Aquatic invertebrate communities of lowland wetlands in New Zealand

Characterising spatial, temporal and geographic distribution patterns

SCIENCE FOR CONSERVATION 305

Department of Conservation
Te Papa Atawhai

This page has been intentionally left blank

Aquatic invertebrate communities of lowland wetlands in New Zealand

Characterising spatial, temporal and geographic distribution patterns

Alastair Suren and Brian Sorrell

SCIENCE FOR CONSERVATION 305

Published by
Publishing Team
Department of Conservation
PO Box 10420, The Terrace
Wellington 6143, New Zealand

Cover: Open water leads at Drummond Wetland, Southland.
Photo: Alastair Suren.

Science for Conservation is a scientific monograph series presenting research funded by New Zealand Department of Conservation (DOC). Manuscripts are internally and externally peer-reviewed; resulting publications are considered part of the formal international scientific literature.
The report is available from the departmental website in pdf form. Titles are listed in our catalogue on the website, refer www.doc.govt.nz under *Publications*, then *Science & technical*.

ISSN 1177-9241 (PDF)
ISBN 978-0-478-14811-4 (PDF)

This report was prepared for publication by the Publishing Team; editing by Amanda Todd and layout by Lynette Clelland. Publication was approved by the General Manager, Research and Development Group, Department of Conservation, Wellington, New Zealand.

CONTENTS

Aquatic invertebrate communities of lowland wetlands in New Zealand

Characterising spatial, temporal and geographic distribution patterns

Alastair Suren and Brian Sorrell

NIWA Christchurch, PO Box 8602, Riccarton, Christchurch 8440, New Zealand
Email: a.suren@niwa.co.nz

A B S T R A C T

This report documents the aquatic invertebrate communities of lowland wetlands throughout New Zealand. It addresses three questions: how do communities vary within and between wetlands; to what extent do communities vary temporally; and how are communities affected by environmental variables? Invertebrate collections from 40 wetlands showed that the fauna was dominated by midges (Chironomidae), aquatic mites (Acarina), Copepoda, Nematoda and Ostracoda. The mud snail *Potamopyrgus antipodarum* and the damselfly *Xanthocnemis zealandica* were also common. A detailed survey of the open-water habitats of two acidic fens and two swamps showed that invertebrate communities varied more between wetlands than they did within wetlands, presumably reflecting differences in water chemistry between fens and swamps. Thus, it may not be necessary to sample specific habitats or plants within wetlands to accurately characterise their invertebrate communities, as long as the range of habitat types is covered. Similarly, analysis of annual data collected at one wetland and of seasonal data collected at two wetlands showed that although invertebrate communities varied temporally, the degree of this variation was small compared with differences within or between wetlands. Thus, wetland invertebrate surveys may not be particularly sensitive to the time of sampling, as community composition is driven by large-scale factors that influence water chemistry and that override temporal changes in the relative abundance of some taxa. Finally, a survey of 40 wetlands throughout the country showed that invertebrate communities are controlled mainly by biogeography, followed by water chemistry—particularly pH. This finding has management implications, as regionally based conservation goals may need to be considered instead of setting goals for specific wetland types.

Keywords: wetlands, invertebrates, swamps, fens, bogs, temporal variation, spatial variation, sampling protocols

Suren, A.; Sorrell, B. 2010: Aquatic invertebrate communities of lowland wetlands in New Zealand: characterising spatial, temporal and geographic distribution patterns. *Science for Conservation 305*. Department of Conservation, Wellington. 64 p.

1. Introduction

High biodiversity value is frequently cited as an important justification for wetland conservation (Mitsch & Gosselink 2000; Junk et al. 2006). Many wetlands are 'ecotones'—transitional habitats between terrestrial and aquatic ecosystems, which have high biological diversity as a result of their diverse mixture of habitats derived from both ecosystems (Decamps & Naiman 1990; Tiner 1999). The blending of deep and shallow aquatic environments within wetlands offers potential habitat for both terrestrial and aquatic flora and fauna. Wetlands with the highest conservation values are often recognised to be those where a range of water regimes and fertilities maximise species diversity (Keddy 2000; Junk et al. 2006). Accurate determination and protection of the biodiversity value of wetlands therefore requires information about aquatic as well as terrestrial biota, including their biogeographic variation and habitat requirements.

Much of the biodiversity value of New Zealand wetlands is poorly understood. Although the vascular plant flora has been described in some detail (Johnson & Brooke 1998; Johnson & Gerbeaux 2004), there is still very little understanding of the physical and chemical drivers of plant species composition. The importance of wetlands for fish and bird habitat is well-documented (Sorrell & Gerbeaux 2004; Williams 2004), but the factors controlling fish and bird productivity in New Zealand wetlands are uncertain, as are the distributions of these organisms throughout the country. Other groups of organisms, such as aquatic invertebrates and algae, have received relatively little attention.

Recent assessments have confirmed that approximately 90% of the original wetland cover of New Zealand has been lost (Ausseil et al. 2008). Furthermore, there has been a disproportionate loss of wetlands of certain types and in certain areas, with particularly heavy losses of lowland systems, and higher losses in eastern and northern regions of the country. In pre-European times (prior to the early 1800s), wetland cover included a diverse range of wetland types, almost all of which offered some open-water habitat (Johnson & Gerbeaux 2004). Given the ongoing pressure on wetlands and their continued loss, coupled with potential nutrient enrichment arising from catchment land-use (Clarkson et al. 2003), assessments of the aquatic habitats and invertebrate communities within New Zealand wetlands are long overdue.

Aquatic invertebrates are found in all freshwater ecosystems, including rivers, lakes and wetlands. They live on or in the bottom substrate, swim in the water column, or live on the surface of the water. There are four major groups of freshwater invertebrates:

- Arthropods, including insects (e.g. mayflies (Ephemeroptera), caddisflies (Trichoptera), stoneflies (Plecoptera), dragonflies (Odonata), and true flies (Diptera), including chironomid midges and blackflies), crustacea (such as freshwater shrimp (e.g. *Paratya*) and amphipods (e.g. *Paraleptamphopus*), as well as zooplankton such as Cladocera (*Daphnia*), ostracods and copepods), and aquatic mites (Acarina).

- Molluscs, such as snails (especially *Potamopyrgus*) and filter-feeding bivalves (e.g. fingernail clams (*Sphaerium* and *Pisidium*) and freshwater mussels (e.g. *Hyridella menziesi* (kākahi), *Cucumerunio websteri*).
- Oligochaetes, typified by a number of different worm species that live in muddy streambeds.
- Nematodes, which are very small, cylindrical, 'worm-like' animals with smooth cuticles.

For convenience, freshwater ecologists have arbitrarily divided aquatic invertebrates into two groups: macroinvertebrates, which are those that are large enough to be retained by a sieve with a mesh size of 500 μm, and meiofauna, which are those that pass through a 500-μm sieve but are retained on a 64-μm sieve (Robertson et al. 2000). This latter group includes recently hatched insect larvae, microcrustacea (such as copepods, ostracods (pea shrimp) and daphnia (water fleas)), as well as animals such as nematodes.

Freshwater invertebrates play a vital role in transferring plant-based organic carbon derived from terrestrial sources (e.g. leaves or woody debris) or aquatic sources (e.g. algae or macrophytes) into animal-based organic carbon, which is then available to predators such as fish and birds. Freshwater invertebrates also have intrinsic biodiversity and ecological values: almost all are native to New Zealand, and many are endemic (i.e. they are not found anywhere else in the world).

1.1 OBJECTIVES

This report describes the first stage of a research programme that aims to document the aquatic invertebrate biodiversity values of lowland wetlands in New Zealand and to present information on variation in community composition in near-pristine wetlands. We selected wetlands mostly with minimal human impacts, with one exception: the Bullock Creek wetland, on the South Island's West Coast. Parts of this wetland had been converted into pasture by 19th-century settlers, with a network of drains dug during the first half of the 20th century. However, grazing had ceased in this wetland approximately 20 years ago, and the site is being managed to restore it to a more natural state (Sorrell et al. 2007). This wetland is also surrounded by undisturbed native bush, so pressures from the surrounding catchment are minimal. This site was part of a restoration programme run collaboratively by the Department of Conservation (DOC), Landcare Research and the National Institute of Water & Atmospheric Research (NIWA), and regular monitoring of the invertebrate communities in this wetland to assess the effect of hydraulic restoration allowed us to examine temporal variability of the invertebrate communities there (see section 3). Selection of mostly unimpacted wetlands was necessary to first obtain knowledge of invertebrate biodiversity, and the factors influencing invertebrate distributions in the absence of anthropogenic disturbances. Identification of the underlying drivers of invertebrate community composition allows evaluation of potential effects of human activities that might influence these drivers.

The aims of the present project were to document:

- The nature of the invertebrate community within wetlands
- The degree of variation in aquatic invertebrate community composition within wetlands versus variation between wetlands
- The amount of temporal variability in wetland aquatic invertebrate communities
- Patterns of natural biogeographic variation in invertebrate species composition across New Zealand, and identification of factors controlling invertebrate species composition in wetlands

The study has the following management goals:

1. The findings will help identify any rare taxa or taxonomic groups, and help us begin to understand more about the spatial distribution of freshwater invertebrates. All data obtained from the wetland work to date will be placed on NIWA's Freshwater Biodata Information System (FBIS: (https://secure.niwa.co.nz/fbis/index.do) as part of what is hoped will become a central repository of wetland invertebrate data.
2. Examination and description of the invertebrate communities of wetlands throughout the country will allow us to identify any regions of particularly high invertebrate biodiversity. Such information will enable DOC and other land managers (such as regional or district councils) to prioritise conservation efforts for different wetlands based on their aquatic biodiversity values. Furthermore, the Dairying & Clean Stream Accord (2003) requires regionally significant wetlands to be defined, in order for farmers to take subsequent action to protect them.
3. Characterisation of the invertebrate communities within wetlands will also provide us with an opportunity to compare the biodiversity of this habitat with that of rivers and lakes. Within New Zealand, most attention to freshwater biodiversity has traditionally been focused on invertebrate communities in running waters or lakes; yet wetlands may support equally high or higher biodiversity, as has been found in Europe (Davies et al. 2008).
4. By understanding how invertebrate communities are controlled by environmental variables in pristine wetlands, and by seeing how these variables are altered by land-use changes, it may be possible to predict the effect of wetland degradation on invertebrate biodiversity. This information has obvious relevance if the adverse impacts of land-use change, nutrient run-off, and changes to hydrological regimes in wetlands are to be minimised. Minimising adverse effects of land-use changes on wetlands is important, not only to ensure maintenance of invertebrate biodiversity in wetlands, but also to ensure that other components of these ecosystems (e.g. fish and wading birds) are unaffected by loss of potential food sources caused by unsustainable land-use activities.
5. The information obtained from studying the aquatic invertebrate communities in pristine wetlands will be a fundamental part of creating a Wetland Macroinvertebrate Community Index score (WMCI score). The WMCI score will be similar to the commonly used MCI score (Stark 1985), which was developed to assess organic pollution in stony-bottomed streams or, more recently, in soft-bottomed streams (Stark & Maxted 2007). It is possible that

separate WMCI scores will need to be developed for swamps and bogs/fens, or for different regions of the country. This score will allow managers to assess the ecological health of particular wetlands based on their invertebrate communities. Its foundation lies in quantifying how invertebrate communities change between pristine wetlands, and wetlands that are subject to increasing degrees of anthropogenic disturbance, and assigning tolerance scores to each taxa depending on their response to distrubance. This latter goal is currently being undertaken as part of a DOC-funded Terrestrial and Freshwater Biodata Information System (TFBIS) programme.

6. A better understanding of aquatic invertebrate biodiversity values of wetlands is considered a requisite step for the completion of the Waters of National Importance (WONI) project, the objective of which is to identify water bodies that require protection to ensure that a full range of freshwater biodiversity is protected throughout the country.

2. General concepts and methodologies

2.1 WETLAND CLASSIFICATION

Wetlands exist in areas of poor drainage where water can accumulate. They can be permanently to intermittently wet, generally have shallow water, and have land margins that support ecosystems of plants and animals that are adapted to wet conditions (Johnson & Gerbeaux 2004). Johnson & Gerbeaux (2004) grouped wetlands using a semi-hierarchical system with four levels:

1. Level 1 is based on differences in hydrosystems (i.e. the broad hydrological and landform setting, and salinity and temperature regimes)
2. Level 2 is based on wetland classes, circumscribed by different combinations of substrate, water regime, nutrients and pH
3. Level 3 deals with structural classes of the vegetation (e.g. forest, rush land, herbfield) or ground surface (rockfield or mudflat)
4. Level 4 deals with species composition of the vegetation

Levels 1 & 2 are mainly concerned with large-scale differences in hydrology and water chemistry between wetlands, while Levels 3 & 4 deal with smaller-scale differences within a wetland that describe the ground surface and vegetation.

There are three main freshwater hydrosystems within New Zealand: Palustrine (swamp, marsh), Riverine, and Lacustrine (lake) (Johnson & Gerbeaux 2004). Although other minor freshwater hydrosystems exist that are of local or restricted significance (e.g. geothermal and nival/ice-sourced), these were not included in the present study, which focused on palustrine wetlands in lowland areas (less than 250 m a.s.l.). Palustrine wetlands are characterised by shallow aquatic environments in which the dominant feature is attached or rooted vegetation, which is emergent permanently or seasonally above freshwater, non-tidal surface water or groundwater (Johnson & Gerbeaux 2004).

New Zealand's wetland classification scheme (Johnson & Gerbeaux 2004) recognises at least nine classes of palustrine wetlands, of which four (bogs, fens, swamps and marshes) are covered in this study. These classes cover most of the palustrine wetlands of New Zealand. Ephemeral wetlands, seepages, pakihi and gumland, and saltmarsh areas were not considered. The four classes being considered broadly follow a hydrological gradient from the dominant water source being precipitation (bogs), to inputs being dominated by surface flow (marshes). Associated with the hydrological gradient are gradients in soil type (from more peaty, organic soils in bogs through to predominantly mineral soils in marshes), chemistry (from low pH in bogs to high pH in swamps and marshes), and fertility (generally increasing from bogs through to swamps). For a complete assessment of wetland invertebrate communities, future sampling > 250 m above sea level, and from the full range of wetland classes is required.

When documenting the invertebrate biodiversity values of pristine wetlands in New Zealand, it is important to note the uneven loss of different wetland classes since European colonisation. Ausseil et al. (2008) documented that swamps and marshes have been most heavily reduced (with 6% and 8% of original cover remaining, respectively, compared with 26% and 19% remaining for bogs and fens, respectively).

2.2 ANTHROPOGENIC EFFECTS ON WETLANDS

Wetlands are faced with a multitude of different pressures from human activities, including alterations of nutrient budgets and hydrological regimes, sedimentation, fire, vegetation clearance, soil disturbance, and biotic invasions from both terrestrial and aquatic organisms (e.g. exotic fish, weedy plant species, stock grazing, and both vertebrate and invertebrate pest species). Some of these pressures may affect only a small portion of a wetland, while others may affect the entire wetland. The threat from biotic invasions by exotic organisms is of particular concern, as this can occur even in wetlands surrounded by unmodified catchments. These pressures may lead to a loss of wetland biodiversity, structure and function. Taken to the extreme, such activities can result in an entire wetland being lost from the landscape. Less extreme results are seen in remnant wetland areas, which can range from simple drainage ditches across what were once waterlogged soils, to small areas of isolated ponds surrounded by highly modified agricultural or urban landscapes. At the other end of the scale, some wetlands still remain in highly unmodified landscapes, where they most likely exist and function as they always have.

In New Zealand, two methods have been developed to assess the degree of human disturbance (and associated pressures) on wetlands (Table 1). The first method (Clarkson et al. 2003) calculates a wetland condition index (WCI), based on changes to five specific indicators, each of which contains a number of indicator components. This method was developed for use in the field by non-experts with a relatively limited amount of training. The second method (Ausseil et al. 2008) calculates a wetland's 'index of ecological integrity' (IEI). This combines six spatial indicators of human activities that degrade wetland biodiversity and function: loss of natural cover; human-made impervious cover; introduced fish; introduced woody weeds; artificial drainage; and nitrate leaching risk. Values of these indicators are derived from a number of GIS databases, allowing national assessments of wetland condition to be made.

TABLE 1. SPECIFIC INDICATORS AND INDICATOR COMPONENTS USED TO ASSESS WETLAND CONDITION (CLARKSON ET AL. 2003), OR ECOLOGICAL INTEGRITY (AUSSIEL ET AL. 2008).

INDEX	INDICATOR	COMPONENTS
Wetland condition	Change in hydrological integrity	• Impact of man-made structures • Water table depth • Dryland plant invasion
	Change in physicochemical parameters	• Fire damage • Degree of sedimentation/erosion • Nutrient levels • Von Post index
	Change in ecosystem intactness	• Loss in area of original wetland • Conductivity barriers
	Change in browsing, predation and harvesting regimes	• Damaged by domestic or feral animals • Introduced predator impacts on wildlife • Harvesting levels
	Change in dominance of native plants	• Introduced plant canopy cover • Introduced plant cover
Ecological integrity	Naturalness of catchment cover Artificial impervious cover (urbanisation, roading) Nutrient enrichment Introduced fish Woody weeds Drainage and disturbance	

This study endeavoured to sample wetlands that were in good condition. Wetlands were first selected with the help of experienced local ecologists who confirmed sites to be amongst those in the best condition in each region. Their overall condition was subsequently confirmed by examination of the IEI from Ausseil et al. (2008). Wetland condition was better in bogs and fens (especially in the South Island) than in swamps and marshes. This imbalance was reflected in this study, with many of the sites being bogs and fens, and only a few swamps and marshes. There have also been strong geographic patterns in loss of wetland habitat, with losses being particularly high in low-lying areas of the North Island, and on the east coast of the South Island. Consequently, no east-coast South Island wetlands were sampled for the work presented in this report, and many of the wetlands that were sampled in the North Island would only have had a moderate ecological integrity (despite representing the best wetlands in the area), as they were exposed to a number of different pressures. They were still included for analysis in this report for the sake of good geographic coverage.

2.3 TYPES OF AQUATIC HABITATS

Sampling was restricted to permanent water bodies in wetlands, which we identified by the presence of macrophytes (water-loving plants). Ephemeral habitats often display marked changes in their invertebrate communities (e.g. Brooks 2000; Fuentes et al. 2005; Strehlow et al. 2005) as different taxa become dominant during the drying–filling cycle. For the purposes of this study, we recognised five types of open-water habitat that occurred in palustrine wetlands (Fig. 1), although not all are necessarily found in any one wetland:

- 'Main channels'—wide, deep, open-water areas flowing slowly through wetlands. Wetland vegetation is generally restricted to the edges of these channels.
- 'Leads'—smaller than channels, and are characterised by shallower, less-open water, and dense wetland vegetation growing in the water. Leads consist of either standing or very slow-moving water and, unlike ponds, have ill-defined margins. Leads are particularly common in flax swamps, where open water is found at the base of each plant.
- 'Large ponds'—arbitrarily defined as being greater than 10 m in diameter, and often fringed with emergent macrophytes. However, the majority of their water surface is open to the sky.
- 'Small ponds'—arbitrarily defined as being < 10 m in diameter, and have discrete margins. They are also often completely fringed with wetland vegetation, which often grows fairly extensively through the pond.
- 'Drains'—obviously man-made. Typified by their straightness, and often have smooth banks. Spoil mounds from the drain are often piled up along the edges. This habitat type was only found at the Bullock Creek wetland.

Depending on its size and class, an individual wetland may support one, some or all of these open-water habitat types. These habitats may or may not support different biological assemblages—something that needs to be considered when designing a sampling or monitoring protocol.

2.4 SAMPLING INVERTEBRATE COMMUNITIES

2.4.1 Sampling technique

The most common methods for collecting aquatic invertebrates from wetlands involve the use of corers, nets or traps (see Batzer et al. 2001). Each method has its own advantages and disadvantages.

Corers

Corers can be used to sample either the animals living in the bottom sediment (i.e. the benthos), or the benthos plus any animals in the water column enclosed within the core. For the former technique, the corer (usually some sort of steel or plastic cylinder of a known diameter) is simply driven into the wetland substrate and then pulled out again, along with the 'plug' of wetland sediment. All inorganic matter is then separated from invertebrates by sieving. The second technique involves stirring the water and underlying substrate into a slurry, which is then collected using buckets or nets (see Sanders 2000). A refinement of this technique

Figure 1. Examples of the different open-water habitats found in wetlands throughout New Zealand:
A. A main channel at Birchfield Swamp, Westland
B. A lead at Groves Swamp, Westland
C. A large pond at Maori Lakes, Westland
D. A small pond at Ruggedy Flats, Stewart Island/Rakiura
E. A man-made drain at Bog Burn, Southland

was successfully used in the Waitaki River catchment (Stark & Suren 2002), where wetlands were sampled using a corer (300-mm diameter by 450-mm high) placed on the bottom of each wetland. The bottom substrate, water column and any aquatic plants enclosed within the corer were agitated into a slurry, and a commercial 'wet dry' vacuum cleaner (run from a 240-V generator) was then used to suck all this material into the large collecting chamber of the vacuum. The corer was sealed at its base with a 50-mm-thick foam flange that ensured a good seal, so that all the water within the corer was removed and collected in the vacuum cleaner. The collected material was then emptied through a

250-µm-mesh sieve to collect all invertebrates and organic matter. The advantage of this method over traditional coring methods is that even fast-swimming taxa are collected in the vacuum cleaner, which is able to quickly remove all the water and stirred-up slurry from the core.

Core samples can also be collected from macrophyte beds. This is relatively easy where the macrophytes are not dense and the corer can be placed quickly around selected stems of plants. However, this is more problematic in dense macrophyte beds, as it is difficult to place the corer quickly over the plants and onto the bottom of the wetland, as the plants become jammed between the corer and the bottom.

The main advantage of core sampling is that a known surface area of the bottom of the wetland, or a known volume of water column and substrate is sampled, allowing quantitative information to be obtained.

A disadvantage of core sampling is that samples can only be taken in water that is shallower than the corer, unless some sort of sleeve is placed over the top of the corer to prevent animals swimming into or out of the corer. In addition, only a relatively small area of each wetland can be sampled, meaning only a small proportion of the overall invertebrate community will be sampled. Although this disadvantage can be minimised by collecting replicate samples, it must be remembered that core samples, in particular, can contain large quantities of organic matter and mud, meaning that samples can take a long time to process (up to 3–4 hours). This can constrain the number of replicates that can be processed when time and money are limiting. Given the close relationship between species richness and area sampled, the collection of only a few core samples may result in the taxonomic richness of a particular wetland being underestimated.

Sweep nets

Sweep nets can be moved through the water column or rapidly pushed (or jabbed) into macrophyte beds and into the substrate to collect invertebrate samples. When using nets, care must be taken to minimise the risk of excessive organic matter clogging the collecting net and reducing sampling efficiency. This can be achieved by regularly emptying the net into sample bottles. The optimal mesh size for the sweep net is a compromise between being too small, in which case the net will very quickly clog, and being too large, in which case some of the smaller invertebrates will not be adequately collected. In practice, most sweep nets have a mesh size of between 250 µm and 1000 µm, with 250-µm nets and 500-µm nets being the most common. It has been reported that this method is more efficient at capturing invertebrates than core sampling (Cheal et al. 1993; Turner & Trexler 1997). It also allows a wide variety of habitats to be sampled.

The disadvantage of the sweep-net method is that it is hard to quantify the amount of habitat sampled so, at best, only percentage abundances of taxa can be determined. However, it is possible to sample for specific time periods (e.g. 2 minutes) or to make a known number of discrete 'jabs' with the net in each habitat, to provide uniformity in the sampling effort. This allows invertebrate abundances to be compared between different wetlands, although possibly not with the same degree of accuracy as if a known surface area had been sampled.

Traps

There are a number of designs of small traps that can be placed in the water column to capture swimming invertebrates (see Radar et al. 2001). These traps are usually deployed for a known period of time, so that comparative quantitative information can be collected between different habitats or wetlands.

The big advantage of this technique is that most of the samples collected will be free of organic matter and contain only those invertebrates of interest. The disadvantages are that traps target only a small proportion of the invertebrate community, and each wetland must be visited on two occasions, once to deploy the traps and once to retrieve them.

Sampling technique used in this study

Since we wanted to characterise the invertebrate communities in a wide variety of wetland habitats and individual wetlands in this study, we decided to use a sweep net (300-µm mesh) to collect invertebrates. Selection of a 300-µm mesh sweep net was a compromise between the mesh size being small enough to collect smaller invertebrates such as microcrustacea, and yet big enough to allow fine silts and detritus to drain through the mesh to minimise clogging. Using the sweep-net meant forfeiting the advantage of collecting quantitative data (as could have been achieved through the use of corers) and, instead, collecting semi-quantitative data. Each sample was collected for 2 minutes to provide some standardisation of sampling effort. This enabled us to estimate relative invertebrate abundances between the different wetlands sampled.

2.4.2 Sample preservation and storage

Once samples have been collected, they can either be processed alive in the field or preserved and processed at a later date in the laboratory. If samples are to be preserved, this needs to be done as soon as possible following collection, most often using 100% isopropanol (IPA). It is important to ensure that sufficient IPA is placed in the sample container to ensure that all the material is properly preserved, and does not start to decompose. This concern is probably more relevant for wetland samples then for river samples, as there is usually much more organic material present in wetland samples.

In this study, we used 750–1000-mL sample containers, which were half to two-thirds (at most) filled with the sample. The container was then filled to the top with IPA, giving a final IPA concentration of at least 60% to minimise the chance of samples decomposing. Identification labels (written on waterproof paper) were placed inside each sample container, and also attached to the outside of each container. All samples were entered into a central sample register spreadsheet as part of NIWA's sample tracking and processing protocol. It is a good idea to follow some sort of sample tracking and registration protocol, especially when large numbers of samples are collected, to ensure that all samples are tracked through all stages of collection, processing and data entry (e.g. see Stark et al. 2001).

2.4.3 Sample processing

Stark et al. (2001) have provided good information on how to collect and process invertebrate samples collected from rivers, and similar methods can be used to process wetland invertebrate samples. However, there are important differences between samples collected from rivers and wetlands. Firstly, wetland samples often contain much higher amounts of organic matter than river samples, making it time-consuming to sift through this organic material to find invertebrates. Secondly, many small, non-insect taxa tend to dominate wetland invertebrate communities (as opposed to the insect-dominated communities found in rivers), and such animals may be under-reported if samples are processed without a microscope. To minimise these problems, we developed a specific protocol to treat wetland samples prior to processing them.

The entire sample was sieved through a coarse (> 4.0 mm) sieve, and all material that passed through this was collected onto a set of nested sieves, with a 1.0-mm sieve on top of a 500-µm, 250-µm and 63-µm sieves. All material retained on the coarse sieve was placed on an inclined, boat-shaped tray, over which water ran (Fig. 2). Macrophyte stems, branches and other large organic matter were spread evenly across the tray and shaken gently in the water current to remove any small animals or other material associated with this large material. All fine material leaving the tray was then passed through the series of nested sieves. In this way, the sample was split into two sizes: a coarse size fraction > 1.0 mm and a finer size fraction < 1.0 mm (but greater than 63 µm). Both size fractions were then processed in their entirety, or sub-sampled so that either ½, ¼, ⅛ or 1/16 of the sample was processed, depending on the amount of material present. The material from each sieve (or subsample) was spread evenly across a small Bogorov tray (Winterbourn & Gregson 1989; Winterbourn et al. 2006) and examined under a dissecting microscope (up to 40× magnification) for invertebrates. A minimum of 400 invertebrates in each sample were identified, and the rest of the sample or subsample was scanned for uncommon taxa (Duggan et al. 2003). This process was repeated for both sieve sizes. All invertebrates were identified to as low a taxonomic resolution as possible, according to the availability of taxonomic keys and the practicality of identifying small taxa such as nematodes, tardigrades and microcrustacea (Suren et al. 2007).

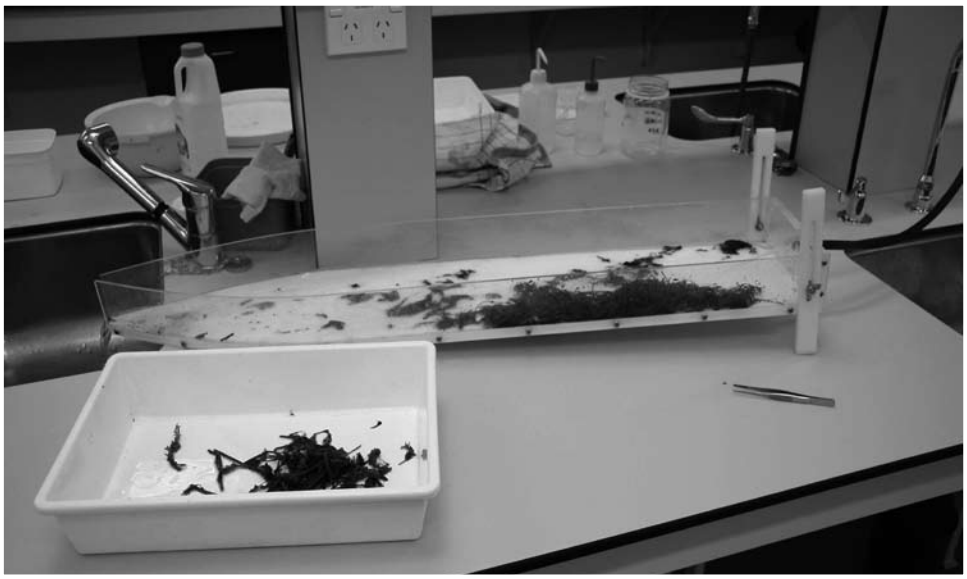


Figure 2. A boat-shaped tray that is used to wash any attached invertebrates from macrophytes and/or twigs that are retained on a 4.0-mm sieve. The tray is inclined and water is run over it. The material is then carefully shaken to dislodge attached invertebrates, which are washed into a collecting sieve in the sink (hidden).

The large quantity of material that comprised the coarse and fine size fractions meant that up to 2 hours were needed to process each fraction, to be sure that the minimum 400 count was adhered to. This meant that it could take up to 4 hours to process a single invertebrate sample from a wetland that contained a large amount of organic matter and mud. These time estimates are close to values obtained by King & Richardson (2002), who found that it took c. 2.6 hours to process samples to a fixed 200 count, and 3.4 hours to process to a fixed 300 count. The long processing time has large implications for the design of any sampling programmes. Development of new techniques to speed up sample processing would consequently have obvious beneficial outcomes that would encourage monitoring wetlands using invertebrates. One such improvement would be to pass the sample through the nested sieves, but only process material trapped on the coarse (> 1 mm) sieve. If it could be demonstrated that there is no loss of information using this method, then considerable time savings could be made.

2.5 EXPERIMENTAL DESIGN

In view of the lack of information about aquatic invertebrate communities in New Zealand wetlands, this study set out to address the following questions:

1. Which invertebrate taxa are found in wetlands? (Addressed by the combination of all studies)
2. To what extent do invertebrate communities differ within and between wetlands? (Spatial study)
3. To what extent do invertebrate communities vary over time, e.g. both seasonally and annually? (Temporal study)
4. How are invertebrate communities affected by environmental variables between different wetlands at a national scale? (National survey)

The work was carried out progressively, so that the results of one study could feed into the sampling design for the following study.

The spatial sampling programme (section 3) was conducted to determine which habitats within a wetland should be sampled to obtain the best representation of the community. This study was carried out in four relatively pristine wetlands that had easy access, as sampling within each wetland was undertaken over a few days. The study investigated whether invertebrate communities varied more between wetlands than within wetlands. The findings from this had implications for future sampling protocols. If, for example, it was found that invertebrate communities varied greatly between different plant species within a pond, or varied between small ponds, large ponds and channels, then any sampling protocol would need to take this into consideration, e.g. by sampling only areas containing submerged vegetation (if these habitats were found to support more taxa than areas without), or by not sampling leads (if these contained only a few of the taxa found in other open-water habitats within a wetland). The rationale behind the spatial sampling programme was to develop a method that most effectively characterised the invertebrate communities in each wetland while collecting as few samples as possible.

The temporal sampling programme (section 4) was carried out after completion of the spatial sampling programme. This investigated temporal changes to invertebrate communities, which also had implications for future survey work. If invertebrate communities vary temporally, then differences between dissimilar wetlands will be masked if samples are collected at different times. Such a scenario could complicate identification of factors regulating invertebrate communities in wetlands. If, however, invertebrate communities vary little over time, or if seasonal variation of individual taxa is similar between wetlands, then between-wetland similarity will remain relatively constant, irrespective of time. Under the latter scenario, surveys of multiple wetlands could be made over a longer time frame, as underlying differences between wetlands would transcend temporal fluctuations.

Finally, we surveyed wetlands throughout New Zealand (section 5) to determine how aquatic invertebrate communities varied in response to catchment, climate, geology, land cover and water quality. We also examined whether there were any regional differences between invertebrate communities. The design strategy for this survey drew on the findings from the spatial and temporal studies, and was focussed only on wetlands with minimal human impacts.

3. Spatial variability of wetland invertebrates—where should we sample?

Wetlands display a large diversity of aquatic habitats, including flowing and standing water, and vegetated and non-vegetated areas. Wetland vegetation can have a large impact on invertebrate communities, as many invertebrates are found on macrophytes, where they seek shelter from predators, and where they can obtain food in the form of algae, detritus and decaying macrophyte tissue. Invertebrate communities may also vary according to plant growth form (submerged, emergent or floating) or morphology (flat, cylindrical or complex). For example, dissected plants have larger surface areas than undissected plants, and thus provide more habitat for epiphytic invertebrates (e.g. Rooke 1986; Cheruvelil et al. 2002). A fundamental consideration for wetland invertebrate ecologists is, therefore, deciding where to sample in order to properly characterise the biodiversity of a particular wetland. Consequently, the first aim of this study was to investigate the spatial variability of wetland invertebrate communities in New Zealand.

3.1 METHODS

3.1.1 Study sites and field methods

Samples were collected from four lowland, coastal wetlands on the west coast of the South Island of New Zealand (Fig. 3). Three wetlands (Mahinapua, Shearer and Kakapotahi) were in Westland, while the Mangarakau Swamp was in the Tasman region. All of these wetlands were sited in areas where human disturbance was minimal. Two sites (Kakapotahi and Shearer) were classified as fens, while the other two sites (Mahinapua and Mangarakau) were classified as swamps. Four of the five open-water habitat types we identified (see section 2.3) were sampled, but each of the four habitats was found in only three of the four wetlands (Table 2).

The dominant terrestrial vegetation at Kakapotahi consisted of a mixture of *Apodasmia similis* rushland and *Gleichenia dicarpa*. The sedge *Baumea teretifolia* and flax *Phormium tenax* also had high cover throughout this wetland. Aquatic plants found in the open-water habitats included *A. similis*, *Glyceria fluitans*, *Myriophyllum robustum* and the tall sedge *Eleocharis sphacelata*, as well as a species of *Sphagnum* (Table 2). Terrestrial vegetation at Shearer was dominated by *G. dicarpa*, *Baumea arthrophylla* and the wire rush *Empodisma minus*. Vegetation in the main channel that meandered through this wetland was dominated by *B. arthrophylla* at its margins, and *E. sphacelata* and the bladderwort *Utricularia australis* in deeper water. Vegetation in the leads and ponds here was dominated by *B. arthrophylla*. Vegetation in the Mahinapua wetland was dominated by dense growths of *P. tenax* and *Carex sinclairii*, with species of *Coprosma* and kahikatea (*Dacrycarpus dacrydioides*) growing in the margins. Aquatic vegetation in the main channels and ponds at Mahinapua

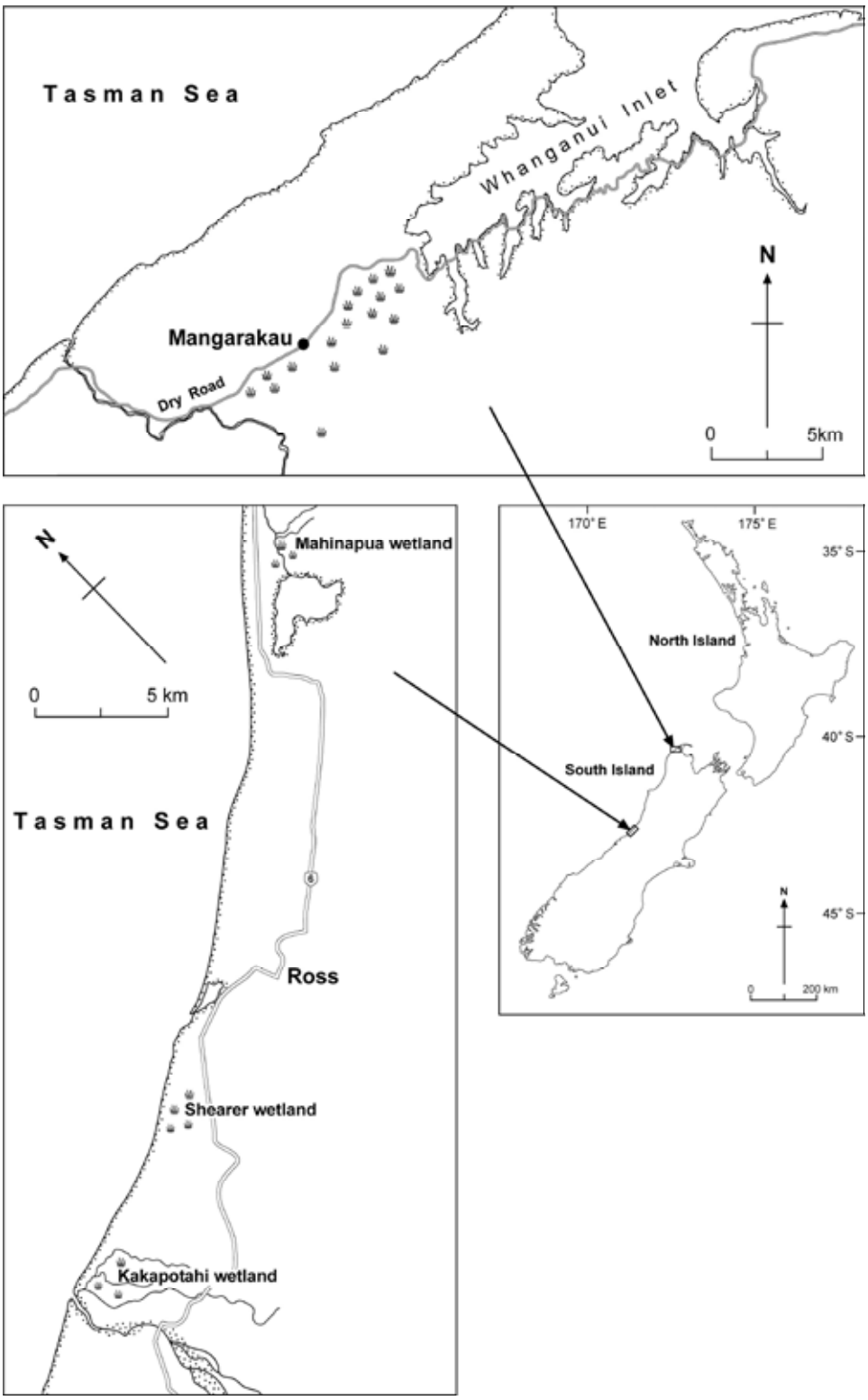


Figure 3. Maps showing the locations of the four wetlands sampled on the West Coast of the South Island as part of the study examining spatial variability of wetland invertebrates.

included *Aponogeton distachyus*, *Callitriche stagnalis*, *P. tenax* and *Myriophyllum propinquum*. Wetland vegetation at Mangarakau Swamp was dominated by species-rich sedgelands comprising four *Baumea* spp. and *Lepidosperma australe*, as well as *G. dicarpa*, *P. tenax* and *Typha orientalis*. The aquatic vegetation at this swamp included tussock (*Carex secta*), and marginal bands of *Baumea*, *E. sphacelata* and *T. orientalis*, with submerged species including two milfoils (*M. propinquum* and *M. robustum*) and *Potamogeton cheesemanii* (Table 2).

TABLE 2. SUMMARY OF THE HABITATS AND AQUATIC PLANTS FOUND IN THE FOUR WETLANDS SAMPLED IN THIS STUDY. THE NUMBER OF HABITATS SAMPLED WITHIN EACH WETLAND IS SHOWN, AS ARE THE NUMBER OF SAMPLES COLLECTED FROM EACH WETLAND, HABITAT AND AQUATIC PLANT TAXON (BRACKETS).

WETLAND (*n*)	HABITAT (*n*)	TAXON (*n*)	GROWTH FORM	MORPHOLOGY
Kakapotahi (25)	1 × main channel (20)	*Eleocharis* (4), *Apodasmia* (4)	Emergent	Cylindrical
	1 × lead (3)	*Glyceria* (4)	Floating	Flat
	2 × small ponds (2)	*Myriophyllum* (4), *Sphagnum* (4)	Submerged	Complex
		No vegetation (5)		
Mahinapua (11)	1 × main channel (5)	*Callitriche* (2), *Myriophyllum* (2)	Submerged	Complex
	1 × big pond (4)	*Phormium* (2)	Emergent	Flat
	1 × small pond (2)	*Aponogeton* (2)		
		No vegetation (3)		
Mangarakau (39)	2 × leads (14)	*Baumea* (14), *Eleocharis* (4)	Emergent	Cylindrical
	1 × big pond (21)	*Carex* (3), *Typha* (10)	Emergent	Flat
	2 × small ponds (4)	*Myriophyllum* (1),	Submerged	Complex
		Potamogeton (5)	Submerged	Flat
Shearer (19)	1 × main channel (12)	*Baumea* (5), *Eleocharis* (5)	Emergent	Cylindrical
	1 × lead (3)	*Utricularia* (2)	Submerged	Complex
	1 × big pond (4)	No vegetation (7)		

Because plant growth form (submerged, emergent or floating) or morphology (flat, cylindrical or complex) can influence invertebrate communities, we allocated plants within each wetland to their appropriate growth form or morphological characteristics (Table 2). We thus wanted to investigate how invertebrate communities varied with respect to the specific predictor variables of 'Wetland', 'Habitat', 'Plant taxon', 'Growth form', and 'Morphology'.

All samples were collected during November–December 2003, to minimise potential seasonal differences in invertebrate community composition. Invertebrates were collected from areas without vegetation and from different macrophytes within individual water bodies, and from different water bodies (e.g. large and small ponds, channels and leads) within each wetland (Table 2) using the protocols described in section 2.4.1. Invertebrate samples were preserved with IPA in the field, and were processed as described in section 2.4.3. Measurements of water chemistry (dissolved oxygen (DO), pH and conductivity) were made at each site using a Horiba® multiprobe. In addition, water samples were collected from each site, filtered through Millipore® GFF glass fibre filters and frozen for nutrient analysis. Upon thawing, samples were analysed for nitrate (NO_3-N), ammonium (NH_4-N), dissolved organic nitrogen (DON), dissolved reactive phosphorus (DRP) and dissolved organic phosphorus (DOP) using standard methods for the Lachat QuikChem Flow Injection Analyser (www.lachatinstruments/apps.asp; viewed December 2009).

3.1.2 Data analysis

Data for each of the water chemistry variables were analysed by Principal Components Analysis (PCA; McCune & Mefford 1997) to see how the spot water chemistry data differed between the wetlands. Individual variables were then correlated against resultant PCA axis 1 and 2 scores to see which were responsible for observed sample groupings. Differences in water chemistry data between the four wetlands were also investigated using ANOVA, and Tukey post-hoc tests (SPSS 2000) to determine where significant differences occurred.

Invertebrate data were analysed to see whether invertebrate communities varied more between wetlands than within wetlands. An ordination analysis (DECORANA, or detrended correspondence analysis—DCA) was used to investigate relationships between the different species assemblages found in each sample. This statistical technique graphically represents the location of samples based on their invertebrate communities, such that samples with similar communities appear close together on a graph, and samples with very different communities appear far apart from each other. Samples are plotted in (usually) two dimensions with arbitrary sample scores. A useful feature of ordination is also the ability to see which environmental and biological data are correlated to the ordination axes, and thus to particular sample groupings. The effects of the five predictor variables ('Wetland', 'Habitat', 'Plant', 'Growth form' and 'Morphology') on ordination scores were examined by Multi-response Permutation Procedures (MRRP; McCune & Mefford, 1997), a non-parametric procedure for testing the hypothesis of no difference between two or more groups of entities. The MRRP calculates the *R* statistic, which varies from 0 (all items within a group differ such that within-group variability is similar to that expected by chance) to 1 (all items within a group are identical, so within-group variability is much less than chance). Finally, all data were analysed using Multiple Regression Trees (MRT; De'ath 2002) to describe how the invertebrate community varied in response to the predictor variables of Wetland, Habitat, 'Plant, Growth form and Morphology. MRT uses selected predictor variables to predict a multivariate response variable, in this case invertebrate community composition. In this way, we could determine which of our measured environmental variables was causing the most variation in invertebrate community composition.

3.2 RESULTS

Spot water chemistry differed greatly between the four wetlands (Fig. 4). The Mahinapua wetland had higher DON, DRP and DOP levels than the other three wetlands (Table 3). Water pH was lowest in the Kakapotahi wetland and highest in the Mangarakau wetland, which also had the highest conductivity. Kakapotahi and Mahinapua had higher NO_3-N concentrations than Shearer and Mangarakau (Table 3).

A total of 75 invertebrate taxa were collected from the four wetlands. Mangarakau wetland supported the highest number of taxa (47), while Shearer supported the lowest (25). The fauna in all wetlands was numerically dominated by *Tanytarsus* and Orthoclad midges (17% and 8% of total density, respectively), and aquatic nematodes (12%). Five other taxa comprised > 5% of total density (harpactacoid copepods, the damselfly *Xanthocnemis zealandica*, ceratopogonid and tanypodinid midges, and the snail *Potamopyrgus antipodarum*). Forty-six taxa were collected only rarely, and occurred at < 5% of sites or had abundances of < 0.01% of total density. The most widespread invertebrates were orthoclad midges and aquatic mites, which were found in 91 of the 94 samples. Other widespread taxa were *Xanthocnemis*, ostracods and cyclopoid copepods, chironomid midges (including *Tanytarsus* and Tanypodinae), nematodes, hydroptilid caddisflies, Ceratopogonidae and Oligochaeta, which all occurred at > 70% of sites. Nineteen taxa were recorded in all four wetlands, while nine taxa were found in three wetlands and 16 taxa were found in two; 31 taxa were restricted to only one wetland. The Kakapotahi wetland supported the most

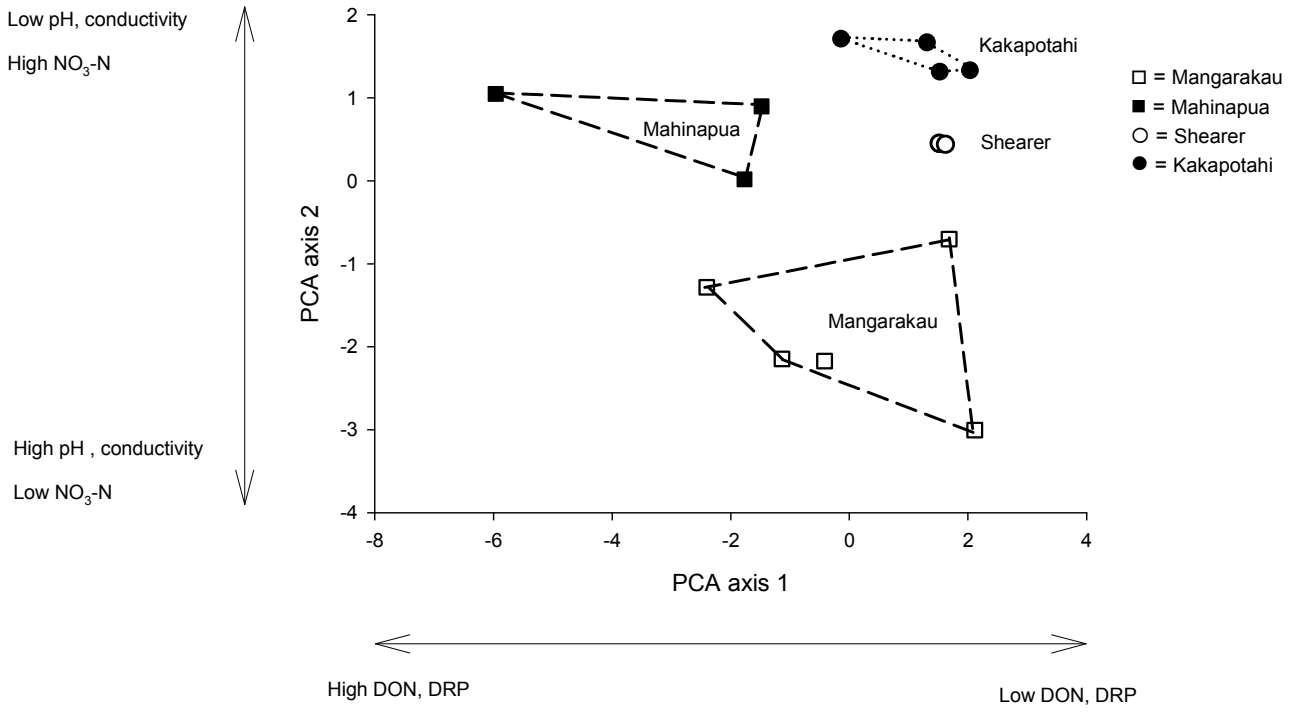


Figure 4. Results of a principle components analysis (PCA) of spot water chemistry data collected from the different habitats within each of the four wetlands surveyed for the spatial study. Significant factors of the PCA axis 1 and 2 scores are also shown. Note that samples from Shearer are superimposed on each other, so that only two of the three samples collected are shown.

TABLE 3. SUMMARY OF WATER QUALITY CONDITIONS (MEAN ± 1 SD) IN EACH OF THE FOUR WETLANDS SAMPLED IN THE SPATIAL STUDY.
DON = dissolved organic nitrogen; DRP = dissolved reactive phosphorus; DOP = dissolved organic phosphorus. Means with different superscript letters are significantly different from each other (Tukeys post-hoc tests, $P < 0.05$).

WETLAND	PH	CONDUCTIVITY (µS/cm)	NH_4-N (µg/L)	NO_3-N (µg/L)	DON (µg/L)	DRP (µg/L)	DOP (µg/L)
Kakapotahi	$4.3 + 0.2^a$	56 ± 2^a	7.1 ± 2.2^a	5.2 ± 1.8^a	173 ± 22^a	0.54 ± 0.22^a	1.8 ± 0.7^a
Mahinapua	5.5 ± 0.2^b	60 ± 10^a	7.4 ± 0.7^a	5.2 ± 2.1^a	268 ± 31^b	2.1 ± 1.0^b	6.3 ± 1.8^b
Mangarakau	6.4 ± 0.5^c	98 ± 19^b	9.8 ± 3.4^b	3.5 ± 0.7^b	204 ± 52^a	0.57 ± 0.35^a	3.5 ± 1.7^a
Shearer	5.2 ± 0.01^b	45 ± 5^a	7.3 ± 1.3^a	3.4 ± 0.1^b	188 ± 7^a	0.61 ± 0.10^a	0.7 ± 0.9^a

unique taxa (12), followed by Mangarakau (10) and Mahinapua (9). Shearer swamp supported only one unique taxon. Within each wetland, the number of taxa restricted to only one habitat varied from 26% to 47%, while the number of taxa found in all habitat types varied from 35% to 50%.

The four wetlands supported distinct invertebrate communities (Fig. 5). Samples from Kakapotahi and Shearer had low axis 1 scores, while Mangarakau had high axis 1 scores, which was positively correlated with the water quality variables of pH ($r^2 = 0.772$) and conductivity ($r^2 = 0.731$). Samples from the Mahinapua wetland had scores intermediate between the low pH fens and Mangarakau (Fig. 5). Correlations of invertebrate densities with the axis 1 and 2 scores showed that specific invertebrates were associated with different wetlands (Fig. 5). For example, 13 taxa had significant positive correlations ($r^2 > 0.3$, $P < 0.05$) to axis 1 scores, and were thus characteristic of sites with high axis 1 scores (i.e. were found at Mangarakau), while nine taxa had similarly significant negative correlations with axis 1 scores; i.e. were found at Shearer and Kakapotahi.

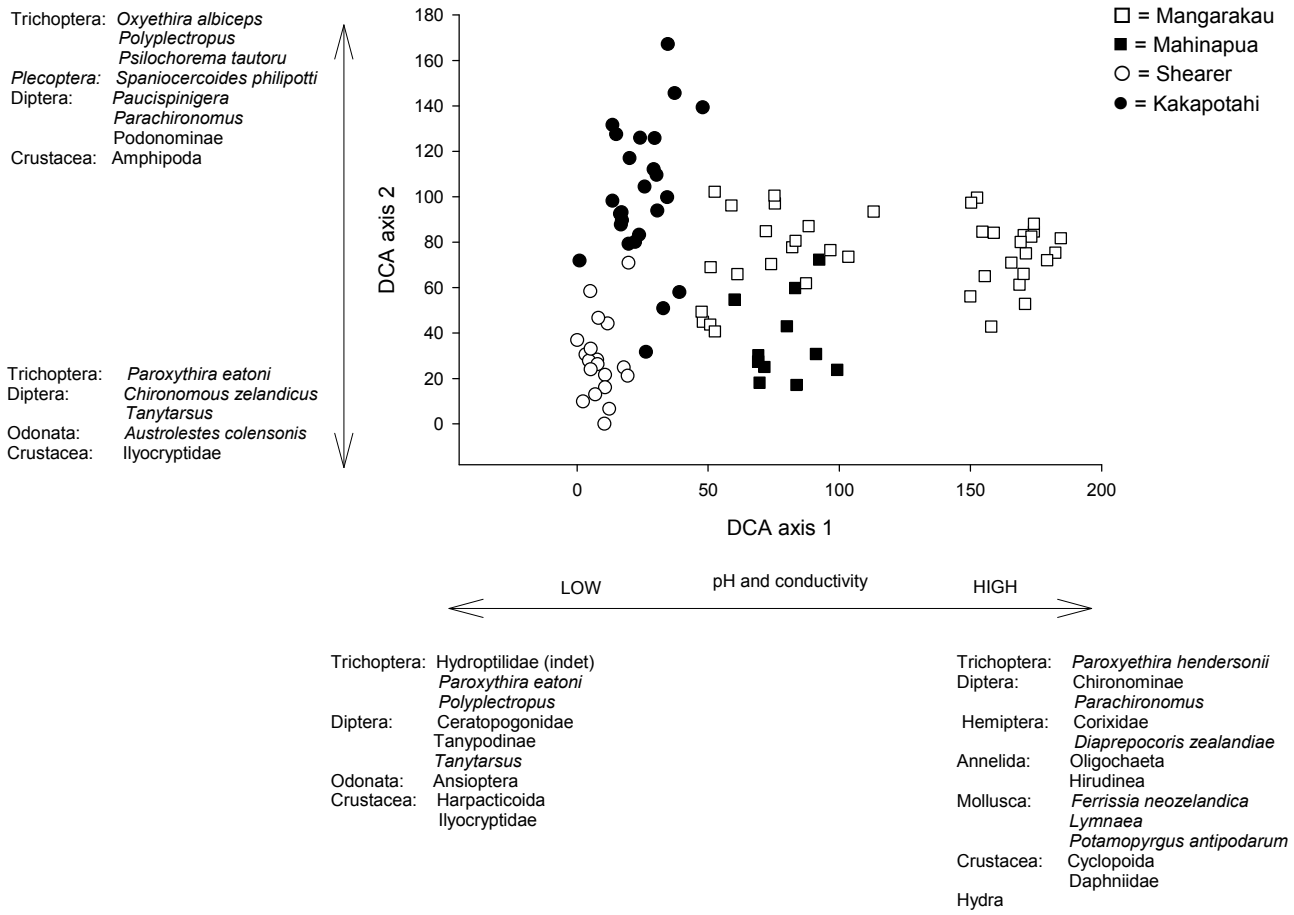


Figure 5. Results of the detrended correspondence analysis (DCA) of invertebrate communities collected from the different habitats within each of the four wetlands surveyed for the spatial study. The different taxa and water quality parameters that displayed significant correlations ($r^2 > 0.2$) to the axis 1 or 2 ordination scores are also shown.

Samples collected from Kakapotahi had higher axis 2 scores than samples collected from Shearer, with the other two wetlands having intermediate scores on this axis. No significant correlations ($P > 0.05$) were observed between axis 2 scores and any of the water quality variables, suggesting that this axis represented an unmeasured gradient. However, significant correlations existed between 13 invertebrate taxa and axis 2 scores (Fig. 5). Examination of densities of these taxa showed that only the caddisflies *Polyplectropus* and *Psilochorema tautoru* were restricted to Kakapotahi; densities of the other 11 taxa varied along this axis and were not restricted to one wetland.

MRPP illustrated how the ordination scores differed according to the characteristics of the sampling site (Wetland, Habitat, Plant, Growth form and Morphology). Most of the differences between ordination scores occurred when samples were coded for different wetlands ($R = 0.198$), although the Habitat and Plant terms also resulted in relatively high within-group homogeneity ($R = 0.140$ and 0.107, respectively). The Growth form and Morphology terms showed little within-group homogeneity ($R = 0.03$ and 0.05, respectively), suggesting that invertebrate communities did not display any strong preference to plants on the basis of their growth form or morphology. The results of the multivariate regression tree generally confirmed these findings, showing that the Wetland term contributed most to the explanatory power of the model (58.2%), followed by Habitat (23.3%), Growth form (12.6%) and Morphology (5.8%). Unlike the

MRPP analysis, the Plant term contributed nothing to the observed variability in the invertebrate community. Such ambiguous results for the importance of the Plant term most likely reflect differences in the two techniques, and are best interpreted as meaning that differences in plant species have less influence on invertebrate composition than either differences between wetlands or habitats.

The number of taxa unique to specific habitats within each wetland was calculated. This showed that approximately 33% of taxa were found in only one habitat in each wetland, 23% were found in two habitats only, and 43% were found in three or more habitats. Based on this result, it was apparent that sampling just one habitat type within a wetland may not have completely characterised the invertebrate communities.

3.3 DISCUSSION

In this spatial study, it was found that invertebrate communities in these natural wetlands varied more between different wetlands than they did between habitats or plants within a wetland. Each of the four wetlands sampled supported distinctive invertebrate communities, presumably reflecting, in part, differences in water chemistry between these two wetland types (fens and swamps). For example, Mangarakau was less acidic and had higher conductivity than the other wetlands, and supported an invertebrate community very different from that in the more acidic wetlands. Molluscs in particular were commonly collected from Mangarakau, but were absent from the lower pH wetlands. Absence of molluscs from the low pH wetlands most likely reflects their inability to obtain enough free calcium for shell maintenance (Crumpton 1978) or the inability of snail eggs to develop in low pH water (Burton et al. 1985). Batzer et al. (2005) also reported a lack of molluscs in water with pH < 6.0 and a similar absence of molluscs has been observed in streams and lakes with low pH (Oekland & Oekland 1986; Oekland 1990).

Our finding of low variability in invertebrate community composition between plant types was somewhat surprising, especially in light of the review by Wissinger (1999), where it was suggested that wetland macroinvertebrates are responsive to variations in plant community structure. Our results suggested that within each of the four wetlands sampled, invertebrate community composition and percentage abundance were relatively similar between areas with and without vegetation. Kratzer & Batzer (2007) also found little variation in invertebrate communities in Okefenokee Swamp, Florida, USA, despite sampling five plant community habitats (marsh prairies, cypress forest, scrub-shrub thickets, deepwater lakes and boat trails) in six discrete areas of the swamp. They attributed this lack of variation to the fact that water quality did not vary greatly throughout the wetland, as a result of its source being almost entirely precipitation-based. If water chemistry is responsible for structuring invertebrate communities, then there are no biological reasons why invertebrate communities would change between different habitats within a wetland, as long as water chemistry within these habitats was similar. The corollary to this is that wetlands with different water chemistry would support different invertebrate communities, despite having similar habitats.

The results of this study suggest that most of the variation in invertebrate communities in wetlands on the west coast of the South Island occurs at the spatial scale of the wetland. Such a finding is likely to be similar throughout the country, assuming that water chemistry within a wetland is relatively uniform and reflective of the particular wetland's hydrosystem. Although invertebrate communities vary at the smaller spatial scale of habitat, plant species or morphology, these variations are not large enough to mask differences between individual wetlands. This means that it may not be necessary to sample a specific habitat or plant type within a wetland in order to properly characterise and compare invertebrate communities, as larger scale processes operating at the wetland level appear to control this. Rather, we suggest sampling from as wide a range of aquatic habitats that are found in a wetland as possible, given the time and cost constraints inherent in collecting too many samples. Furthermore, rather than concentrating on collecting samples from vegetated and non-vegetated areas, or a particular plant taxon, we suggest collecting samples from as many micro-habitats as possible within a water body, and pooling these, asssuming the water chemistry and hydrological variation is generally consistent across the wetland. Consequently, our subsequent sampling protocol was to identify different types of aquatic habitat within a wetland, and to try to sample a representative number of each. Within each habitat, two replicate samples were collected from a range of micro-habitats including vegetated and non-vegetated areas. Up to three water bodies within each wetland were chosen, giving a total of six samples per wetland.

4. Temporal variation—when should we sample?

The spatial study outlined in section 3 was carried out over a 3-week period during the austral spring (November–December 2003) to minimise potential seasonal effects that may have altered the invertebrate communities. However, future nationwide inventories of wetlands may need to consider potential interannual or seasonal variation in invertebrate communities that could obscure or exaggerate differences between wetlands.

If wetland invertebrates vary interannually or seasonally, and if this affects our ability to discriminate between different wetlands, then sampling may need to be restricted to particular seasons. Unless this is taken into account, it will be difficult to identify potential factors regulating invertebrate communities in perennial wetlands. In contrast, if invertebrate communities vary little over time, or if seasonal variation in the abundance of individual taxa is similar between different wetlands, then variation between wetlands will remain relatively constant. Under such a scenario, surveys of multiple wetlands encompassing a wide range of environmental conditions could be conducted at any time of the year, because the underlying differences between wetlands would transcend those caused by temporal fluctuations.

This second sampling programme investigated temporal variability in invertebrate communities and whether this would affect our ability to discriminate between wetlands. This consisted of two separate studies: the first study investigated interannual variation, while the second study investigated seasonal variation.

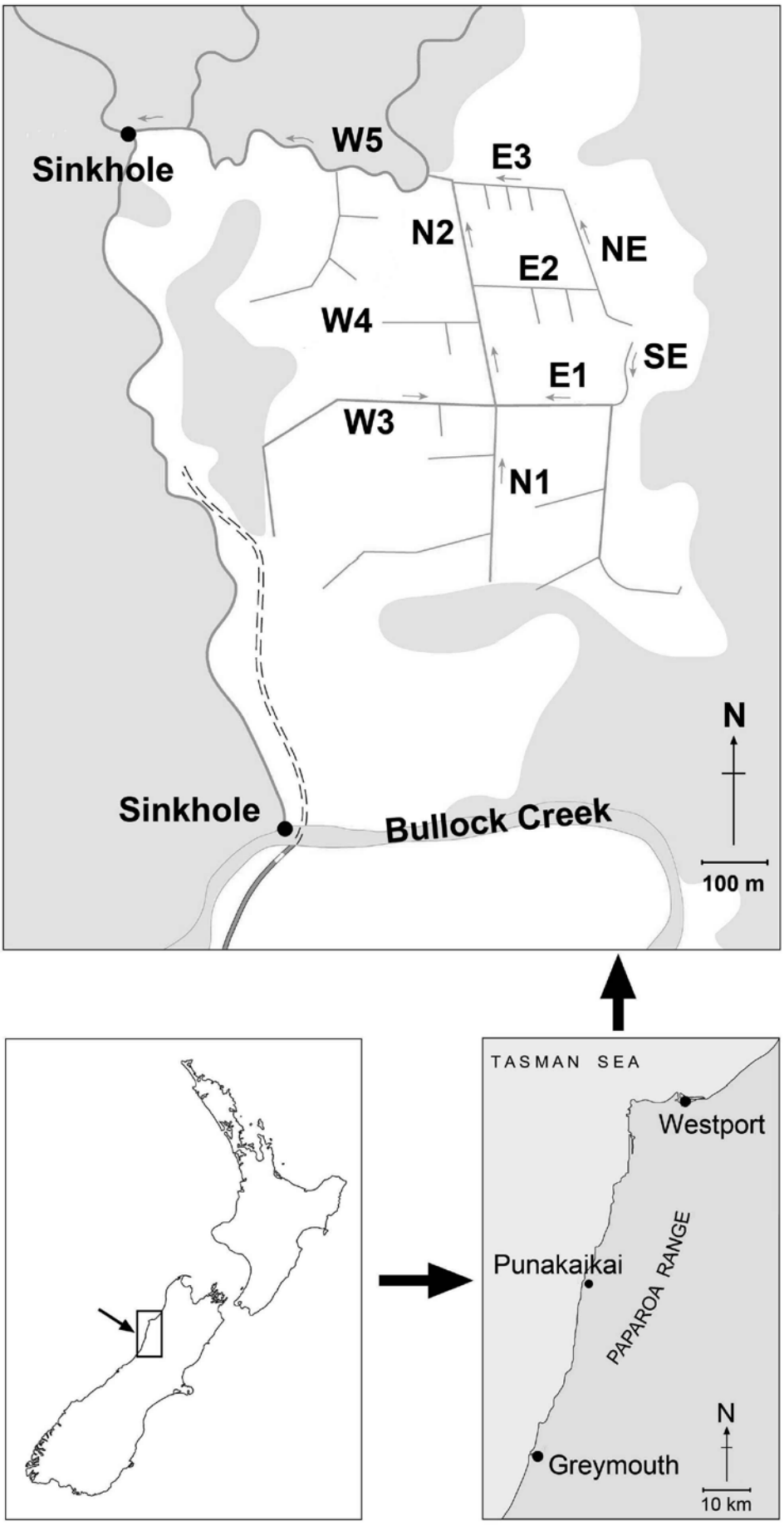
4.1 STUDY SITES AND METHODS

4.1.1 Interannual variation

The first study was conducted in the Bullock Creek wetland: an enclosed depression in a steep karst landscape in the Paparoa Ranges on the west coast of the South Island. The study area was a 100-ha palustrine fen within the wetland, surrounded by tall limestone cliffs and indigenous forest of southern beech (*Nothofagus* spp.) and podocarp conifers (Podocarpaceae). Climatic conditions in the area (obtained from a climate recording station at Westport, approximately 40 km north of the wetland) are characterised by cool seasonal temperatures (mean temperature = 12.5°C, mean winter minimum = 2.9°C, mean summer maximum = 25°C), and relatively high amounts of unpredictable rain (mean monthly rainfall = 170 mm).

Most of the wetland was converted into pasture for grazing by 19th-century settlers, and a network of drains was established during the first half of the 20th century (Fig. 6). The wetland is a mosaic of vegetation types, separated by the drainage network. In wetter areas remote from drains, the vegetation is dominated by native wetland species, including the sedges *Carex sinclairii* and *Baumea rubiginosa*, flax (*Phormium tenax*), and the peat-forming moss

Figure 6. Map showing the location of the Bullock Creek wetland, and diagrammatic representation of the main drainage network.



Sphagnum cristatum. In contrast, drier and more disturbed areas, especially areas close to drains, are dominated by alien pasture grasses and weeds (e.g. *Agrostis stolonifera*, *Holcus lanatus*, *Lotus pedunculatus*, *Ranunculus repens*). The entire site passed into public ownership in 1986, and is currently being managed and restored for conservation and biodiversity values by DOC.

A large central drain (N2) runs north through the wetland into the headwaters of Cave Creek (Fig. 6). These headwaters then flow west into a submergence. During base flow, water flows down this submergence, but during periods of high rainfall, the submergence is unable to cope with the volume of floodwater and the water flow reverses, flooding the fen and discharging south into Bullock Creek (Sorrell et al. 2007). Water input to the fen is therefore a combination of rainfall and overland floods, including the backflow from the sinkhole. A number of smaller side branches drain the western and eastern parts of the wetland. At the time of sampling, some drains (N1, W3, W4, E2) had steep, unvegetated banks with no instream macrophytes. Other drains (E1, E3, SE, NE and N2) were lined with overhanging vegetation and supported a range of aquatic macrophytes.

Invertebrates were sampled from ten sampling stations within the Bullock Creek wetland (Fig. 6) using a sweep net (300-µm mesh) that was repeatedly jabbed into vegetation or moved around the bottom of each drain to collect the benthos. Care was taken to empty the net regularly as it filled. Samples were collected for approximately 2 minutes from an area of c. 2 m^2 in each drain. Samples were collected during each summer (December–January) from 1999 to 2003. Invertebrate samples were preserved using 100% IPA, and processed as previously described (section 2.3.3). Measurements of water chemistry (DO, pH and conductivity) were made at each drain on each sampling occasion using a Horiba® multiprobe (Sorrel et al. 2007). Waterway width, depth and bank height were measured at five locations within each waterway. The depth of organic matter was measured by pushing a steel rod into the substrate until it hit solid material underneath. Five sediment samples were collected from each waterway and ashed (550°C: 8 h) to determine the % organic matter content. The remaining inorganic fraction was then passed through a series of nested sieves (4 mm, 2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm and 0.064 mm) for size analysis. The substrate size was expressed as the D_{16}, D_{50} and D_{84}, which represented the 16th, 50th and 84th percentile, respectively.

All invertebrate data were examined for normality and fourth-root transformed where necessary—log transformation was not as effective at normalising the data. We used non-metric multidimensional scaling (NMDS) ordination to see whether invertebrate communities in the drains differed between sampling locations, and whether these differences persisted over time.

4.1.2 Seasonal variation

Samples for the second study were collected from Mahinapua and Shearer wetlands, which are situated approximately 10 km and 30 km southwest of Hokitika, respectively. These wetlands were also included in the spatial variability study (section 3; Fig. 3). Climatic conditions in the area (obtained from a climate recording station at Ross, approximately equidistant from both wetlands) are characterised by cool seasonal temperatures (mean temperature = 15.7°C, mean winter minimum = 4°C, mean summer maximum = 30°C), and relatively high amounts of unpredictable rain (mean monthly rainfall = 277 mm).

Duplicate invertebrate samples were collected semi-quantitatively every 3–4 months over an 18-month period from each of three open-water habitats within each wetland using the same hand-held sweep net as used in other studies (sections 3 and 4.1.1). All samples were preserved immediately following collection using 100% IPA. Spot measurements of water chemistry (temperature, pH and conductivity) were made at each habitat within each wetland using a Horiba® multiprobe. Water level was monitored against a known benchmark placed at a discrete point in the main channel in each wetland.

Taxonomic richness was calculated for each sample, as was the percentage abundance of the 11 most common taxa, each of which contributed > 2% to total density. A repeated measures ANOVA (SPSS 2000) was used to assess whether selected invertebrate metrics differed between the wetlands and over time. The wetland × time interaction term showed whether the metrics behaved in the same way in both wetlands. A repeated measures ANOVA was also used to determine whether measured water quality metrics differed between each wetland over time. An ordination was then carried out on the percentage abundance data, and resultant ordination scores were assigned to each wetland and to each sampling occasion. These scores were then analysed to see whether samples differed more as a result of differences between wetlands or sampling occasions.

4.2 RESULTS

4.2.1 Interannual variation

Ordination of the invertebrate data collected from the waterways of the Bullock Creek wetland gave three distinct clusters, with samples from the stream site (W5) having lower axis 1 scores than samples collected from the drains, and samples collected from unvegetated drains in the wetland (N1, N2, W3 and W4) having higher axis 2 scores than samples collected from vegetated drains (E1, E2, E3, NE and SE) (Fig. 7). These differences persisted throughout the 4 years, despite evidence of some interannual variation in the invertebrate communities within each habitat, as shown by small shifts in ordination scores. However, at no time did the invertebrate communities converge in their species composition.

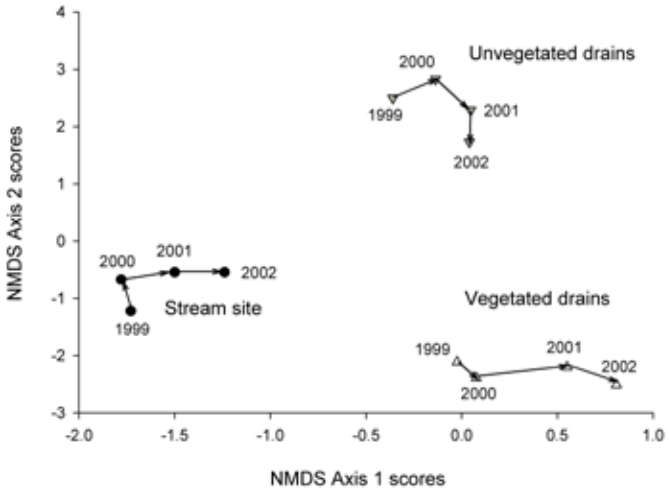


Figure 7. Non-metric multidimensional scaling (NMDS) ordination of invertebrate communities collected from drain bottoms in the Bullock Creek wetland, showing the three discrete groups found in the drains, and temporal differences in calculated NMDS scores for the different groups. For clarity, only the centroids of each group have been shown. Note that although community composition changed over time, at no time did we lose the ability to discriminate between the three sampling locations.

Densities of individual invertebrate taxa differed significantly between sites. Insects such as Ephemeroptera (*Deleatidium*, *Neozephlebia* and *Zephlebia*), Trichoptera (*Costachorema*, *Psilochorema*, *Oxyethira* and *Pycnocentria*) and Diptera (*Austrosimulium*, Eriopterini and Orthocladiinae) were significantly more common in the stream site (W5); dipterans (Chironominae, *Chironomus* and *Paradixa*), the amphipod *Paraleptamphopus*, copepods, the hempiteran *Microvelia*, and Collembola were significantly more common in the acidic drains; and Mollusca (*Potamopyrgus* and *Sphaerium*), microcrustacea (Cladocera and Ostracoda), nematodes and the corixid *Sigara* were more common in the more circum-neutral vegetated drains. The occurrence

of Ephemeroptera and Trichoptera, and *Austrosimulium* and Eriopterini at the stream site is not surprising, as these invertebrates are common to streams throughout the West Coast region. The fauna of the drains was more typical of that found in wetlands throughout the country, being dominated by midges, molluscs, micro-crustacea and nematodes.

These consistent differences in invertebrate communities between the sampling sites during the 4-year period most likely reflected differences in water chemistry and physical habitat conditions (Table 4). Water pH, in particular, varied greatly between the waterways within Bullock Creek: the stream site (W5) and the vegetated drains (most of which were found in the northeastern part of the wetlwnd) had relatively neutral pH, while the unvegetated drains (most of which were in the southwestern part) had lower pH. Such a large pH variability within a wetland appears unusual: indeed, this wetland had the highest within-wetland pH variability (with a range of 3.9 pH units) of 154 wetlands surveyed throughout the country, where the median variability was only 0.6 pH units. The large variability within the Bullock Creek wetland most likely reflects the underlying geology within the wetland: low pH limestone intersecting with higher pH quartz-bearing rocks. Habitat conditions also varied between the waterways, with the stream site in particular differing from the wetland drains in terms of having slightly wider channels and deeper water than the drains, larger streambed sizes, and less benthic organic matter.

TABLE 4. SUMMARY OF PHYSICO-CHEMICAL CONDITIONS MEASURED IN THE THREE WATERWAY TYPES SAMPLED IN THE BULLOCK CREEK WETLAND DURING THE INTERANNUAL VARIATION STUDY.
The mean and range (min–max) is given for each variable. Means with different superscript letters are significantly different from each other (Tukeys post-hoc tests, $P < 0.05$).

VARIABLE	STREAM SITE (W5)	UNVEGETATED SITES (N1, W3, W4, E2)	VEGETATED SITES (E1, E3, SE, NE, N2)
pH	7.1^{a}	5.8^{b}	6.8^{a}
	(6.8–7.5)	(5.2–7.4)	(5.7–8.0)
Conductivity (mS/cm)	0.130^{a}	0.047^{b}	0.157^{a}
	(0.110–0.150)	(0.015–0.085)	(0.030–0.300)
Dissolved O_2 (mg/L)	10.1^{a}	5.9^{b}	9.4^{a}
	(9.5–10.3)	(3.4–9.4)	(7.7–12.7)
Temperature (°C)	$10.1^{a,b}$	12.1^{b}	10.3^{a}
	(8.9–11.7)	(9.0–16.5)	(7.7–13.6)
Width (m)	1.97^{a}	1.22^{b}	$1.78^{a,b}$
	(1.12–2.70)	(0.25–3.1)	(0.65–3.4)
Water depth (m)	0.40^{a}	0.25^{b}	0.29^{b}
	(0.30–0.48)	(0.06–0.80)	(0.09–0.56)
Depth of organic matter (m)	0.01^{a}	0.23^{b}	0.69^{c}
	(0–0.05)	(0.0–0.44)	(0.35–0.98)
Bank height (m)	2.42^{a}	1.07^{b}	0.86^{b}
	(2.2–2.58)	(0.2–1.4)	(0.25–1.50)
% macrophyte cover	20%	0%	60%
			(25%–90%)
Substrate size (mm)			
D_{16}	0.1	0.032	0.064
D_{50}	0.7	0.075	1.2
D_{84}	4.2	0.28	2.6
% organic matter	0.9^{a}	11.3^{b}	19.9^{b}
	(0.7–1.3)	(2.6–26.1)	(1.4–41.3)

4.2.2 Seasonal variation

Over the 15-month period of the seasonal study, measured water quality parameters always remained distinctive between the two wetlands sampled. Water pH was always higher at Mahinapua than at Shearer, and although this changed over time, it did not follow any seasonal patterns. Water levels in both wetlands varied over time, and reflected the unpredictable rainfall patterns in the area. Variation was higher at Mahinapua than at Shearer, but at no time did any of the sampling sites dry. Spot water temperature was higher at Shearer (Fig. 8). Conductivity was low (< 100 µS/cm) at both wetlands, but was usually slightly higher at Mahinapua (except in February 2006). Such distinctive water chemistry signatures presumably reflect the different hydrological source of water in each wetland: rainfall-dominated hydrology at Shearer and lake floodplain hydrology at Mahinapua (Johnson & Gerbeaux 2004). We expect such differences in water quality to persist over time and to result in consistently distinctive invertebrate communities within each wetland, as was found in the interannual study at Bullock Creek (section 4.2.1).

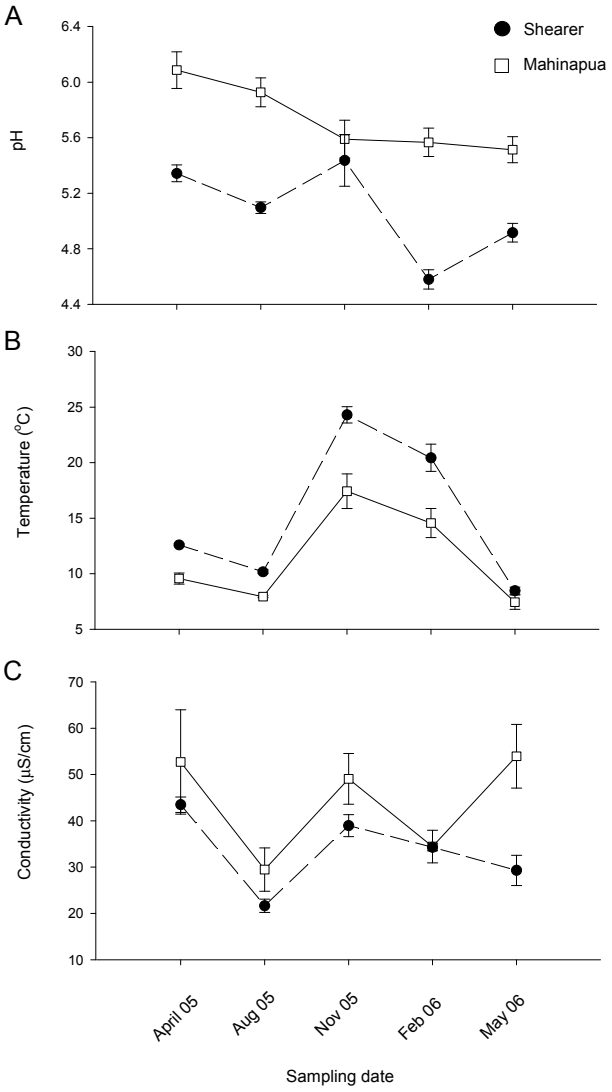


Figure 8. Seasonal differences in pH (A), temperature (B) and conductivity (C) in the Shearer (black circles) and Mahinapua (open squares) wetlands over the 15-month study period (mean ± 1 SEM, n = 3).

A total of 58 taxa were collected during the seasonal variation study. Mahinapua supported more taxa (50) than Shearer (38). Taxonomic richness varied over time in both wetlands, but in different ways: richness increased over time at Mahinapua, but was low each autumn (April–May) in Shearer (Fig. 9A). Relative abundances of six of the 11 most common taxa differed between wetlands (Table 5), with three taxa (Cyclopoida, Orthocladiinae and *Xanthocnemis*) being more common in the Mahinapua wetland, and three taxa (Hydroptilidae, Nematoda and *Tanytarsus*) more common in Shearer (Fig. 9B–L). Relative abundances of two taxa (Harpacticoida and Ilyocryptidae) displayed spring or summer maxima and autumn minima at both wetlands (Fig. 9B & C), while relative abundance of *Tanytarsus* peaked in autumn, and was lowest in spring at both wetlands (Fig. 9D). Relative abundances of Nematoda peaked in spring at Shearer Swamp only (Fig. 9E), while *Paroxyethira* had highest relative abundances in Autumn at Mahinapua (Fig. 9F). Relative abundances of six of the 11 taxa (Acarina, cyclopoid copepods, small unidentified hydroptilid caddisflies, orthoclad and tanypodinid midges, and *Xanthocnemis*) varied significantly ($P < 0.05$) over time, but without obvious seasonal patterns in either wetland (Fig. 9G–L).

Five taxa had significant wetland × time interaction terms (Table 5), suggesting that their relative abundances varied inconsistently over time between the two wetlands. Relative abundances of orthoclad midges, cyclopoid copepods and *Paroxyethira* varied over time at Mahinapua but not at Shearer, where they were found only rarely (Fig. 9F, H & J). In contrast,

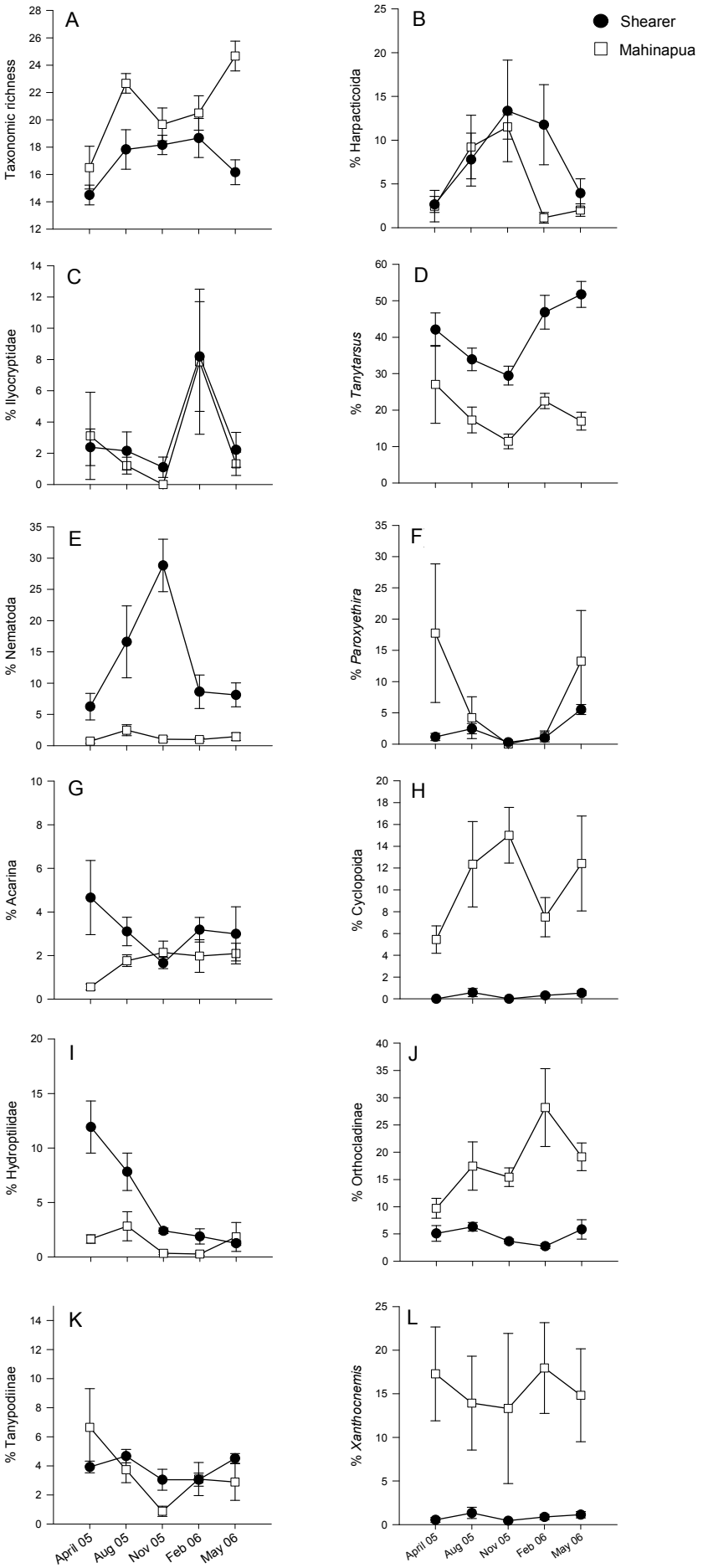


Figure 9. Seasonal patterns in taxonomic richness (A) and the percentage abundance of the 11 most common taxa (B–L) found in Shearer (black circles) and Mahinapua (open squares) wetlands over the 15-month study period (mean ± 1 SEM, $n = 6$).

TABLE 5. DENSITIES OF THE 11 MOST COMMON TAXA COLLECTED FROM THE TWO WETLANDS (MAHIANAPUA AND SHEARER) IN THE SEASONAL STUDY, AND TAXONOMIC RICHNESS, SHOWING COMPONENTS OF THE REPEATED MEASURE ANOVA MODEL TESTING FOR DIFFERENCES BETWEEN WETLANDS OVER TIME, AND THE INTERACTION. SIGNIFICANT EFFECTS ($P < 0.05$) ARE SHOWN IN BOLD.

TAXA	SOURCE	SS	DF	MEAN SQUARES	*F*-RATIO	*P*-VALUE
Acarina	Wetland	0.23	1	0.23	4.56	0.058
	Error	0.49	10	0.05		
	Time	0.31	4	0.08	0.66	0.627
	Time × Wetland	0.43	4	0.11	0.91	0.469
	Error	4.77	40	0.12		
Cycloipoida	Wetland	26.16	1	26.16	87.56	**<0.001**
	Error	2.99	10	0.30		
	Time	1.78	4	0.44	6.58	**<0.001**
	Time × Wetland	1.43	4	0.36	5.31	**0.002**
	Error	2.69	40	0.07		
Harpacticoida	Wetland	1.77	1	1.77	2.50	0.145
	Error	7.07	10	0.71		
	Time	3.81	4	0.95	6.93	**<0.001**
	Time × Wetland	1.86	4	0.47	3.39	**0.018**
	Error	5.49	40	0.14		
Hydroptilidae	Wetland	4.69	1	4.69	29.35	**<0.001**
	Error	1.59	10	0.16		
	Time	3.62	4	0.90	7.77	**<0.001**
	Time × Wetland	0.96	4	0.24	2.07	0.103
	Error	4.65	40	0.12		
Ilyocryptidae	Wetland	3.03	1	3.03	3.51	0.090
	Error	8.63	10	0.86		
	Time	5.07	4	1.27	7.21	**0.000**
	Time × Wetland	1.11	4	0.28	1.57	0.200
	Error	7.04	40	0.18		
Nematoda	Wetland	10.04	1	10.04	14.96	**0.003**
	Error	6.71	10	0.67		
	Time	2.56	4	0.64	4.40	**0.005**
	Time × Wetland	1.82	4	0.45	3.12	**0.025**
	Error	5.83	40	0.15		
Orthocladinae	Wetland	4.88	1	4.88	51.47	**<0.001**
	Error	0.95	10	0.09		
	Time	0.31	4	0.08	1.86	0.137
	Time × Wetland	0.82	4	0.20	4.93	**0.003**
	Error	1.65	40	0.04		
Paroxyethira	Wetland	0.45	1	0.45	0.40	0.539
	Error	11.21	10	1.12		
	Time	7.26	4	1.82	13.49	**0.000**
	Time × Wetland	1.94	4	0.49	3.61	**0.013**
	Error					
Tanypodinae	Wetland	0.54	1	0.54	2.38	0.154
	Error	2.27	10	0.23		
	Time	0.999	4	0.25	5.10	**0.002**
	Time × Wetland	0.48	4	0.12	2.45	0.062
	Error	1.96	40	0.05		
Tanytarsus	Wetland	3.79	1	3.79	28.45	**0.000**
	Error	1.33	10	0.13		
	Time	0.77	4	0.19	3.11	**0.026**
	Time × Wetland	0.12	4	0.03	0.49	0.738
	Error	2.47	40	0.06		

Continued on next page

Table 5 continued

TAXA	SOURCE	SS	DF	MEAN SQUARES	*F*-RATIO	*P*-VALUE
Xanthocnemis	Wetland	13.85	1	13.85	17.32	**0.002**
	Error	7.99	10	0.80		
	Time	1.58	4	0.39	3.62	**0.013**
	Time × Wetland	0.99	4	0.25	2.26	0.080
	Error	4.37	40	0.11		
Richness	Wetland	209.07	1	209.07	14.61	**0.003**
	Error	143.07	10	14.31		
	Time	193.73	4	48.43	7.71	**0.000**
	Time × Wetland	106.60	4	26.65	4.24	**0.006**
	Error	251.27	40	6.28		

the relative abundance of Nematoda varied greatly over time at Shearer, but was relatively constant (and low) at Mahinapua. In both wetlands, the relative abundance of harpacticoid copepods was low in autumn and then increased to a peak in late spring; however, it then declined markedly in summer at Mahinapua, whilst remaining high in summer before declining in winter at Shearer.

Despite the observed temporal changes to the invertebrate communities in Mahinapua and Shearer, each wetland always supported discrete invertebrate communities, with no overlap at any time during the study (Fig. 10), despite inconsistent changes to relative abundances of some of the common taxa. Thus, there appeared to be consistent differences in the invertebrate communities between the two wetlands, so that the community composition of the low pH wetland always differed from that of the higher pH wetland.

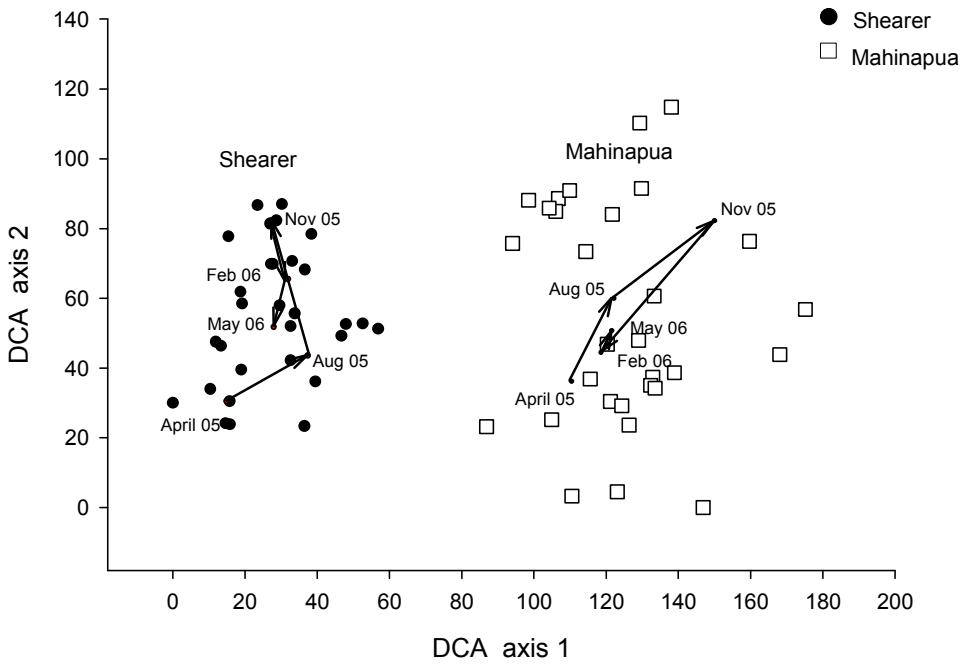


Figure 10. Detrended correspondence analysis (DCA) ordination of invertebrate communities collected from the Shearer and Mahinapua wetlands showing the temporal trajectories of communities in each wetland during the study.

4.3 DISCUSSION

This study sought to determine the degree of temporal variability in invertebrate communities in perennial wetlands, and whether such variability would confound surveys of wetlands conducted over seasons, or years. Our results consistently demonstrated that although invertebrate communities within wetlands varied both interannually and seasonally, the degree of this temporal variation was relatively small compared with larger scale differences operating either within a wetland as a result of variable environmental conditions (Bullock Creek) or between wetlands (Mahinapua and Shearer). This suggests that the composition of invertebrate communities within wetlands is largely constrained by overarching factors, such as water chemistry, which exert their influence over long time-scales. Consequently, as long as water quality and physical conditions differ between wetlands, so too will the invertebrate communities. Thus, surveys of invertebrate communities in New Zealand wetlands may not be particularly sensitive to the time of sampling. This result suggests that any comparisons of invertebrate samples collected from wetlands throughout the country at different times can still be made, as the fauna characteristic of, for example, low pH fens will always be distinct from that of higher pH swamps.

Of relevance to this finding are those from studies into temporal dynamics of river-dwelling invertebrates. For example, Scarsbrook (2002) studied the invertebrate communities of 26 New Zealand rivers over 9 years and showed that they fluctuated around a relatively stable state at each site, with little evidence of trajectories or sudden shifts. A similar finding was highlighted by Winterbourn (1997), in a 5-year study of invertebrate communities in three mountain streams. Other studies (Weatherley & Ormerod 1990; Armitage & Gunn 1996) have reported only slight changes in community composition in streams where habitat conditions remain relatively constant, and confirm Scarsbrook's contention that communities undergo significant changes in composition only when habitat conditions change significantly.

While relative abundances of some invertebrates varied aseasonally, others such as micro-crustacea (harpacticoid copepods and ilyocryptid cladocera) and *Tanytarsus* did show seasonal patterns, most likely reflecting the more stable habitat conditions within wetlands[1]. This contrasts with the lack of seasonality displayed by many common invertebrates found in New Zealand rivers such as the common mayfly *Deleatidium* in gravel-bed streams (Winterbourn 1974; Huryn 1996; Greenwood & McIntosh 2004), or midges in alpine (Suren 1991) or subalpine (Boothroyd 1988) streams. Lack of seasonality in invertebrate densities in rivers may be a response to their unpredictable flow regimes (Towns 1981; Winterbourn et al. 1981; Boothroyd 1988) and destruction of invertebrate populations during floods (Matthaei et al. 2000; Biggs et al. 2001). Consequently,

[1] It could be argued that the observed seasonal pattern of these mostly small invertebrates may be due to sampling error caused by relatively few replicates and large mesh size (relative to dominant taxa). However, this is unlikely, as any inefficiency due to our large sieve size would have been constant over time. Furthermore, although many of the smaller taxa may have passed through the 0.3-mm mesh, the reality is that this mesh size soon became clogged with detritus, etc., meaning that the net was likely to capture even small animals. The error terms associated with our sample size (six replicates per wetland) was also less then the estimate of the mean, and seasonal patterns were detected in the data even with this low degree of replication.

many invertebrates in rivers display highest densities during periods of stable flow, irrespective of season (Scrimgeour 1991; Holomuzki & Biggs 1999; Suren & Jowett 2006).

In contrast, wetlands do not experience the same types of disturbances as a result of floods as rivers—particularly those associated with high velocity and substrate movement. Although water depth may increase during a flood, fast, bed-moving flows similar to those that disturb river invertebrates are unlikely. For example, Sorrell et al. (2007) found that although water depth at Bullock Creek increased by up to seven times during a rainfall period, velocity only doubled, from 0.2 m/s to 0.4 m/s. Even this higher velocity would not have caused the gravel-bed substrate of the drains to move.

Disturbances in wetlands would, instead, most likely occur as a result of desiccation, when habitats such as leads or small ponds dry, which would usually occur in ephemeral wetlands or during times of drought. Permanent wetlands (and, particularly, habitats such as big ponds or channels) such as those sampled here, would rarely (if ever) dry, except in exceptional circumstances. Invertebrate communities differ between permanent and temporary wetlands (e.g. Batzer & Wissinger 1996; Wellborn et al. 1996; Wissinger et al. 2009), reflecting, amongst other things, a loss of taxa that cannot complete their life cycle in habitats that dry. Because all the wetlands studied here were permanent, factors associated with drying would not control the invertebrate communities. Instead, seasonal variables such as climate (e.g. temperature, daylight hours) may control the relative abundance of different invertebrate taxa. The fact that five of the nine taxa examined in this study showed clear seasonal patterns in at least one wetland support this contention.

4.4 CONCLUSIONS

Prior to this work, we were faced with two major questions: what sort of habitats do we need to sample within wetlands to best characterise their invertebrate communities, and what are the implications of temporal changes in invertebrate communities with respect to our ability to discriminate between wetlands on the basis of these communities? The results of the spatial study showed that invertebrate communities varied more between different wetlands than they did between habitats or plants within a wetland. Such differences presumably reflected differences in water chemistry between wetlands. If water chemistry was responsible for structuring invertebrate communities, there would be no biological reasons why invertebrate communities would change between different habitats within a wetland, as long as water chemistry within these habitats was similar. This caveat was demonstrated at the Bullock Creek wetland, where considerable differences existed between the drains. Such differences were most likely attributable to the large variation in pH in this wetland—caused by the proximity of different geological formations which would have influenced water chemistry at a local scale. Based on these findings, we suggest that invertebrates be collected from a wide range of aquatic habitats within a wetland, and that within each habitat as many micro-habitats as possible are sampled, including vegetated and non-vegetated areas. Sweep nets, used as described in section 2.3, are ideally suited for this task.

The temporal study showed that although the relative abundances of some wetland invertebrate taxa change over time, the effect of these changes is relatively small, and does not influence our ability to discriminate between wetlands on the basis of their invertebrate communities. This is a similar finding to that in river ecosystems, where community composition fluctuates around a relatively stable state at each site. The implication here is that the outcomes of large-scale surveys of invertebrate communities throughout New Zealand wetlands may not be particularly sensitive to the time of sampling, as the faunal differences between different wetlands are expected to transcend those caused by seasonal changes. As such, the invertebrate fauna of fens will always be distinct from that of swamps.

5. National distribution patterns

This section describes the findings from a large-scale survey of wetlands throughout New Zealand. The objectives of this third sampling programme were to better document the invertebrate biodiversity of lowland wetlands throughout New Zealand and to investigate the factors responsible for community composition. If invertebrate communities show strong regional differences, such knowledge will be vital from a conservation perspective. For example, conservation strategies implemented to maintain wetland biodiversity values may depend on the distribution of specific invertebrate taxa and may differ in regions that show particularly high biodiversity values such as high endemism.

5.1 METHODS

5.1.1 Field and laboratory methods

We sampled 40 lowland wetlands in ten geographic regions throughout New Zealand (Fig. 11). These correspond to the regions used by Ausseil et al. (2008), with the exception that we recognised only one Northland region (as opposed to three), and that we recognised South Westland (south of the Whataroa River) as distinct from one region (Westland). Wetlands were chosen to encompass as wide a range of latitude as possible, and to have a wide range of water chemistry and plant communities. To minimise potential effects of land-use activities on invertebrate communities, only wetlands with minimal human activities in their catchments were sampled. Such wetlands were selected with the help of experienced local ecologists who confirmed sites to be amongst those with the best condition in each region. Furthermore, wetlands were restricted to low-elevation areas (i.e. < 250 m a.s.l.) to minimise any influence that altitude may have on wetland invertebrates (which is currently unknown). Also, wetlands in lowland areas have experienced the highest loss due to land development, so remnant wetlands in these areas are more likely to be of interest to conservation managers

Within each wetland, different types of open-water habitat were identified (i.e. small or large ponds, leads, or channels; see section 2.2), and three habitats were selected, from which duplicate invertebrate samples were collected semi-quantitatively using a hand-held sweep net (300-µm mesh; see section 2.3.1 and Suren et al. (2007) for further information), giving six samples per wetland.

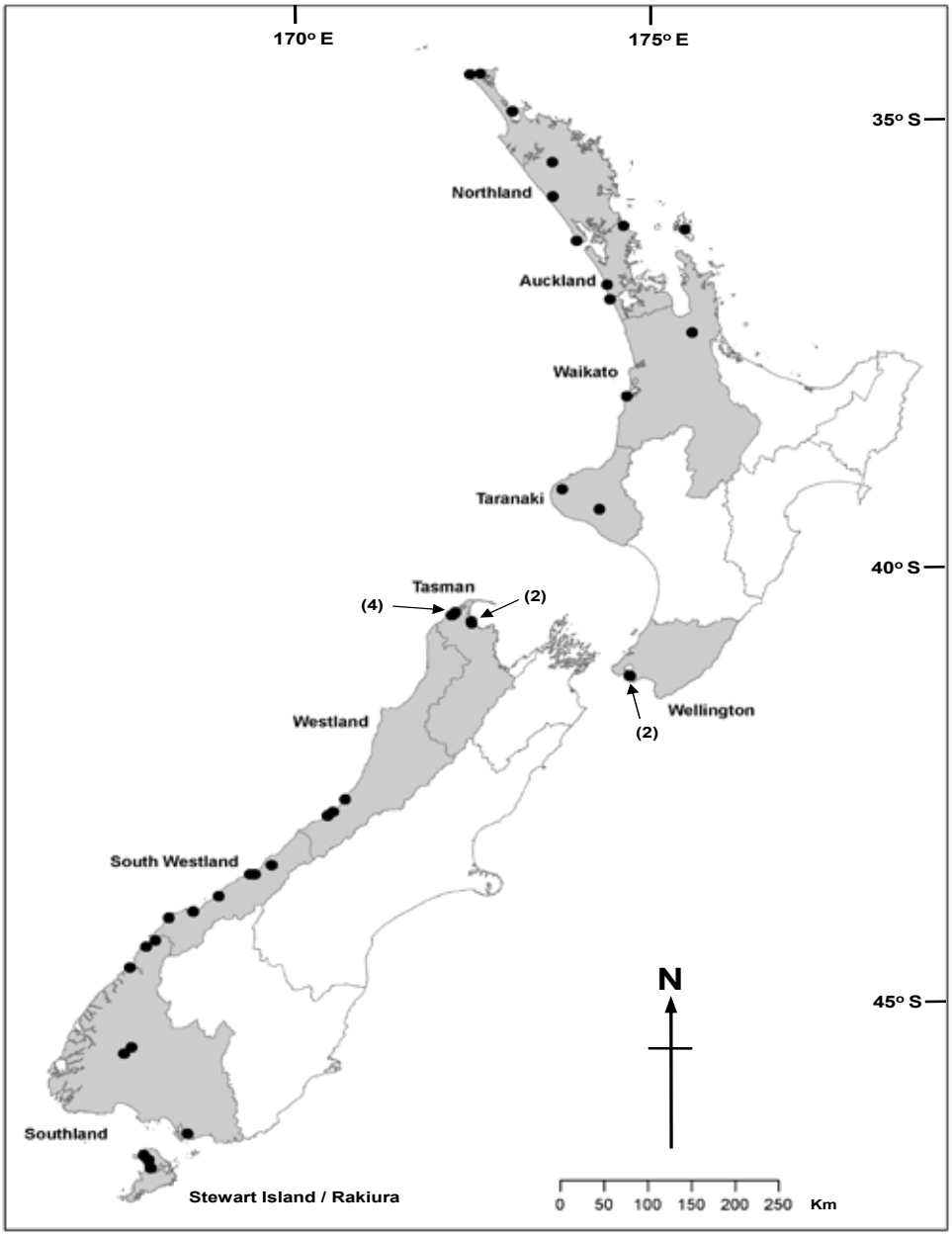


Figure 11. Map of New Zealand showing the location of the 40 wetlands sampled in ten geographic regions throughout the country.

The location of each sample was recorded using a Garmin® GPS. Spot measurements of water chemistry (temperature, pH and conductivity) were also made at each habitat within each wetland using a Horiba® multiprobe. Water samples were collected and filtered (Millipore® GFF filters) and stored frozen (–18°) prior to analysis. Invertebrate samples were processed according to the protocol outlined in section 2.3.3 and in Suren et al. (2007). All water samples were analysed for nutrients (NH_4-N, NO_3-N, DRP, TDP and TDN) using standard methods (see section 3.1.1.).

5.1.2 Physical data

Physical data were collected according to a spatial hierarchy of three levels (Table 6). The smallest level ('microscale') was at the habitat scale, and was based on conditions within each wetland sampled. These variables included water quality data (pH, conductivity and nutrients), the spatial coordinates of each sampling site (based on GPS eastings and northings), and the type of aquatic

TABLE 6. LIST OF ENVIRONMENTAL VARIABLES OBTAINED FROM EACH WETLAND. VARIABLES WERE MEASURED IN THE FIELD (WATER QUALITY, EASTING AND NORTHING) OR DERIVED FROM GIS DATABASES.

SPATIAL SCALE	VARIABLE TYPE	VARIABLE	DESCRIPTION
Sample (Microscale)	Water quality	pH	Wetland water pH
		Cond	Spot conductivity (µS/cm)
		Spot_Temp	Spot water temperature (°C)
		NH4	Ammonia concentration (mg/L)
		NO3	Nitrate-N concentration (mg/L)
		DRP	Dissolved reactive phosphorus (mg/L)
		TDP	Total dissolved phosphorus (mg/L)
		TDN	Total dissolved nitrogen (mg/L)
	Spatial	Easting	GPS derived easting (NZMS Series 260)
		Northing	GPS derived northing (NZMS Series 260)
	Physical	Type (4)	Channel, Lead, Small Pond, Large Pond
Wetland (Mesoscale)	Physical	Area	Wetland area (ha)
		DistToSea	Distance to sea (km)
		Elevation	Mean wetland elevation (m a.s.l.)
		Slope	Mean wetland slope (°)
		Ecological Integrity Index	Pressure index (0–1)
		Region (10)	Region 1 to 10
	Geology	Alluvium	% alluvium
		Calc	% calcium dominated rocks
		Glacial	% glacial material
		Hard	% of hard rock in the catchment
		Peat	% peat
		Phos	% phosphorus bearing rocks
	Landcover	Bare	% bare cover
		ExoticForest	% exotic foreign
		IndigForest	% indigenous forest
		Pasture	% pasture cover
		Scrub	% scrub cover
		Tsock	% tussock
		Wetland	% wetland
		MiscLandCover	% miscellaneous land cover (e.g. urban, snow, ice)
Regional (Macroscale)	Climate	TCold	Average annual minimum temperature (°C)
		TWarm	Average annual maximum temperature (°C)
		SolarSum	Average annual summer solar radiation (W/m)
		SolarWin	Average annual winter solar radiation (W/m)
		AnnRain	Average annual rainfall (mm)
		PET	Potential evapotranspiration (mm)
		Rain10	Number of days with >10 mm rain per month
		Rain20	Number of days with >20 mm rain per month
		Rain50	Number of days with >50 mm rain per month
		Rain100	Number of days with >100 mm rain per month
		Rain200	Number of days with >200 mm rain per month

habitat. These habitat variables were treated as dummy variables, and recorded as either channel, lead, large pond or small pond. The next level of the hierarchy (mesoscale) described the wetland, and included variables such as wetland area, distance to sea, mean elevation, geology, dominant vegetation within the wetland and wetland condition, as assessed by the index of ecological integrity (IEI), extracted from the GIS databases developed by Ausseil et al. (2008). The different geographic regions were also included in this level, and coded as dummy variables (e.g. Region1, Region2, … Region9, Region10). The macroscale level in the hierarchy ('regional') included all climatic data, such as temperature, solar radiation, annual rainfall, and potential evapotranspiration (Table 6).

All microscale variables were collected in the field. Other wetland-related and climatic variables were derived from GIS databases, including the New Zealand Land Cover Database (LCDB), and the Freshwater Environments of New Zealand (FWENZ) database (Wild et al. 2005; Leathwick et al. 2007). Polygon boundaries were placed around each wetland and their catchment, based on a digital elevation model with a 20-m resolution. Catchment boundaries in hilly areas were easily defined by the DEM, while those in less steep regions were not as clear. In these cases, each catchment boundary was examined in detail and altered according to aerial photographs and field-based observations. A total of 55 variables were thus obtained for each sample: 14 mesoscale variables, 30 wetland variables, and 11 regional variables (Table 6).

The geological variables included the percentage of alluvium and peat in the catchment, the percentage of calcium- and phosphorus-bearing rocks, and an assessment of the degree of rock hardness (i.e. propensity to produce sediment). The land cover variables indicated the percentage of the catchment that was covered by six different land-use categories: bare, exotic forest, indigenous forest, pasture, scrub and tussock.

The climatic variables included average winter and summer temperature (°C) and solar radiation (W/m^2), as well as average annual rainfall (mm), and average annual potential evapotranspiration (mm). Five variables expressing rainfall intensity were also calculated, showing the number of days per month where more than 10, 20, 50, 100 and 200 mm of rain fell. This gave an index of rainfall intensity (Wild et al. 2005).

5.1.3 Statistical analysis

The 55 measured or derived environmental variables were examined for collinearity. Highly correlated variables were then removed, leaving 40 variables. Four complementary multivariate analyses were run on the data.

Firstly, an ordination was performed (using detrended correspondence analysis (DCA); McCune & Mefford 1997) on the log-transformed percentage data, to see whether discrete invertebrate communities existed in the 40 wetlands. This statistical technique graphically represents the location of samples based on their invertebrate communities, such that samples with similar communities appear close together on a graph, and samples with very different communities appear far apart from each other. Samples were plotted in two dimensions with arbitrary sample scores. A useful feature of the DCA technique is the calculation of a separate *gradient length* along both axes 1 and 2. This is a measure of the degree to which species composition changes along the ordination axis. A large gradient length (> 4) indicates almost complete species turnover along

the ordination axis, so that samples at opposite ends of an axis share no taxa in common. Invertebrate percentage abundance data and environmental variables (log-transformed to achieve normality) were regressed against the DCA ordination scores to see which taxa and which environmental variables were responsible for observed groupings in the data.

Secondly, biological data were classified by TWINSPAN analysis (McCune & Mefford 1997) to see if invertebrate communities formed discrete assemblages. TWINSPAN is a dichotomous classification technique that at each level of its division produces 2, 4 and 8 and groupings after the first, second and third divisions, respectively. As with any classification, there is a trade-off between the number of groups that are created, and the classification strength: the more groups there are, the less the differences between them. Differences in measured environmental parameters between the TWINSPAN groups were assessed by ANOVA.

Thirdly, a Bray-Curtis similarity matrix was created for the percentage abundance data, so that samples which supported identical communities had a similarity of 1, and samples that had no taxa in common had a similarity of 0. Each wetland sample was then allocated to a particular grouping based on island, region, wetland type (i.e. bog, fen, swamp, shallow water) and pH (see below). Analysis of similarity (ANOSIM) was then used to see whether the invertebrate communities differed between these groups. This technique tests the hypothesis of no differences between groups of samples, using permutation/randomisation methods on the Bray-Curtis similarity matrix. The method calculates an *R* statistic, which can range from 0 (no differences in sample groups) to 1 (all sample groups are different to each other).

Finally, stepwise multiple regression analysis (SPSS 2000) was used to see how relative abundances of the 20 most common taxa collected in all wetlands were related to the 40 measured environmental variables. Stepwise multiple regressions were also done for the calculated DCA ordination scores, and taxonomic richness. The independent variables included all environmental data previously used in the ordination analysis. Both forwards and backwards regression models were run, with $\alpha = 0.05$ for variables to be entered and removed from the model. The model with the highest r^2 value was subsequently chosen.

5.2 RESULTS

5.2.1 Physical conditions

Wetland size varied greatly, from a minimum of 3.8 ha (Longfords, near Collingwood, South Island), to a maximum of 9692 ha (Kopuatai Peat Dome, near Hamilton, North Island) (Table 7). Just over half of the wetlands surveyed were less than 100 ha in size. The average distance to the sea was 4.7 km (Table 7). As expected, climatic conditions (e.g. temperature, solar radiation and rainfall) varied greatly between wetlands (Table 7), most likely reflecting the broad latitudinal gradient included in the study. For all wetlands, the calculated Ecological Integrity Index was relatively high (average = 0.65), although two wetlands (Corbett Reserve and Lake Tomarata) had very low index scores (< 0.2). The low scores reflected the fact that these relatively small wetlands (< 5 ha) were surrounded by highly modified landscapes dominated by pasture, or pasture and exotic forest. However, both still had relatively untouched riparian margins that

TABLE 7. SUMMARY STATISTICS OF THE 40 SELECTED ENVIRONMENTAL VARIABLES SHOWING MEAN, MINIMUM AND MAXIMUM VALUES OF ALL 40 SURVEYED WETLANDS.

TYPE	VARIABLE	MIN	AVERAGE	MAX
Water quality	pH	3.9	5.9	8.9
	Cond	20.0	167.7	3810.0
	Spot_Temp	7.4	16.4	23.6
	NH4-N	1	27	1367
	NO3-N	0.5	16.6	312.0
	DRP	0.2	8.6	530.0
	TDN	84.5	403.6	1420.0
	Water types (4)		(categorical)	
Physical	Area	3.8	667.0	9692.0
	Distance to Sea	0.8	4.7	35.3
	Slope	0.0	1.8	7.4
	Elevation	2	35	227
	Ecological Integrity Index	0.197	0.650	0.959
	Region (10)		(categorical)	
Geology	Alluvium	0.0	0.4	1.0
	Hard	1.0	2.7	4.3
	Phos	1.0	2.0	4.1
Landcover	Bare	0.0	0.3	10.0
	ExoticForest	0.0	1.1	30.0
	IndigForest	0.0	11.3	73.7
	MiscLandCover	0.0	0.7	11.0
	Pasture	0.0	12.3	100.0
	Scrub	0.0	42.3	98.0
	Tsock	0.0	2.2	84.0
	Wetland	0.0	23.8	92.5
Climate	TCold	3.8	7.9	12.6
	SolarWin	345.1	543.1	740.0
	Rain100	0.001	0.107	0.307
	Rain200	0.000	0.004	0.011

were dominated by native wetland vegetation, so in the interest of maintaining a national coverage of wetlands, we decided to still include these wetlands in the analysis, despite their less than pristine status.

Catchment land cover varied greatly between the different wetlands, with some wetlands being surrounded mostly by pasture, and others being found in catchments dominated by scrub, tussock or indigenous forest (Table 7). A very wide range of water quality conditions were encountered; for example, pH ranged by a factor of five, and conductivity showed almost 200-fold variation (Table 7). Nutrient concentration also varied widely between wetlands, with the greatest variation in DRP and NH_4-N (where concentrations differed by up to 2600 and 1370 times, respectively), and the least variation in TDN (where concentration variation was only 17-fold).

5.2.2 Invertebrate communities

A total of 133 taxa were identified from the 40 wetlands. Across all wetlands, the fauna was dominated by chironomid midges (*Tanytarsus*—11.1%; Orthocladiinae—4.9; and Tanypodinae—4.0%), aquatic mites (7.5%), cyclopoid

and harpacticoid copepods (7.2% and 5.2%, respectively), nematodes (7.0%) and ostracods (6.2%). With the exception of midges, aquatic insects made up a small proportion of relative abundance, with the most common insects being the damselfly *Xanthocnemis zealandicus* (3.2%) and the hydroptilid caddisfly *Oxyethira* (1.8%). The most widespread taxa were Acarina, which were found at 90% of sites, followed by nematodes and cyclopoid copepods (88% of sites), oligochaetes, *Xanthocnemis*, Orthocladiinae and Ceratopogonidae (all found at approximately 80% of sites). The most diverse invertebrate groups were the Diptera (31 taxa), Trichoptera (25 taxa) and Crustacea (21 taxa).

A plot of cumulative taxonomic richness against the number of wetland samples (arranged in a latitudinal gradient from north to south) shows that a distinct plateau was reached after about the 24th wetland, at which point 116 taxa (or 88% of the total richness) had been recorded. After this, the number of new taxa found in each wetland decreased considerably (Fig. 12). A similar trend was observed if the wetlands were arranged in a different order (unpubl. data). Taxonomic richness differed greatly between the ten regions surveyed, with the lowest richness in Taranaki and Stewart Island/Rakiura, and the highest richness in Northwest Nelson and Southland (Table 8). No unique taxa were found in any of the North Island wetlands, whereas 14 unique taxa were found in wetlands in Northwest Nelson, and six unique taxa in wetlands in both Southland and Westland (Tables 8 and 9). Nineteen taxa were found in wetlands in all regions, including two damselflies (*Austrolestes* and *Xanthocnemis*), three hemipterans and four microcrustacea (two cladoceran and copepod families), as well as water mites, oligochaetes, nematodes and tardigrades (Table 9).

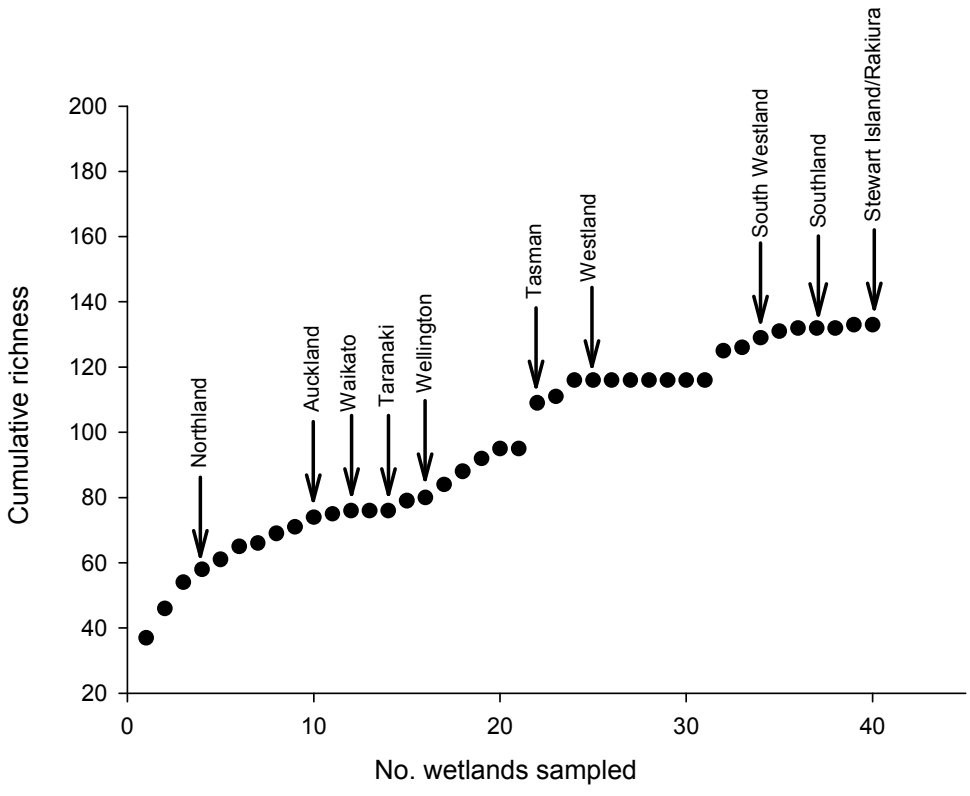


Figure 12. Plot of cumulative taxonomic richness versus the number of wetland samples collected, with the wetlands arranged in a latitudinal gradient from north to south.

TABLE 8. THE NUMBER OF WETLANDS SAMPLED, TAXONOMIC RICHNESS AND NUMBER OF UNIQUE TAXA IN EACH OF THE TEN REGIONS WITHIN NEW ZEALAND. NUMBER OF SAMPLES TAKEN FROM EACH REGION ARE GIVEN IN PARENTHESES.

REGION	NO. WETLANDS (SAMPLES)	TAXONOMIC RICHNESS	NO. UNIQUE TAXA
Northland	4 (24)	61	0
Auckland	6 (36)	64	0
Waikato	2 (12)	49	0
Taranaki	2 (12)	47	0
Wellington	2 (12)	52	0
Northwest Nelson	6 (36)	96	14
Westland	3 (21)	70	6
South Westland	9 (54)	77	7
Southland	3 (18)	82	6
Stewart Island/Rakiura	3 (18)	45	1

TABLE 9. LIST OF TAXA EITHER UNIQUE TO THE NORTHWEST NELSON, WESTLAND OR SOUTHLAND REGIONS, OR COSMOPOLITAN THROUGHOUT ALL 40 WETLANDS SAMPLED.

INVERTEBRATE GROUP	NORTHWEST NELSON	WESTLAND	SOUTHLAND	ALL REGIONS
Odonata				*Austrolestes colensonis* *Xanthocnemis*
Ephemeroptera	*Austroclima sepia* *Zephlebia versicolor*		*Oniscigaster wakefieldi*	
Plecoptera	*Cristaperla*	*Acroperla* *Taraperla*		
Hemiptera	Corixidae			*Anisops assimilis* *Sigara* *Microvelia*
Trichoptera	*Psilochorema nemorale*	*Paroxyethira tillyardi* *Psilochorema acheir* *Triplectidina*	*Hydrobiosis* sp.	
Coleoptera	Ptilodactylidae		*Rhantus* *Homeodytes* Elmidae	
Diptera	*Harrisius pallidus* Forcipomyiinae Syrphidae Tanyderidae	Staphylinidae		Ceratopogonidae *Chironomus zelandicus* Orthocladiinae *Tanytarsus* Tanypodiinae
Collembola				Collembola
Crustacea	*Tenagomysis chiltoni* Ostracoda sp. G *Paranephrops planifrons*		Macrothricidae	Chydoridae Cyclopoida Daphniidae Harpacticoida
Acarina				Acarina
Mollusca	*Hyridella menziesi*			
Nematoda				Nematoda
Oligochaeta				Oligochaeta
Tardigrada				Tardigrada

5.2.3 Multivariate analyses

The DCA ordination of the invertebrate data showed relatively large gradient lengths on axis 1 (3.76) and axis 2 (2.44), suggesting a high degree of species turnover along each of these axes. Correlations of invertebrate data with the DCA scores showed that microcrustacea and molluscs, leeches (Hirudinea), worms (Oligochatea) and flatworms (Platyhelminthes) were characteristic of samples with high axis 1 scores (Fig. 13). Correlations with environmental data showed that wetlands with high winter temperatures, high solar winter radiation, large amounts of hard sedimentary rock and pasture land-use in the catchment, and with high pH, were characteristic of samples with high axis 1 scores. Low axis one scores were characterised by high densities of three midge taxa (Chironominae, Tanypodinae and *Tanytarsus*), hydroptilid caddisflies (*Paroxyethira*) and aquatic mites (Acarina) (Fig. 13). These sites were colder, had less winter solar radiation, more alluvium in their catchment, and low pH waters.

Correlations of invertebrate density with the DCA axis 2 scores showed that four microcrustacea (cyclopoids, *Daphnia*, *Ilyocryptus* and ostracods), Acarina, Hirudinea and Platyhelminthes were characteristic of samples with high axis 2 scores, while three crustacea (amphipods, isopods and the freshwater

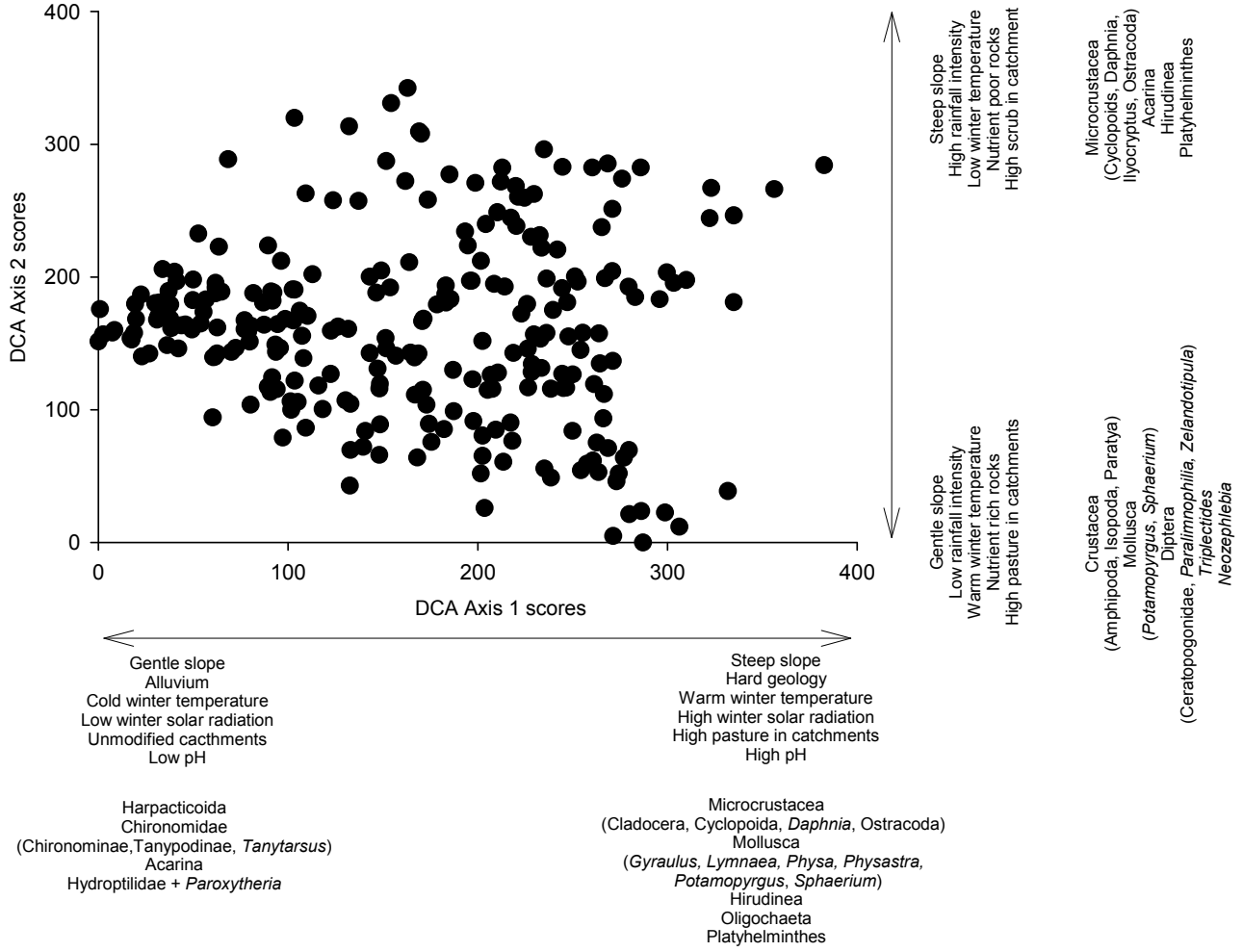


Figure 13. Detrended correspondence analysis (DCA) of invertebrate data collected in the 40 wetlands sampled throughout New Zealand showing group membership according to region. The invertebrate taxa and environmental parameters that showed significant correlations ($r^2 > 0.4$, $P < 0.01$) to the axis 1 or 2 ordination scores are also shown.

shrimp *Paratya*), two molluscs (*Potamopyrgus* and *Sphaerium*), three diptera (Ceratopogonidae, *Paralimnophilia* and *Zelandotipula*), the leptocerid caddisfly *Triplectides*, and the mayfly *Neozephlebia* were characteristic of sites with low axis 2 scores. Environmental parameters such as water quality, climate (rainfall and temperature) and land-use variables also differed along axis 2 (Fig. 13).

The TWINSPAN analysis was arrested after the second division, producing four groups (Fig. 14). Further divisions yielded less-powerful differences between the smaller groups (unpubl. data). The first division was primarily based on a geographical separation between the North and South Islands, while the second division was based more on regions. Thus, samples collected from Tasman were separate from those from South Westland, Westland, Southland and Stewart Island/ Rakiura. Within the North Island samples, wetlands in Northland were grouped separately from those from Auckland, Taranaki and Wellington. Wetlands from the Waikato were found in all four sample groups, suggesting that their faunas were relatively cosmopolitan. ANOVA of environmental variables showed that the biggest difference between the four TWINSPAN groups was due to wetland pH, followed by average annual minimum temperature and winter solar radiation. On the basis of these results, we created three distinct pH classes: low pH wetlands (< 5.5); medium pH wetlands (5.6–6.5); high pH wetlands (> 6.5).

ANOSIM showed that there were very similar differences in invertebrate community composition when all the wetlands were grouped according to island, region, pH group or wetland type (Figs 15, 16 & 17). Calculated *R* values were similar, suggesting that these factors were equally important in structuring the invertebrate community composition.

Stepwise regression models for the 20 most commonly collected taxa, as well as the DCA axis 1 and 2 ordination scores and taxonomic richness were relatively powerful, with an average r^2 of 0.58 (Table 10). Highest predictive power ($r^2 > 0.700$) came from models for Amphipoda, Cladocera, Platyhelminthes, Tanypodinae, and DCA axis 1 scores. All of the 40 environmental variables used in the analysis were included in a least one of the resultant models, which generally contained many significant explanatory variables. All regression models had at least half of the 40 independent variables in the final regression

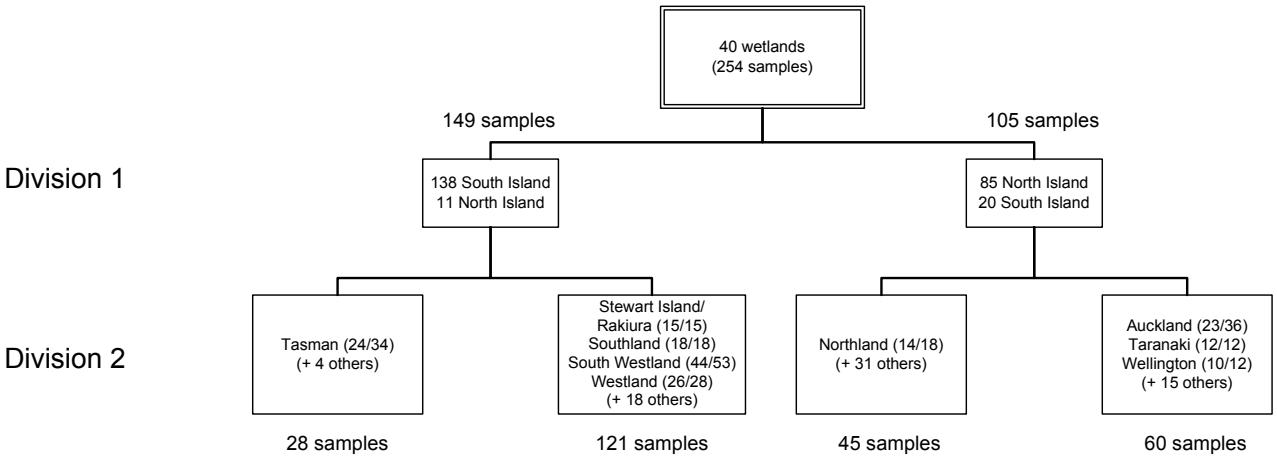


Figure 14. Results of the TWINSPAN analysis (arrested after the second division) showing the number of samples in each sample grouping and the location of each sample (North or South Island) in the first division, or the Region in the second division. For the second division, only the most common regions in each group are shown, along with the number of wetlands in each region in the group, and the total number of wetlands in that region (in parentheses).

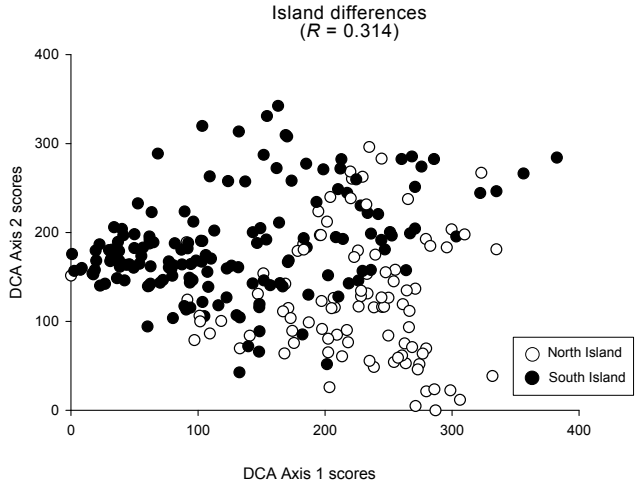


Figure 15. Detrended correspondence analysis (DCA) of invertebrate data collected from the 40 wetlands, showing membership according to either the North or South Islands. Also shown is the result of the ANOSIM analysis for between island differences.

equation (Table 10). At least three of the dummy variables coding for region were selected in all the regression models, emphasising the importance of this spatial variable in influencing invertebrate distributions. Other commonly selected variables included Alluvium, Conductivity and SolarWin (19 models), pH (18 models), and Rain100, Region 1, 5, 6 and 7 (17 models). The dummy coded regional variables were the most powerful variables in six of the resultant models, and second most powerful in eight models. Water pH was the most powerful predictor variable in four models, while alluvium and phosphorus-bearing rocks, indigenous forest and pasture, and one of the region variables were the most powerful variables in two models. Other important variables included exotic forest and scrub, the amount of winter solar radiation and TDN, each of which was the second most powerful variable in two models (Table 10).

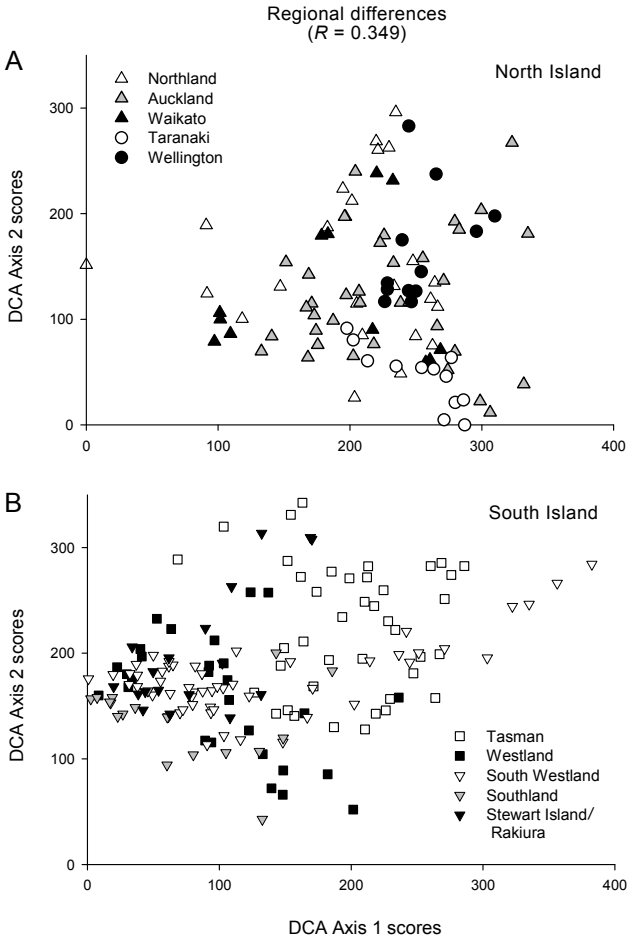


Figure 16. Detrended correspondence analysis (DCA) of invertebrate data collected from the 40 wetlands showing membership according to regions (partitioned into North Island (A) and South Island (B)). Also shown is the result of the ANOSIM analysis for between-region differences.

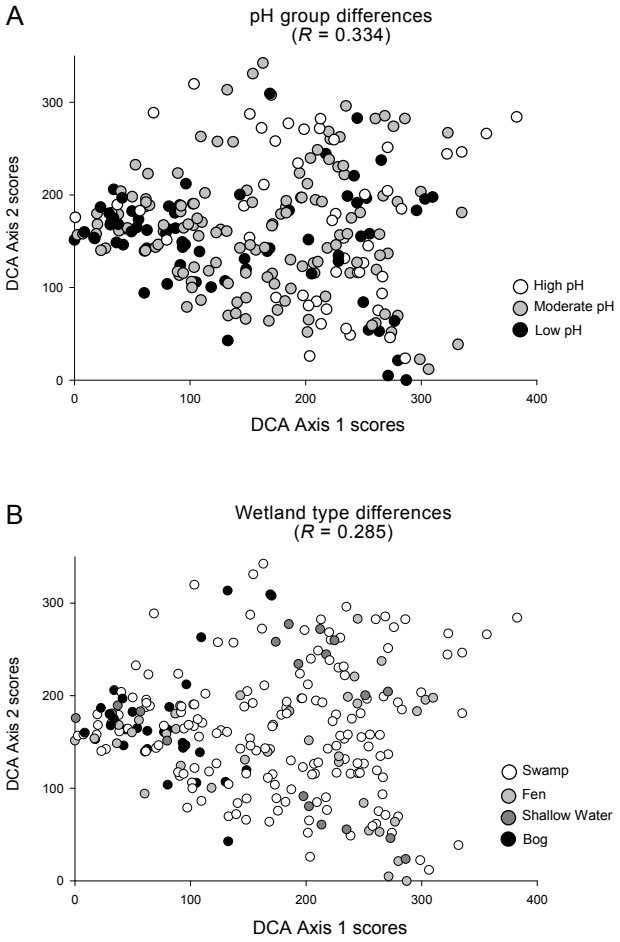


Figure 17. Detrended correspondence analysis (DCA) of invertebrate data collected in the 40 wetlands showing membership according to the pH derived groups (A), or the type of wetland (B) that samples were collected from. Also shown is the result of the ANOSIM analysis for differences between pH groups or wetland types.

TABLE 10. RESULTS OF STEPWISE MULTIPLE REGRESSION ANALYSIS ON COMMON INVERTEBRATE TAXA, DCA ORDINATION AXIS 1 AND 2 SCORES, AND TAXONOMIC RICHNESS SHOWING THE TWO MOST POWERFUL PREDICTOR VARIABLES SELECTED FOR EACH MODEL, AS WELL AS THE NUMBER OF VARIABLES IN EACH MODEL, THE MODEL *F*-RATIO, AND RESULTANT r^2 VALUE. ALL VARIABLES IN THE MODEL WERE SELECTED AT A SIGNIFICANCE LEVEL OF $\alpha = 0.05$. DIRECTION OF RELATIONSHIP IS INDICATED BY + (POSITIVE) OR – (NEGATIVE).

DEPENDENT VARIABLE	1ST VARIABLE	2ND VARIABLE	TOTAL NUMBER OF VARIABLES	MODEL *F*-RATIO	r^2 VALUE
Acarina	pH (–)	Region1 (+)	22	16.36	0.570
Amphipoda	Indigenous forest (–)	Wetland (–)	29	28.99	0.713
Ceratopogonidae	Region1 (+)	Region6 (–)	22	12.40	0.502
Cladocera	Region3 (–)	SolarWin (+)	22	38.62	0.758
Corynocera	Pasture (–)	Alluvium (+)	23	21.50	0.672
Cyclopoida	Phos (+)	Scrub (–)	25	14.23	0.536
Daphniidae	Lead (–)	TDN (+)	25	13.14	0.516
Harpacticoida	Region7 (+)	Exotic forest (+)	25	19.49	0.613
Ilyocryptidae	Hard (–)	Region3 (+)	22	7.90	0.391
Nematoda	Exotic forest (+)	IEI (+)	26	10.98	0.471
Oligochaeta	Region5 (–)	Phos (+)	22	9.20	0.428
Orthocladiinae	Indigenous Forest (+)	Scrub (+)	22	14.25	0.536
Ostracoda Species A	Region2 (+)	Region8 (+)	22	12.59	0.545
Ostracoda Species C	Pasture (–)	Alluvium (+)	27	15.23	0.615
Ostracoda Species H	Region7 (+)	Hard (+)	22	13.73	0.527
Platyhelminthes	Bare (+)	Region1 (+)	22	45.20	0.786
Potamopyrgus antipodarum	pH (+)	Region9 (+)	25	20.21	0.621
Tanypodinae	Phos (–)	Region8 (+)	22	29.24	0.704
Tanytarsus	pH (–)	TDN (+)	22	20.39	0.624
Xanthocnemis zelandicus	Wetland (+)	SolarWin (+)	22	9.27	0.430
DCA Axis 1 scores	pH (+)	Exotic forest (–)	27	30.83	0.726
DCA axis 2 scores	Alluvium (+)	Phos (–)	22	27.41	0.690
Richness	Alluvium (+)	Region4 (–)	23	12.103	0.548

5.3 DISCUSSION

5.3.1 Physical conditions

The range of wetlands sampled in this study represented the great diversity of lowland wetlands throughout New Zealand. Climatic variables changed in a predictable manner, with strong latitudinal temperature and solar radiation gradients between the extremes of the two Northland wetlands, and the three Stewart Island wetlands, some 1450 km to the south. Other climatic variables such as Rain100 or Rain 200 varied markedly throughout the country, but without obvious pattern.

Land cover varied greatly among wetlands, despite our desire to restrict sampling to the more pristine wetlands within each region. Although some of these differences reflected natural vegetation changes (for example, catchments dominated by tussock, scrub or indigenous forest), other wetlands were located in catchments dominated by pasture or exotic pine plantations. These wetlands also generally had lower ecological integrity scores. Their inclusion in the survey reflected our decision to survey as broad a spatial extent of New Zealand wetlands as possible, while still trying to minimise changes due to land use and other human activities.

There were strong gradients in pH, conductivity and nutrient regimes across the 40 wetlands, which partially reflected latitudinal trends in water quality variables. Thus, pH, conductivity, DRP and TDN were higher on average in North Island wetlands, and NO_3 was higher in South Island wetlands. The higher pH and conductivity in the North Island wetlands confirms the predominance of swamps in the North Island, and fens and bogs in the South Island. The higher DRP and TDN concentrations in the North Island wetlands may also be a result of these inherent differences in wetland classification, or may reflect the fact that the North Island wetlands were in more modified catchments than wetlands in the South Island. Catchments dominated by pasture or pine were more common in the North Island, whereas catchments dominated by native bush, tussock or scrub were more common in the South Island. Catchments modified by agriculture tend to have higher exports of nutrients such as DRP and TDN, whereas catchments dominated by native bush are known to be net exporters of NO_3 (Howard-Williams & Pickmere 1986).

5.3.2 Invertebrate communities

The invertebrate fauna of the sampled wetlands closely resembled the wetland fauna in other biogeographic regions, e.g. Australia (Robson & Clay 2005), USA (Whiles & Goldowitz 2005) and Europe (Oertli et al. 2002; Nicolet et al. 2004). Despite the predominance of non-insect groups (crustacea, nematodes, oligochaetes and snails), aquatic insects were the most diverse class, with 93 taxa recognised. However, the diversity of the non-insect groups was likely under-represented, because of identification to a coarser taxonomic level. Currently, there are no taxonomic identification guides that would have allowed identification of these groups to the same level as the aquatic insects. Some of the aquatic insects found in our surveys are more commonly found in rivers and streams, and are not regarded as 'typical' wetland inhabitants. For example, the presence of swimming mayflies such as *Nesameletus* and *Oniscigaster* in two South Westland sites, and the occurrence of two mayflies (*Austroclima* and *Zephlebia*) and the stonefly *Cristaperla* in one of the Northwest Nelson wetlands reflected the fact that these wetlands had channels, or small, slow-flowing streams flowing through them.

Comparison of the invertebrates found in the wetlands with those found in nationwide surveys of rivers and lakes reveals how invertebrate community composition differs between the three ecosystems (Table 11). Three taxa (the snail *Potamopyrgus antipodarum*, Oligochaeta and Orthocladiinae) were dominant members of the community in each ecosystem. The dipteran family Chironomidae were also common to all three ecosystem types, although the taxonomic composition differed between rivers, lakes and wetlands. Midges of the subfamily Diamesinae appear to be relatively common in rivers, and were found in Lake Coleridge. However, there was no record of this midge subfamily having been found in wetlands to date. The riverine fauna was dominated by aquatic insects (not including chironomid midges), whereas the lake and wetland fauna had more microcrustacea (e.g. copepods, ostracods, *Daphnia*) and aquatic mites. Absence of microcrustacea from riverine ecosystems most likely reflects the fact that they would simply be washed away from these fast-flowing systems, whereas lakes and wetlands represent far more stable environments for animals that are weak swimmers. The snail, *Potamopyrgus antipodarum*, was the

TABLE 11. LIST OF THE TEN MOST COMMON TAXA FOUND IN SURVEYS OF WETLANDS, RIVERS AND LAKES THROUGHOUT NEW ZEALAND. TAXA IN BOLD ARE FOUND IN ALL ECOSYSTEM TYPES.

WETLANDS* (n = 40)		RIVERS† (n = 975)		LAKES‡ (n = 9)	
TAXON	% ABUNDANCE	TAXON	% ABUNDANCE	TAXON	% ABUNDANCE
Tanytarsus	11.1	*Deleatidium*	21.0	***Potamopyrgus antipodarum***	29.2
Acarina	7.5	**Orthocladiinae**	9.6	**Oligochaeta**	5.6
Cyclopoida	7.2	Elmidae	9.2	Ostracoda	4.3
Nematoda	7.0	*Pycnocentrodes*	7.7	*Chironomus*	3.2
Harpacticoida	5.2	*Aoteapsyche*	4.9	*Cladopelma*	2.8
Orthocladiinae	4.9	***Potamopyrgus antipodarum***	4.9	*Daphnia*	2.8
Potamopyrgus antipodarum	**4.7**	**Chironominae**	**4.3**	*Sigara*	**2.7**
Ceratopogonidae	4.6	Diamesinae	4.2	*Gundlachia*	2.6
Oligochaeta	4.2	Ostracoda	3.9	Acarina	2.3
Tanypodinae	4.1	**Oligochaeta**	3.5	**Orthocladiinae**	2.1

* Wetland data sourced from the national survey data outlined in section 5.

† River data sourced from regional councils (Environment Waikato, West Coast Regional Council, Otago Regional Council, Environment Canterbury), NIWA surveys, and selected University of Canterbury theses.

‡ Lake data sourced from NIWA lake survey data.

dominant invertebrate in lakes, but was less common in wetlands, and absent from wetlands with a pH <6.6. Snails tend to be absent from low pH waters because of the associated low concentrations of free calcium (Oekland 1990).

5.3.3 Invertebrate–environment relationships

Despite the high taxonomic turnover observed in the ordination, 19 of the 133 taxa encountered were found in one or more samples from all wetlands, and many of these were also the most abundant. Part of the differences in taxonomic composition between wetlands could be attributable to the different habitats that were sampled in each of the wetlands (e.g. presence of slow-flowing channels in some wetlands, and not others), and the fact that some taxa were restricted to flowing habitats (e.g. presence of the mayflies *Nesamaletus* and *Oniscigaster* in South Westland wetlands).

The results of the TWINSPAN analysis showed clearly that invertebrate communities formed discrete groupings on the basis of geographic differences: inter-island differences were responsible mainly for groupings at the first division, and regional differences at the second. The resultant groups differed mostly on the basis of pH and climate-related variables. The DCA ordination also identified pH and climate-related variables as being responsible for structuring the invertebrate communities. Given the large differences in climate between the ten regions, it is not surprising that ANOSIM showed that pH and geographic location were of equal importance in structuring the invertebrate community composition.

The stepwise multiple regression (SMR) indicated that invertebrate communities are controlled by many different variables acting together, which collectively have a high influence on overall invertebrate distribution patterns rather than any single variable. As with the DCA, TWINSPAN and ANOSIM, the SMR models identified Region and pH as being some of the most powerful predictor variables.

Selection of the Region variable emphasises the fact that wetlands in the ten regions supported different invertebrate communities, and differed with respect to environmental parameters such as water quality, climate and land cover. Selection of the pH variable suggests that water pH (and therefore the class of wetland) plays an important role in structuring invertebrate communities, as has been found in other studies (Batzer & Wissinger 1996; Nicolet et al. 2004). This implies that there are, indeed, fundamental differences in the invertebrate communities of high pH swamps and lower pH fens/bogs.

The level of taxonomic resolution used in this study may have constrained our ability to detect patterns in the biological data, as well as to examine links between biota and environmental variables. Of the 20 taxa examined in the stepwise regression analysis, three were identified to the level of sub-class or higher, while 12 were identified to family or lower. Identifying some taxa to higher levels (and therefore 'lumping' taxa into broad groups) potentially ignores major habitat differentiation existing within specific groups. However, the level of taxonomic resolution used in this study was a result of a number of constraints, including lack of suitable identification guides (as previously mentioned), time and funding constraints, and the analytical strategy. Although we acknowledge the inherent problems in lumping taxa into broad groups, studies by Bowman & Bailey (1997) and Hewlett (2000) have shown that the effect of taxonomic resolution on our ability to describe the structure of freshwater invertebrate communities, and examine relationships between biota and environmental variables, are not as large as previously imagined. For example, Bowman & Bailey (1997) found identifying invertebrates to Genus, Family, Order, Class or Phylum had little effect on the resultant classification of sites. Hewlett (2000) found very similar correlations between environmental variables and invertebrates when identified to Species, Genus and Family. One reason for this is the aptly named 'hierarchical response to stress' (Pearson & Rosenberg 1978), which suggests that subtle environmental changes need identifications to species level, while greater environmental changes can be detected at higher taxonomic levels. Thus, large environmental differences between low pH fens and higher pH swamps would still be detectable, even if invertebrates were not identified to Species or Genus.

Fish have a large effect on wetland invertebrates through predation (Diehl 1992; Mallory et al. 1994; Tangen et al. 2003; Hornung & Foote 2006), with lower densities of large-bodied invertebrates such as Odonata, Coleoptera and Hemiptera being found in wetlands with fish. Examination of the freshwater fisheries database showed that 30 fish species were found in the 26 wetlands for which we had fisheries information (Table 12). The most common fish included shortfin and longfin eels, common and redfin bullies, inanga and kōkopu—all of which are known to consume aquatic invertebrates (McDowall 1990). The introduced mosquito fish *Gambusia* was observed in a least one wetland during sampling (Kaipeha, in Northland), so predation by this species may have altered the invertebrate community composition at this site—although a total of 35 invertebrate taxa were collected from this wetland, and this number was also the median number of taxa in all the 40 wetlands sampled. It is evident that further studies are needed to determine whether predation from introduced or native fish is responsible for structuring invertebrate community composition in New Zealand wetlands.

TABLE 12. LIST OF THE FISH SPECIES FOUND IN, OR WITHIN 5 km OF WETLANDS SURVEYED IN THIS STUDY.

Data were found for only 26 of the 40 wetlands; absence of data from the other 14 wetlands does not necessarily indicate an absence of fish from these wetlands, but more likely the lack of detailed investigation of these areas. All data obtained from the Freshwater Fish Database (www.niwa.co.nz/our-services/online-services/freshwater-fish-database; viewed December 2009).

COMMON NAME	SCIENTIFIC NAME	NUMBER OF WETLANDS (n = 26)
Shortfin eel	*Anguilla australis*	17
Common bully	*Gobiomorphus cotidianus*	15
Longfin eel	*Anguilla dieffenbachia*	15
Inanga	*Galaxias maculatus*	13
Giant kōkopu	*Galaxias argentus*	10
Banded kōkopu	*Galaxias fasciatus*	9
Redfin bully	*Gobiomorphus huttoni*	8
Black mudfish	*Neochannia*	6
Brown trout	*Salmo trutta*	6
Mosquito fish	*Gambusia affinis*	6
Goldfish	*Carassius auratus*	5
Catfish	*Ameiurus nebulosus*	4
Common smelt	*Retropinna retropinna*	4
Kōaro	*Galaxias brevipennis*	4
Kōura	*Paranephrops planifrons*	4
Perch	*Perca fluviatilis*	3
Torrentfish	*Cheimarrichthys fosteri*	3
Grey mullet	*Mugil cephalus*	2
Lamprey	*Geotria australis*	2
Rudd	*Scardunius erythrophthalmus*	2
Black flounder	*Rhombosolea retiaria*	1
Dart goby	*Parioglossus marginalis*	1
Giant bully	*Gobiomorphus gobioides*	1
Gollum galaxias	*Galaxias gollumoides*	1
Koi carp	*Cyprinus carpio*	1
Northland (burgundy) mudfish	*Neochanna heleios*	1
Shortjaw kōkopu	*Galaxias postvectus*	1
Tench	*Tinca tinca*	1
Upland bully	*Gobiomorphus breviceps*	1
Yelloweyed mullet	*Aldrichetta forsteri*	1

6. Conservation significance of wetlands for invertebrates and management implications

Invertebrate community composition has previously been shown to be linked to water pH (e.g. Batzer & Wissinger 1996; Evans et al. 1999; Nicolet et al. 2004), but our results indicate that it is also structured by inherent regional or biogeographical differences. This finding may have conservation and management implications. If swamps and fens/bogs are not uniformly distributed across regions, more conservation efforts may need to be placed into one wetland type in one particular region, and another wetland type in another region. If distributions of some invertebrates are controlled by biogeographic differences, then there are major implications for setting conservation and restoration goals for wetlands at a national level throughout the country; instead, regionally based conservation goals may need to be considered.

The regional differences found in this study are not surprising, especially given that invertebrate distribution patterns are controlled by many processes, including evolution, physiological and behavioural adaptations, climatic changes, sea level rise and glaciation, volcanic activity, dispersal ability, and human impacts (Boothroyd 2000). Some invertebrates (e.g. chironomid genera such as *Cricotopus*, *Eukieferiella*, *Chironomus* and *Polypedilum*; oligochaete genera such as *Nais* and *Tubifex*; and Trichoptera genera such as *Oxyethira* and *Oecetis*) are cosmopolitan, occurring throughout New Zealand (Boothroyd 2000). Other invertebrate groups, such as stoneflies and mayflies, show strong geographic patterns in their distributions e.g. stoneflies have greater diversity in Northwest Nelson and South Westland, and Trichoptera have greater diversity in the central regions of New Zealand (Boothroyd 2000). In this study, the highest numbers of unique invertebrate taxa were found in Northwest Nelson, mirroring a finding from Scarsbrook et al. (2007), who found that this region was identified as a biodiversity hotspot for spring macroinvertebrates.

The fauna of wetlands throughout New Zealand was numerically dominated by five major invertebrate groups: chironomid midges, aquatic mites, microcrustacea (including copepods and ostracods), and aquatic nematodes. The New Zealand chironomid fauna is becoming relatively well known, with keys provided by Boothroyd (2001), Winterbourn et al. (2006), and the NIWA quick guide series (see www.niwa.co.nz/our-science/aquatic-biodiversity-and-biosecurity/tools; viewed February 2010). Unfortunately, our ability to easily and accurately identify many of the other common wetland invertebrate groups to Family, Genus or Species is still limited, due to the lack of suitable identification guides. For example, to the best of our knowledge, keys to only some aquatic mites (e.g. Cook 1983; Olsen 2007: www.niwa.co.nz/our-science/aquatic-biodiversity-and-biosecurity/research-projects/all/freshbiodiversity/tools#id; viewed February 2010), and copepods (Chapman & Lewis 1976) exist, and we are not aware of any keys to the freshwater ostracods or aquatic nematodes in New Zealand. Therefore, the biodiversity values of the wetlands we sampled cannot be fully evaluated. In the absence of more detailed keys, different morphological groups of each taxon can only be given a unique voucher identification.

Many of the invertebrate groups that we could not identify belonged to the meiofauna (i.e. animals that can pass through a 500-µm sieve). Although these animals are, by definition, small, that should not imply that they are not important. Firstly, they are significant in their own right from a biodiversity perspective and, indeed, many types of copepods, ostracods and nematodes may be found only in New Zealand. Second, meiofauna may attain very high densities within aquatic environments and, consequently, may contribute significantly to organic carbon turnover and energy transfer within wetlands (O'Doherty 1985; Strayer & Likens 1986; Palmer 1992). Unlike aquatic insects, which have mobile adult phases, members of the meiofauna do not emerge from the aquatic environment, and so all carbon that has been taken up by the animals remains within a particular wetland. Finally, members of the meiofauna, such as microcrustacea, are also often important components in the diets of small larval fish (McDowall 1990).

The data obtained during the above work forms the first broad-scale attempt to describe the overall distributional patterns of wetland invertebrate fauna in New Zealand. Such information is currently lacking, reflecting a paucity of national surveys of wetland invertebrates, and the lack of a suitable, centralised national database repository for such information. All data generated by this combined DOC- and FRST-funded work examining wetland invertebrates will be entered onto NIWA's FBIS database, with the ultimate aim of producing a national database to describe invertebrate distribution patterns. The information could then be used to generate spatially explicit species distribution maps, which arguably provide the clearest way of conveying species information to a wide audience.

The three studies presented in this report were all carried out in relatively pristine wetlands that were limited to lowland areas at an altitude of less than 250 m a.s.l. Although we are generally aware of the different pressures facing wetlands (e.g. nutrient enrichment, land-use intensification, changes to hydraulic regime, or invasion by weedy plants), we know little about how these pressures influence and affect invertebrate communities. This is currently being addressed through the creation of a wetland Macroinvertebrate Community Index score (WMCI score) for different wetland invertebrates, which is being funded from TFBIS. It is envisioned that the WMCI will result in the development of specific tolerance values for the different invertebrate taxa found within wetlands, indicating their sensitivity to different wetland pressures. The results of the national survey (section 5) highlighted the inherent differences in invertebrate communities between (amongst other things) low pH fens and bogs, and higher pH swamps. Therefore, it may be necessary to create separate WMCI scores for the invertebrate communities in these two different wetland types. However, the current survey work being implemented for the WMCI score is restricted to sampling wetlands that are less than 250 m a.s.l., and is focused on permanent wetlands with open-water habitat. Since there is a clear gap in our knowledge as to how invertebrate communities respond to an altitudinal gradient, further research is needed to address this. The Arawai Kākāriki wetland in the upper Ashburton catchment, which has recently come under the management of DOC, would be an ideal location for such a study to see how invertebrates from these higher altitude wetlands (600–900 m a.s.l.) differ from those in lower elevation wetlands.

Quantitative information about factors that regulate invertebrate abundance and/or biomass in different wetlands is also lacking. Although the work summarised in this report has focused on understanding mechanisms responsible for structuring invertebrate communities within wetlands, it has not attempted to rigorously quantify differences in secondary productivity between the different wetlands. We know little about the energy flow and energy dynamics in wetlands in New Zealand. The links between primary productivity (by algae, macrophytes or the detrital food chain) and invertebrate productivity in wetlands are not particularly well known within New Zealand or elsewhere (Batzer & Wissinger 1996). However, links between invertebrate productivity and bird productivity are well established, with many studies showing clear correlations between the abundance of aquatic invertebrates in wetlands and wetland birds (Goss-Custard 1970; Hockey et al. 1992; Yates et al. 1993; Sanders 2000). At least 11 native New Zealand wetland birds feed to some extent on immature aquatic invertebrates or their adult life stages. In addition, many of the popular game species of bird also rely heavily at some stage in their life cycles on aquatic invertebrates. Given the strong reliance of wetland birds on invertebrate productivity, it is essential to better understand the factors influencing invertebrate productivity, especially when making management decisions about how to best maintain or enhance wetland productivity. Such factors are still relatively unknown, as shown by Sanders (2000) who studied the effectiveness of substrate manipulation tools in created wetlands to increase the food supply of waders in the upper Waitaki basin. Here, ponds were constructed at six sites, and a number of manipulations were carried out, such as raking the substrate to bring coarse material to the top, adding pea straw to ponds, or adding stones to ponds with a silty substrate. Food supplies in newly created wetlands developed rapidly (within 3 months), and ponds with stony substrates contained low invertebrate biomass when compared with ponds with soft substrates. However, Sanders found no technique of wetland construction achieved consistently positive results. He concluded that wetland managers should not expect substratum manipulations that work at some sites to work at others. Such findings make it difficult to predict the effects of wetland enhancement or creation programmes on higher trophic levels, such as wading birds. Therefore, further detailed studies investigating factors responsible for invertebrate distribution and productivity throughout wetlands, and exploring links between invertebrate consumers and higher consumers are required if we are to properly manage and protect New Zealand's wetlands and their ecological communities.

6.1 CONCLUSIONS

In the past, wetlands have been viewed as 'barriers to progress' (Hunt 2007; Hansford & Daly 2010), and their management has historically been driven by a desire to drain them. This has led to a large loss of wetland area throughout New Zealand (up to 90%), particularly in lowland areas in eastern and northern regions of the country. Part of the reason for this loss is a lack of basic knowledge of the immense ecosystem services that wetlands can provide, and the strong economic and social imperatives that are placed on land-use intensification, which often leads to wetland drainage. Such imperatives may be reduced if the true ecosystem values of wetlands are acknowledged by society. Although some

of these values are becoming realised, wetlands still remain largely unknown and, consequently, potentially unappreciated. The studies presented in this report are intended to increase our awareness of just one component of these threatened habitats: their invertebrate communities. These have mostly been overlooked by freshwater ecologists and are also, by and large, unknown to other people.

We found that wetlands can support very diverse invertebrate communities, which are fundamentally different from those of rivers and lakes. The fauna is dominated by five major invertebrate groups: chironomid midges, aquatic mites, copepods, ostracods and aquatic nematodes. In the absence of diagnostic keys to some of these groups, it is difficult to fully document the true biodiversity values of wetlands. This task would be greatly assisted by the creation of identification keys to these less well-known animals. The meiofauna in particular is a major component of wetland invertebrate fauna, yet this group has received scant attention from freshwater ecologists when compared with macro-invertebrates (Robertson et al. 2000). Further studies are warranted on these organisms, not only to better document their biodiversity, but also to better understand their role in organic carbon turnover and energy transfer within wetlands.

Our work has also shown that invertebrate community composition is structured by inherent regional or biogeographical differences, as well as water chemistry differences between wetland types (section 5). National conservation efforts need to recognise this so that specific conservation objectives are not just set for the different wetland types, but also for specific regions, if necessary. However, this work was carried out mainly in relatively unmodified and low-elevation wetlands, and we presently do not know how invertebrates respond to the multiple pressures that wetlands face. Ongoing work funded by agencies such as DOC, FRST and regional councils is currently assessing how wetland invertebrate communities respond to changes in wetland health brought about by land-use changes.

This report is also intended to increase public awareness of the invertebrate communities in wetlands, and to provide some assistance with recommending sampling programmes. We reviewed different sampling techniques used to collect aquatic invertebrates (section 2.4.1) and showed that the collection of semi-quanititative data using a sweep-net provided us with sufficiently accurate information to meet our objectives. We also showed that most of the variability in invertebrate communities occurred at the spatial scale of the wetland (section 3), most likely reflecting inherent water quality differences between different wetlands. Invertebrate communities varied much less between different open-water habitats within a wetland, or between different plant species. We thus recommend sampling in different open-water habitats within each wetland to get a good assessment of the invertebrate communities; although, in some instances, assessment of temporary wetland habitats may also be advocated. Our protocol was to collect duplicate samples from each of three open-water habitats, giving a total of six samples per wetland.

However, it must be remembered that our study was limited to only a small selection of New Zealand wetlands, and a similar analysis to determine whether our findings are similar elsewhere would be beneficial. In particular, more impacted wetlands could be sampled to better understand the effect of reductions in wetland condition on invertebrate communities. For example, it would be useful to obtain information on how invertebrate communities differ

between wetlands with and without invasive willows; what effect increased habitat fragmentation has on wetland invertebrate communities as wetland area decreases and surrounding catchment modifications increase; and whether nutrient run-off and the potentially associated algal blooms have a large effect on invertebrate communities. We also restricted our study to perennial wetlands, so the applicability of these results to ephemeral wetlands is unknown, as they may contain different invertebrates (e.g. Strehlow et al. 2005). For example, Wissinger et al. (2009) found that permanent wetlands near Cass, in the Southern Alps/Ka Tiritiri o te Moana, had almost twice the number of species as temporary wetlands, and the fauna of temporary wetlands was dominated by chironomids, water bugs, beetles and crustaceans, while these animals were less common in permanent habitats which were, instead, dominated by snails, worms, caddisflies, dragonflies and damselflies.

We also described how wetland samples are processed, but acknowledge that sample processing can take considerable time and resources, which may represent a barrier to organisations interested in examining wetland invertebrates. It is likely that sampling programmes may need to alter the number of replicates collected within a wetland to meet budgetary constraints. Future work is urgently needed to investigate potential gains in sample efficiency by refining the current processing methodology described in this report. Currently, the entire sample collected from a wetland is sieved through a series of nested sieves, and the contents of each sieve is picked through to identify and count invertebrates. There may be efficiency gains to be made if only the coarser sieve fraction is processed, which may reduce sample processing time with only a small loss of information to the data. Modifications to processing efficiencies are urgently needed to identify a more cost-effective methodology for processing invertebrate samples. Such a methodology may result in greater uptake of using invertebrates to monitor wetland health and better documentation of the invertebrate biodiversity of these fascinating ecosystems.

Finally, we acknowledge that collecting invertebrate samples is only the first step in using invertebrates to assess wetland health. Aquatic invertebrates are routinely used to assess the ecological condition of rivers and lakes (e.g. Stark 1985; Plafkin et al. 1989; Chessman 1995), reflecting their relative ease of collection and identification, and the fact that their long life spans (weeks–months–years) allow them to act as integrators of antecedent environmental conditions. Within New Zealand, the MCI (Stark 1985, 1993) and the more recently developed soft-bottomed versions (Stark & Maxted 2007) are widely used by regional councils and other organisations to assess the biological condition of streams and rivers. No such indices are used for New Zealand wetlands. However, Chessman et al. (2002) developed a biotic index for invertebrates in western Australian wetlands, and several invertebrate indices have also been developed in North America to describe wetland health (Apfelbeck 2001; Helgen & Gernes 2001). It is likely that a similar index could be developed here, which was the rationale behind the creation of the WMCI.

As with wetlands themselves, their invertebrate communities have remained relatively elusive, understudied and underappreciated. It is hoped that the studies presented here will help people to understand which invertebrates are found in wetlands, and which environmental variables they appear to be responding to. It is also hoped that this report will be an impetus for individuals and organisations

to start their own sampling and monitoring programmes of wetland invertebrate communities. An increased understanding of the importance of these animals, the roles they play and how they are affected by changes to the environment may lead to better management of not only invertebrate communities, but also of the wetlands they are so initimately linked to.

7. Acknowledgements

Funding for the studies presented in the report came from the New Zealand Department of Conservation (Science Investigation No. 3595; Biodiversity of Lowland Wetlands), with additional support from the Foundation for Research, Science and Technology, Contract Number C09X0508 (Maintaining and Restoring Wetlands). We thank DOC (Punakaiki Visitor Centre) for arranging access to he Bullock Creek sites, Ted Brennan (DOC, Hokitika) for allowing us access to the Shearer wetland, and Peter Simpson (formerly of DOC, Northland) for arranging access to wetlands throughout Northland. We also acknowledge the assistance and cooperation of landowners throughout the country for granting us access to many wetlands on or near their properties. Review comments from Cathy Kilroy (NIWA Christchurch), Amanda Todd (DOC, Wellington) and Hugh Robertson (DOC, Christchurch), and an anonymous reviewer are acknowledged.

8. References

Apfelbeck, R.S. 2001: Development of biocriteria for wetlands in Montana. Pp. 141–166 in Rader, R.G.; Batzer, D.P.; Wissinger, S.A. (Eds): Bioassessment and management of North American freshwater wetlands. John Wiley & Sons, Inc., New York.

Armitage, P.D.; Gunn, R.J.M. 1996: Differential response of benthos to natural and anthropogenic disturbance in three lowland streams. *Internationale Revue der gesamten Hydrobiologie 81*: 161–181.

Ausseil, A.-G.; Gerbeaux, P.; Chadderton, W.L.; Stephens, T.; Brown, D.J.; Leathwick, J. 2008: Wetland ecosystems of national importance for biodiversity. Criteria, methods and candidate list of nationally important inland wetlands. Discussion Document. Landcare Research Contract Report LC0708/158, prepared for the Department of Conservation. 162 p.

Batzer, D.P.; Dietz-Brantley, S.E.; Taylor, B.E.; DeBiase, A.E. 2005: Evaluating regional differences in macroinvertebrate communities from forested depressional wetlands across eastern and central North America. *Journal of the North American Benthological Society 24*: 403–414.

Batzer, D.P.; Shurtleff, A.S.; Rader, R.B. 2001: Sampling invertebrates in wetlands. Pp. 339–354 in Rader, R.B.; Batzer, D.P.; Wissinger, S.A. (Eds): Bioassessment and management of North American freshwater wetlands. John Wiley and Sons, Inc., New York.

Batzer, D.P.; Wissinger, S.A. 1996: Ecology of insect communities in nontidal wetlands. *Annual Review of Entomology 41*: 75–100.

Biggs, B.J.F.; Duncan, M.J.; Suren, A.M.; Holomuzki, J.R. 2001: The importance of bed sediment stability to benthic ecosystems. Pp. 423–449 in Mosley, M.P. (Ed.): Gravel-bed rivers. New Zealand Hydrological Society, Christchurch.

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

Boothroyd, I.K.G. 1988: Temporal and diel emergence of Chironomidae (Diptera: Insecta) from a New Zealand stream. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 23*: 1399–1404.

Boothroyd, I.K.G. 2001: Preliminary key to the Orthocladiinae larvae (Chironomidae: Insecta) of New Zealand. NIWA Technical Report, National Institute of water and Atmospheric Research, Hamilton. 32 p.

Bowman, M.F.; Bailey, R.C. 1997: Does taxonomic resolution affect the multivariate description of the structure of fresh water benthic macroinvertebrate communities? *Canadian Journal of Fisheries and Aquatic Sciences 54*: 1802–1807.

Brooks, R.T. 2000: Annual and seasonal variation and the effects of hydroperiod on benthic macroinvertebrates of seasonal forest ("Vernal") ponds in Central Massachusetts, USA. *Wetlands 20*: 707–715.

Burton, T.M.; Stanford, R.M.; Allan, J.W. 1985: Acidification effects on stream biota and organic matter processing. *Canadian Journal of Fisheries and Aquatic Sciences 42*: 669–675.

Chapman, M.A.; Lewis, M.H. 1976: An introduction to the freshwater Crustacea of New Zealand. William Collins (NZ) Ltd, Auckland. 261 p.

Cheal, F.; Davis, J.A.; Growns, J.E.; Bradley, J.S.; Whittles, F.H. 1993: The influence of sampling method on the classification of wetland macroinvertebrate communities. *Hydrobiologia 257*: 47–56.

Cheruvelil, K.; Soranno, P.; Madsen, J.; Roberson, M. 2002: Plant architecture and epiphytic macroinvertebrate communities: the role of an exotic dissected macrophyte. *Journal of the North American Benthological Society 21*: 261–277.

Chessman, B.C. 1995: Rapid assessment of rivers using macroinvertebrates: a procedure based on habitat-specific sampling, family-level identification and a biotic index. *Australian Journal of Ecology 20*: 122–129.

Chessman, B.C.; Trayler, K.M.; Davis, J.A. 2002: Family- and species-level biotic indices for macroinvertebrates of wetlands on the Swan Coastal Plain, Western Australia. *Marine and Freshwater Research 53*: 919–930.

Clarkson, B.R.; Sorrell, B.K.; Reeves, P.N.; Champion, P.D.; Partridge, T.R.; Clarkson, B.D. 2003: Handbook for monitoring wetland condition. Coordinated monitoring of New Zealand wetlands. Ministry for the Environment, Sustainable Management Fund Project, Wellington. 73 p.

Cook, D.R. 1983: Rheophilic and hyporheic water mites of New Zealand. *Contributions of the American Entomological Institute 21*: 224.

Crumpton, W.J. 1978: The biology of six South Island ponds. *Journal of the Royal Society of New Zealand 8*: 179–206.

Davies, B.; Biggs, J.; Williams, P.; Whitfield, M.; Nicolet, P.; Sear, D.; Bray, S.; Maund, S. 2008: Comparative biodiversity of aquatic habitats in the European agricultural landscape. *Agriculture, Ecosystems and Environment 125*: 1–8.

De'ath, G. 2002: Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology 83*: 1105–1117.

Decamps, H.; Naiman, R.J. 1990: Towards an ecotone perspective. Pp. 1–5 in Naiman, R.J.; Decamps, H. (Eds): Ecology and management of aquatic-terrestrial ecotones. UNESCO Paris, and Parthenon Publishing Group, Camforth, UK.

Diehl, S. 1992: Fish predation and benthic community structure: the role of omnivory and habitat complexity. *Ecology 73*: 1646–1661.

Duggan, I.C.; Collier, K.C.; Lambert, P. 2003: Evaluation of invertebrate biometrics and the influence of subsample size using data from some Westland, New Zealand, lowland streams. *New Zealand Journal of Marine and Freshwater Research 36*: 117–128.

Evans, D.L.; Streever, W.J.; Crisman, T.L. 1999: Factors influencing aquatic invertebrate distribution and comparisons between natural and created marsh communities. Pp. 81–104 in Batzer, D.P.; Rader, R.B.; Wissinger, S.A. (Eds): Invertebrates in freshwater wetlands of North America. John Wiley and Sons, New York.

Fuentes, C.; Green, A.J.; Orr, J.; Olafsson, J.S. 2005: Seasonal variation in species composition and larval size of the benthic chironomid communities in brackish wetlands in Southern Alicante, Spain. *Wetlands 25*: 289–296.

Goss-Custard, J.D. 1970: The responses of redshank (*Tringa totanus* (L.)) to spatial variation in the density of their prey. *Journal of Animal Ecology 39*: 91–113.

Greenwood, M.; McIntosh, A. 2004: Influence of environmental conditions on nymphal development and abundance of *Deleatidium fumosum* mayflies. *New Zealand Natural Sciences 29*: 55–66.

Hansford, D.; Daly, P. 2010: Wetlands. *New Zealand Geographic 101*: 48–73.

Helgen, J.C.; Gernes, M.C. 2001: Monitoring the condition of wetlands: indexes of biological integrity using invertebrates and vegetation. Pp. 167–185 in Rader, R.B.; Batzer, D.J.; Wissinger, S.A. (Eds): Bioassessment and management of North American freshwater wetlands. John Wiley & Sons Inc., New York.

Hewlett, R. 2000: Implications of taxonomic resolution and sample habitat for stream classification at a broad geographic scale. *Journal of the North American Benthological Society 19*: 352–361.

Hockey, P.A.R.; Navarro, R.A.; Kalejta, B.; Velasquez, C.R. 1992: The riddle of the sands: why are shore bird densities so high in southern estuaries? *American Naturalist 140*: 961–979.

Holomuzki, J.R.; Biggs, B.J.F. 1999: Distributional responses to flow disturbance by a stream-dwelling snail. *Oikos 87*: 36–47.

Hornung, J.P.; Foote, A.L. 2006: Aquatic invertebrate responses to fish presence and vegetation complexity in western boreal wetlands, with implications for water bird productivity. *Wetlands 26*: 1–12.

Howard-Williams, C.; Pickmere, S. 1986: Nutrient retention and processing in New Zealand streams: the influence of riparian vegetation. *New Zealand Agricultural Science 20*: 110–114.

Hunt, J. 2007: Wetlands of New Zealand: a bitter-sweet story. Random House, New Zealand Ltd.

Huryn, A.D. 1996: Temperature-dependent growth and life cycle of *Deleatidium* (Ephemeroptera: Leptophlebiidae) in two high-country streams in New Zealand. *Freshwater Biology 36*: 351–361.

Johnson, P.N.; Brooke, P.A. 1998: Wetland plants of New Zealand. Manaaki Whenua Press, Lincoln. 319 p.

Johnson, P.N.; Gerbeaux, P. 2004: Wetland types in New Zealand. Coordinated monitoring of New Zealands wetlands. Department of Conservation and Ministry for the Environment, Wellington. 184 p.

Junk, W.J.; Brown, M.; Campbell, I.C.; Finlayson, M.; Gopal, B.; Ramberg, L.; Warner, B.G. 2006: The comparative biodiversity of seven globally important wetlands: a synthesis. *Aquatic Sciences 68*: 400–414.

Keddy, P.A. 2000: Wetland ecology: principles and conservation. Cambridge University Press, Cambridge. 614 p.

King, R.S.; Richardson, C.J. 2002: Evaluating sub sampling approaches and macroinvertebrate taxonomic resolution for wetland bioassessment. *Journal of the North American Benthological Society 21*: 150–171.

Kratzer, E.B.; Batzer, D.P. 2007: Spatial and temporal variation in aquatic macroinvertebrates in the Okefenokee Swamp, Georgia, USA. *Wetlands 27*: 127–140.

Leathwick, J.; Julian, K.; Elith, J.; Ferrier, S.; Snelder, T. 2007: A biologically-optimised environmental classification of New Zealand rivers and streams. Unpublished NIWA Client Report HAM2007-043, prepared for the Department of Conservation.

Mallory, M.L.; Blancher, P.J.; Weatherhead, P.J.; McNicol, D.K. 1994: Presence or absence of fish as a cue to macroinvertebrate abundance in boreal wetlands. *Hydrobiologia 279/280*: 345–351.

Matthaei, C.D.; Arbuckle, C.J.; Townsend, C.R. 2000: Stable surface stones as refugia for invertebrates during disturbance in a New Zealand stream. *Journal of the North American Benthological Society 19*: 82–93.

McCune, B.; Mefford, M.J. 1997: PC-ORD. Multivariate analysis of ecological data. Version 3.0. MjM Software Design, Gleneden Beach, Oregon.

McDowall, R.M. 1990: New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland. 553 p.

Mitsch, W.J.; Gosselink, J.G. 2000: Wetlands. John Wiley and Sons, New York. 920 p.

Nicolet, P.; Biggs, J.; Fox, G.; Hodson, M.J.; Reynolds, C.; Whitfield, M.; Williams, P. 2004: The wetland plants and macro invertebrate assemblages of temporary ponds in England and Wales. *Biological Conservation 120*: 261–278.

O'Doherty, E.C. 1985: Stream-dwelling copepods: their life history and ecological significance. *Limnology and Oceanography 30*: 554–565.

Oekland, J. 1990: Effects of acidic water on freshwater snails: results of a study of 1000 lakes throughout Norway. *Environmental Pollution 78*: 127–130.

Oekland, J.; Oekland, K.A. 1986: The effects of acid deposition on benthic animals in lakes and streams. *Experientia 42*: 471–486.

Oertli, B.; Joye, D.A.; Castella, E.; Juge, R.; Cambin, D.; Lachavanne, J.-B. 2002: Does size matter? The relationship between pond area and biodiversity. *Biological Conservation 104*: 59–70.

Olsen, D. 2007: Quick guide to major groups of freshwater Acari. www.niwa.co.nz/our-science/aquatic-biodiversity-and-biosecurity/research-projects/all/freshbiodiversity/tools#id (viewed February 2010).

Palmer, M.A. 1992: Incorporating lotic meiofauna into our understanding of faunal transport processes. *Limnology and Oceanography 37*: 329–341.

Pearson, T.H.; Rosenberg, R.R. 1978: Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Annual Review of Oceanography and Marine Biology 16*: 299–311.

Plafkin, J.L.; Barbour, M.T.; Porter, K.D.; Gross, S.K.; Hughes, R.M. 1989: Rapid bioassessment protocols for use in streams and rivers: benthic macroinvertebrates and fish. 170 p.

Rader, R.B.; Batzer, D.P.; Wissinger, S.A. 2001: Bioassessment and management of North American freshwater wetlands. John Wiley and Sons, Inc., New York. 469 p.

Robertson, A.L.; Rundel, S.D.; Schmid-Araya, J.M. 2000: An introduction to a special issue on lotic meiofauna. *Freshwater Biology 44*: 1–10.

Robson, B.J.; Clay, C.J. 2005: Local and regional macroinvertebrate diversity in the wetlands of a cleared agricultural landscape in south-western Victoria, Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems 15*: 403–414.

Rooke, J.B. 1986: Seasonal aspects of the invertebrate fauna of three species of plants and rock surfaces in a small stream. *Hydrobiologia 134*: 81–87.

Sanders, M.D. 2000: Enhancing food supplies for waders: inconsistent effects of substratum manipulations on aquatic invertebrate biomass. *Journal of Applied Ecology 37*: 66–76.

Scarsbrook, M. 2002: Persistence and stability of lotic invertebrate communities in New Zealand. *Freshwater Biology 47*: 417–431.

Scarsbrook, M.; Barquin, J.; Gray, D. 2007: New Zealand coldwater springs and their biodiversity. *Science for Conservation 278*: 72.

Scrimgeour, G.J. 1991: Life history and annual production of a net spinning caddisfly *Aoteapsyche colonica* (Trichoptera: Hydropsychidae) in an unstable New Zealand river. *New Zealand Natural Sciences 18*: 31–38.

Sorrell, B.K.; Gerbeaux, P. 2004: Wetland ecosystems. P. 764 in Harding, J.S.; Mosley, M.P.; Pearson, C.P.; Sorrell, B.K. (Eds): Freshwaters of New Zealand. New Zealand Hydrological Society Inc., New Zealand Limnological Society Inc., Christchurch.

Sorrell, B.K.; Partridge, T.R.; Clarkson, B.R.; Jackson, R.J.; Chague-Goff, C.; Ekanayke, J.; Payne, J.; Gerbeaux, P.; Grainger, N.P.J. 2007: Soil and vegetation responses to hydrological manipulation in a partially drained polje fen in New Zealand. *Restoration Ecology 15*: 361–383.

SPSS 2000: Systat, Version 10. SPSS, Chicago, Illionis.

Stark, J.D. 1985: A Macroinvertebrate Community Index of water quality for stony streams. *Water & Soil Miscellaneous Publications 87*: 1–53.

Stark, J.D. 1993: Performance of the Macroinvertebrate Community Index: effects of sampling method, sample replication, water depth, current velocity, and substratum on index values. *New Zealand Journal of Marine and Freshwater Research 27*: 463–478.

Stark, J.D.; Boothroyd, I.K.G.; Harding, J.S.; Maxted, J.R.; Scarsbrook, M.R. 2001: Protocols for sampling macroinvertebrates in wadeable streams. New Zealand Macroinvertebrate Working Group Report No. 1. Ministry for the Environment, Sustainable Management Fund Project No. 5103. 57 p.

Stark, J.D.; Maxted, J.R. 2007: A biotic index for New Zealand's soft bottom streams. *New Zealand Journal of Marine and Freshwater Research 41*: 43–61.

Stark, J.D.; Suren, A.M. 2002: Project Aqua: environmental study—aquatic ecosystems: macroinvertebrates. NIWA Unpublished Client Report CHC02/96. 176 p.

Strayer, D.; Likens, G.E. 1986: An energy budget for the zoobenthos of Mirror Lake, New Hampshire. *Ecology 67*: 303–313.

Strehlow, K.; Davis, J.; Sim, L.; Chambers, J.; Halse, S.A.; Hamilton, D.; Horwitz, P.H.J.; McComb, A.; Froend, R. 2005: Temporal changes between ecological regimes in a range of primary and secondary salinised wetlands. *Hydrobiologia 552*: 17–31.

Suren, A.M. 1991: Bryophytes as invertebrate habitat in two New Zealand alpine streams. *Freshwater Biology 26*: 399–418.

Suren, A.M.; Jowett, I.G. 2006: Effects of floods versus low flows on invertebrates in a New Zealand gravel-bed river. *Freshwater Biology 51*: 2207–2227.

Suren, A.M.; Lambert, P.; Image, K.L.; Sorrell, B.K. 2007: Variation in wetland invertebrate communities in lowland acidic fens and swamps. *Freshwater Biology 53*: 727–744.

Tangen, B.A.; Butler, M.G.; Ell, M.J. 2003: Weak correspondence between macroinvertebrates and assemblages and land use in Prairie Pothole region in wetlands, USA. *Wetlands 23*: 104–115.

Tiner, R.W. 1999: Wetland indicators: a guide to wetland identification, delineation, classification and mapping. CRC Press, Boca Raton, Florida. 392 p.

Towns, D.R. 1981: Life histories of benthic invertebrates in a Kauri forest stream in northern New Zealand. *Australian Journal of Marine and Freshwater Research 32*: 191–211.

Turner, A.M.; Trexler, J.C. 1997: Sampling aquatic invertebrates from marshes: evaluating the options. *Journal of the North American Benthological Society 16*: 694–709.

Weatherley, N.S.; Ormerod, S.J. 1990: The constancy of invertebrate assemblages in soft-water streams: implications for the prediction and detection of environmental change. *Journal of Applied Ecology 27*: 952–964.

Wellborn, G.A.; Skelly, D.K.; Werner, E.E. 1996: Mechanisms creating community structure along a freshwater habitat gradient. *Annual Review of Ecology and Systematics 27*: 337–363.

Whiles, M.R.; Goldowitz, B.S. 2005: Macroinvertebrates communities in Central Platte River wetlands: patterns across a hydrologic gradient. *Wetlands 25*: 462–472.

Wild, M.; Snelder, T.; Leathwick, J.; Shanker, U.; Hurren, H. 2005: Environmental variables for the Freshwater Environments of New Zealand River Classification. Unpublished NIWA Client Report CHC2004-086, prepared for the Department of Conservation. 31 p.

Williams, M. 2004: Bird communities of lakes and wetlands. Pp. 26.1–26.11 in Harding, J.S.; Mosley, M.P.; Pearson, C.P.; Sorrell, B.K. (Eds): Freshwaters of New Zealand. Caxton Press, Christchurch.

Winterbourn, M.J. 1974: The life histories, trophic relations and production of *Stenoperla prasina* (Plecoptera) and *Deleatidium* sp. (Ephemeroptera) in a New Zealand river. *Freshwater Biology 4*: 507–524.

Winterbourn, M.J. 1997: New Zealand mountain stream communities: stable yet disturbed? Pp 31–54 in Streit, B.; Stadler, T.; Lively, C.M. (Eds): Evolutionary ecology of freshwater animals. Birkhauser-Verlag, Basel, Switzerland.

Winterbourn, M.J.; Gregson, K.L.D. 1989: Guide to the aquatic insects of New Zealand. *Bulletin of the Entomological Society of New Zealand 9*: 1–96.

Winterbourn, M.J.; Gregson, K.L.D.; Dolphin, C.H. 2006: Guide to the aquatic insects of New Zealand. *Bulletin of the Entomological Society of New Zealand 14*: 1–108.

Winterbourn, M.J.; Rounick, J.S.; Cowie, B. 1981: Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research 15*: 321–328.

Wissinger, S.A. 1999: Ecology of wetland invertebrates: synthesis and applications for conservation and management. Pp. 1043–1086 in Batzer, D.P.; Rader, R.B.; Wissinger, S.A. (Eds): Invertebrates in freshwater wetlands of North America: ecology and management. John Wiley and Sons, New York.

Wissinger, S.A.; Greig, H.; McIntosh, A. 2009: Absence of species replacements between permenent and temporary lentic communities in New Zealand. *Journal of the North American Benthological Society 28*: 12–23.

Yates, M.G.; Goss-Custard, J.D.; McGrorty, S.; Lakhani, K.H.; Durell, S.E.A.L.V.D.; Clarke, R.T.; Rispin, W.E.; Moy, L.; Yates, T.; Plant, R.A.; Frost, A.J. 1993: Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. *Journal of Applied Ecology 30*: 599–614.

This page has been intentionally left blank

What are the characteristics of invertebrate communities in healthy lowland wetlands in New Zealand?

This report describes the first stage of a research programme that aims to document the aquatic invertebrate biodiversity values of lowland wetlands in New Zealand and to present information on variation in community composition in near-pristine wetlands. It addresses three questions: how do communities vary within and between wetlands; to what extent do communities vary temporally; and how are communities affected by environmental variables? Identifying the underlying drivers of invertebrate community composition will allow evaluation of the potential effects of human activities on them.

Suren, A.; Sorrell, B. 2010: Aquatic invertebrate communities of lowland wetlands in New Zealand: characterising spatial, temporal and geographic distribution patterns. *Science for Conservation 305*. 64 p.

New Zealand Government