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Invertebrate community structure in streams of the Manawatu–Wanganui region, New Zealand: the roles of catchment versus reach scale influences

RUSSELL G. DEATH AND MICHAEL K. JOY
Institute of Natural Resources – Ecology, Massey University, Palmerston North, New Zealand

SUMMARY

1. Invertebrate communities at 187 least impacted streams in the Manawatu–Wanganui region of New Zealand were sampled between February and May 2000 to investigate the relative influence of catchment and reach scale environmental influences on community structure.
2. Of the 138 biological (fish and periphyton), local habitat and catchment scale descriptors used to examine invertebrate community patterns, alkalinity and conductivity were the most consistently influential predictors.
3. Of the 52 geographical information system (GIS)-derived catchment variables (catchment geology, catchment land use, rainfall and topography) only per cent catchment in pasture, indigenous forest, coastal sand, crushed argillite and wind blown sand were associated with any measures of the invertebrate communities.
4. Grouping of communities based on GIS data in general, did not generate distinct community types. Groupings based on river catchment, conductivity and alkalinity however, did produce distinct communities.
5. Streams with very low alkalinity were dominated by Ephemeroptera, Plecoptera and Trichoptera that were gradually replaced by Mollusca, Crustacea and Chironomidae as alkalinity increases.
6. Habitat characteristics measured at the scale of the reach were more closely linked with measures of invertebrate community structure than any GIS derived variables or river classifications.

Keywords: geographic information systems, geology, geomorphology, habitat, invertebrate community structure, vegetation, water chemistry

Introduction

The abundance and distribution of lotic invertebrates is controlled by a number of physical and biological variables that are in turn influenced by both the local and regional characteristics of a river catchment (Power *et al*., 1988; Quinn & Hickey, 1990; Allan, 1995; Richards, Johnson & Host, 1996). Several studies using geographical information systems (GIS) have shown landscape characteristics, such as surficial geology, channel geomorphology and vegetation, influence invertebrate communities in streams draining those landscapes (Richards *et al*., 1996; Harding, Winterbourn & McDiffett, 1997; Wiley, Kohler & Seelbach, 1997; Townsend *et al*., 2003). This, in turn has led to the development of a number of GIS-based classification systems, such as ecoregions (Harding, 1994; Omernik, 1995) and the New Zealand river environment classification (REC) (Snelder & Biggs, 2002), that are hypothesised to predict biotic conditions within a river catchment. In contrast to

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Correspondence: Russell G. Death, Institute of Natural Resources – Ecology, Massey University, Private Bag 11-222, Palmerston North, New Zealand.
E-mail: r.g.death@massey.ac.nz

GIS-based studies, much of the emphasis in stream ecology has focused on examining the effects of reach-level site characteristics on stream invertebrates (Allan, 1995; Wiley *et al.*, 1997). Clearly factors acting at both scales are likely to be important; however, elucidating the relative contributions of each of the factors remains a challenge in stream ecology.

Much of the focus on landscape and catchment-scale analysis of invertebrate communities has been on the influence of land-use practices. These studies have shown that anthropogenic changes to land use, and the associated instream habitat changes, often have an overriding influence on invertebrate community structure (e.g. Quinn & Hickey, 1990; Richards *et al.*, 1997; Townsend *et al.*, 1997, 2003). Not surprisingly, there have been very few studies that have attempted to look at large scale patterns in invertebrate communities of streams and rivers that are relatively unimpacted by human activity (but see Corkum, 1989; Harding *et al.*, 1997) because of the logistical problems of trying to find a wide cross section of such streams over a large geographical area.

A full understanding of how 'natural' stream invertebrate communities are structured, however, depends on examining the influence of reach and catchment scale variables in streams that have not been drastically altered by human activity. Like many approaches to examining large-scale regional ecological patterns (Blackburn & Gaston, 1998), surveys of river biotas are beset with a number of problems for addressing such issues (Manel, Williams & Ormerod, 2001). They rely on correlation implying cause and effect, often reveal confounding patterns, and may lack replication or controls. However, recognising that they have weaknesses, such studies currently provide one of the few pragmatic solutions to examining large-scale patterns in ecological communities (Corkum, 1989). In this study we sample invertebrate communities on one occasion in 187 streams spread over 22 000 km^2 of the central North Island of New Zealand. Although this region includes a significant area of land modified by human activities we chose sites spread throughout the region that were considered to be the least impacted possible. We then examined whether catchment scale variables drawn from a GIS or reach scale variables measured at the site were better descriptors of invertebrate community structure.

Methods

Study area

The Manawatu–Wanganui Region covers 22 179 km^2 of the south west of the North Island of New Zealand and is delineated by the catchment boundaries of the three major rivers in the region, the Whanganui, Rangitikei and Manawatu Rivers (Fig. 1). The region includes considerable areas of steep mudstone country, uplifted ranges and rich alluvial plains, resulting in a diversity of stream types ranging from braided cobble to silt dominated lowland rivers, and from an acidic volcano-fed river to small spring fed mountain streams. Study sites spanned 40°45′S to 39°30′S and from sea level to 820 m a.s.l. The predominant land use in the region is pastoral farming with some cropping, while most of the region above 500 m a.s.l. has relatively unmodified native vegetation.

Site selection

The study was designed to cover all major stream types in the Manawatu–Wanganui region. To achieve this, 200 relatively unimpacted sites were selected over the region (Fig. 1). Emphasis was placed on sites having the most natural catchment vegetation, channel morphology, and minimal human impacts (e.g. Hughes, 1995). In order to have sites over the full range of elevations and stream types some moderately impacted but best available catchments were included at lower elevations (Hughes, Larson & Omernik, 1986). Sites were also selected in a stratified design

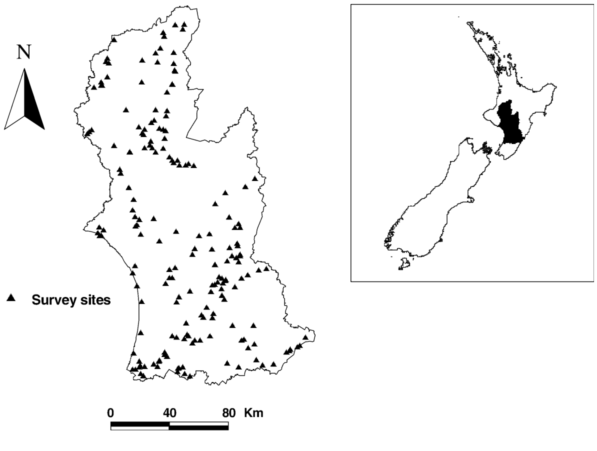

Fig. 1 Location of sample sites in the Manawatu–Wanganui Region, New Zealand.

within the seven lotic ecoregions for the Manawatu–Wanganui region (Harding, 1994). The selection of sites occurred in two phases: the first phase was a 'desk-top' exercise using expert knowledge of streams combined with geographic information. The second phase occurred after sampling, with the inclusion of up to date information from the field. This left 187 sites that were considered to be best management sites for any given area of the region (Hughes *et al.*, 1986).

Macroinvertebrate sampling

Sites were sampled over the Austral summer–autumn period, between February and May 2000. Macroinvertebrate samples were collected within a 50-m reach from riffles using a kick net (250 μm mesh). Samples were taken by disturbing the substrate while moving upstream for 1 min and preserved in 10% formalin. In the laboratory 100 randomly selected invertebrates were subsampled using a Marchant subsampling box (Marchant, 1989). A sample of 100 individuals from New Zealand streams has been shown by Duggan, Collier & Lambert (2002) to give a similar quantification of community composition to more intensive sampling, although it can be expected to underestimate taxon richness. We also processed entire samples from 18 (10%) randomly selected sites and found high multivariate similarity in community structure between the 100-individual subsamples and the complete sample (Minimum, Median and Maximum relative Sorensen distances were 0.15, 0.22 and 0.61, respectively). However, it needs to be recognised that, as with any survey, this study represents reduced precision for individual sites in return for greater spatial coverage (Manel, Buckton & Ormerod, 2000). Taxonomic precision used in the analysis was to the lowest possible resolution (usually genus) following Winterbourn (2000) and Winterbourn, Gregson & Dolphin (2000).

Reach scale habitat measurements

Physicochemical measures. A number of physical and chemical characteristics were recorded at each site concurrently with the invertebrate sampling. Conductivity (automatically adjusted to 25 °C) and water temperature were measured with a YSI model 85 meter. An Orion Quickcheck model 106 pocket meter was used to measure pH. A 500 mL water sample was collected and frozen for measurement of alkalinity, soluble reactive phosphorous and nitrate. Alkalinity was determined by potentiometric titration (Horizons Regional Council laboratory, Palmerston North). Soluble reactive phosphorus concentrations were obtained using the Ascorbic acid method, and nitrate using the Cadmium Reduction method (APHA, 1998).

Water velocity was determined by timing the movement of the modal concentration of a slug of flourescein sodium dye over 100 m of the reach sampled. Maximum water depth and width were measured using a staff at five equidistant points longitudinally along the sample reach. Mean and median substratum particle sizes were determined using standard granulometry techniques (*sensu* Wolman, 1954; Quinn & Hickey, 1990) on 70–100 randomly selected stones at each site. Substrate embeddedness was subjectively assessed at each site after moving substrate (1 = loosely packed; 4 = tightly packed).

The Pfankuch channel stability index (Pfankuch, 1975; Death & Winterbourn, 1994) was used to assess the stability of the stream banks and bed. The index involves summing the scores in 15 environmental characteristics (scored according to their perceived importance) within predetermined criteria. The lower the total score the more stable the stream channel. Three totals relate to three regions of the stream channel; upper banks, lower banks, and stream bottom. The percentage of backwater, pool, still, run, riffle, rapid, undercut or debris jams was visually estimated over 100 m of the sampled reach. Riffles were classified as areas of fast, shallow water with a broken-surface appearance; pools were areas of slow deep water with a smooth surface appearance, whereas runs were intermediate in character. Rapids were classified as areas of fast cascading deep water. The percentage areas covered by surrounding land use and riparian vegetation (native, exotic forest, scrub, crop/pasture, tussock and other) were also estimated visually at each site.

Biological measures. The potential influence of higher and lower trophic levels in the stream food web on the invertebrate communities was examined by concurrent sampling of the fish and periphyton present at each site. Each site was sampled by single pass electric fishing using a battery powered electric fishing machine (EFM300; NIWA Instrument Systems, Christchurch, New Zealand), operated at 150–300 V. Single pass electrofishing is a suitable survey method for assessing distribution of freshwater fish in New Zealand as all species are collected with equal probability on the first pass (Jowett & Richardson, 1996). Fish were identified to species, counted and returned. At least two examples of each habitat type (e.g. riffles, runs, pools, rapids) were included in each sampling reach. Individual fish seen and positively identified to species but not captured during or after electrofishing were also recorded, to give a minimum estimate of density.

Relative abundance of fish at all sites was calculated by dividing the number of fish by the area fished (mean width × length × 100) to give the minimum density of fish per 100 m^2. Juvenile eels (<300 mm length) were treated as separate operational taxonomic units (OTUs) from the two species of adult eel in the analysis and the two trout species encountered [rainbow trout (*Oncorhychus mykiss* Richardson) and brown trout (*Salmo trutta* Linnaeus) which were most common] were combined into a single OTU. For more details on the fish communities see Joy & Death (2002).

Periphyton abundance was assessed by collecting 6.15 cm^2 circular scrapings (Davies & Gee, 1993) from five randomly selected stones, which were kept dark and cool before being frozen in the laboratory. Pigments were extracted by soaking the samples in 90% acetone for 24 h at 5 °C in the dark. Absorbancy was measured with a Cary 50 Conc. UV-Visible spectrophotometer^{TM} (Varian, Mulgrave, Australia) and chlorophyll *a* and phaeophytin were calculated using the method of Steinman & Lamberti (1996).

Catchment GIS derived habitat measures

The catchment scale variables for each site (Appendix 1) were derived from a number of GIS sources to yield two distinct forms of data. These were continuous data on the percentages of a site's upstream catchment in different land use, geology and climate categories and categorical site characterisations (e.g. type of land cover, geology, ecoregion) based on that underlying continuous data.

The continuous GIS data on terrain, geology and land cover were obtained from the New Zealand REC derived from a 30 m Digital Elevation Model (Snelder *et al.*, 1998; Snelder & Biggs, 2002). For each section of the region's river network (average length = 700 m) the area of catchment occupied by various categories (e.g. geological categories include; greywacke, limestone etc.) is recorded (Snelder & Biggs, 2002). The geology rock type classifications for this dataset were sourced from the New Zealand Land Resources Inventory (NZLRI) that classifies geology into 55 categories at a scale of 1 : 50 000. Land cover catchment proportions came from the New Zealand Land Cover Database (NZLCDB). The LCDB defines land cover in 17 categories (e.g. indigenous forest, exotic forest, pastoral farming) and is derived from digitising satellite images at a mapping scale of 1 : 50 000. For rainfall and climate variables, surfaces of annual mean precipitation, annual mean evapotranspiration and annual mean air temperature were estimated from thin plate splines fitted to meteorological station data. More detailed information on the REC and the underlying data can be found in Snelder *et al.* (1998) and Snelder & Biggs (2002). All data were associated with each corresponding sample site using the geoprocessing extension of ARCVIEW (ArcView, 1999). The total distance from the site to the coast along the waterway was also calculated for each site by summing the reach lengths from the site to the sea. This yielded 52 GIS derived variables (Appendix 1).

Categorical data were also derived predominately from the REC site classifications based on a number of the above variables (e.g. source of flow, geology, land cover, network position and valley landform, Table 3) (Snelder *et al.*, 1998). The lotic ecoregion classification for each site from Harding (1994) was used as a further categorical dataset.

Data analysis

As an initial step in the analysis, linkages between the individual reach and catchment scale predictor variables and some univariate measures of community structure (number of taxa, Berger Parker dominance index, relative abundance of the six most abundant taxa, and relative abundance of orders) were explored with the Spearman rank correlation procedure in SAS (2000). To allow for the possibility that environmental variables may be acting on species in combination, rather than individually, new predictor variables representing collective measures were generated by principal components analysis (PCA) or non-metric multidimensional scaling (NMS) (fish data only). Each of the datasets for water chemistry, physical habitat, fish communities, riparian conditions, land cover and geology were run through their respective ordinations and the site scores generated for each of the first three axes also used in the correlation analysis. The three axes explained between 9 and 53% of the variation in their respective datasets. As correlation of multiple variables will generate a number of spurious correlations by chance alone (Rice, 1989), and as this is exploratory analysis, only the strongest correlations are reported.

Patterns in community composition were examined using NMS with the PC-ORD statistical package (McCune & Mefford, 1999). The relative Sorensen distance measure was used to measure similarity between samples. Examination of stress patterns in 500 iterations of the data suggested three dimensions were appropriate for the final ordination. Stress of the final configuration was also compared with that generated from random runs of the data to establish that the observed patterns in all dimensions were real (Kruskal & Wish, 1978). Relationships between the ordination axes and the measured local and regional environmental variables were examined using simple correlation (SAS, 2000). To minimise type 1 errors associated with multiple correlations a Bonferroni correction was applied to probabilities (Rice, 1989). As above, a reduced dataset of ordination axis scores from the predictor variables was also used in the analysis.

Although every effort was made to choose 'unimpacted' sites there is no statistical methodology for doing this in New Zealand streams. Joy & Death (2003) have developed a New Zealand RIVPACS (River InVertebrate Predictive And Classification System) predictive model for statistically evaluating whether a site is impacted (i.e. observed taxa number/expected taxa number must be greater than that for the lowest 10% of O/E values for the reference sites). We applied this criterion to the 187 sites and removed any sites with O/E < 0.84, this left 123 sites, which can be considered unimpacted based on the taxa collected. We repeated the analytical procedures for this subset, hitherto referred to as 'reference' sites.

To evaluate if the regional scale categorical GIS data could be used to differentiate distinct groups of invertebrate community, rather than gradients of change, analysis of similarities (ANOSIM) using the ANOSIM routine in the PRIMER statistical package (Clarke & Warwick, 1994) was used to compare communities between ecoregions, river catchments and REC classes. ANOSIM is a nonparametric procedure that evaluates whether the average similarities (measured in this case with a Bray–Curtis distance measure) between samples within groups are closer than the average similarities of all pairs of replicates between groups (Clarke & Warwick, 1994).

Results

Invertebrate communities

One hundred and five taxa were collected in the 187 streams. Half of these were recorded at fewer than 5% of the sites. The mayflies *Deleatidium* (present at 92% of sites) and *Coloburiscus humeralis* (72%), beetle larvae Elmidae (84%), caddisflies Hydrobiosidae (76%), *Aoteapsyche* spp. (65%) and *Olinga feredayi* (47%), chironomids Orthocladiinae (73%), Megalopteran *Archichauliodes diversus* (63%), snail *Potamopyrgus antipodarum* (47%) and Simuliidae (43%) were the taxa most often present at a site. The numerically dominant taxon at individual sites was usually one of *Deleatidium* (most common at 89 sites), *P. antipodarum* (19 sites), Elmidae (19 sites), Orthocladiinae (15 sites), *C. humeralis* (14 sites) or Amphipoda (5 sites). Fifteen other taxa, principally Ephemeroptera, Plecoptera and Trichoptera, were the most common taxa at one to three sites each (total 26 sites).

Individual taxa and orders

Of the 138 biological and habitat variables examined, number of taxa was most strongly, and negatively linked with the per cent of the catchment in dairy farming and dominance was most strongly, and positively, linked with the per cent catchment base rock composed of windblown sand, however neither relationship was particularly convincing (Table 1). The relative abundance of Ephemeroptera showed a strong negative relationship with conductivity. Positive relationships were found between Plecoptera and per cent catchment in native forest, Trichoptera and trout abundance and Diptera with per cent base rock in crushed argillite.

Water chemistry had the strongest links with relative abundances of two of the most common taxa,

Table 1 Spearman rank correlation coefficients comparing relative abundance of individual taxa (six most abundant), orders (relative abundance) and diversity with the environmental factor that was most strongly correlated with the dependent variable. Environmental factors were chosen from the full suite of 120 measures and 18 PCA or NMS scores

Taxa	Variable	*r*
Deleatidium sp.	Chemical PCA 1 [combination alkalinity (+) conductivity (+) and salinity (+)]	−0.47
Potamopygrus antipodarum (Grey)	Conductivity	0.48
Elmidae	% base rock as crushed argillite	0.38
Orthocladiinae	Chlorophyll *a*	0.36
Coloburiscus humeralis (Walker)	Riparian PCA1 [combination % native (−), % pasture (+) and % willows (+)]	−0.40
Amphipoda	% macrophytes	0.35
Ephemeroptera	Conductivity	−0.43
Plecoptera	Land use PCA 2 [combination % native (+) and % pasture (−)]	0.54
Trichoptera	Trout abundance	0.28
Diptera (not Chironomidae)	% base rock as crushed argillite	−0.27
Chironomidae	Chlorophyll *a*	0.36
Crustacea	% land use in coastal sands	0.34
Mollusca	Conductivity	0.48
Number of taxa	% catchment in dairy farming	−0.36
Berger Parker index	% base rock in wind blown sand.	0.26
Invertebrate NMS axis 1 (187 sites)	Chemical PCA 1 [combination alkalinity (+) conductivity (+) and salinity (+)]	−0.69
Invertebrate NMS axis 1 (123 sites)	Alkalinity/Salinity	0.49

the leptophlebiid mayfly *Deleatidium* and the hydrobiid snail *P. antipodarum* showing a negative and positive relationship, respectively (Table 1). *Coloburiscus humeralis* was most strongly negatively associated with riparian PCA 1 [a combination of per cent riparian vegetation that is native (−), pasture (+) and willow (+)]. Positive relationships were found between Elmidae and per cent base rock in crushed argillite, Amphipoda and per cent macrophytes and Orthocladiinae with periphyton biomass (i.e. chlorophyll *a*).

Gradients of community structure

The NMS ordination (Fig. 2) yielded a final stress of 15.78 with axis one explaining 50% and axis two 22% of the variation in the data, indicating that the observed ordination was a valid representation of real patterns in the data (Clarke, 1993; McCune & Grace, 2002). *Deleatidium*, *C. humeralis* and *O. feredayi* were the principal taxa associated with sites to the right of axis 1 and O. albiceps, Orthocladiinae and *P. antipodarum* with sites to the left (Table 2). *Deleatidium* and Elmidae were similarly the principal taxa associated with sites to the bottom of axis 2 and Amphipoda with sites to the top of axis 2.

Alkalinity ($r = -0.67$), conductivity ($r = -0.61$), salinity ($r = -0.60$), per cent pasture ($r = -0.53$), and per cent macrophytes ($r = -0.48$) were negatively associated with axis 1 while per cent indigenous forest ($r = 0.46$) and average elevation ($r = 0.45$) were both positively correlated. Several other variables had significant, but considerably weaker relationships with axis 1, 2 and 3. Correlating the invertebrate ordination axis 1 scores with environmental variables replaced by their corresponding PCA or NMS scores chemical axis 1 (a combination of alkalinity and conductivity) ($r = -0.69$), land-use axis 2 [a combination of per cent pasture (−) and per cent indigenous forest (+)] ($r = 0.54$) and fish community axis 3 ($r = 0.47$) were the only significant correlations.

The NMS ordination of the 'reference site' subset (123 sites) produced a similar pattern to that for the full dataset although the axes are plotted in opposite directions to the full dataset (Fig. 2). Axis one again has sites that are dominated by *Deleatidium* ($r = -0.71$) at one end and Orthocladiinae ($r = 0.62$), *P. antipodarum* ($r = 0.49$), and *O. albiceps* ($r = 0.37$) at the other end. Furthermore, water chemistry [alkalinity ($r = 0.49$), salinity ($r = 0.49$) and conductivity ($r =$

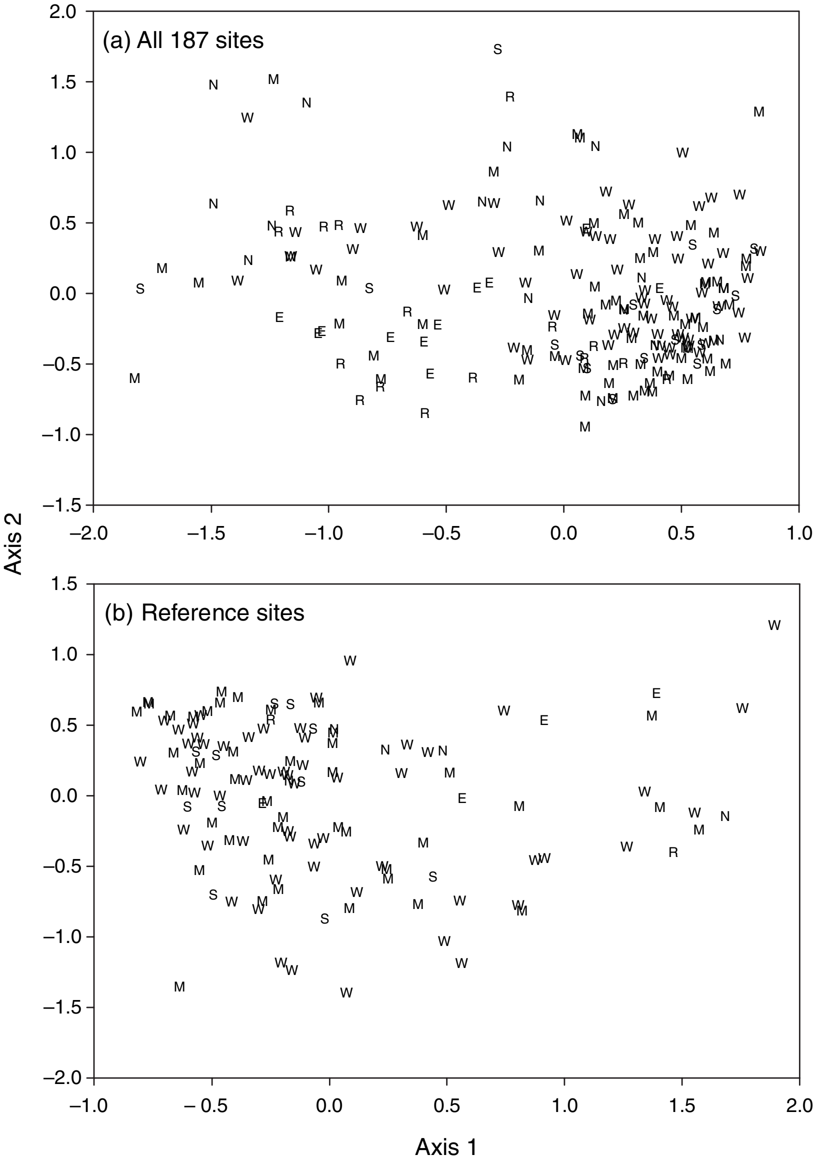

Fig. 2 Plot of axis 1 versus axis 2 of a non-metric multidimensional scaling analysis for invertebrate samples collected at (a) all 187 streams and (b) 123 'reference' streams (O/E < 0.84) in the Manawatu–Wanganui region between February and May 2000. Sites are represented by codes for the river catchment they were collected in M, Manawatu River; R, Rangitikei River; W, Whanganui River; E, Eastern rivers (East of divide); N, Northern rivers (North of Manawatu river); S, Southern rivers (South of Manawatu River).

0.41)] are again positively linked with the Orthocladiinae/*P. antipodarum*/*O. albiceps* communities and per cent indigenous forest ($r = -0.36$) with the mayfly dominated communities. Axis 1 explained 48% and axis 2 21% of the variation in the data with a final stress of 15.73.

Effects of categorical variables on community structure

The only significant difference between communities grouped on ecoregion, river catchment or REC class occurred between river catchment, geology REC and source of flow REC (Table 3, Fig. 3). Although the only difference between communities in the source of flow categories was between Low Elevation sites and those with Mountain or Hill based flows.

As alkalinity and conductivity have both been shown to be strongly associated with community structure above, we also divided communities into approximately equal groups of sites based on their measured alkalinity and conductivity and analysed the resulting groups using ANOSIM. In both cases there were strong differences between the groups (Table 3).

Of the groupings of communities considered, those for the alkalinity classes seem to be the most distinct.

Table 2 Correlation coefficients for taxa and NMS axes from the ordination of invertebrate data collected at 187 streams in the Manawatu–Wanganui region between February and May 2000. Only Bonferroni-corrected significant correlation coefficients are presented

	Axis 1	Axis 2	Axis 3
Deleatidium	0.62	−0.55	−0.54
Coloburiscus humeralis (Walker)	0.49		
Olinga fereday (McLachlan)	0.35		
Archichauliodes diversus (Walker)	0.33		
Austroperla cyrene (Newman)	0.30		
Megaloptoperla grandis (Kimmins)	0.27		
Paradixa harris (Tonnoiri)		0.38	
Paranephrops planifrons (Archey)		0.35	
Neozephlebia scita (Walker)		0.28	
Potamopygrus antipodarum (Grey)	−0.60		
Orthocladiinae	−0.51		−0.30
Oxyethira albiceps (McLachlan)	−0.43		
Amphipoda	−0.33	0.42	
Chironomidae pupae	−0.33		
Hirudinea	−0.29		
Oligochaeta	−0.29		
Platyhelminthes	−0.28		
Elmidae		−0.58	0.30
Eriopterini			−0.31

The mean relative abundance of orders in each of the five classes is presented in Fig. 4. Communities exhibit a steady increase in the relative abundance of Crustacea, Mollusca and to a lesser extent Chironomidae as alkalinity increases. Concomitant with this is a decline in the relative abundance of Ephemeroptera and Trichoptera.

Discussion

Determinants of invertebrate community structure

This study differs from similar investigations of macroecological patterns in stream invertebrate environment relationships (e.g. Richards *et al.*, 1996; Harding *et al.*, 1997; Wiley *et al.*, 1997; Townsend *et al.*, 2003) in that we have attempted only to sample streams that are minimally impacted by human activities. We have collected a spatially extensive dataset of invertebrate communities from relatively unimpacted streams in the central North Island of New Zealand. Associated with those samples we have compiled or measured an extensive array of biological (mainly fish), habitat characteristics, and GIS derived site descriptors to examine their relative contribution to explaining the observed patterns in the invertebrate communities. Of the 138 variables considered, water chemistry (alkalinity, conductivity and salinity) was the most consistent and influential descriptor of invertebrate community structure. Even when sites, whose pristine status was dubious, were removed from the analysis alkalinity was still the variable most strongly linked with community structure. Conductivity, and alkalinity when it is measured, have similarly been found to be strong predictors of community structure throughout the world in the development of reference site bioassessment models (e.g. RIVPACS, AUSRIVAS) where only relatively unimpacted sites are sampled (e.g. Moss *et al.*, 1987; Marchant *et al.*, 1997; Hawkins *et al.*, 2000).

Measures of conductivity and alkalinity are often taken to be surrogate measures of algal productivity, geology or land use in studies where these variables are not measured directly. In this study we had quantified or estimated all these other variables directly and yet conductivity and alkalinity were still more strongly linked with community structure. Some taxa, such as the Mollusca, may be responding directly to chemical characteristics of the water such as $CaCO_3$ concentration for shell formation, but it is hard to see why animals such as *Deleatidium* should be so tightly linked with alkalinity.

Perhaps measuring alkalinity is a better gauge of the longer term combined effects of variables such as algal productivity, geology or land use that have traditionally been associated with patterns in invertebrate distribution. For example algal productivity

Table 3 Analysis of similarity (ANOSIM) results testing for differences in groups of invertebrate community collected in 187 Manawatu–Wanganui streams. Allocation of stream communities to groups is based on river catchment, ecoregion, River Environment Classification (REC) classes (source of flow, geology, landcover, network position and valley landform), alkalinity and conductivity. Derivation of REC classes can be found in Snelder *et al.* (1998) and Snelder & Biggs (2002) and lotic ecoregions in Harding (1994). Global R indicates significant differences over all groups, however, significant individual group comparisons are also presented

Grouping class	Global R	*P*	Classes that are significantly different	Classes
River catchment	0.135	0.001	M,R M,E M,W	M Manawatu River
			M,N S,R S,E	R Rangitikei River
			S,N R,E R,W	W Whanganui River
			R,N E,W W,N	E Eastern rivers (East of divide)
				N Northern rivers (North of Manawatu river)
				S Southern rivers (South of Manawatu River)
Lotic ecoregion	0.023	0.20	CM,EL	CM Central mountains
			CM,WA	EL Eastern lowlands
			CM,TO CM,VP	MN Manawatu Plains
			EL,WO EL,TO	TO Taupo Plateau
			WA,WO	WO Waikato Hill Country
			WA,TO	WA Wairarapa Highlands
			TO,VP	VP Volcanic Plateau
Source of flow REC*	0.133	0.015	H,L L,M	M Mountain
				H Hill
				L Low elevation
Geology REC†	0.199	0.001	HS,M HS,SS	AL Alluvium
			HS,AL HS,VA	HS Hard sedimentary
			HS,VB M,SS	SS Soft sedimentary
			M,AL M,VA	VB Volcanic basic
			SS,AL SS,VA	VA Volcanic acidic
			AL,VA	M Mixed
Landcover REC‡	0.01	0.36	IF,EF IF,B	B Bare
				IF Indigenous forest
				P Pasture
				T Tussock
				S Scrub
				EF Exotic forest
Network position REC§	0.029	0.22		LO Low order
				MO Middle order
				HO High order
Valley landform REC¶	−0.033	0.91		HG High gradient
				MG Medium gradient
				LG Low gradient
Alkalinity class	0.203	0.001	A,C A,E A,D	A <20 mg L^{-1} CaCO$_3$
			B,E B,D C,E	B 21–40 mg L^{-1} CaCO$_3$
			C,D E,D	C 41–60 mg L^{-1} CaCO$_3$
				D 61–100 mg L^{-1} CaCO$_3$
				E >100 mg L^{-1} CaCO$_3$
Conductivity class	0.176	0.001	A,C A,D A,E	A <80 μs cm^{-1}
			B,C B,D B,E	B 81–120 μs cm^{-1}
			C,D C,E D,E	C 121–160 μs cm^{-1}
				D 161–260 μs cm^{-1}
				E >260 μs cm^{-1}

REC rules:

*M: >50% annual rainfall volume above 1000 m a.s.l., H: 50% annual rainfall volume between 400 and 100 m a.s.l., and L: 50% annual rainfall volume below 400 m a.s.l.

†Class is the spatially dominant geology category unless combined soft sedimentary geological categories exceed 25% of catchment area in which case class = SS.

‡Class is spatially dominant land cover category unless P exceeds 25% of catchment area in which case class = P.

§LO: stream order 1 and 2, MO: stream order 3 and 4, and HO: stream order ≥5.

¶HG: valley slope > 0.04, MG: 0.02 ≥ valley slope ≤ 0.04, and LG: valley slope < 0.02.

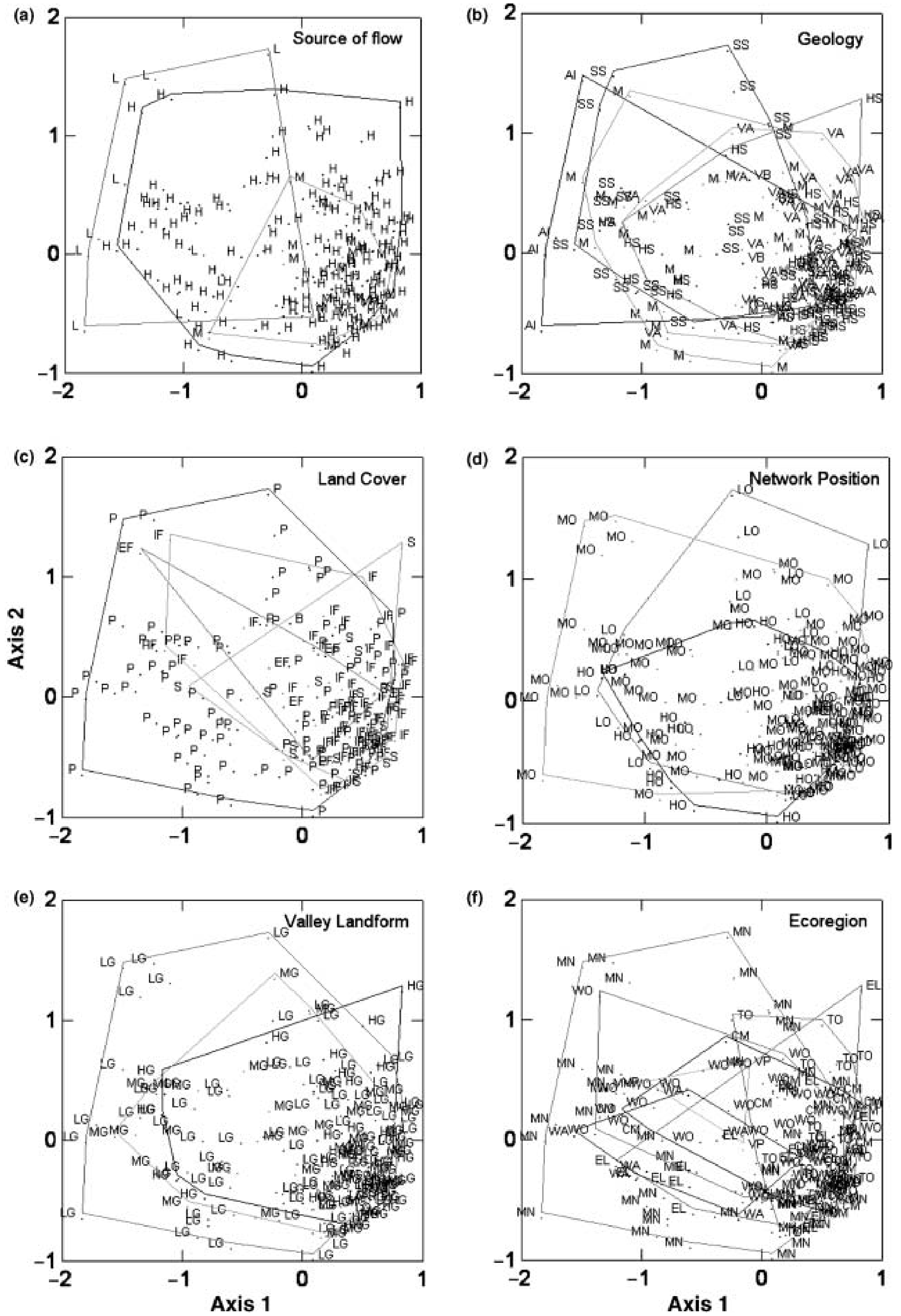

Fig. 3 Plot of axis 1 versus axis 2 of a non-metric multidimensional scaling analysis for invertebrate samples collected at 187 streams in the Manawatu–Wanganui region between February and May 2000. Sites are plotted based on River Environment Classification classes (a) source of flow, (b) geology, (c) land cover, (d) network position and (e) valley landform, and (f) ecoregion. See Table 3 for group codes for each REC or ecoregion class.

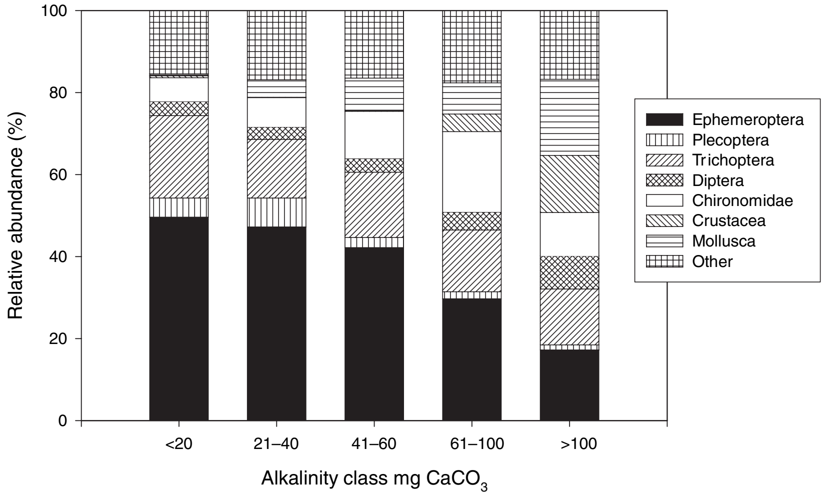

Fig. 4 Mean relative abundance of higher order taxa collected in streams from each of five alkalinity classes in the Manawatu–Wanganui region between February and May, 2000.

may not be accurately characterised by measuring periphyton biomass if it has been recently scoured by flooding. Similarly characterising land use as per cent pasture may not differentiate between the effects of low stocking levels and intensive agriculture (Harding *et al.*, 1999). We attempted to address this by replacing actual environmental measures with PCA scores for similar types of data (e.g. geology categories) but relationships were no better than those for individual variables.

Regardless of the reason, there are clear differences in invertebrate communities between streams that differ in alkalinity and conductivity. Streams with very low alkalinity and conductivity are dominated by Ephemeroptera, Plecoptera and Trichoptera that are gradually replaced by Mollusca, Crustacea and Chironomidae as alkalinity increases. Clearly not all taxa will be responding directly to changes in alkalinity or conductivity; amphipods, for example, are most strongly associated with the percentage of macrophytes in the stream, but this in turn is correlated with low gradient streams and high alkalinity. Similarly Chironomidae are associated with higher biomasses of periphyton that are likely to be found in streams with higher conductivity.

Reach scale versus catchment scale determinants of community structure

The availability and relative ease with which large numbers of catchment level variables can be retrieved from geographic information systems is an attractive prospect to stream ecologists for explaining patterns in community structure (Allan & Johnson, 1997). Hitherto implicated determinants of stream community structure such as catchment land use and geology can now be examined directly as potential predictor variables of instream fauna (Newson & Newson, 2000; Snelder & Biggs, 2002). If such patterns exist there is considerable potential for using GIS to categorise stream types and their associated biota and thus allow catchment wide management decisions to be made more accurately. The aim of our study was to compare the ability of reach and landscape scale GIS derived regional site characteristics to determine instream invertebrate community structure.

Of the 52 catchment scale GIS variables considered, only the land use categories (per cent pasture, indigenous forest, and coastal sand), and the geological categories (per cent crushed argillite and wind blown sand) were shown to be potential descriptors of community structure but even then these were generally weaker descriptors than reach level measures. Reach scale measurements of water chemistry, substrate composition, channel stability, riparian vegetation and fish communities were clearly the best predictors of community structure. Even communities from groups of streams derived using GIS, such as Ecoregions and REC classes, did not appear to be particularly distinctive. Geology was really the only discriminator and may in fact just reflect patterns in alkalinity rather than the other way around. Characterising sites based on water chemistry or river catchment (e.g. Rangitikei, Whanganui) was as good if not better in differentiating communities.

It would be premature to dismiss GIS data altogether as many of the potential predictor variables and classifications are in the early stages of development (Snelder & Biggs, 2002). The GIS will only be as good as the data that generated it (Richards *et al.*, 1997) and, for example, geology maps (from the NZLRI) in particular are notoriously unreliable in New Zealand (V. E. Neal, pers. comm.). Decisions about how rivers are classified using GIS-rule based systems are also continuing to be refined (Snelder & Biggs, 2002). However, we conclude that currently available GIS data in New Zealand are not as good at predicting invertebrate communities in these relatively unimpacted streams as reach scale measures.

Richards *et al.* (1996, 1997), in a study of 45 central Michigan rivers, encompassing a wide cross-section of land use types from forest and wetlands to intensive agriculture, have also found that local reach-scale characteristics (e.g. substrate type, stream width, canopy cover) are better predictors of community composition and species traits than the GIS derived catchment scale variables (e.g. surficial geology and land use). Sponseller, Benfield & Valett (2001) and Sponseller & Benfield (2001) also found both invertebrate communities and the breakdown of leaf material, respectively were more tightly linked with channel characteristics than any catchment scale variables. In contrast, Corkum (1989) in an extensive survey of 100 rivers in north-western North America found invertebrate communities were more tightly linked with biogeographic factors (e.g. geology, vegetation and land use) than on site variables. Furthermore, investigations focused on the effects of land use management have generally found the catchment scale variables associated with land use good predictors of community structure (e.g. Quinn & Hickey, 1990; Townsend *et al.*, 1997; Harding *et al.*, 1998; Townsend *et al.*, 2003).

Reach scale habitat characteristics of a stream will be determined, in part by factors acting at the scale of the catchment (Hynes, 1975) and it is thus not surprising that the above studies suggest both reach and catchment characteristics of a stream or river can be important in determining the invertebrate communities that live there. Evaluating which variables are more important is difficult from the above studies as they cover widely differing ranges of stream type, and evaluate different combinations of reach and catchment scale habitat characteristics. However, with an increasing need to develop predictive models of invertebrate community structure for bioassessment and resource management it is important that progress is made in evaluating what, of the wide array of available GIS data can be successfully used to determine invertebrate communities. Certainly in New Zealand the current GIS tools, the REC and lotic ecoregions, do not appear to predict the invertebrate communities of these central North Island streams with much accuracy, although it is possible to build predictive bioassessment models for New Zealand stream invertebrates with the careful selection of variables (Joy & Death, 2003).

In conclusion invertebrate community structure at these unimpacted New Zealand streams appears to be most strongly influenced by characteristics at the scale of the sample reach, such as water chemistry. Although catchment level variables must ultimately influence these reach habitat characteristics (Hynes, 1975; Frissell *et al.*, 1986) the instream measures recorded at the time of collection were much more strongly linked with community structure than any corresponding catchment level factors. Perhaps this is really not all that surprising given the size and relative mobility of most aquatic invertebrates. Environmental variables acting at the scale of the reach can have a more direct and thus stronger influence than any of the larger scale variables generating those habitats in the first place. Results from this and similar studies (e.g. Richards *et al.*, 1996, 1997) emphasise that caution needs to be used in ecological and resource management investigations using GIS data to predict instream biota. Although the quantity and ease of access of previously unavailable GIS data is appealing, the link between this data and the associated stream communities is far from a certainty.

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Appendix 1 Reach and catchment site characteristics recorded at the study sites between February and May 2000 or derived from GIS databases

Biological measures	
Galaxias fasciatus (Gray)	no. m^{-2}
Gobiomorphus cotidianus (McDowall)	no. m^{-2}
Gobiomorphus basalis (Gray)	no. m^{-2}
Elver *Anguilla* spp.	no. m^{-2}
Galaxias maculatus (Jenyns)	no. m^{-2}
Galaxias brevipinnis (Günther)	no. m^{-2}
Paranephrops planifrons (Archey)	no. m^{-2}
Anguilla dieffenbachia (Gray)	no. m^{-2}
Parataya curvirostris	no. m^{-2}
Gobiomorphus huttoni (Ogilby)	no. m^{-2}
Anguilla australis (Richardson)	no. m^{-2}
Galaxias postvectis (Clarke)	no. m^{-2}
Trout	no. m^{-2}
Gobiomorphus breviceps (Stokell)	no. m^{-2}
Retropinna retropinna (Richardson)	no. m^{-2}
Gobiomorphus breviceps (Stokell)	no. m^{-2}
Perca fluviatilis (Linnaeus)	no. m^{-2}
Cheimarrichthys fosteri (Haast)	no. m^{-2}
Galaxias divergens (Stokell)	no. m^{-2}
Mugil spp.	no. m^{-2}
Cyprinus spp.	no. m^{-2}
Geotria australis (Gray)	no. m^{-2}
No fish present	
Chlorophyll *a*	µg cm^{-2}
Phaeophytin	µg cm^{-2}
Water chemistry	
pH	
Alkalinity	mg L^{-1} $CaCO_3$
Conductivity	µs cm^{-1}
Salinity	ppm
Nitrate	mg L^{-1} NO_3-N
Reactive Phosphorous	mg L^{-1} PO_4^- P
Temperature	°C
Physical characteristics measured at site	
Easting	Map co-ords
Northing	Map co-ords
Reach length	m
Elevation	m (a.s.l.)
Reach slope (over surveyed reach)	m km^{-1}
Width (mean ± SD)	m
Depth (mean ± SD)	mm
Velocity	m s^{-1}
Mean and median substrate size	mm
Embededness	
Pfankuch stability score	
Upper	
Lower	
Bottom	
Total	
Proportion of reach surveyed composed of	
Still water	%
Backwater	%
Pool	%
Run	%
Riffle	%
Rapid	%
Undercut	%
Macrophytes	%
Debris jam	%
Land use and riparian vegetation at site	
Proportion of catchment at site composed of	
Exotic forest	%
Native forest	%
Dairy farming	%
Sheep/Beef farming	%
Urban	%
Proportion of riparian (10–20 m) vegetation at site composed of	
Native forest	%
Exotic forest	%
Pasture	%
Willow	%
Raupo reeds	%
Exposed gravel bed	%
GIS derived site characteristics	
Distance from coast	km
Euclidean distance from coast	km
Overall slope (site to sea)	m km^{-1}
Stream order	Strahler
Average catchment elevation	M
Elevation above sample reach	M
Elevation below sample reach	M
Total catchment rainfall	Annual rainfall × catchment area
Total catchment area	km^2
GIS derived catchment geology (entered as baserock and toprock separately) (from New Zealand Land Resources Inventory)	
Argillite	%
Argillite – crushed	%
Undifferentiated floodplain alluvium	%
Conglomerate or breccia	%
Gravels	%
Greywacke	%
Lahar deposits	%
Windblown sands	%
Loess	%
Mudstone of fine siltstone	
Banded	%
Jointed	%
Massive	%

Appendix 1 (*Continued*)

Biological measures	
Ashes older than Taupo pumice	%
Sandstone or coarse siltstone – massive	%
Taupo and Kaharoa breccia and volcanic alluvium	%
Unconsolidated clays, silts, sands, tephra and breccias	%
Lava, ignimbrite and other ‘hard’ volcanic rocks	%
GIS derived catchment land cover (from New Zealand Land Cover Database)	
Pastoral land	%
Horticultural land	%
Indigenous forest	%
Planted forest	%
Scrub	%
Tussock	%
Coastal sands	%
Bareground	%