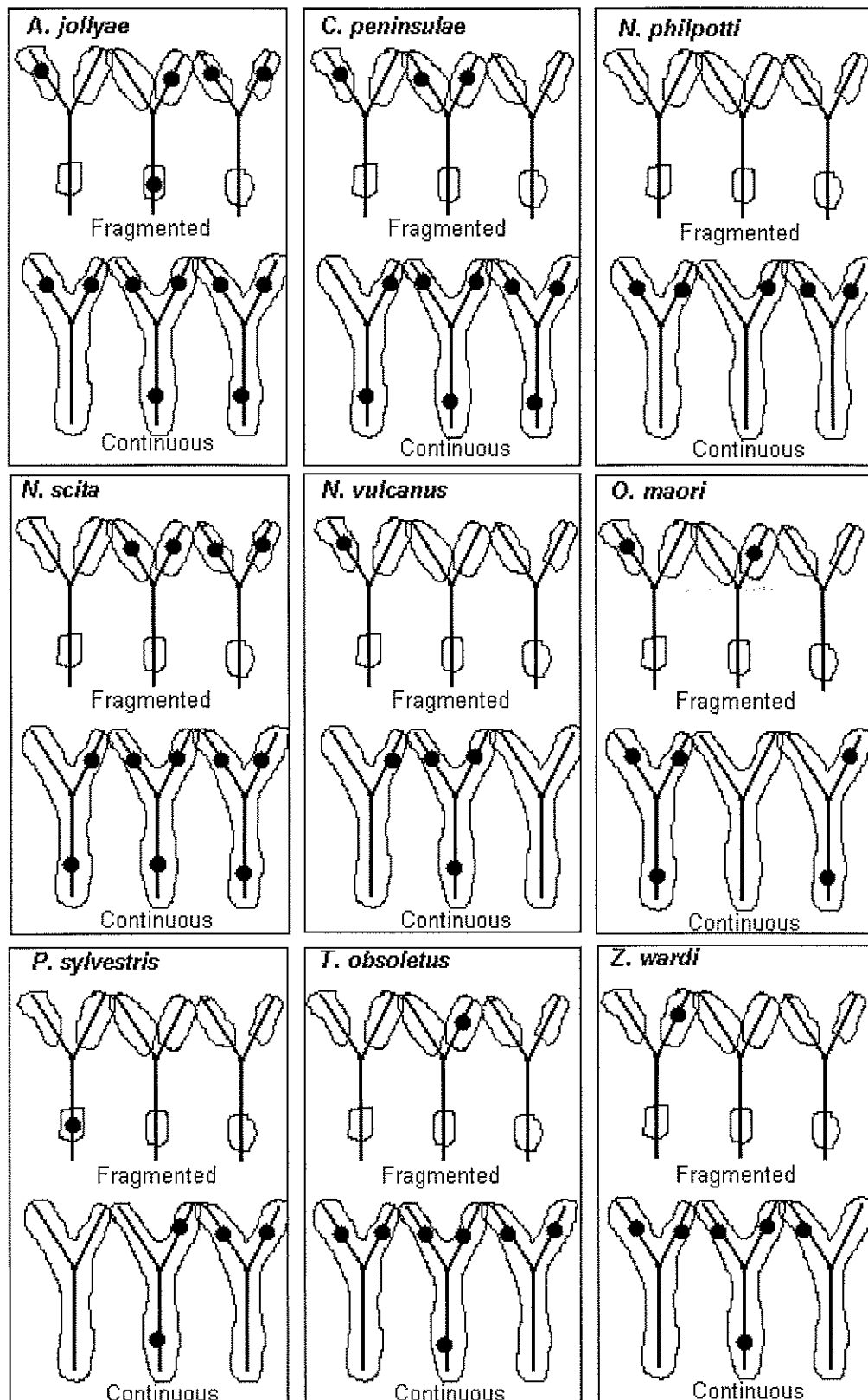


Figure 3.8: Distributions of nine taxa in continuous forest versus fragmented forest. Circles indicate the presence of the species at given catchment locations

The majority of the occurrences in the fragmented catchments (of the species which were present more often in the continuous forest catchments) were in the headwaters (Fig 3.8). Two species believed to be endemic to the region, *Costachorema peninsulae* and *Zelandobius wardi*, seemed to favour the continuous forest and were found only in the headwaters of the fragmented catchments (Table 3.2, Fig 3.8).

Discussion

Many studies have shown higher invertebrate taxonomic richness in conjunction with forest as opposed to other land use (Harding and Winterbourn 1995, Benstead et al. 2003). However some have shown no significant difference in taxonomic richness between forest and agricultural land use (Quinn et al. 1997), while others report streams with pastoral land use to have higher taxonomic richness than forested streams (Death and Zimmermann 2005). My findings from Banks Peninsula show that higher taxonomic richness occurred in catchments with continuous riparian forest than the catchments with fragmented riparian forest surrounded by agricultural land use. My findings are also consistent with Harding et al. (2006) which also sampled streams on Banks Peninsula and found taxonomic richness to be higher in continuous forest sites than fragmented forest sites.

Harding et al. (2006) also found significantly higher numbers of EPT taxa in continuous forest than in the forest fragments, a finding which my results did not support. The inclusion of the headwater fragmented sites to the downstream fragments used by Harding et al. (2006) appears to remove the significance from this pattern. If I remove the headwater fragmented sites and one outlier in my data set then a significant difference does occur in EPT taxonomic richness between fragmented

and continuous forest, with continuous forest having significantly greater diversity (t-test $t_{1,9} = -4.305$ $p = 0.002$).

Canopy cover constrains macroinvertebrate abundance and biomass by limiting primary production, with open pasture streams supporting greater densities of benthic invertebrates than forested streams (Quinn et al. 1997, Nyström et al. 2003, Death and Zimmermann 2005). In this study macroinvertebrate densities have been shown to be significantly higher in the fragmented forest catchments than the continuous forest. However, closer inspection reveals that the only significant difference comes from the downstream fragments which are located beneath open land (Fig 3.2B). It appears that the communities within the downstream fragments may be taking advantage of the processing inefficiencies of the upstream communities as postulated by Vannote et al (1980). The light levels and shading were similar between all the sites (Chapter 2). Therefore, increased local primary production within the downstream fragments is an unlikely explanation for the elevated macroinvertebrate densities. However, there was no significant difference in periphyton standing crops, as interpreted from the concentration of chlorophyll a, between sites (Chapter 2). Therefore periphyton growth, and primary production, would logically have to be greater at in the downstream fragments to maintain similar periphyton levels with the greater abundance of grazers and collector browsers that would be consuming it (Fig 3.2B, 3.5B), or the agricultural land use is supporting higher abundances in the downstream fragments through upstream subsidies.

An increase in stream temperature could increase the metabolic rate of periphyton increasing the rate of photosynthesis. Although there was no significant difference in the stream temperatures recorded during this study (Chapter 2) they were only one off measurements and repeated measures taken by Harding et al.

(2006) found the stream temperatures in the downstream fragments in Kaituna valley and Pigeon Bay were significantly higher than those of the Narbey stream and the Okuti River. Solar (shortwave) radiation is the most important contributor to stream water surface temperature in small streams (Sinokrot and Stefan 1993). In the catchments with fragmented riparian forest the streams would have 10-30x higher levels of incident light as they pass through open pasture (Quinn et al. 1997). Therefore it could be assumed that the mean stream temperature of the downstream fragmented sites is higher than the stream temperature at the other sites.

Elevated stream temperatures would also increase the metabolic rate of the stream invertebrates and micro organisms, such as fungi and bacteria (Cummins 1974). This could lead to increased microbial processing of CPOM within the downstream fragments compared to the other sites and provide the invertebrate community with greater food supplies in the form of FPOM. Greater metabolic rate for the invertebrates would allow the shredders present to process more CPOM creating greater FPOM. Shredders convert only c. 40% of CPOM ingested, the rest is egested as FPOM faeces (Cummins 1974). A greater metabolic rate may also allow the local invertebrate fauna to capitalize on the food resources available before they are carried downstream out of reach.

The changes in proportions of Ephemeroptera and Trichoptera from headwaters to downstream may reflect predation pressures by fish. The larger downstream reaches could support greater densities of fish predators and larger fish. Although I did not sample fish communities in this study work by Eikaas et al. (2005a, 2005b) on Banks Peninsula streams has shown that fish abundance declines rapidly away from the sea. The caddisfly fauna that played a more important role in the downstream sites than the headwater sites was comprised mainly of cased caddis

P. evecta and *Olinga* (Fig 3.7BE). Cases might make invertebrates less vulnerable to predation, whereas, none of the mayflies are protected from predation in such a fashion. Nyström et al. (2003) found that the presence of a trout raised the abundance and biomass of cased and shelled invertebrates.

However these trends in the fauna could be explained by environmental changes in the stream along the headwaters to downstream gradient. Faunal shifts predicted by the River Continuum Concept (RCC) (Vannote et al. 1980) may also be occurring in these systems although the differences in stream size between my headwater and downstream reaches were generally only one stream order. Though there is some debate to the applicability of the RCC to New Zealand streams and Winterbourn et al. (1981) have suggested that the short steep topography and physically unstable habitat partially explains the presence of a depauperate invertebrate fauna. This study did not detect a shift in the functional feeding groups that matches the shift from mayfly dominated headwaters to caddisfly dominated lower reaches. Moreover my findings indicate that catchment land use may have greater effect on the relative proportions of the functional feeding groups present in the fauna, than the position on the stream continuum. Other studies support the theory that catchment land use effects food web structure and the relative proportions of functional feeding groups (Quinn et al. 1997, Woodward and Hildrew 2002).

The fragmented forest streams follow the relationship proposed by the RCC better than the continuous forest streams, with increases in grazers and collector browsers from upstream to downstream. The continuous forest streams however did not follow this trend, with significant increases in shredders from upstream to downstream.

The larvae of most New Zealand native aquatic insects show little evidence of food specialisation which makes interpretation of functional feeding trends problematic (Winterbourn et al. 1981). Many collector/browsers will also lightly graze the substrate and several of the taxa categorised as “shredders” also graze, and shift their feeding modes as they mature. This clouding of the distinctions between feeding groups makes interpretation of the functional feeding groups more difficult. Gut content analysis would be the only way to determine which individuals were feeding on what at any given time and such analysis was not undertaken in this study.

The MCI scores show the downstream fragmented sites to be marginally more impacted than the other sites. With more pollution tolerant taxa present in relation to pollution intolerant taxa than at the other sites. However, the QMCI shows no difference between the fragmented or continuous catchments or the within catchment location. Therefore even though there are more pollution tolerant taxa present the community is still dominated by relatively intolerant species.

My ordination indicates that there are communities that are more likely to only be found in the continuous forest, with the majority of the continuous forest sites being tightly clustered. The patterns also indicate that some of the headwater sites in the fragmented catchments have similar fauna to the continuous forest catchments. The species that showed a preference for forest link the continuous forest sites to headwater sites in the fragmented catchments, more closely than to the downstream sites. Therefore the headwater fragmented sites probably have physical conditions more similar to those of the continuous forest streams than the downstream sites in the fragmented catchments. This makes sense, as headwater reaches are not affected by the condition of streams upstream of them as downstream reaches are.

Endemic species on the peninsula seemed to occur in the continuous forest as was the natural condition of the peninsula before the arrival of humans (Harding 2003, Eikaas et al. 2005b). Two endemic species, *C. peninsulae* and *Z. wardi* had a clear preference for the continuous forest sites and were only found in the headwater sites in the fragmented forest catchments. The other two endemic species found during this study were *Hydrobiosis styx* and *Neocurupira chiltoni*. Both were found in two more continuous forest sites than fragmented forest sites. As found by Harding (2003) *N. chiltoni* was very widely dispersed and appeared in the majority of sites sampled. As we know virtually nothing about the ecological requirements of these endemic species it is difficult to postulate what specific mechanisms control the distribution of these rare species.

Catchments with fragmented forest differed from catchments with continuous forest especially in the lower reaches. Streams (and the invertebrate communities therein) in downstream forest fragments were more impacted by surrounding land use than headwater streams in forest fragments and streams in continuous forest. Downstream reaches in fragmented catchments were characterised by poor taxonomic richness and under representation of endemic and 'forest' taxa.

Chapter 4: Adult stream invertebrate dispersal between forest fragments

Introduction

Forest fragmentation can threaten the persistence of metapopulations of many species dependent on forest habitats by disconnecting populations (Shirley 2006, Zartman and Shaw 2006). The fragmentation of riparian buffers not only affects the benthic invertebrate communities, directly but can affect the adult dispersal by disconnecting favourable oviposition and larvae habitat and consequently affecting the recruitment along stream reaches.

Adults of many stream insects require days or even weeks to fully sexually mature after emergence (Beer-Stiller and Zwick 1995, Collier and Smith 2000). During this adult phase some are susceptible to high temperatures and desiccation and may be reliant on forested riparian conditions for survival (Collier and Smith 2000). The presence of landscape patches with large open expanses may severely hinder dispersal. Some stream invertebrate taxa feed in the riparian zone during their adult phase and their fecundity may be dependent on the quality and quantity of the food available in the riparian vegetation (Smith and Collier 2000).

This study focuses on the effects of forest fragmentation on the adults of three orders Ephemeroptera, Plecoptera and Trichoptera (EPT) comparing the catch of adults flying along forest streams to the catch above downstream forest fragments and beneath headwater forest fragments.

I hypothesized that the EPT catch would be more diverse in the continuous forest compared to the forest fragments. If forested habitats are preferred habitat then within fragmented catchments I would further expect that there would be greater

upstream flight into the headwater fragments and greater upstream flight out of the downstream fragments than downstream flight into them.

Methods

Malaise trapping

Malaise trapping occurred during the October and November 2005 at the downstream sites FL1, FP1, FK1, CH1, CB1, CO1 detailed in chapter 2. Malaise traps were set up across the middle of the stream channel with the central trap wall touching the stream surface. The Malaise traps used were double sided, providing both upstream and downstream flight catches. They were deployed for 4 weeks, cleared every 2 weeks and the ethanol in the collection jar was replaced. Samples were returned to the lab in c.90% ethanol.

Sticky trapping

Sticky trapping was conducted over a two week period in November 2005 during which traps were left deployed for a week before being replaced. Sticky trapping occurred at all downstream sites and a single headwater site from each of the fragmented catchments, i.e. sites (CH1, CO1, CB1, FL1, FL2, FP1, FP2, FK1 and FK3) as detailed in Chapter 2. Within continuous forest sites the lowermost trap was deployed at the benthic sampling site used in chapter 3 and further traps were deployed progressively upstream from there. In the fragmented catchments, downstream sites started at the forest-pasture edge on the upstream side of the forest fragment. Headwater sites started at the downstream edge of the forest fragment and were deployed into the pasture.

Sets of sticky traps were deployed at 0 m, 16 m, 32 m and 64 m from the forest edge (from arbitrary point of origin in the continuous forest streams) into

pasture. The sticky traps consisted of two sheets of type “P”, A4 size, clear copier transparency stapled to each other on either side of green plastic 50mm square trellis, cropped to just larger than A4 size. The sheets were liberally coated by brush with the insect barrier Tanglefoottm. Each set of traps consisted of 3 sticky traps all at approximately equal heights above the stream surface. The traps were suspended between 1.2m and 1.8m above the stream surface dependant on availability of suitable anchorage points, either vegetation or warratahs. The full traps were placed in snap lock bags and refrigerated until insects were identified.

Identification

In the laboratory, malaise trap samples were poured into trays and Ephemeroptera, Plecoptera and Trichoptera were separated from other insects and identified under a microscope (40x magnification). EPT taxa on the sticky traps were counted and identified without being removed from the sheets. Traps with large catches of Trichoptera were sub-sampled for Trichoptera with a randomly selected quarter of the sheet counted. EPT taxa were identified using Ward (2003), Town and Peters (1996) and with the assistance of Prof. Winterbourn. Taxa were identified to genus and species level where possible, however, the identification of hydrobiosid caddisflies to this level was problematic, and therefore taxa were grouped to family level for analysis to remove possible error.

Analysis

To test for differences between continuous and fragmented forest and flight direction two-Way ANOVAs were conducted on the Malaise trap data. Two-way ANOVAs were also conducted on the sticky trap data to look for forest cover and

flight direction differences. Three-way ANOVAs were then used on the sticky trap data to incorporate distance from the fragments as a factor. Two-way ANOVAs were run on the data from the different flight directions separately to focus on the site type differences and distance. All analyses were performed using Sigma Stat (Systat Software 2004).

Results

Malaise traps

During the trapping period 2131 EPT adults were collected. These individuals came from 16 families representing >24 species. The majority of the catch (58%) was comprised of Trichoptera (Table 4.1). However the majority of the downstream flight catch was mayflies (Fig 4.1A, Table 4.1). In general mayflies were frequently caught on both upstream and downstream sides of the malaise traps (Table 1). Stoneflies were also caught in greater proportions, though not significantly so, on the upstream sides of the traps (Fig 4.1A, Table 4.1). A significantly greater percentage of caddisflies were caught flying upstream than downstream (Two-way ANOVA $F_{1,11} = 5.987$ $p=0.040$) (Fig 4.1A, Table 4.1).

Table 4.1: Malaise trap catch by order, with percentages of flight direction and of total catch

	Ephemeroptera	Plecoptera	Trichoptera	Total
Upstream flight	342	31	902	1275
Downstream flight	442	81	333	856
Combined Catch	784	112	1235	2131
% Upstream flight	43.6%	27.7%	73.0%	59.8%
% Downstream flight	56.4%	72.3%	27.0%	40.2%
% Combined catch	36.8%	5.3%	58.0%	N/A

Within the mayflies Leptophlebiidae were the dominant family in both forest types (Fig 4.1C). The family Coloburiscidae, which contains only the single species

Coloburiscus humeralis, contributed a visibly greater proportion of the mayfly taxa in the continuous forest than the fragment forest (Fig 4.1C). Only a single ephememerid was collected, *Ichthyotus bicolor*, flying upstream in one of the fragmented catchments (Fig 4.1C). Members of the family Nesameletidae were also rare (Fig 4.1C).

The stonefly taxa were predominantly members of the family Gripopterygidae (Fig 4.1B), primarily *Zelandoperla decorata*. *Stenoperla prasina* a member of the family Eustheniidae was the only non gripopterygid stonefly collected and it was only collected on the upstream (downstream flight) side (Fig 4.1B).

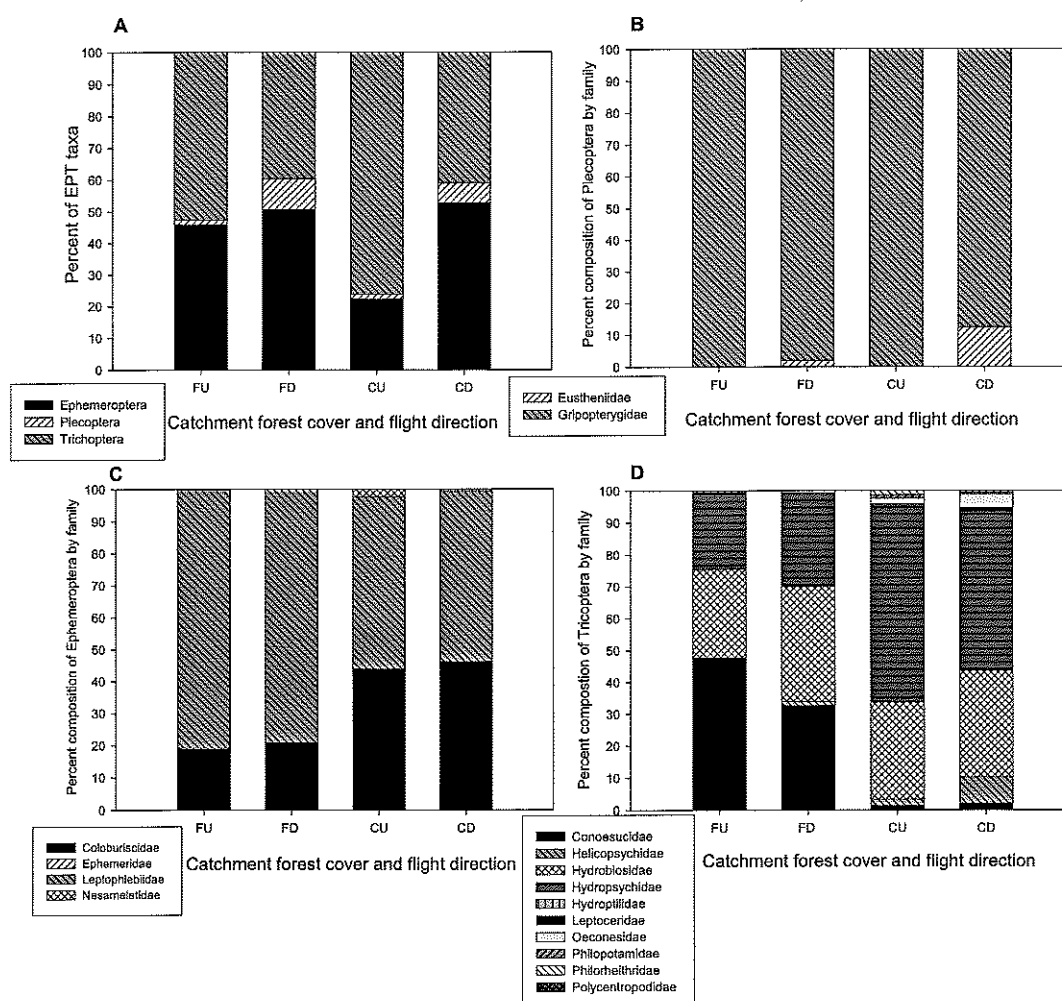


Figure 4.1: Catch percentages from the Malaise traps, at the order and within order levels, showing fragmented or continuous forest and flight direction. F= Fragmented forest, C= Continuous forest, U= Upstream flight, D= Downstream flight.

The caddisfly families were more variable (Fig 4.1D). Members of the Conoesucidae formed a large portion of the catch in the fragmented forest, contributed very little to the overall caddisfly catch in the continuous forest (Fig 4.1D). This led to a significant difference in the percentage of caddisflies that conoesucids formed between fragmented and continuous forest (Two-way ANOVA $F_{1,11} = 49.715$ $p < 0.001$). The proportion of the total caddisfly catch comprised of hydrobiosid caddisflies was similar between the forest cover types and in upstream and downstream flight (Fig 4.1D). The hydropsychid caddisfly *Aoteapsyche* showed the opposite trend to the conoesucids, contributing a significantly greater percentage of the population in continuous forest than in fragmented forest (Two-way ANOVA $F_{1,11} = 9.479$ $p = 0.015$) (Fig 4.1D). The helicopsychids featured more prominently in the continuous forest but not significantly so (Fig 4.1D). The only other family to differ significantly between fragmented and continuous forest was Oeconesidae, which formed a significantly greater percentage in the continuous forest than in the fragmented forest where it was almost absent (Two-way ANOVA $F_{1,11} = 7.007$ $p = 0.029$) (Fig 4.1D).

Sticky Traps

Approximately 32,000 EPT adults were caught during the sticky trapping, roughly 90% of which were Trichoptera (Table 4.2). The catch was comprised of 15 families and >22 species.

The majority of the catch was Trichoptera across all site types except in continuous forest where downstream flight was primarily mayflies (Fig 4.2A). Continuous forest sites differed significantly from the fragmented sites in their proportions of Ephemeroptera and Trichoptera in the total catch (Two-way ANOVA $F_{2,17} = 14.788$ $p < 0.001$ and $F_{2,17} = 14.934$ $p < 0.001$ respectively) (Fig 4.2A). Plecoptera

formed less than 1% of the catch at any of the sites and consequently did not significantly differ in percent of catch between site types or flight direction (Fig 4.2A). Overall Plecoptera were 0.07% of the total catch with only 22 individuals collected (Table 4.2). Aside from continuous forest sites there was very little difference in catch composition between flight directions (Fig 4.2A). The continuous forest sites had significant differences in flight direction with a greater percentage of the downstream flight being Ephemeroptera and greater percentage of the upstream flight being Trichoptera (Holm-Sidak comparison $t = 2.502$ $p = 0.028$) (Fig 4.2A). Overall, Trichoptera followed the same pattern, with 61% caught flying upstream and 39% caught flying downstream (Table 4.2, Fig 4.2A). However Ephemeroptera were caught in roughly equal numbers flying upstream and downstream (Table 4.2).

Table 4.2: Sticky trap catch displayed by order, with percentages of flight direction and of total catch

	Ephemeroptera	Plecoptera	Trichoptera	Total
Upstream flight	1388	11	17485	18963
Downstream flight	1459	11	11207	12754
Combined Catch	2847	22	28692	31717
% Upstream flight	48.8 %	50.0 %	60.9 %	59.8 %
% Downstream flight	51.2 %	50.0 %	39.1 %	40.2 %
% Combined catch	9.0 %	0.07 %	90.5 %	N/A

Plecopterans were rarely caught which made the relative percentages of plecopteran families highly variable and failed to conform to normal distribution. Therefore, there were no statistically significant differences between plecopteran families and site types or flight directions. However, the families Austroperlidae (*Austroperla cyrene*) and Eustheniidae (*S. prasina*) were only caught in the continuous forest and the only Eustheniidae collected was caught flying downstream (Fig 4.2B). Members of the family Gripopterygidae, including *Z. decorata* and *Zelandobius wardi*, made up the remainder of the plecopteran catch (Fig 4.2B).

The percentages of families comprising the Ephemeroptera catch was similar across all site types and both flight directions (Fig 4.2C). The majority of the catch was the family Leptophlebiidae, dominated by *Deleatidium sp.* (Fig 4.2C). The rest of the catch was the family Coloburiscidae, except for a single *I. bicolour*, which was caught flying upstream from a downstream forest fragment (Fig 4.2C). No members of the family Nesameletidae were collected in sticky traps.

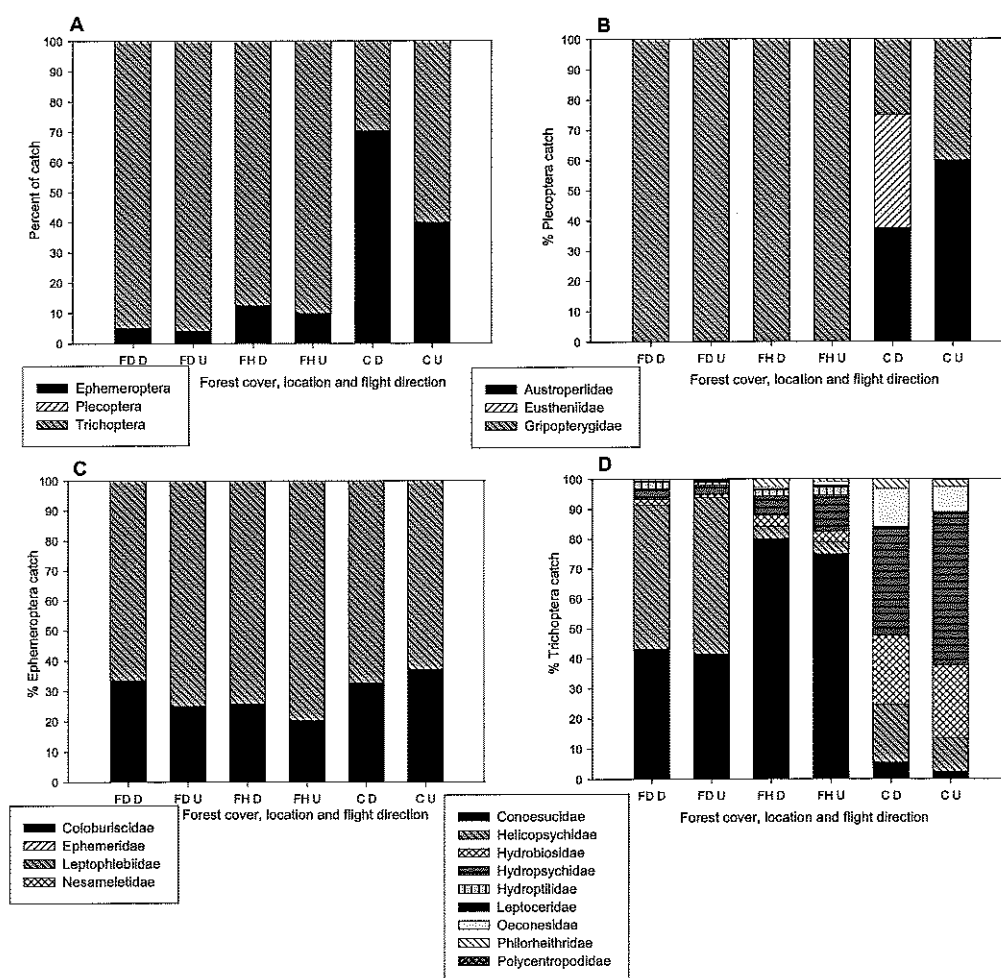


Figure 4.2: Catch percentages from the sticky traps, at the order and family levels, showing fragmented downstream, fragmented headwaters or continuous forest and flight direction. FD= Fragmented downstream, FH= Fragmented headwaters, C= Continuous forest, U= Upstream flight, and D= Downstream flight.

As with the Malaise traps there was considerable variation in the trichopteran catch. There was a significant difference in Conoesucidae catch between site types

(Two-way ANOVA $F_{2,17}=9.122$ $p=0.004$). The fragmented headwater sites had the greatest percentage conoesucids accounting for c.80% of the catch in both flight directions (Fig 4.2D). At the fragmented downstream sites, conoesucids comprised only c.40% of the trichopteran catch while they formed c.80% in the fragmented headwaters, however, they were not significantly different (Fig 4.2D). The continuous forest sites had significantly lower percentages of Conoesucids than both the fragmented headwater (Holm-Sidak comparison $t= 3.580$ unadjusted $p=0.00378$ critical level $=0.025$), and the fragmented downstream sites (Holm-Sidak comparison $t= 3.807$ unadjusted $p=0.00250$ critical level $=0.017$) (Fig 4.2D).

The Helicopsychidae played a more important role in the fragmented downstream sites, than the fragmented headwater or continuous forest sites, forming over 40% of the catch (Fig 4.2D). However, again this was not a significant difference.

Hydrobiosids formed a significantly greater part of the catch in the continuous forest than in the fragmented forest sites (Two-way ANOVA $F_{2,17}= 4.374$ $p=0.037$). The hydropsychid *Aoteapsyche* was also significantly more prevalent in the continuous forest (Two-way ANOVA $F_{2,17}= 5.313$ $p=0.022$), as was the oeconesid *Oeconesus maori* (Two-way ANOVA $F_{2,17}= 11.570$ $p=0.002$) and the philorheithrid *Philorheithrus agilis* (Two-way ANOVA $F_{2,17}= 5.582$ $p=0.019$).

Longitudinal stratification

The total daily catch rate of EPT insects increased along the 0-64m transect from the forest edge in both the headwater and the downstream fragmented sites (Fig 4.3A). This was true for both upstream and downstream flight (Fig 4.4A, 4.5A). This was due mainly to the large influence of the Trichoptera which comprise the majority

of the catch (Fig 4.3D, 4.4D, 4.5D). However, the ephemeropteran catch rate in the fragmented catchments also increased further from the forest edge (Fig 4.3C). The same pattern occurred in both upstream and downstream flight although in varying intensities (Fig 4.4C, 4.5C).

The catch rate of Plecoptera was too small and sporadic to show any real patterns, and there were no significant differences between site types, flight direction or over longitudinal distance from forest edge (Fig 4.3B, 4.4B, 4.5B).

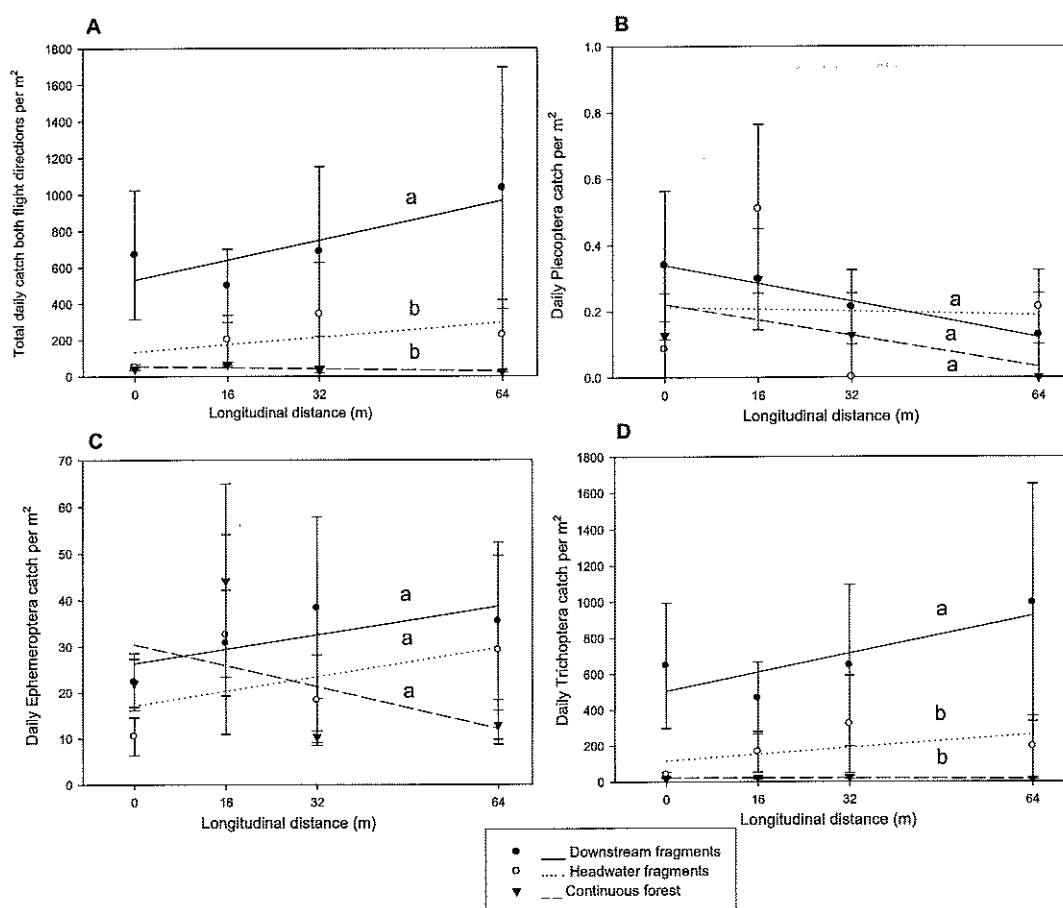


Figure 4.3: Combined upstream and downstream catches showing total daily catch rate per m² (± 1 S.E) and that of the EPT orders along a longitudinal gradient. Letters show the results of two-way ANOVA and Holm-sidak pairwise comparisons where means of groups with the same letter are not significantly different, $p > 0.05$.

The total daily EPT catch rate in the continuous forest was very low in comparison to the catch rate in the open near fragmented forest (Fig 4.3A, 4A, 5A). It

remained consistently low and decreased slightly upstream over the longitudinal distance in total catch and in each flight directions (Fig 4.3A, 4A, 5A). Not surprisingly this pattern was repeated in the all the orders although there appears to be no decrease over distance in the downstream flight catch rate of Trichoptera (Fig 4.3, 4.5).

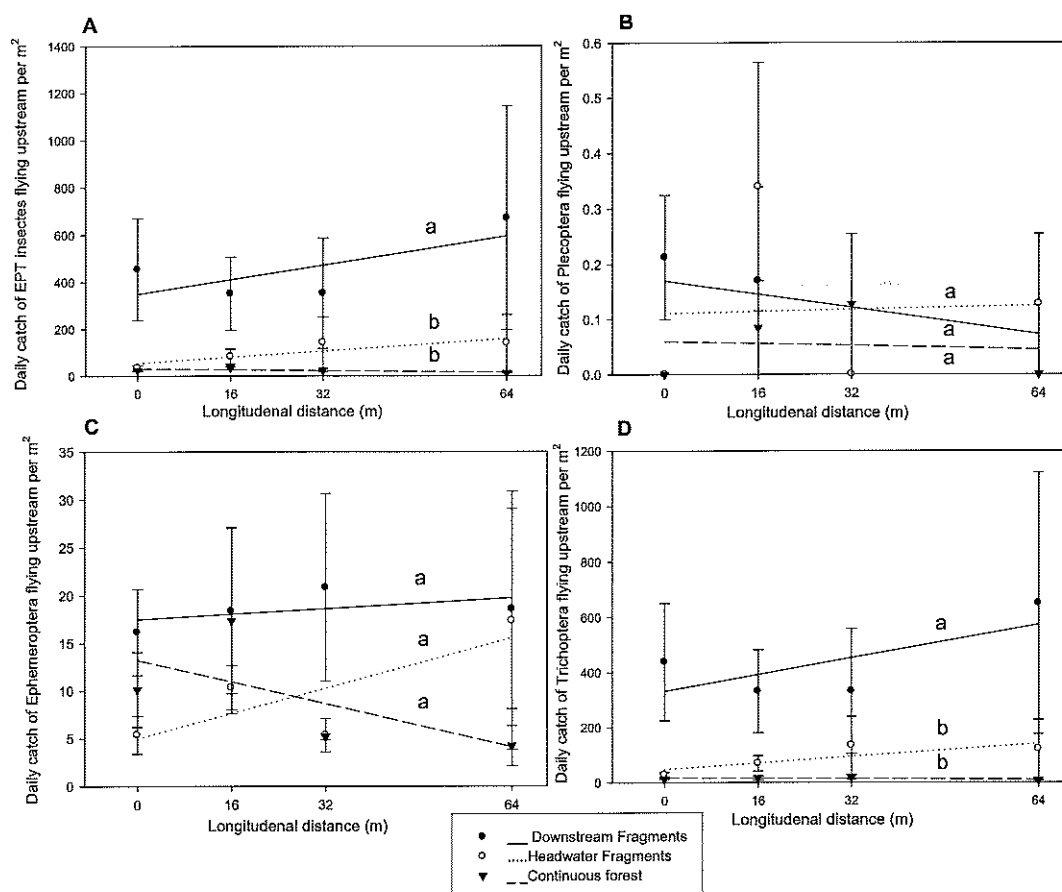


Figure 4.4: Upstream flight catches showing daily catch rate per m² (± 1 S.E) of the EPT orders along a longitudinal gradient. Letters show the results of two-way ANOVA and Holm-sidak pairwise comparisons where means of groups with the same letter are not significantly different, $p > 0.05$.

There were significant differences in the combined total daily catch rate between the different site types (Two-way ANOVA $F_{2,35} = 6.307$ $p = 0.006$) (Fig 4.3A). The combined total daily catch rate in the fragmented downstream sites was significantly greater than both the fragmented headwater sites (Holm-Sidak comparison $t = 2.586$ unadjusted $p = 0.0162$ critical level = 0.025) and the continuous

forest sites (Holm-Sidak comparison $t=3.401$ unadjusted $p=0.00235$ critical level=0.017) (Fig 4.3A).

The same was true with the Trichopteran catch with fragmented downstream sites having significantly greater daily catch rates than the fragmented headwater sites (Holm-Sidak comparison $t= 2.606$ unadjusted $p= 0.0155$ critical level=0.025) and the continuous forest sites (Holm-Sidak comparison $t= 3.431$ unadjusted $p=0.00219$ critical level=0.017) (Fig 4.3D).

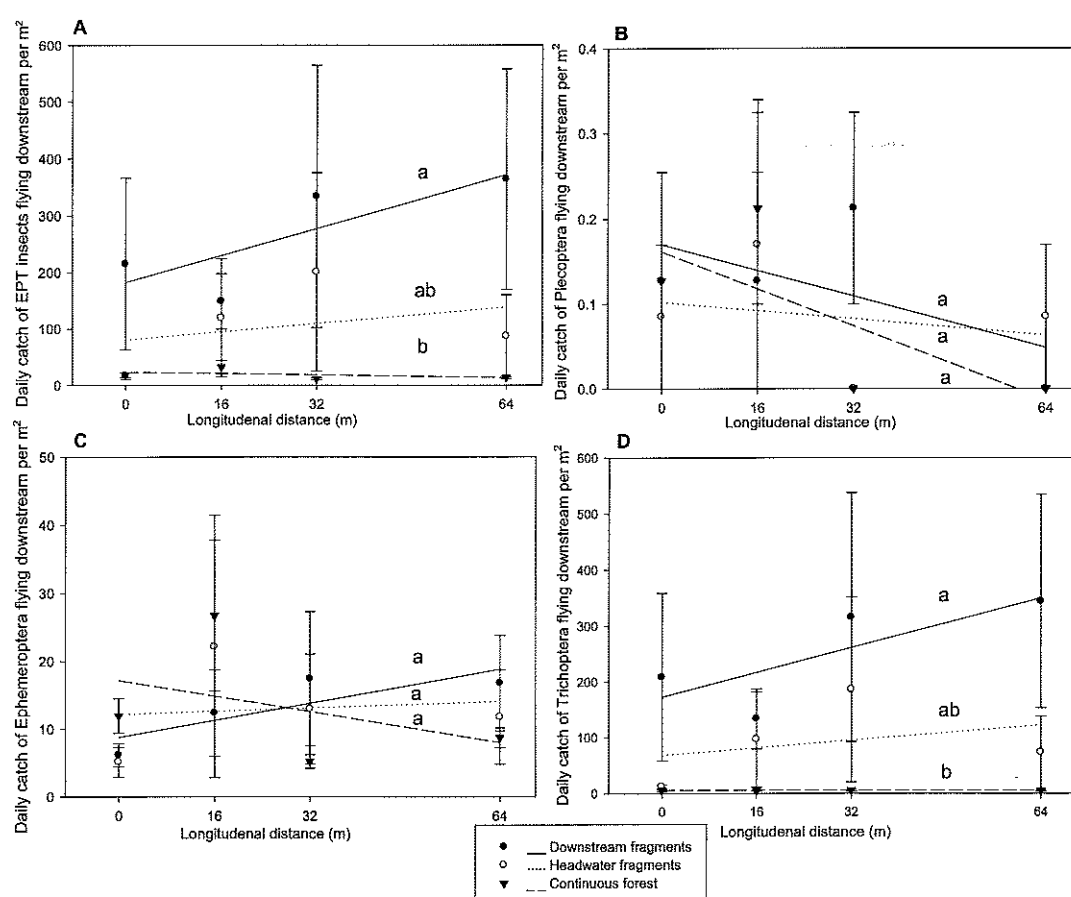


Figure 4.5: Downstream flight catches showing daily catch rate per m² (± 1 S.E) of the EPT orders along a longitudinal gradient. Letters show the results of two-way ANOVA and Holm-sidak pairwise comparisons where means of groups with the same letter are not significantly different, $p>0.05$.

Upstream flight by itself demonstrated the same patterns, with significant differences in both EPT catch rate (Two-way ANOVA $F_{2,35}= 6.785$ $p=0.005$) and Trichoptera catch rate (Two-way ANOVA $F_{2,35}= 6.686$ $p=0.005$) between the site types (Fig 4.4AD). The EPT daily catch rate in the fragmented downstream sites was

also significantly greater than both the fragmented headwater sites (Holm-Sidak comparison $t = 2.845$ unadjusted $p = 0.009$ critical level = 0.025) and the continuous forest sites (Holm-Sidak comparison $t = 3.449$ unadjusted $p = 0.002$ critical level = 0.017) (Fig 4.4A). In regard to the Trichopteran catch fragmented downstream sites had significantly greater daily catch rates than the fragmented headwater sites (Holm-Sidak comparison $t = 2.824$ unadjusted $p = 0.009$ critical level = 0.025) and the continuous forest sites (Holm-Sidak comparison $t = 3.424$ unadjusted $p = 0.002$ critical level = 0.017) (Fig 4.4D).

There were also significant differences in the downstream flight in both total catch rate (Two-way ANOVA $F_{2,35} = 4.579$ $p = 0.021$) and trichopteran catch rate (Two-way ANOVA $F_{2,35} = 4.929$ $p = 0.016$) (Fig 4.5AD). However, unlike the combined flight direction and the upstream flight, the fragmented downstream sites were not different from the fragmented headwater sites, they were only significantly different from the continuous forest sites in both total catch rate (Holm-Sidak comparison $t = 2.984$ unadjusted $p = 0.006$ critical level = 0.017) and trichopteran catch rate (Holm-Sidak comparison $t = 3.095$ unadjusted $p = 0.005$ critical level = 0.017) (Fig 4.5AD).

Comparisons between benthic and adult catch

Interestingly the composition of adult catches from malaise traps differed from the composition found in benthic samples of the larval community (Fig 4.6A). The percentage of the adult plecopoterans was far greater in the downstream flight of the malaise traps than it was in either the benthic samples or the upstream flight in the malaise traps (Fig 4.6AB). However the variation between catches was so great that there was no significant difference between any of the catch groups (Fig 4.6B).

While there was variation in the percentages Ephemeroptera comprised between the benthic sampling and malaise traps there was no significant difference between the relative percentages of the catches of the benthic samples and either of the flight directions within both the fragmented forest sites and the continuous forest sites (Fig 4.6AC). However there was a significant (t-test $t = -3.023$ $df=4$ $p = 0.039$) difference in the upstream and downstream flight catch percentages in the continuous forest (Fig 4.6C).

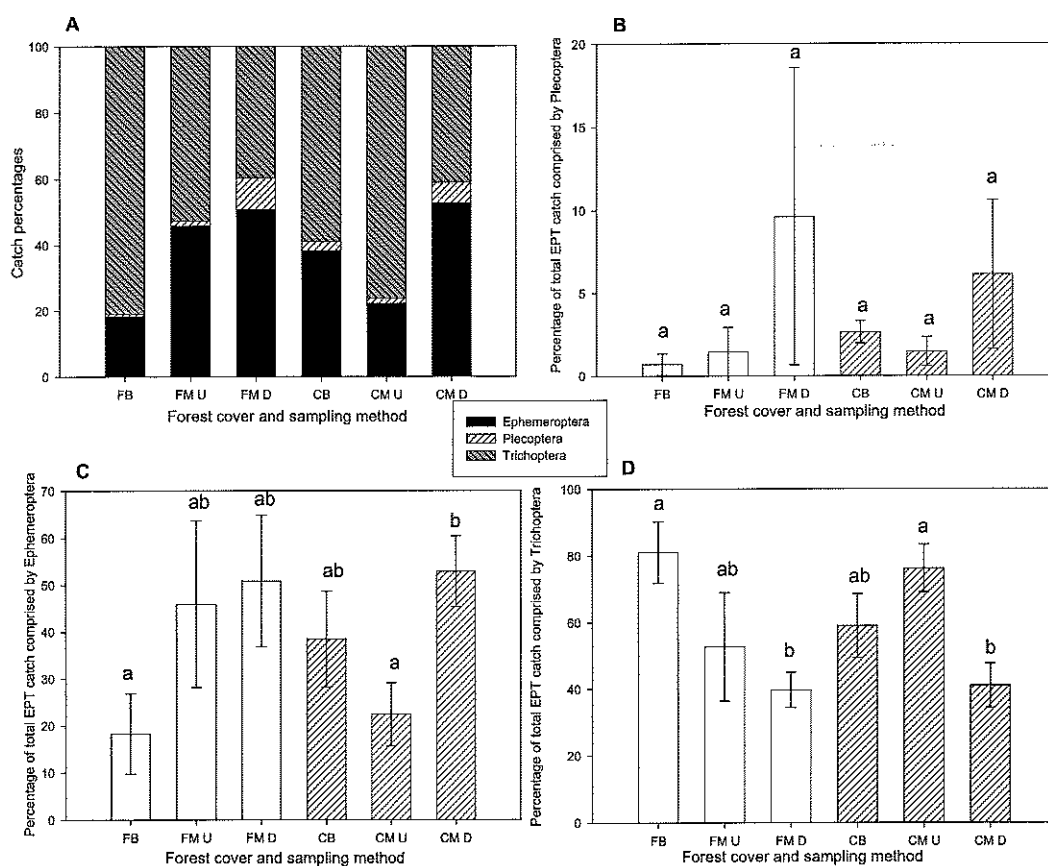


Figure 4.6: Comparisons of catch percentages of the EPT orders (± 1 S.E) between the benthic sampling and the malaise traps. F = fragmented, C= continuous, B = benthic, M= malaise, U= upstream flight, D= downstream flight. Letters show the results of t-tests where means of groups with the same letter are not significantly different, $p>0.05$.

The percentage of the catch formed by Trichoptera was lower in the malaise traps than in the benthic sampling in the fragmented sites and the downstream flight in the continuous forest (Fig 4.6AD). The percentage of Trichoptera in the downstream flight malaise trap catch in the fragmented sites was significantly (t-test t

= 3.912 df=4 $p = 0.017$) lower than the percentage of Trichoptera in the benthic samples (Fig 4.6D). However, the upstream flight in the continuous forest went against the trend with a greater proportion of Trichoptera than the benthic samples (Fig 4.6D).

The sticky trap catches and benthic samples showed a similar pattern with the fragmented sites having higher EPT densities than the continuous forest. However, the catches in both fragmented downstream and fragmented headwater reaches were larger than expected from the benthic data (Fig 4.7A). Although due to the high variance in the sticky trap catch within the fragmented sites there was no significant difference (Fig 4.7A). If the catch in the fragmented downstream sites was regarded as the expected catch from an invertebrate community of size X, then the catch in continuous forest was significantly (t-test $t = 39.062$ df=4 $p < 0.001$) smaller than expected (Fig 4.7).

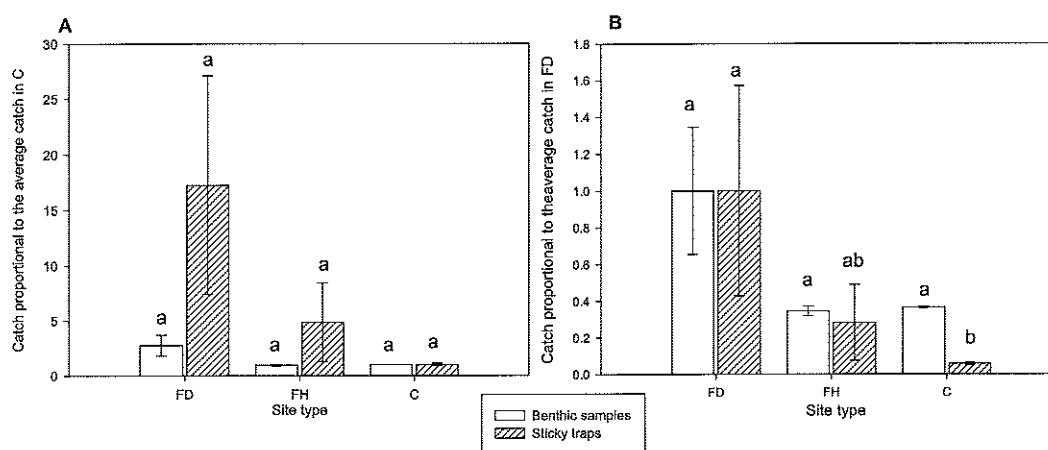


Figure 7: Comparison of the benthic densities and sticky trap catches of EPT invertebrates (± 1 S.E) across the different site types. A) Both the benthic and sticky trap catches were divided by their respective catch in the continuous forest to render them comparable as proportions B) Both the benthic and sticky trap catches were divided by their respective catch in the fragmented downstream sites to render them comparable as proportions. FD= Fragmented downstream, FH = Fragmented headwaters, C = Continuous forest. Letters show the results of t-tests where means of groups with the same letter are not significantly different, $p > 0.05$.

Discussion

Although studies on adult aquatic insects are becoming more common much is still unknown about the flight patterns, duration and behaviour of many of our New Zealand species. Commonly studies focus on a single technique, light trapping, malaise trapping, or sticky trapping, and each method has both advantages and disadvantages. In this study I combined both malaise and sticky trapping techniques in order to gain not only a measure of the diversity of the taxa but also some measure of adult density.

Catch compositions were more varied in the continuous forest than the fragmented forest in both the malaise trapping and sticky trapping. Ephemeroptera made up a greater proportion of the overall catch in continuous forest in the sticky traps but not the malaise traps. Catch rate in the sticky traps increased out from the forest edge, in both the downstream and headwater reaches, mainly due to the increase in the catch of Trichoptera.

The two trapping methods showed markedly different trapping efficiency for Trichoptera in the fragmented downstream sites, whereas the trichopteran catches were similar in the continuous forest sites. This may have been due to the differences in physical conditions inside the fragments and upstream, or sticky traps proved more effective at trapping conoesucids and helicopsychids in the open upstream of the fragments. The hydrobiosid and hydropsychid caddisflies did not have the same increase in catch out in the open. They also formed a greater percentage of the catch in the continuous forest. Therefore they may be more dependent on forest conditions.

The Philorheithrid *P. agilis* comprised a greater percentage of the sticky trap catch in the continuous forest than the fragmented forest was also present in decent proportions in the fragmented headwaters. This suggests that the conditions

downstream of the headwater fragments were closer to that of the continuous forest than the reaches upstream of the downstream fragments were. The hydrobiosid and hydropsychid caddisflies also contributed greater proportions in the fragmented headwater sites than the fragmented downstream sites, adding weight to the theory that the headwater fragmented sites are more similar to the continuous forest sites.

Adult catches above the downstream fragments were significantly greater than the catch rates in both the continuous forest and reaches beneath the headwater fragments. The difference between the headwater and downstream fragments could be explained by the difference in stream size and therefore potential size of the stream community. However airspace above the stream channel is dependant on the size of the stream and the sticky traps would have taken up a greater proportion of this space in the headwater sites than the downstream sites, therefore should have theoretically trapped a greater proportion of the community. Unless the traps were exerting some form of attraction, and catching a greater number of insects than random flight would account for.

The comparison of the sticky trap catches to the benthic densities suggests two possibilities, either the benthic invertebrate densities are far greater in the open between the fragments or sticky trap effectiveness increases in the open. The benthic densities of EPT may be greater in the open primarily due to trichopteran taxa such as Conoesucidae and Helicopsychidae. Death and Zimmermann (2005) found benthic invertebrate densities to be twice as high in the open as in forest, however this was all benthic invertebrates not solely EPT taxa. Harding and Winterbourn (1995) also found greater benthic invertebrate densities in open pasture than in forest, both pine and native beech, and while Trichoptera densities in pasture slightly exceeded those in forest the overall density of EPT taxa did not. Therefore while a greater

invertebrate density could be expected in the pasture land between the forest fragments it should not be large enough to explain the 5-6 fold average increase in adult catch in the fragmented sites, when using the proportions from the continuous forest sites as the expected catch. Given that, when the catch from the fragmented downstream sites was used as the expected catch, the sticky trap catch in the continuous forest was significantly lower than the proportional benthic density of EPT taxa. I suggest that there were differences in the effectiveness of the sticky traps in the continuous forest compared to in the open between the fragmented sites.

The females of several species of caddisfly are known to produce pheromones to attract males (Bjostad 1996, Larsson and Hansson 1998). It has been theorised that trichopteran males may be attracted to females stuck on sticky traps by pheromones they release. However, this would have led to elevated catches of Trichoptera across all the sites, and the catch in the continuous forest was not large. All the Trichoptera catches are relatively proportional to their relative benthic larval densities so this mechanism is unlikely to explain the higher catches. Unless there is a threshold level for attraction, requiring a certain number of females to be caught before there is a high enough concentration of pheromones released from the one spot to preferentially attract males to the sticky trap, rather than any other nearby female. The fragmented sites had higher concentrations of Trichoptera which would increase the probability that females would be trapped by chance, potentially allowing this mechanism to establish. However this should lead to a sex bias in favour of males on the traps. Unfortunately the sex ratio of the Trichoptera collected by sticky trapping was not analysed in this study.

The Ephemeroptera catch also increased out into the open along with the Trichoptera catch and they are not thought to use the same pheromonal attraction as

the Trichoptera. Therefore some other factor may be influencing the catch in the open. I propose that light may be affecting the catch rate. It is a major difference between the sites, both the fragmented headwaters and downstream sites are out in the open and exposed to high levels of direct light while the traps in the continuous forest get very little light. EPT invertebrates have compound eyes, compound eyes increase the sensitivity to light at a cost of resolution, giving them good low light vision which some taxa use for night flying (Gullan and Cranston 2000). However the bright light conditions in the open may impair their vision making them less likely to notice the trap and take appropriate action to avoid the trap. Insects can also see polarized light and in some cases are attracted to it (Gullan and Cranston 2000). Mayflies in particular have been documented to be attracted to polarised light (Kriska et al. 1998, Bernath et al. 2001). Light is polarized when it reflects off shiny surfaces and the sticky traps are shiny and would therefore polarize light. Therefore in the open where the sticky traps are more likely to have light striking them, the plane polarized light reflecting from the traps may be attracting insects to them. This could partially account for the significantly lower catches in the continuous forest as the light levels would be lower, more within the optimum operating range of a compound eye, and there would be less plane polarized light reflecting off the traps, which means the insects would be less likely to be attracted to the traps and possibly more likely to see them in time to avoid them.

Wind may have had an affect on the catch rate. Other studies have shown that dispersal of insects can be wind assisted (Gatehouse 1997, Caceres and Soluk 2002, Briers et al. 2004). There would be greater wind velocities in the open than in the forest (Davies-Colley et al. 2000). Therefore it stands to reason that there would be greater wind assisted catch in the fragmented sites compared to the continuous forest

sites, as insects being carried by the wind would have less control over their flight and may be less likely to avoid the traps.

Temperature may also have had an effect on the catch rate. Temperatures would be higher in the open than in the forest (Davies-Colley et al. 2000). The higher temperatures in the open could lead to a longer daily period of activity of the invertebrates. A longer daily period of activity means more hours flying per day which could lead to the increased catches seen in the open sites. Briers et al. (2003) in a study in Wales found that plecopteran catch rate was positively correlated to daily temperature. In New Zealand, Ward et al. (1996) found that catch numbers of caddisflies strongly depended on air temperature.

The main differences in flight direction that occurred in the malaise traps were in the continuous forest sites. The proportions of both Ephemeroptera and Trichoptera differed between the upstream and downstream flight. Given that this data was based on percentages of total catch the catch of only one of the orders needs to differ to make both proportions significantly different. The difference was caused by the decrease in the Ephemeroptera catch on the downstream side of the malaise traps at these sites, and the apparent preference of Trichoptera to fly upstream. The decrease in the Ephemeroptera catch may have been due to the fact that the sites were located near the bottom edge of the continuous forest and less Ephemeroptera may have been flying upstream from the open land beneath the forest. The near 50:50 split of flight directions in the Ephemeroptera catch in the sticky traps suggest that as a group Ephemeroptera had no real preference for flight direction. This gives support to Humphries and Ruxton's (2002) theory that upstream flight is not required to counter drift and insure continuation of populations in headwaters.

Plecoptera appeared in greater numbers on the upstream side of the malaise traps but their catch rate was also highly variable. This may have been due to larvae drifting downstream and emerging on the malaise trap. The variability may have been caused by the differences in the position of the bottom edge of the malaise traps in relation to the stream surface and position of the trap in relation to the main current within the stream. I suggest drift to explain the differences in the plecopteran catch in the malaise traps due to the presence of exuviae on the upstream side of some malaise traps at the end of trapping. The downstream catch in the malaise traps of Ephemeroptera may also be boosted by drift.

The downstream flight catch of Trichoptera was lower than the upstream flight in both the trapping regimes. Given that 60% of the Trichoptera in the sticky traps and 73% of the Trichoptera in the malaise traps were caught flying upstream it suggests that at least some of the Trichopteran taxa are preferentially flying upstream. Other studies in New Zealand have found preferential upstream flight in some Trichopteran species (Winterbourn and Crowe 2001). Winterbourn and Crowe (2001) found that the more abundant forest dwelling caddisfly species were over represented on the downstream side of sticky traps indicating that the majority were flying upstream.

The differences in the directional flight of the Ephemeroptera and the Trichoptera, with Ephemeroptera showing no preference for flight direction and Trichoptera having a preference for upstream flight, may be explained by morphological characteristics of their larvae. Humphries and Ruxton (2002) debate that a preference for upstream flight is unnecessary as small scale movements and density dependence at some point in the larval stage are all that are required for invertebrates to overcome the 'drift paradox'. The larvae of Ephemeroptera and

Trichoptera differ greatly morphologically and therefore in benthic and lotic movement and mobility. The generally more mobile Ephemeroptera larvae may more easily be able to move back upstream if displaced by drift than the often cased and less mobile Trichoptera. In the terms of energetics larval Ephemeroptera would use less energy travelling back upstream than a cased Trichoptera larva would expend hauling its case upstream. Therefore Trichoptera are more likely to require/use upstream flight to overcome the drift paradox and maintain persistent populations in streams. Density dependence in the larval stages would make this upstream flight beneficial to the fitness of the offspring of the individual flying upstream, as the upstream reaches would have lower densities due to drift, allowing greater growth and less competition (Anholt 1995). The flying adult phase would also be the most energetically efficient phase to undertake the upstream movement as they are going to fly a given distance as an adult they may as well fly a given distance upstream, rather than struggling against the current trying to move upstream as a larvae.

Chapter 5: Conclusions

Concluding comments

Catchments with continuous forest had the greatest diversity in the benthic community and this was mirrored in the adult community. The headwater fragments in the catchments with fragmented forest were more likely to contain a high diversity of taxa and taxa which have a preference for forested streams than the downstream fragments, due to the less impacted conditions of the headwater streams. Given that the original condition of Banks Peninsula was almost completely forested (Porteous 1987, Harding 2003, Eikaas et al. 2005) it is not surprising that the local stream invertebrate fauna is better suited to life in forested streams, and that the forested stream or reaches with conditions most closely resembling forested streams had the highest diversities.

However invertebrate densities were highest in the downstream fragments, in the conditions least like those of a continuous forest stream. The same appeared to be true for the adult communities, with the highest catches being recorded out in the open pasture 64m from the forest fragment edge. Therefore forest stream conditions may be unable to support the high densities of invertebrates as open or partially open stream conditions. Other studies have also shown higher densities of invertebrates in open pasture streams than forested streams, although usually not of Trichoptera (Harding and Winterbourn 1995, Quinn et al. 1997). Supporting the theory that macroinvertebrate density and biomass in New Zealand streams are limited by canopy cover, and dependent on light and in stream primary production (Nyström et al. 2003). Given the predominance of evergreen trees within the native flora New Zealand streams receive asynchronous inputs

of leaves and combined with the depauperate shredder taxa (Winterbourn et al. 1981), may help explain the limiting nature of canopy cover on biomass.

Implications for management

The results of my study indicate that the establishment of native forest in the riparian zones of the headwater streams on Banks Peninsula is liable to be the most efficient method of maintaining stream invertebrate biodiversity. The steep topography of headwater areas in Banks Peninsula would also have been the least profitable to clear for farming. Forests in the headwaters could help to maintain populations of the endemic species as well as the forest specialist taxa, although my findings indicate that even headwater sites in fragmented catchments do not have the same diversity as catchments with continuous forest.

Establishment of riparian vegetation linking headwater forest fragments to downstream forest fragments could markedly improve the condition of the downstream forest fragments and improve their capacity to provide habitat for forest specialist taxa and potentially the apparently forest favouring endemics. Narrow riparian strips would increase shading on the stream reducing solar heating and mitigating some of the diurnal fluctuations of stream in open land (Sinokrot and Stefan 1993, Rutherford et al. 1997). This could prevent stream temperatures reaching lethal levels for temperature sensitive taxa, which open streams can easily achieve during summer months (Quinn et al. 1994). These riparian strips would also act as dispersal corridors for the adults, some of which are sensitive to desiccation and air temperature (Collier and Smith 2000).

Riparian vegetation also provides additions of leaf litter along the river continuum. A riparian margin of 2-5m has been shown to supply around 22% of the leaf litter expected from a mature riparian forest (Oelbermann and Gordon 2000). This would add variety to the food resources available in the stream which may in turn allow greater diversity between the fragments. However leaf litter within a reach is dependent retention of litter and stream flow (Winterbourn 1976, Lepori et al. 2005). Coarse substrate such as large boulders or coarse woody debris may initially could be added to lower reaches to aid in the retention of leaf litter and other CPOM (Lepori et al. 2005). Over time the riparian buffers would also add their own coarse woody debris to the streams.

Multiple fragments of forest along the stream continuum could be another method of management. Fragments should extend at least 50m either side of the stream to ensure forest microclimatic conditions above the stream (Davies-Colley et al. 2000). For greatest effect the forest fragment would need to cover a several hundred metres of the stream. Scarsbrook and Halliday (1999) found that conditions in a stream transitioning from pasture to forest reverted to expected forest conditions within 300m. However repetitions of fragments along the river continuum may decrease the distance required to achieve forest conditions. Insuring that fragments were not too far apart would at least prevent the thermal regime reaching open pasture stream, and hence potentially detrimental, conditions. Allowing distances between fragments of no more than 150m in 1st order streams, 500m in 2nd order streams and 1.5km in 3rd order streams should maintain stream water temperatures beneath 20°C, the suggested safe limit for sensitive taxa (Quinn et al. 1994, Rutherford et al. 1997).

Fragments in the headwaters would support the more forest specialist taxa while fragments along the stream would supply allochthonous inputs and mediate temperature fluctuations. The downstream fragments could support high biomass of macroinvertebrates which in turn may support a greater biomass of fish, both native and exotic sports fish.

Scattered fragments would leave reaches of the stream in the open. Open reaches in the streams produced greater densities of flying adults which would provide food for insectivorous birds and other terrestrial fauna. Given the high amount of temporal variation in the flight of New Zealand stream invertebrates (Winterbourn and Crowe 2001), these aquatic terrestrial subsidies could occur year round.

Limiting the distance between fragments would insure high potential rates of migration between metapopulations of forest specialist/preferring taxa within the fragments. It would also limit the time adults would have to spend flying in the open, in potentially too warm and desiccating conditions (Collier and Smith 2000), before re-entering forest and the more moderate conditions within.

References

- Anholt, B. R. 1995. Density dependence resolves the stream drift paradox. *Ecology* **76**:2235-2239.
- Beer-Stiller, A., and P. Zwick. 1995. Biometric studies of some stoneflies and a mayfly (Plecoptera and Ephemeroptera). *Hydrobiologia* **299**:169-178.
- Benstead, J. P., and C. M. Pringle. 2004. Deforestation alters the resource base and biomass of endemic stream insects in eastern Madagascar. *Freshwater Biology* **49**:490-501.
- Benstead, J. P., C. M. Pringle, and M. M. Douglas. 2003. Relationships of stream invertebrate communities to deforestation in eastern Madagascar. *Ecological Applications* **13**:1473-1490.
- Bernath, B., G. Szedenics, G. Molnar, G. Kriska, and G. Horvath. 2001. Visual ecological impact of "Shiny black anthropogenic products" on aquatic insects: Oil reservoirs and plastic sheets as polarized traps for insects associated with water. *Archives of Nature Conservation and Landscape Research* **40**:89-109.
- Bjostad, L. B. 1996. Sex pheromone of caddisfly *Hesperophylax occidentalis* (Banks) (Trichoptera: Limnephilidae). *Journal of Chemical Ecology* **22**:103-121.
- Boothroyd, I. K. G., J. M. Quinn, E. R. Langer, K. J. Costley, and G. Steward. 2004. Riparian buffers mitigate effects of pine plantation logging on New Zealand streams: 1. Riparian vegetation structure, stream geomorphology and periphyton. *Forest Ecology and Management* **194**:199-213.
- Boothroyd, I. K. G., and J. Stark. 2000. Use of invertebrates in monitoring. Pages 344-373 in M. J. Winterbourn and K. J. Collier, editors. *New Zealand Stream invertebrates: Ecology and Implications for Management*. New Zealand Limnological Society.
- Briers, R. A., H. M. Cariss, and J. H. R. Gee. 2003. Flight activity of adult stoneflies in relation to weather. *Ecological Entomology* **28**:31-40.
- Briers, R. A., J. H. R. Gee, H. M. Cariss, and R. Geoghegan. 2004. Inter-population dispersal by adult stoneflies detected by stable isotope enrichment. *Freshwater Biology* **49**:425-431.
- Broadmeadow, S., and T. R. Nisbet. 2004. The effects of riparian forest management on the freshwater environment: A literature review of best management practice. *Hydrology and Earth System Sciences* **8**:286-305.
- Caceres, C. E., and D. A. Soluk. 2002. Blowing in the wind a field test of overland dispersal and colonization by aquatic invertebrates. *Oecologia* **131**:402-408.
- Collier, K. 1993. Review of the status, distribution, and conservation of freshwater invertebrates in New Zealand. *New Zealand Journal of Marine & Freshwater Research* **27**:339-356.
- Collier, K. J. 2004. Invertebrate community dynamics in soft-bottomed streams of northern New Zealand: A spatio-temporal hierarchy. *New Zealand Journal of Marine and Freshwater Research* **38**:1-18.
- Collier, K. J., and B. J. Smith. 2000. Interactions of adult stoneflies (Plecoptera) with riparian zones I. Effects of air temperature and humidity on longevity. *Aquatic Insects* **22**:275-284.

- Cummins, K. W. 1974. Structure and Function of Stream Ecosystems. *Bioscience* **24**:631-641.
- Cummins, K. W., M. J. Klug, R. G. Wetzel, R. C. Petersen, K. F. Suberkropp, B. A. Manny, J. C. Wuycheck, and F. O. Howard. 1972. Organic enrichment with leaf leachate in experimental lotic ecosystems. *Bioscience* **22**:719-722.
- Davies-Colley, R. J., G. W. Payne, and M. v. Elswijk. 2000. Microclimate gradients across a forest edge. *New Zealand Journal of Ecology* **24**(2):111-121.
- Death, R. G., and E. M. Zimmermann. 2005. Interaction between disturbance and primary productivity in determining stream invertebrate diversity. *Oikos* **111**:392-402.
- Didham, R. K., P. M. Hammond, J. H. Lawton, P. Eggleton, and N. E. Stork. 1998. Beetle species responses to tropical forest fragmentation. *Ecological Monographs* **68**:295-323.
- Eikaas, H., J. S. Harding, A. R. McIntosh, and A. D. Kliskey. 2005a. The effect of terrestrial habitat fragmentation on fish populations in small streams: A case study from New Zealand. *Norsk Geografisk Tidsskrift* **59**:269-275.
- Eikaas, H. S., A. R. McIntosh, and A. D. Kliskey. 2005b. Catchment- and site-scale influences of forest cover and longitudinal forest position on the distribution of a diadromous fish. *Freshwater Biology* **50**:527-538.
- Fahrig, L. 2003. Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **34**:487-515.
- Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global Consequences of Land Use. *SCIENCE* **309**:570-574.
- Gatehouse, A. G. 1997. Behaviour and ecological genetics of wind-bourne migration by insects. *Annual review of Entomology* **42**:475-502.
- Giller, P. S. 2005. River restoration: seeking ecological standards. Editor's introduction. *Journal of Applied Ecology* **42**:201-207.
- Gomi, T., R. C. Sidle, and J. S. Richardson. 2002. Understanding processes and downstream linkages of headwater systems. *Bioscience* **52**:905.
- Goodsell, P. J., and S. D. Connell. 2002. Can habitat loss be treated independently of habitat configuration? Implications for rare and common taxa in fragmented landscapes. *Marine Ecology-Progress Series* **239**:37-44.
- Gullan, P. J., and P. S. Cranston. 2000. Sensory systems and behaviour. Pages 83-110 in *The Insects: An Outline of Entomology*. Blackwell Science.
- Hanski, I. 2005. Landscape fragmentation, biodiversity loss and the societal response. The longterm consequences of our use of natural resources may be surprising and unpleasant. *EMBO Reports* **6**:388-392.
- Harding, J. S. 2003. Historic deforestation and the fate of endemic invertebrate species in streams. *New Zealand Journal of Marine and Freshwater Research* **37**:333-345.
- Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones Iii. 1998. Stream biodiversity: The ghost of land use past. *Proceedings of the National Academy of Sciences of the United States of America* **95**:14843-14847.

- Harding, J. S., K. Claassen, and N. Evers. 2006. Can forest fragments reset physical and water quality conditions in agricultural catchments and act as refugia for forest stream invertebrates? *Hydrobiologia** in press.
- Harding, J. S., and M. J. Winterbourn. 1995. Effects of contrasting land use on physico-chemical conditions and benthic assemblages of streams in a Canterbury (South Island, New Zealand) river system. *New Zealand Journal of Marine and Freshwater Research* **29**:479-492.
- Humphries, S., and G. D. Ruxton. 2002. Is there really a drift paradox? *Journal of Animal Ecology* **71**:151-154.
- Jowett, I. G., J. Richardson, B. J. F. Biggs, C. W. Hickey, and J. M. Quinn. 1991. Microhabitat preferences of benthic invertebrates and the development of generalised *Deleatidium* spp. habitat suitability curves, applied to four New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* **25**:187-199.
- Kiffney, P. M., J. S. Richardson, and J. P. Bull. 2003. Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams. *Journal of Applied Ecology* **40**(6):1060-1076.
- Kriska, G., G. Horváth, and S. Andrikovics. 1998. Why do mayflies lay their eggs en masse on dry asphalt roads? Water-imitating polarized light reflected from asphalt attracts ephemeroptera. *Journal of Experimental Biology* **201**:2273-2286.
- Larsson, M. C., and B. S. Hansson. 1998. Receptor neuron responses to potential sex pheromone components in the caddisfly *Rhyacophila nubila* (Trichoptera: Rhyacophilidae). *Journal of Insect Physiology* **44**:189-196.
- Lepori, F., D. Palm, and B. Malmqvist. 2005. Effects of stream restoration on ecosystem functioning: detritus retentiveness and decomposition. *Journal of Applied Ecology* **42**:228-238.
- Malcolm, I. A., C. Soulsby, D. M. Hannah, M. J. Donaghy, and A. F. Youngson. 2004. The influence of riparian woodland on the spatial and temporal variability of stream water temperatures in an upland salmon stream. *Hydrology and Earth System Sciences* **8**:449-459.
- McCune, B., and M. J. Mefford. 1999. Multivariate Analysis of Ecological Data. *in* PC-ORD for Windows. MjM Software, Gleneden Beach, Oregon, USA.
- McGlone, M. S. 1989. The Polynesian settlement of New Zealand in relation to environmental and biotic changes. *The New Zealand Journal of Ecology* **12**:115-130.
- Medina-Vogel, G., V. S. Kaufman, R. Monsalve, and V. Gomez. 2003. The influence of riparian vegetation, woody debris, stream morphology and human activity on the use of rivers by southern river otters in Lontra provocax in Chile. *ORYX* **37**:422-430.
- Meleason, M. A., and J. M. Quinn. 2004. Influence of riparian buffer width on air temperature at Whangapoua Forest, Coromandel Peninsula, New Zealand. *Forest Ecology and Management* **191**:365-371.
- Molán, A., and I. Hanski. 1998. Metapopulation dynamics: Effects of habitat quality and landscape structure. *Ecology* **79**:2503-2515.
- Naiman, R. J., and M. G. Turner. 2000. A future perspective on north America's freshwater ecosystems. *Ecological Applications* **10**:958-970.

- Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial-aquatic linkages: Riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology* **80**:2435-2441.
- Nyström, P., A. R. McIntosh, and M. J. Winterbourn. 2003. Top-down and bottom-up processes in grassland and forested streams. *Oecologia* **136**:596-608.
- Oelbermann, M., and A. M. Gordon. 2000. Quantity and Quality of Autumnal Litterfall into a Rehabilitated Agricultural Stream. *Journal of Environmental Quality* **29**:603-611.
- Perry, C. D., G. Vellidis, D. L. Thomas, and R. Lowrance. 1999. Watershed-scale water quality impacts of riparian forest management. *Journal of Water Resources Planning and Management* **125**:117-125.
- Petersen, I., Z. Masters, A. G. Hildrew, and S. J. Ormerod. 2004. Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology* **41**:934-950.
- Pfankuch, D. J. 1975. Stream Reach Inventory and Channel Stability Evaluation USDA Forest Service Northern region. Missoula, Montana, USA.
- Pichancourt, J. B., F. Burel, and P. Auger. 2006. Assessing the effect of habitat fragmentation on population dynamics: An implicit modelling approach. *Ecological Modelling* **192**:543-556.
- Porteous, T. 1987. The Banks Peninsula landscape. Queen Elizabeth II national trust (NZ), Wellington.
- Quinn, J. M., A. B. Cooper, R. J. Davies-Colley, J. C. Rutherford, and R. B. Williamson. 1997a. Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill-country streams. *New Zealand Journal of Marine and Freshwater Research* **31**:579-597.
- Quinn, J. M., A. B. Cooper, M. J. Stroud, and G. P. Burrell. 1997b. Shade effects on stream periphyton and invertebrates: an experiment in streamside channels. *New Zealand Journal of Marine and Freshwater Research* **31**:665-683.
- Quinn, J. M., and C. W. Hickey. 1990. Characterisation and classification of benthic invertebrate communities in 88 New Zealand rivers in relation to environmental factors. *New Zealand Journal of Marine and Freshwater Research* **24**:387-409.
- Quinn, J. M., G. L. Steele, C. W. Hickey, and M. L. Vickers. 1994. Upper thermal tolerances of twelve New Zealand stream invertebrate species. *New Zealand Journal of Marine and Freshwater Research* **28**:391-397.
- Rutherford, J. C., S. Blackett, C. Blackett, L. Saito, and R. J. Davies-Colley. 1997. Predicting the effects of shade on water temperature in small streams. *New Zealand Journal of Marine and Freshwater Research* **31**:707-721.
- Scarsbrook, M. R., and J. Halliday. 1999. Transition from pasture to native forest land-use along stream continua: effects on stream ecosystems and implications for restoration. *New Zealand Journal of Marine and Freshwater Research* **33**:293-310.
- Shirley, S. M. 2006. Movement of forest birds across river and clearcut edges of varying riparian buffer strip widths. *Forest Ecology and Management* **223**:190-199.
- Sinokrot, B. A., and H. G. Stefan. 1993. Stream temperature dynamics: measurements and modeling. *Water Resources Research* **29**:2299-2312.
- Smith, B. J. 2001. Larval Hydrobiosidae. *in* Biodiversity identification workshop, Christchurch.

- Smith, B. J. 2003a. Quick guide to the common MCI Plecoptera. *in*. NIWA.
- Smith, B. J. 2003b. Quick guide to the MCI cased Tricoptera. *in*. NIWA.
- Smith, B. J. 2003c. Quick guide to the MCI Hydrobiosidae *in*. NIWA.
- Smith, B. J. 2003d. Quick guide to the MCI Leptophlebiidae Ephemoptera. *in*. NIWA.
- Smith, B. J. 2003e. Quick guide to the MCI non-cased Tricoptera (excluding Hydrobiosidae). *in*. NIWA.
- Smith, B. J. 2003f. Quick guide to the MCI non-Chironomidae Diptera. *in*. NIWA.
- Smith, B. J., and K. J. Collier. 2000. Interactions of adult stoneflies (Plecoptera) with riparian zones II. Diet. *Aquatic Insects* **22**:285-296.
- Systat Software. 2004. Sigmastat for Windows *in* Sigmastat Systat Software, Inc.
- Towns, D. R., and W. L. Peters. 1996. Leptophlebiidae (Insecta: Ephemeroptera). Manaaki Whenua Press, Lincoln, Canterbury, N.Z.
- Townsend, C. R., A. G. Hildrew, and J. Francis. 1983. Community structure in some southern English streams: the influence of physicochemical factors. *Freshwater Biology* **13**:521-544.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**:130-137.
- Vuori, K., and I. Joensuu. 1996. Impact of Forest Drainage on the Macroinvertebrates of a Small Boreal Headwater Stream: Do Buffer Zones Protect Lotic Biodiversity? *Biological Conservation* **77**:87-95.
- Wallace, J. B., T. F. Cuffney, S. L. Eggert, and M. R. Whiles. 1997. Stream organic matter inputs, storage and export for Satellite Branch at Coweets Hydrological Laboratory North Carolina ,USA. *Journal of the North American Benthological Society* **16**:67-74.
- Ward, J. B. 2003. New Zealand Trichoptera: Keys to Adults. Canterbury Museum, Christchurch
- Ward, J. B., I. M. Henderson, B. H. Patrick, and P. H. Norrie. 1996. Seasonality, sex ratios and arrival pattern of some New Zealand caddis (Trichoptera) to light-traps. *Aquatic Insects* **18**:157-174.
- Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. *Journal of Geology* **30**:377-392.
- Wilson, H. 2005. Hinewai: Information and Map. Manuka Press, Christchurch.
- Winterbourn, M. J. 1976. Fluxes of litter falling into a small beech forest stream. *New Zealand Journal of Marine and Freshwater Research* **10**(3):399-416.
- Winterbourn, M. J., and A. L. M. Crowe. 2001. Flight activity of insects along a mountain stream: is directional Flight adaptive? *Freshwater Biology* **46**:1479-1489.
- Winterbourn, M. J., K. L. D. Gregson, and C. H. Dolphin. 2000. Guide to the Aquatic Insects of New Zealand 3rd edition. Entomological Society of New Zealand Auckland.
- Winterbourn, M. J., J. S. Rounik, and B. Cowie. 1981. Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine & Freshwater Research* **15**:321-328.

- Wissmar, R. C. 2004. Riparian corridors of Eastern Oregon and Washington: Functions and sustainability along lowland-arid to mountain gradients. *Aquatic Sciences* **66**:373-387.
- Woodward, G., and A. G. Hildrew. 2002. Food web structure in riverine landscapes. *Freshwater Biology* **47**:777-798.
- Young, A., and N. Mitchell. 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. *Biological Conservation* **67**:63-72.
- Zartman, C. E., and A. J. Shaw. 2006. Metapopulation extinction thresholds in rain forest remnants. *American Naturalist* **167**:177-189.

Acknowledgements

I would like to thank all those people who helped me with my fieldwork; Anna Hosking, Jeff Brown, Julia Jenkins, Laura Young, Michelle Greenwood, Duncan Gray, Rebecca Neumegen, Patrick Duncan. Also to the guys who decided to keep me company on a couple of site scouting trips Manu and Nick.

I would like to thank my supervisor Jon Harding and my co-supervisor Raphael Didham for attempting to keep me on track and heading in the right direction.

Special thanks go to Prof. Mike Winterbourn, without his assistance I would probably still be attempting to identify the adult samples.

I would like to thank the many landowners who allowed me access to the streams on their land, with out which I would never have been able to do this study. Special thanks go to Hugh Wilson, Maurice White Native Forest Trust and DoC. Also to Tim Coop for showing interest in the work I was doing.

Thanks to my parents for feeding me whenever I decided to raid their house for food during write up.

I would like to thank my friends for putting up with me. Honourable mention goes to Ben Burrows for late night coffee sessions in the staffroom.

Appendix 1: Species presence absence in fragmented sites

	FL 1	FL 2	FL 3	FP 1	FP 2	FP 3	FK 1	FK 2	FK 3
Ephemeroptera	-	-	-	-	-	-	-	-	-
<i>Austroclima jollyae</i>	0	1	0	1	0	1	0	1	1
<i>Coloburiscus humeralis</i>	1	1	1	1	1	1	1	1	1
<i>Deleatidium</i>	1	1	1	1	1	1	1	1	1
<i>Ichthyotus bicolor</i>	1	0	0	0	0	0	0	0	0
<i>Neozephlebia scita</i>	0	0	0	0	1	1	0	1	1
<i>Nesameletus ornatus</i>	0	0	0	0	0	1	0	0	0
<i>Nesameletus vulcanus</i>	0	1	0	0	0	0	0	0	0
<i>Zephlebia</i>	0	0	0	0	0	0	0	0	0
Plecoptera	-	-	-	-	-	-	-	-	-
<i>Austroperla cyrene</i>	0	1	1	0	1	1	0	0	1
<i>Stenoperla prasina</i>	0	0	0	0	0	0	0	0	0
<i>Zelandobius wardi</i>	0	0	1	0	0	0	0	0	0
<i>Zelandoperla decorata</i>	1	1	1	1	1	1	1	0	0
Trichoptera	-	-	-	-	-	-	-	-	-
<i>Aoteapsyche</i> spp.	1	1	1	1	1	1	1	1	1
<i>Confluens</i>	0	1	0	0	0	0	0	0	0
<i>Costachorema peninsulae</i>	1	1	0	0	1	1	0	0	0
<i>Helicopsyche</i>	1	1	1	1	1	1	0	1	1
<i>Hudsonema alienum</i>	0	0	0	0	0	0	0	0	0
<i>Hudsonema amabile</i>	0	0	0	0	0	0	1	0	0
Hydrobiosidae	0	1	0	1	0	0	0	0	1
<i>Hydrobiosis</i> sp.	1	1	1	0	0	1	1	0	0
<i>Hydrobiosis gollanis</i>	0	0	0	0	0	0	0	0	0
<i>Hydrobiosis parumbripennis</i>	1	0	1	1	1	1	0	0	1
<i>Hydrobiosis soror</i>	0	0	0	1	1	0	0	1	0
<i>Hydrobiosis styx</i>	0	0	1	0	0	0	0	1	0
<i>Hydrobiosella stenocerca</i>	1	0	1	0	1	1	0	1	1
<i>Neurochorema</i> sp.	0	0	1	0	0	0	0	0	0
<i>Oeconesus maori</i>	0	1	0	0	0	1	0	0	0
<i>Olinga</i>	1	1	1	1	1	1	1	1	1
<i>Polypsectropus purelis</i>	0	0	1	0	0	1	0	1	1
<i>Psilochorema bidens</i>	0	0	0	0	0	0	0	1	1
<i>Psilochorema tautoru</i>	0	0	0	1	0	1	1	0	0
<i>Psilochorema</i> spp.	0	1	1	0	1	1	1	1	1
<i>Pycnocentria evecta</i>	1	1	1	1	1	1	1	0	0
<i>Pycnocentria forcipata</i>	0	0	0	0	0	0	0	0	0
<i>Pycnocentria sylvestris</i>	1	0	0	0	0	0	0	0	0
<i>Pycnocentria</i> sp a	0	0	0	0	0	0	0	0	0
<i>Pycnocentrodes</i> sp.	1	0	0	1	1	1	1	1	0
<i>Philorheithrus agilis</i>	0	1	0	1	1	1	1	1	1
<i>Triplectides obsoletus</i>	0	0	0	0	0	1	0	0	0
<i>Zelolessica cheira</i>	0	0	0	0	0	0	0	0	1

Mecoptera	-	-	-	-	-	-	-	-	-
<i>Nannochorista philpotti</i>	0	0	0	0	0	0	0	0	0
Megaloptera	-	-	-	-	-	-	-	-	-
<i>Archichauliodes diversus</i>	1	1	1	1	1	1	1	1	1
Diptera	-	-	-	-	-	-	-	-	-
<i>Aphrophila neozelandica</i>	1	1	0	1	1	1	0	1	0
<i>Austrosimulium</i>	1	1	1	1	1	1	1	0	0
Chironomidae	-	-	-	-	-	-	-	-	-
Chironominae	0	1	0	1	1	0	1	0	0
Diamesea	0	1	1	0	0	0	0	0	0
Orthocladinae	1	1	1	1	1	1	1	1	1
Tanypodinae	1	1	1	1	1	1	0	1	1
Empididae	1	1	0	0	1	1	0	1	0
Eriopterini	0	0	0	0	0	0	0	0	0
Hexatomini	0	0	0	0	0	0	0	0	0
limonia	0	0	1	1	1	0	0	0	1
<i>Neocurupira chiltoni</i>	1	1	0	1	1	1	0	0	0
<i>Nothodixa</i>	1	0	1	0	1	1	0	1	1
<i>Psychodidae</i>	0	0	0	0	0	0	0	0	0
<i>Tanyderidae</i>	1	0	0	0	0	0	0	1	1
<i>Ceratopogonidae</i>	0	0	0	0	0	0	0	0	0
Mollusca	-	-	-	-	-	-	-	-	-
<i>Potamopyrgus antipodarum</i>	1	1	1	1	1	1	1	1	1
<i>Psysa acuta</i>	0	0	0	0	0	0	1	0	0
<i>Sphaerium novaezelandiae</i>	1	0	1	1	0	0	0	0	1
Coleoptera	-	-	-	-	-	-	-	-	-
Elmidae	1	1	0	0	0	1	0	1	1
Hydraenidae	0	1	0	1	1	1	1	1	1
Hydrophilidae	0	0	1	0	0	0	0	0	1
Ptilodactylidae	0	0	0	0	0	0	0	0	0
Scirtidae a	0	1	0	0	0	0	0	0	1
Scirtidae b	0	0	0	0	0	0	0	1	1
Oligochaetae-Oligochaete	0	0	1	1	1	1	1	1	1
Crustacea-Ostracoda	1	0	1	0	0	0	0	0	0
Collembola	1	0	0	0	0	0	0	1	0
Mite-Acari	1	0	0	0	0	0	0	0	0
Nematodes-Flatworm	1	1	1	0	1	0	1	1	1

Appendix 2: Species presence absence in continuous forest sites, benthic samples

	CH 1	CH 2	CH 3	CB 1	CB 2	CB 3	CO 1	CO 2	CO 3
Ephemeroptera	-	-	-	-	-	-	-	-	-
<i>Austroclima jollyae</i>	0	1	1	1	1	1	1	1	1
<i>Coloburiscus humeralis</i>	1	0	1	1	1	1	1	1	1
<i>Deleatidium</i>	1	1	1	1	1	1	1	1	1
<i>Ichthyotus bicolor</i>	0	0	0	0	0	0	0	0	0
<i>Neozephlebia scita</i>	1	0	1	1	1	1	1	1	1
<i>Nesameletus ornatus</i>	0	0	0	0	0	0	0	0	0
<i>Nesameletus vulcanus</i>	0	0	1	1	1	1	0	0	0
<i>Zephlebia</i>	0	0	0	0	0	0	0	1	0
Plecoptera	-	-	-	-	-	-	-	-	-
<i>Austroperla cyrene</i>	0	1	1	0	1	1	1	1	1
<i>Stenoperla prasina</i>	1	0	0	0	1	0	0	0	0
<i>Zelandobius wardi</i>	0	1	1	1	1	1	0	1	0
<i>Zelandoperla decorata</i>	1	0	1	1	1	1	1	1	0
Trichoptera	-	-	-	-	-	-	-	-	-
<i>Aoteapsyche</i> spp.	1	0	1	1	1	1	1	1	1
<i>Confluens</i>	0	0	0	1	1	0	1	1	0
<i>Costachorema peninsulae</i>	1	0	1	1	1	1	1	1	1
<i>Helicopsyche</i>	1	0	0	1	0	0	1	1	1
<i>Hudsonema alienum</i>	0	0	0	0	0	0	0	1	0
<i>Hudsonema amabilis</i>	0	0	0	0	0	0	0	0	0
Hydrobiosidae	1	1	1	0	0	0	0	1	1
<i>Hydrobiosis</i> sp.	0	0	0	0	0	1	1	0	1
<i>Hydrobiosis gollanis</i>	0	0	0	1	0	1	0	1	0
<i>Hydrobiosis parumbripennis</i>	0	0	1	0	0	1	1	0	1
<i>Hydrobiosis soror</i>	0	0	0	0	0	1	1	0	0
<i>Hydrobiosis styx</i>	0	0	1	1	1	0	0	1	0
<i>Hydrobiosella stenocerca</i>	1	0	0	1	1	0	0	0	1
<i>Neurochorema</i> sp.	0	0	0	0	0	0	0	0	0
<i>Oeconesus maori</i>	1	1	1	0	0	0	1	0	1
<i>Olinga</i>	1	0	0	1	1	1	1	1	1
<i>Polypsectropus purelis</i>	0	0	0	1	1	1	0	1	1
<i>Psilochorema bidens</i>	0	0	1	0	0	0	0	0	0
<i>Psilochorema tautoru</i>	0	0	0	0	0	0	0	0	0
<i>Psilochorema</i> spp.	0	1	1	1	1	1	1	1	1
<i>Pycnocentria evecta</i>	1	0	0	1	0	1	1	1	1
<i>Pycnocentria forcipata</i>	0	0	1	0	0	0	0	0	0
<i>Pycnocentria sylvestris</i>	0	0	0	1	0	1	0	1	1
<i>Pycnocentria</i> sp a	0	0	1	0	0	0	0	0	0
<i>Pycnocentroides</i> sp.	1	1	1	1	0	0	1	1	0
<i>Philorheithrus agilis</i>	1	0	1	1	1	1	1	1	1
<i>Triplectides obsoletus</i>	0	1	1	1	1	1	0	1	1
<i>Zelolessica cheira</i>	0	0	0	0	1	1	0	0	0

Mecoptera	-	-	-	-	-	-	-	-	-
<i>Nannochorista philpotti</i>	0	1	1	0	0	1	0	1	1
Megaloptera	-	-	-	-	-	-	-	-	-
<i>Archichauliodes diversus</i>	1	0	0	1	1	1	1	1	1
Diptera	-	-	-	-	-	-	-	-	-
<i>Aphrophila neozelandica</i>	1	1	0	0	0	1	1	1	1
<i>Austrosimulium</i>	1	1	0	1	1	1	1	0	0
Chironomidae	-	-	-	-	-	-	-	-	-
Chironominae	0	0	0	1	1	1	0	0	0
Diamesea	0	0	0	1	1	0	0	0	0
Orthocladinae	1	1	1	1	1	1	1	1	1
Tanypodinae	1	1	0	1	1	1	1	1	1
Empididae	1	1	0	0	1	1	1	1	1
Eriopterini	0	0	0	1	0	0	0	0	0
Hexatomini	0	0	0	0	0	0	0	1	0
limonia	0	0	0	0	0	0	0	0	1
<i>Neocurupira chiltoni</i>	1	0	1	1	1	1	1	1	0
<i>Nothodixa</i>	1	1	1	1	1	0	0	0	1
<i>Psychodidae</i>	0	0	0	1	0	0	0	0	0
<i>Tanyderidae</i>	0	0	0	0	0	0	0	1	1
<i>Ceratopogonidae</i>	0	0	0	1	0	0	0	0	0
Mollusca	-	-	-	-	-	-	-	-	-
<i>Potamopyrgus antipodarum</i>	1	1	1	1	1	1	1	1	1
<i>Psysa acuta</i>	0	0	0	0	0	0	0	0	0
<i>Sphaerium novaezealandiae</i>	1	0	0	0	1	0	0	1	1
Coleoptera	-	-	-	-	-	-	-	-	-
Elmidae	1	1	0	1	1	0	0	0	0
Hydraenidae	1	0	1	1	1	1	1	1	1
Hydrophilidae	0	0	0	0	0	0	0	0	0
Ptilodactylidae	0	0	1	0	0	0	0	0	0
Scirtidae a	0	1	1	1	0	0	0	0	1
Scirtidae b	0	0	0	0	0	0	0	0	0
Oligochaetae-Oligochaete	1	1	1	1	1	1	1	1	1
Crustacea-Ostracoda	0	0	1	1	0	0	0	1	0
Collembola	0	1	1	0	1	0	0	1	0
Mite-Acari	0	1	1	1	0	1	0	1	1
Nematodes-Flatworm	0	1	1	1	1	0	1	1	1

Appendix 3: Abundance in fragmented forest sites, benthic samples number of inds/m²

	FL 1	FL 2	FL 3	FP 1	FP 2	FP 3	FK 1	FK 2	FK 3
<i>Austroclima jollyae</i>	0	53	0	869	0	5	0	43	48
<i>Coloburiscus humeralis</i>	357	347	48	581	1264	1061	5	384	592
<i>Deleatidium</i>	875	1408	1877	144	469	1029	1253	2021	1643
<i>Ichthybotus bicolor</i>	5	0	0	0	0	0	0	0	0
<i>Neozephlebia scita</i>	0	0	0	0	16	53	0	373	1152
<i>Nesameletus ornatus</i>	0	0	0	0	0	32	0	0	0
<i>Nesameletus vulcanus</i>	0	5	0	0	0	0	0	0	0
<i>Zephlebia</i>	0	0	0	0	0	0	0	0	0
<i>Austroperla cyrene</i>	0	5	11	0	11	0	0	0	5
<i>Stenoperla prasina</i>	0	0	0	0	0	0	0	0	0
<i>Zelandobius wardi</i>	0	0	0	0	0	0	0	0	0
<i>Zelandoperla decorata</i>	69	69	5	5	21	59	11	0	0
<i>Aoteapsyche</i> spp.	843	256	469	2379	1083	1744	32	843	85
<i>Confluens</i>	0	0	0	0	0	0	0	0	0
<i>Costachorema peninsulae</i>	11	0	0	0	16	0	0	0	0
<i>Helicopsyche</i>	368	325	213	5	11	213	0	43	59
<i>Hudsonema alienum</i>	0	0	0	0	0	0	0	0	0
<i>Hudsonema amabile</i>	0	0	0	0	0	0	16	0	0
Hydrobiosidae	0	0	0	0	0	0	0	0	5
<i>Hydrobiosis</i> sp.	21	48	69	0	0	5	32	0	0
<i>Hydrobiosis gollanis</i>	0	0	0	0	0	0	0	0	0
<i>Hydrobiosis soror</i>	0	0	0	21	5	0	0	16	0
<i>Hydrobiosis styx</i>	0	0	5	0	0	0	0	11	0
<i>Hydrobiosis parumbripennis</i>	11	0	32	101	64	37	0	0	5
<i>Hydrobiosella stenocerca</i>	5	0	192	0	5	5	0	117	219
<i>Neurochorema</i> sp.	0	0	5	0	0	0	0	0	0
<i>Oeconesus maori</i>	0	5	0	0	0	5	0	0	0
<i>Olinga</i>	512	1083	224	3600	251	1285	85	736	304
<i>Polyplectropus purelis</i>	0	0	27	0	0	11	0	5	11
<i>Psilochorema bidens</i>	0	0	0	0	0	0	0	5	5
<i>Psilochorema tautoru</i>	0	0	0	11	0	53	11	0	0
<i>Psilochorema</i> spp.	0	0	11	0	0	0	5	27	21
<i>Pycnocentria evecta</i>	384	555	37	7941	37	400	11563	0	0
<i>Pycnocentria forcipata</i>	0	0	0	0	0	0	0	0	0
<i>Pycnocentria sylvestris</i>	32	0	0	0	0	0	0	0	0
<i>Pycnocentria</i> sp a	0	0	0	0	0	0	0	0	0
<i>Pycnocentrodes</i> sp.	5	0	0	11	11	315	485	0	0
<i>Philorhethrus agilis</i>	0	37	0	16	64	43	21	27	5
<i>Triplectides obsoletus</i>	0	0	0	0	0	5	0	0	0
<i>Zelolessica cheira</i>	0	0	0	0	0	0	0	0	0
<i>Nannochorista philpotti</i>	0	0	0	0	0	0	0	0	0
<i>Archichauliodes diversus</i>	256	107	5	48	32	112	0	80	128
<i>Aphrophila neozelandica</i>	32	16	0	27	16	5	0	16	0

<i>Austrosimulium</i>	165	139	144	181	27	16	160	0	0
Chironominae	0	21	0	37	5	0	16	0	0
Diamesea	0	11	27	0	0	0	0	0	0
Orthocladinae	139	128	32	1104	475	69	11	251	347
Tanypodinae	21	27	21	11	11	53	0	128	27
Empididae	11	11	0	0	27	5	0	11	0
Eriopterini	0	0	0	0	0	0	0	0	0
Hexatomini	0	0	0	0	0	0	0	0	0
Limonia	0	0	5	5	0	0	0	0	5
<i>Neocurupira chiltoni</i>	235	165	0	21	16	11	0	0	0
<i>Nothodixa</i>	0	0	5	0	5	0	0	16	21
<i>Psychodidae</i>	0	0	0	0	0	0	0	0	0
<i>Tanyderidae</i>	5	0	0	0	0	0	0	11	5
<i>Ceratopogonidae</i>	0	0	0	0	0	0	0	0	0
<i>Potamopyrgus antipodarum</i>	704	1115	1173	773	80	155	1696	149	27
<i>Psysa acuta</i>	0	0	0	0	0	0	32	0	0
<i>Sphaerium novaezealandiae</i>	5	0	32	11	0	0	0	0	5
Elmidae	69	59	0	0	0	43	0	5	0
Hydraenidae	0	48	0	21	48	117	0	187	251
Hydrophilidae	0	0	0	0	0	0	0	0	5
Ptilodactylidae	0	0	0	0	0	0	0	0	0
Scirtidae a	0	21	0	0	0	0	0	0	48
Scirtidae b	0	0	0	0	0	0	0	16	32
Oligochaetae-Oligochaete	0	0	5	5	27	37	21	5	27
Crustacea-Ostracoda	0	0	5	0	0	0	0	0	0
Collembola	5	0	0	0	0	0	0	5	0
Mite-Acari	5	0	0	0	0	0	0	0	0
Nematodes-Flatworm	53	245	107	0	0	0	0	85	320

Appendix 4: Abundance in continuous forest sites, benthic samples number of inds/m²

	CH 1	CH 2	CH 3	CB 1	CB 2	CB 3	CO 1	CO 2	CO 3
<i>Austroclima jollyae</i>	0	11	464	80	69	69	48	667	251
<i>Coloburiscus humeralis</i>	219	0	53	603	992	784	1019	3797	2213
<i>Deleatidium</i>	576	347	144	539	571	923	1109	1147	1264
<i>Ichthybotus bicolor</i>	0	0	0	0	0	0	0	0	0
<i>Neozephlebia scita</i>	112	0	347	91	171	48	101	523	699
<i>Nesameletus ornatus</i>	0	0	0	0	0	0	0	0	0
<i>Nesameletus vulcanus</i>	0	0	37	85	53	203	0	0	0
<i>Zephlebia</i>	0	0	0	0	0	0	0	27	0
<i>Austroperla cyrene</i>	0	0	208	0	101	0	0	11	16
<i>Stenoperla prasina</i>	5	0	0	0	16	0	0	5	0
<i>Zelandobius wardi</i>	0	176	69	27	69	53	0	0	0
<i>Zelandoperla decorata</i>	139	0	37	91	27	37	53	16	0
<i>Aoteapsyche</i> spp.	53	0	11	373	373	709	379	816	779
<i>Confluens</i>	0	0	0	11	11	0	21	75	11
<i>Costachorema peninsulae</i>	0	0	5	16	48	16	11	21	0
<i>Helicopsyche</i>	848	0	0	112	0	0	80	27	32
<i>Hudsonema alienum</i>	0	0	0	0	0	0	0	5	0
<i>Hudsonema amabile</i>	0	0	0	0	0	0	0	0	0
Hydrobiosidae	0	5	21	0	0	0	0	5	16
<i>Hydrobiosis</i> sp.	0	0	0	0	0	5	5	0	0
<i>Hydrobiosis gollanis</i>	0	0	0	5	0	16	0	11	0
<i>Hydrobiosis soror</i>	5	0	0	0	0	11	5	0	0
<i>Hydrobiosis styx</i>	0	0	5	0	16	0	0	0	0
<i>Hydrobiosis parumbripennis</i>	0	0	5	0	0	0	5	0	11
<i>Hydrobiosella stenocerca</i>	0	0	0	48	69	0	0	0	5
<i>Neurochorema</i> sp.	0	0	0	0	0	0	0	0	0
<i>Oeconesus maori</i>	11	75	11	0	0	0	0	0	16
<i>Olinga</i>	1077	0	0	1701	315	219	1024	1611	485
<i>Polypsectropus purelis</i>	0	0	0	5	16	16	0	16	5
<i>Psilochorema bidens</i>	0	0	5	0	0	0	0	0	0
<i>Psilochorema tautoru</i>	0	0	0	0	0	0	0	0	0
<i>Psilochorema</i> spp.	0	32	21	11	11	11	11	21	27
<i>Pycnocentria evecta</i>	549	0	0	85	0	139	27	11	0
<i>Pycnocentria forcipata</i>	0	0	5	0	0	0	0	0	0
<i>Pycnocentria sylvestris</i>	0	0	0	32	0	5	0	64	5
<i>Pycnocentria</i> sp a	0	0	5	0	0	0	0	0	0
<i>Pycnocentrodes</i> sp.	197	5	5	64	0	0	5	5	5
<i>Philorhethrus agilis</i>	165	0	37	53	53	123	43	336	395
<i>Tripletides obsoletus</i>	0	0	5	5	21	0	0	0	0
<i>Zelolessica cheira</i>	0	0	0	0	43	16	0	0	0
<i>Nannochorista philpotti</i>	0	11	32	0	0	5	0	27	21
<i>Archichauliodes diversus</i>	155	0	0	192	16	16	128	267	229
<i>Aphrophila neozelandica</i>	37	5	0	0	0	11	21	107	69

<i>Austrosimulium</i>	0	725	0	16	16	5	5	0	0
Chironominae	0	0	0	11	75	155	0	0	0
Diamesea	0	0	0	5	11	0	0	0	0
Orthocladinae	69	224	235	155	672	123	64	171	245
Tanypodinae	64	5	0	16	11	5	32	139	59
Empididae	5	0	0	0	48	5	5	27	43
Eriopterini	0	0	0	5	0	0	0	0	0
Hexatomini	0	0	0	0	0	0	0	5	0
Limonia	0	0	0	0	0	0	0	0	5
<i>Neocurupira chiltoni</i>	139	0	0	37	0	5	5	5	0
<i>Nothodixa</i>	5	27	27	0	16	0	0	0	0
<i>Psychodidae</i>	0	0	0	5	0	0	0	0	0
<i>Tanyderidae</i>	0	0	0	0	0	0	0	16	11
<i>Ceratopogonidae</i>	0	0	0	5	0	0	0	0	0
<i>Potamopyrgus antipodarum</i>	160	357	139	37	5	101	32	32	645
<i>Psysa acuta</i>	0	0	0	0	0	0	0	0	0
<i>Sphaerium novaezealandiae</i>	5	0	0	0	5	0	0	149	43
Elmidae	176	5	0	192	5	0	0	0	0
Hydraenidae	272	0	128	485	117	117	309	709	331
Hydrophilidae	0	0	0	0	0	0	0	0	0
Ptilodactylidae	0	0	5	0	0	0	0	0	0
Scirtidae a	0	0	21	5	0	0	0	0	5
Scirtidae b	0	0	0	0	0	0	0	0	0
Oligochaetae-Oligochaete	21	5	27	5	21	0	53	133	32
Crustacea-Ostracoda	0	0	16	11	0	0	0	48	0
Collembola	0	21	32	0	16	0	0	11	0
Mite-Acari	0	5	5	11	0	5	0	5	5
Nematodes-Flatworm	0	48	139	11	27	0	59	437	192

Appendix 5: Species presence absence in Malaise traps

	FP1	FK1	FL1	CO1	CH1	CB1
Ephemeroptera	-	-	-	-	-	-
<i>Austroclima jollyae</i>	0	0	1	1	1	1
<i>Coloburiscus humeralis</i>	1	0	1	1	1	1
<i>Deleatidium</i>	1	1	1	1	1	1
<i>Ichthybotus bicolor</i>	0	0	1	0	0	0
<i>Neozephlebia scita</i>	1	0	1	1	1	1
<i>Nesameletus sp.</i>	0	0	1	0	1	1
<i>Zephlebia</i>	0	0	0	0	0	0
Plecoptera	-	-	-	-	-	-
<i>Acroperla triviculata</i>	0	0	1	1	1	1
<i>Austroperla cyrene</i>	0	0	0	0	0	0
<i>Stenoperla prasina</i>	0	0	1	0	0	1
<i>Zelandobius wardi</i>	0	0	0	1	0	0
<i>Zelandoperla decorata</i>	0	1	1	1	1	0
Trichoptera	-	-	-	-	-	-
Conoesucidae	-	-	-	-	-	-
<i>Confluens</i>	0	0	0	0	1	0
<i>Olinga</i>	1	1	1	1	1	1
<i>Pycnocentria sp.</i>	1	1	1	0	0	1
<i>Pycnocentrodes sp.</i>	1	1	1	0	0	0
Helicophidae	-	-	-	-	-	-
<i>Zelolessica cheira</i>	0	0	0	0	0	0
Helicopsychidae	0	0	0	0	0	0
<i>Helicopsyche</i>	0	0	1	1	1	1
Hydrobiosidae	1	1	1	1	1	1
Hydropsychidae	-	-	-	-	-	-
<i>Aoteapsyche</i>	1	1	1	1	1	1
Hydroptilidae	0	1	0	0	0	0
Leptoceridae	-	-	-	-	-	-
<i>Hudsonema</i>	0	1	1	0	0	1
<i>Triplectides obsoletus</i>	0	1	1	0	0	1
Oeconesidae	-	-	-	-	-	-
<i>Oeconesus maori</i>	0	0	1	1	1	1
Philopotamidae	0	0	0	0	0	0
<i>Hydrobiosella stenocerca</i>	0	0	0	1	0	1
Philorheithridae	-	-	-	-	-	-
<i>Philorheithrus agilis</i>	1	0	1	1	1	0
Polycentropodidae	-	-	-	-	-	-
<i>Polypsectropus purelis</i>	0	1	0	0	0	0