

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 \pm 1 SEM, $n = 6$).

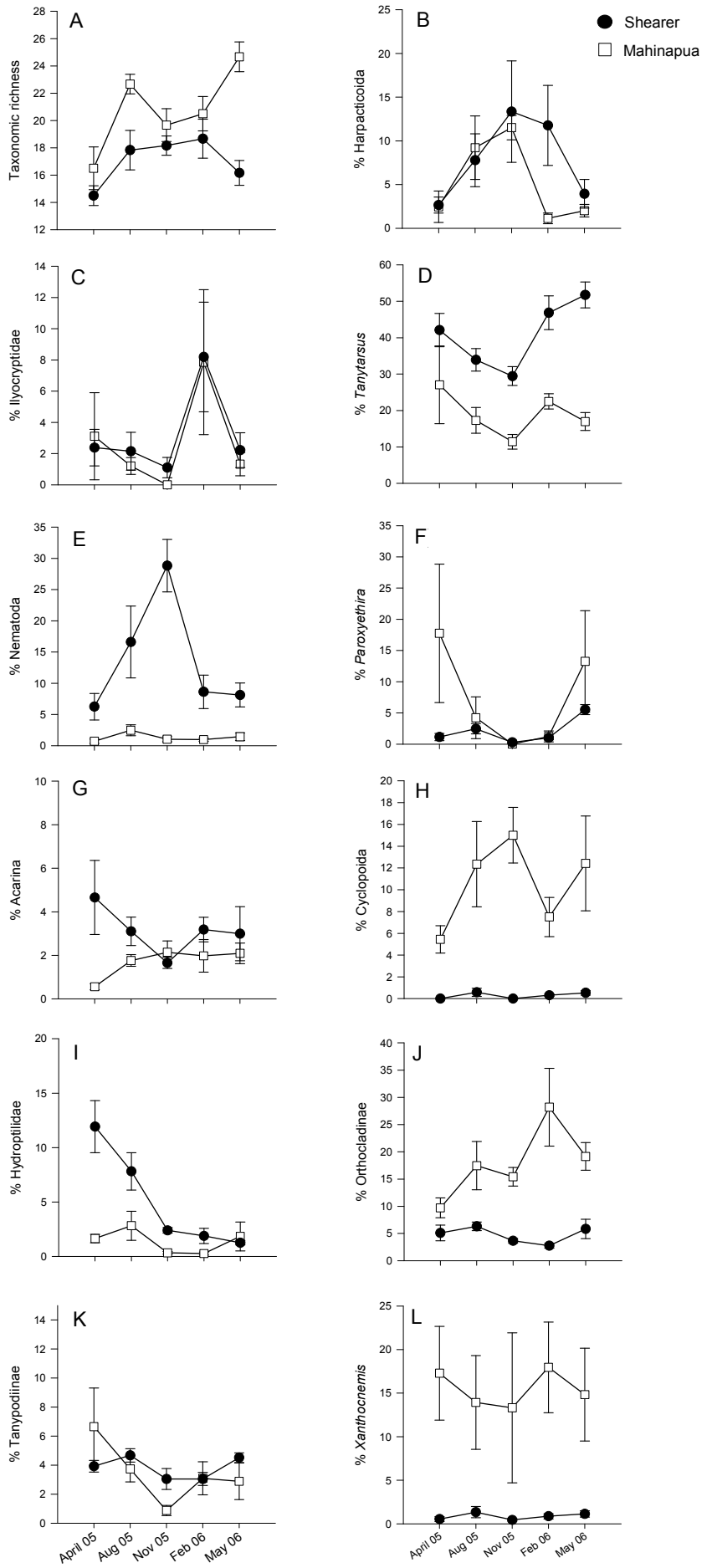


TABLE 5. DENSITIES OF THE 11 MOST COMMON TAXA COLLECTED FROM THE TWO WETLANDS (MAHIANAPUA AND SHEARER) IN THE SEASONAL STUDY, AND TAXONOMIC RICHNESS, SHOWING COMPONENTS OF THE REPEATED MEASURE ANOVA MODEL TESTING FOR DIFFERENCES BETWEEN WETLANDS OVER TIME, AND THE INTERACTION. SIGNIFICANT EFFECTS ($P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

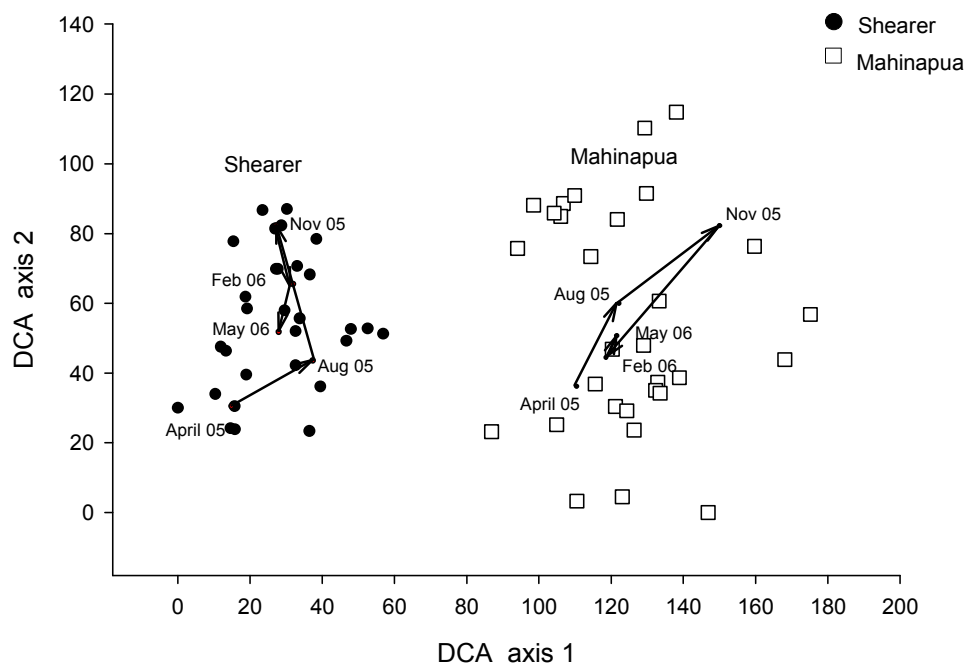
Table 5 continued

TAXA	SOURCE	SS	DF	MEAN SQUARES	F-RATIO	P-VALUE
<i>Xanthocnemis</i>	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 wetlands¹. 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 than 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.

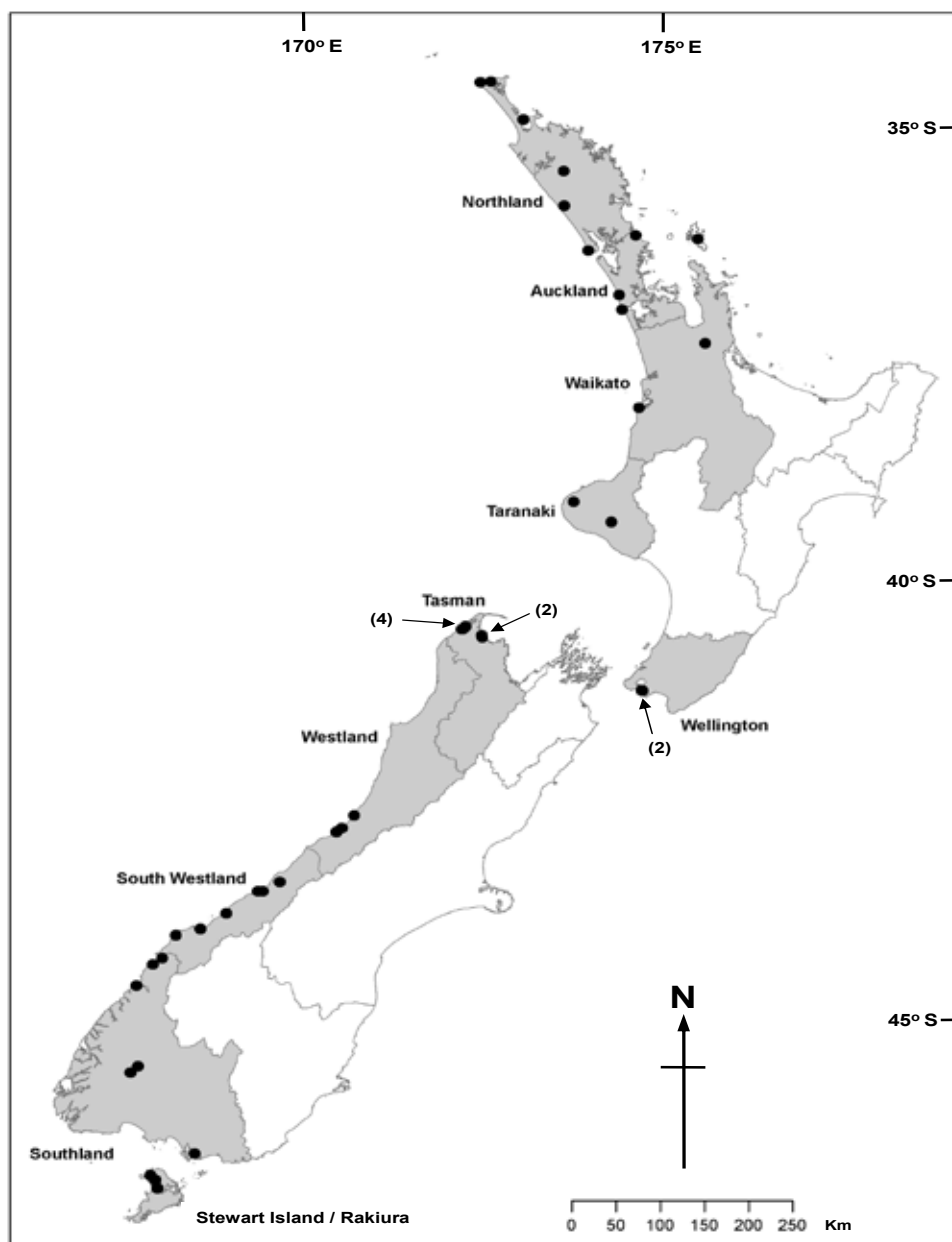
5.1 METHODS

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- μ m 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 ($\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, 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 ($\mu\text{S}/\text{cm}$)
		Spot_Temp	Spot water temperature ($^{\circ}\text{C}$)
		NH ₄	Ammonia concentration (mg/L)
		NO ₃	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
DistToSea			Distance to sea (km)
Elevation			Mean wetland elevation (m a.s.l.)
Slope			Mean wetland slope ($^{\circ}$)
Ecological Integrity Index			Pressure index (0-1)
Geology		Region (10)	Region 1 to 10
		Alluvium	% alluvium
		Calc	% calcium dominated rocks
		Glacial	% glacial material
		Hard	% of hard rock in the catchment
Landcover	Peat	% peat	
	Phos	% phosphorus bearing rocks	
	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 ($^{\circ}\text{C}$)
		TWarm	Average annual maximum temperature ($^{\circ}\text{C}$)
		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
	NH ₄ -N	1	27	1367
	NO ₃ -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 NH₄-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%; Orthoclaadiinae—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.

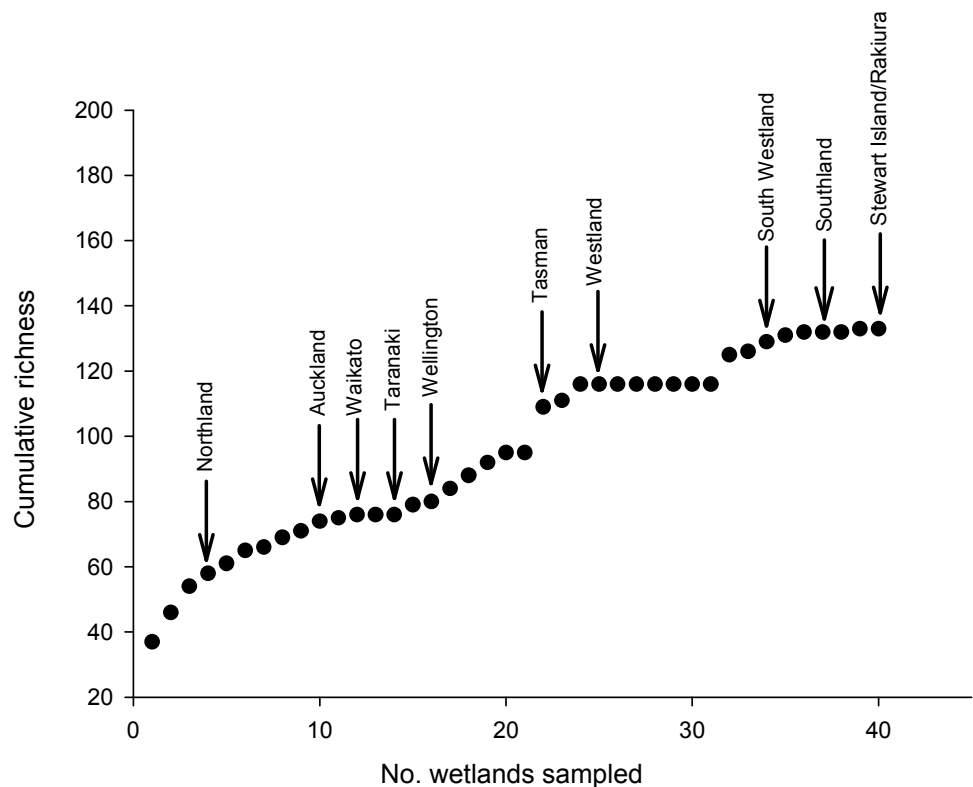


TABLE 8. THE NUMBER OF WETLANDS SAMPLED, TAXONOMIC RICHNESS AND NUMBER OF UNIQUE TAXA IN EACH OF THE TEN REGIONS WITHIN NEW ZEALAND. NUMBER OF SAMPLES TAKEN FROM EACH REGION ARE GIVEN IN PARENTHESES.

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				<i>Austrolestes colensonis</i> <i>Xanthocnemis</i>
Ephemeroptera	<i>Austroclima sepia</i> <i>Zephebia versicolor</i>		<i>Oniscigaster wakefieldi</i>	
Plecoptera	<i>Cristaperla</i>	<i>Acroperla</i> <i>Taraperla</i>		
Hemiptera	Corixidae			<i>Anisops assimilis</i> <i>Sigara</i> <i>Microvelia</i>
Trichoptera	<i>Psilochorema nemorale</i>	<i>Paroxyethira tillyardi</i> <i>Psilochorema acheir</i> <i>Triplectidina</i>	<i>Hydrobiosis</i> sp.	
Coleoptera	Ptilodactylidae		<i>Rbantus</i> <i>Homeodytes</i> Elmidae	
Diptera	<i>Harrisius pallidus</i> Forcipomyiinae Syrphidae Tanyderidae	Staphylinidae		Ceratopogonidae <i>Chironomus zelandicus</i> Orthoclaadiinae <i>Tanytarsus</i> Tanypodiinae
Collembola				Collembola
Crustacea	<i>Tenagomysis chiltoni</i> Ostracoda sp. G <i>Paranebrops planifrons</i>		Macrothricidae	Chydoridae Cyclopoida Daphniidae Harpacticoida
Acarina				Acarina
Mollusca	<i>Hyridella menziesi</i>			
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

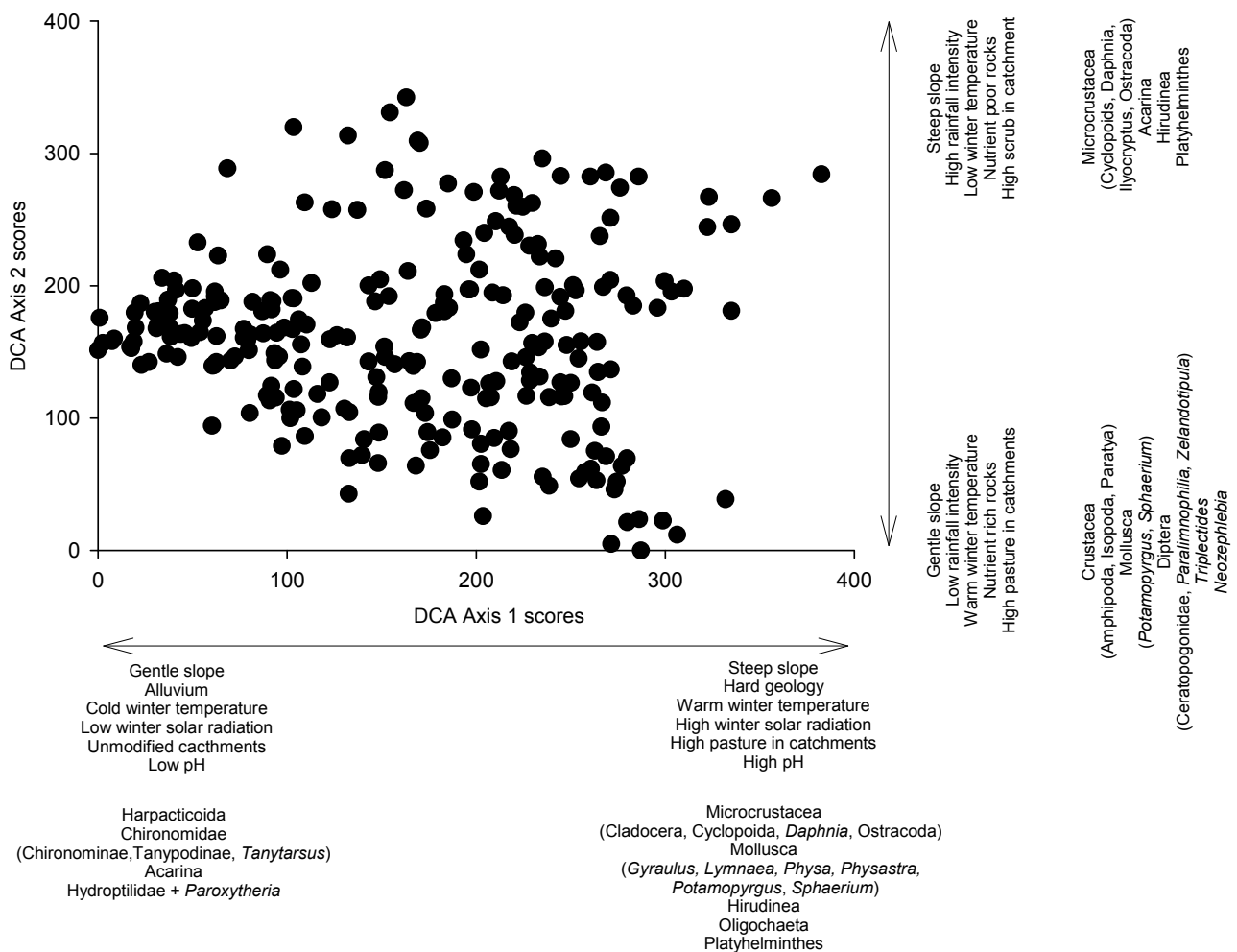


Figure 13. Detrended correspondence analysis (DCA) of invertebrate data collected in the 40 wetlands sampled throughout New Zealand showing group membership according to region. The invertebrate taxa and environmental parameters that showed significant correlations ($r^2 > 0.4$, $P < 0.01$) to the axis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

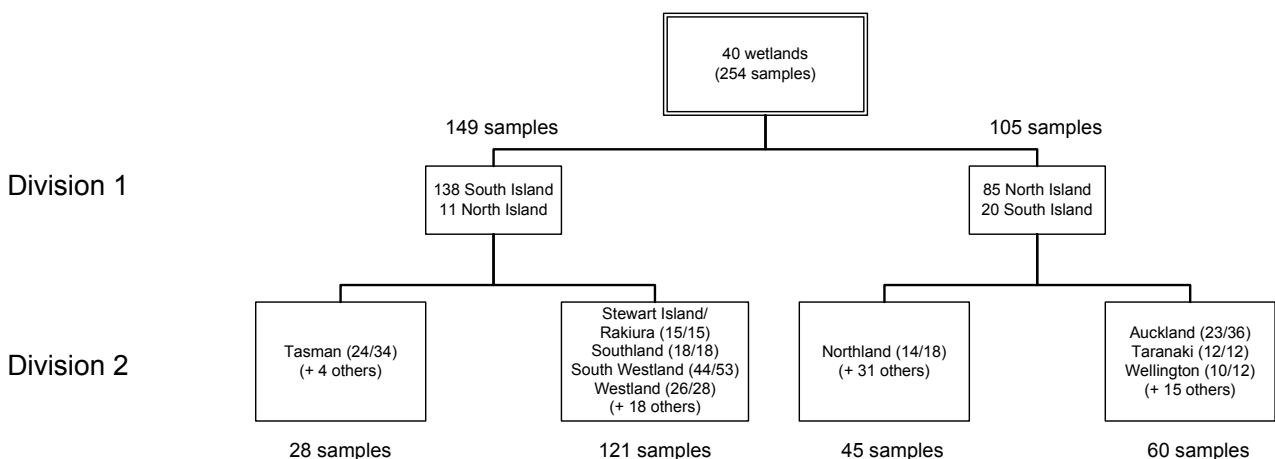


Figure 14. Results of the TWINSpan analysis (arrested after the second division) showing the number of samples in each sample grouping and the location of each sample (North or South Island) in the first division, or the Region in the second division. For the second division, only the most common regions 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).

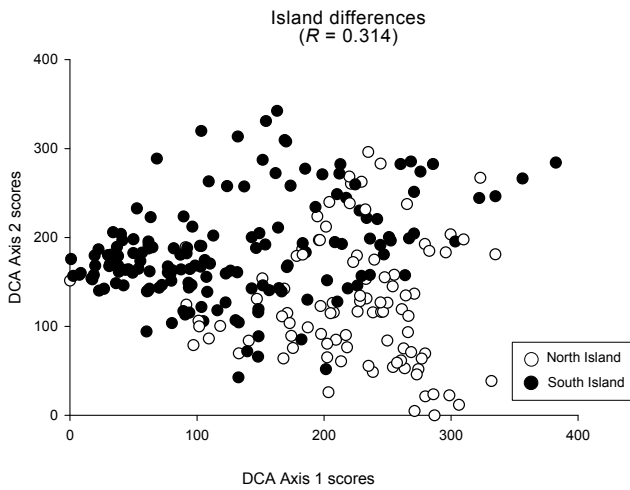


Figure 15. Detrended correspondence analysis (DCA) of invertebrate data collected from the 40 wetlands, showing membership according to either the North or South Islands. Also shown is the result of the ANOSIM analysis for between island differences.

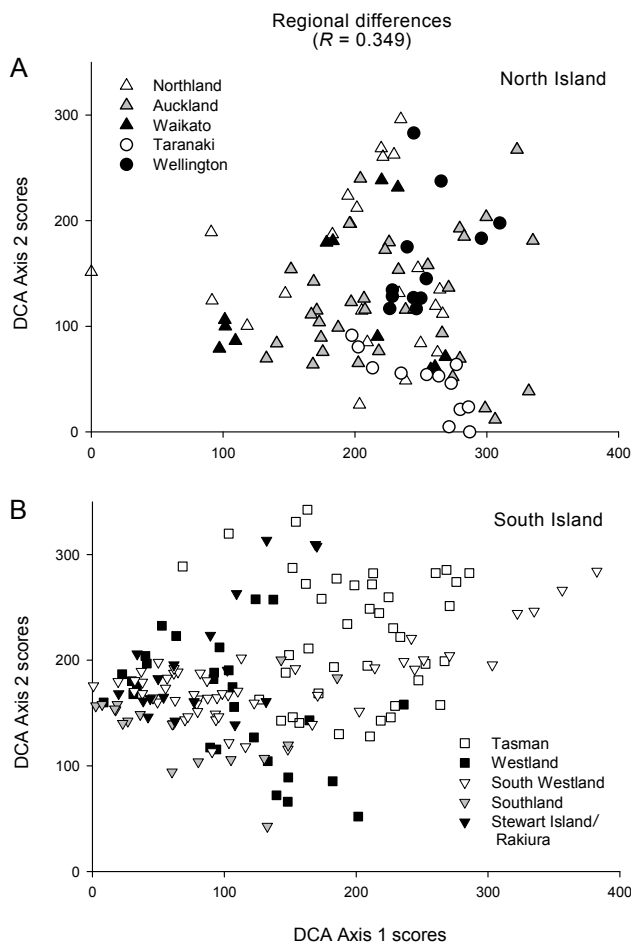


Figure 16. Detrended correspondence analysis (DCA) of invertebrate data collected from the 40 wetlands showing membership according to regions (partitioned into North Island (A) and South Island (B)). Also shown is the result of the ANOSIM analysis for between-region differences.

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).

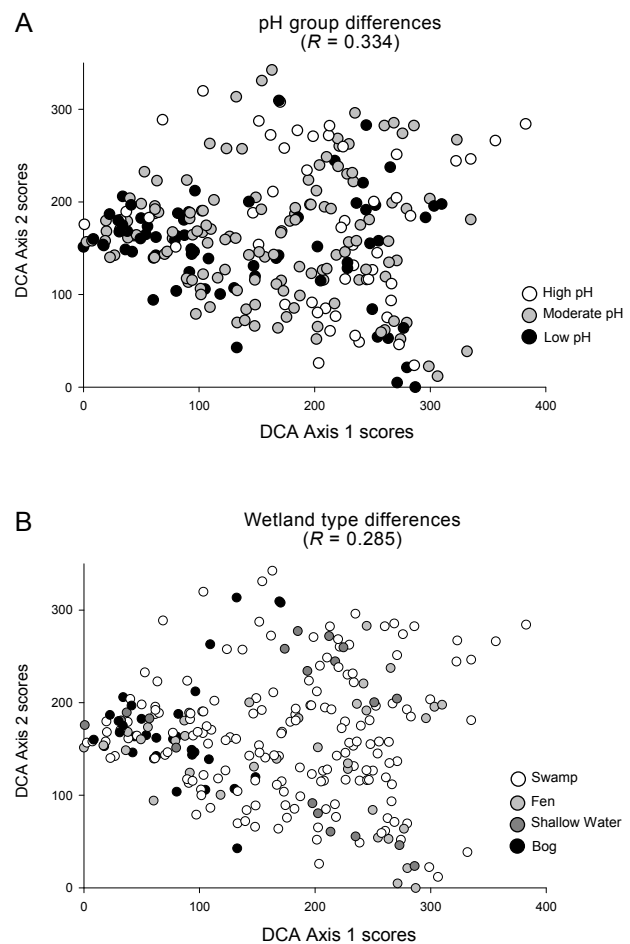


Figure 17. Detrended correspondence analysis (DCA) of invertebrate data collected in the 40 wetlands showing membership according to the pH derived groups (A), or the type of wetland (B) that samples were collected from. Also shown is the result of the ANOSIM analysis for differences between pH groups 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 <i>F</i> -RATIO	<i>r</i> 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
Orthocladinae	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
<i>Potamopyrgus antipodarum</i>	pH (+)	Region9 (+)	25	20.21	0.621
Tanypodinae	Phos (-)	Region8 (+)	22	29.24	0.704
<i>Tanytarsus</i>	pH (-)	TDN (+)	22	20.39	0.624
<i>Xanthocnemis zelandicus</i>	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 NO₃ 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 NO₃ (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
<i>Tanytarsus</i>	11.1	<i>Deleatidium</i>	21.0	<i>Potamopyrgus antipodarum</i>	29.2
Acarina	7.5	Orthoclaadiinae	9.6	Oligochaeta	5.6
Cyclopoida	7.2	Elmidae	9.2	Ostracoda	4.3
Nematoda	7.0	<i>Pycnocentroides</i>	7.7	<i>Chironomus</i>	3.2
Harpacticoida	5.2	<i>Aoteapsyche</i>	4.9	<i>Cladopelma</i>	2.8
Orthoclaadiinae	4.9	<i>Potamopyrgus antipodarum</i>	4.9	<i>Daphnia</i>	2.8
<i>Potamopyrgus antipodarum</i>	4.7	Chironominae	4.3	<i>Sigara</i>	2.7
Ceratopogonidae	4.6	Diamesinae	4.2	<i>Gundlachia</i>	2.6
Oligochaeta	4.2	Ostracoda	3.9	Acarina	2.3
Tanypodinae	4.1	Oligochaeta	3.5	Orthoclaadiinae	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 *Nesameletus* 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 (<i>n</i> = 26)
Shortfin eel	<i>Anguilla australis</i>	17
Common bully	<i>Gobiomorphus cotidianus</i>	15
Longfin eel	<i>Anguilla dieffenbachia</i>	15
Inanga	<i>Galaxias maculatus</i>	13
Giant kōkopu	<i>Galaxias argenteus</i>	10
Banded kōkopu	<i>Galaxias fasciatus</i>	9
Redfin bully	<i>Gobiomorphus buttoni</i>	8
Black mudfish	<i>Neochanna</i>	6
Brown trout	<i>Salmo trutta</i>	6
Mosquito fish	<i>Gambusia affinis</i>	6
Goldfish	<i>Carassius auratus</i>	5
Catfish	<i>Ameiurus nebulosus</i>	4
Common smelt	<i>Retropinna retropinna</i>	4
Kōaro	<i>Galaxias brevipennis</i>	4
Kōura	<i>Paranephrops planifrons</i>	4
Perch	<i>Perca fluviatilis</i>	3
Torrentfish	<i>Cheimarrichthys fosteri</i>	3
Grey mullet	<i>Mugil cephalus</i>	2
Lamprey	<i>Geotria australis</i>	2
Rudd	<i>Scardinius erythrophthalmus</i>	2
Black flounder	<i>Rhombosolea retiaria</i>	1
Dart goby	<i>Partoglossus marginalis</i>	1
Giant bully	<i>Gobiomorphus gobioides</i>	1
Gollum galaxias	<i>Galaxias gollumoides</i>	1
Koi carp	<i>Cyprinus carpio</i>	1
Northland (burgundy) mudfish	<i>Neochanna beleios</i>	1
Shortjaw kōkopu	<i>Galaxias postvectus</i>	1
Tench	<i>Tinca tinca</i>	1
Upland bully	<i>Gobiomorphus breviceps</i>	1
Yelloweyed mullet	<i>Aldrichetta forsteri</i>	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- μ m 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-quantitative 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 intimately 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 the 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 Orthoclaadiinae 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.; Gowns, 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.
- Cheruvilil, 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.; Traylor, 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.
- Hurn, 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 Zealand's 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 permanent and temporary lentic communities in New Zealand. *Journal of the North American Benthological Society* 28: 12–23.
- Yates, M.G.; Goss-Custard, J.D.; McGroarty, 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.

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. 64p.