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SEASONAL AND YEAR TO YEAR VARIATION IN THE MACROINVERTEBRATE COMMUNITIES OF NEW ZEALAND FOREST STREAMS



A thesis submitted in partial fulfilment of the requirements for the degree of

Master of Science in Ecology

at Massey University, Palmerston North, New Zealand

STEPHEN MARK MINCHIN 2002 One of the ultimate advantages of an education is simply coming to the end of it. - B.F. Skinner

ABSTRACT

The bed movement of 42 streams in the Ruahine Forest Park, Urewera National Park, and Cass-Craigieburn region was predicted from each stream's channel and catchment characteristics. While a stepwise regression was relatively unsuccessful in predicting tracer particle movement, an artificial neural network analysis achieved strong correlations with measured tracer particle data.

Forty-three streams in the Ruahine and Tararua Forest Parks were sampled in the summers of 1996 and 2001, and the macroinvertebrate communities compared. Changes in community structure between the two surveys did not correlate with any measured environmental characteristics including stream bed movement and change in periphyton biomass. MCI scores changed by a mean of 12.8 points between the two surveys, and the number of sites attaining an MCI score indicative of a 'pristine' stream dropped from 40 to 29. This appears to be related to a change in stream temperature, with streams that were cooler in 2001 than in 1996 showing an increase in MCI, while those which were warmer showed a decrease. Changes such as these could have a marked effect on biomonitoring programmes that use reference sites similar to these streams. In both 1996 and 2001, a greater number of taxa were collected from sites with more periphyton - taxon richness appears to asymptote at chlorophyll *a* concentrations greater than 5 $\mu g/cm^2$.

Twelve streams within the Ruahine Forest Park were sampled every three months between June 2000 and May 2001. Both periphyton biomass and macroinvertebrate taxon richness tended to decrease with bed movement. While macroinvertebrate community structure showed marked changes over the study period, these changes were not linked to bed movement or variation in periphyton level. The seasonal changes observed in these streams are not significantly different to the changes seen between the summers of 1996 and 2001 - community structure was no more stable between two summers separated by five years than it was between the seasons of a single year.

Eight artificial channels were laid on the bed of the Turitea Stream. At the onset of the experiment, half of the channels contained neither invertebrates nor periphyton cover, while the other half had no invertebrates but an initial periphyton layer. Drift samples indicate that approximately one in four drifting invertebrates colonised the channels during the 14 day study period, with benthic taxon richness reaching a peak after only four days. Colonisation was not affected by periphyton biomass. Some of the less common taxa that were present in the water column did not colonise the channels within 14 days.

EXPLANATION OF THE TEXT

This thesis is a combination of four individual papers, which has resulted in some repetition in the introductions and methods of some chapters.

Appendix 6 contains a fifth paper, which was presented at the 2001 Societas Internationalis Limnologiae Congress, held at the Clayton Campus of Monash University, Melbourne, Australia. This paper is to appear in Volume 28 of the Proceedings of the International Association of Theoretical and Applied Limnology, and is referred to within this thesis as 'Minchin & Death in press'.

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I would like to dedicate this thesis to my grandparents. Only one of you lasted long enough to see this produced, so Grandma, I'm expecting you to read it four times to make up the difference. Thank you for all of your financial support - without your generosity, I don't think that I would have made it this far. As with my parents, I hope that having me finish this thesis will make it seem worthwhile.

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Chapter 1:

GENERAL INTRODUCTION



Stream bed movement is perhaps the most frequently cited cause of disturbance and structuring of macroinvertebrate communities (e.g., Robinson & Minshall 1986; Resh *et al.* 1988; Matthaei *et al.* 1996; Townsend *et al.* 1997; Bond & Downes 2000, McCabe & Gottelli 2000). Disturbances, here defined as 'any relatively discrete event in time that removes organisms and opens up space or other resources which can be utilized by individuals of the same or different species' (Pickett & White 1985), may be particularly important in New Zealand stream communities due to the unpredictable nature of this country's hydrological regime (Winterbourn *et al.* 1981; Death & Winterbourn 1995).

Macroinvertebrate community structure is also affected by anthopogenic changes such as pollution or the removal of riparian vegetation. The invertebrate community may therefore be used as an indicator of waterway degradation (e.g., Stark 1985), but it is not clear how much change occurs naturally within a year, from year to year, or as a result of disturbances (Townsend *et al.* 1987), and it may be difficult to distinguish between natural and anthropogenic fluctuations. Changes in the communities of pristine 'reference sites' may influence the accuracy of stream biomonitoring programmes (Scarsbrook 2002), as it is the degree of difference between test and reference sites which determines our ability to identify degradation.

Scarsbrook (2002) has concluded that New Zealand macroinvertebrate communities may 'fluctuate around a relatively stable state', with greater inter-annual fluctuation at sites with more variable flows. A number of studies have investigated macroinvertebrate community change between years (e.g., Scarsbrook 2002; Townsend *et al.* 1987) and others have looked at change within a single year (e.g., Death & Winterbourn 1994), but few have compared these two quite different time scales. The purpose of this study is to determine what it is that causes change in the communities of forest streams over two time scales (intra-annual and between two summers separated by five years), with particular focus on disturbances by bed movement as a factor driving community change. Robinson & Minshall (1986) suggest that the factors which structure a community will differ according to season, while it makes intuitive sense that the factors will be similar in the same season of different years.

This study examines the effects of bed movement and periphyton biomass on the macroinvertebrate communities in Ruahine and Tararua Forest Park streams. The questions which this thesis aimed to investigate were:

 Is temporal variation of macroinvertebrate communities greater in streams which have greater bed movement?

2) Do macroinvertebrate communities vary more between years or between seasons within a single year, and is this related to stream bed movement?

3) Can the differences in spatial and temporal patterns between stream communities be explained by periphyton biomass?

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Chapter 2:

PREDICTING STREAM BED MOVEMENT FROM CHANNEL AND CATCHMENT CHARACTERISTICS



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ABSTRACT

The channel and catchment characteristics of 42 streams in the Ruahine Forest Park, Urewera National Park, and Cass-Craigieburn region were used in an attempt to predict each stream's bed movement. Data on tracer particle movement were used to assess the predictive potential of the models. Stepwise regression was relatively unsuccessful, but artificial neural network analysis achieved strong correlations with tracer particle data. Although the neural network model was not verified against an external data set, the 'leave-one-out' testing procedure was able to predict tracer particle data with a high level of accuracy.

INTRODUCTION

The hydrological regime of a stream and any associated bed movement are one of the main determinants of macroinvertebrate community structure (Resh *et al.* 1988). Consequently, bed movement is frequently measured in studies of macroinvertebrate communities, although there is little agreement as to exactly how this should be done (Downes *et al* 1998; Duncan *et al.* 1999; Death in press).

The majority of methods used to assess bed movement fall into one of three groups. Qualitative indices of bed stability are often quite simple to use, and require little time to be spent at a site but suffer from subjectivity of scoring (Duncan *et al.* 1999). In stream invertebrate studies, the Pfankuch stability index (Pfankuch 1975) is perhaps the most widely used of these indices (e.g., Death 1995; Death & Winterbourn 1995; Townsend *et al.* 1997b), but there is some doubt as to whether the Pfankuch index is a good measure of bed movement as it has been found to correlate poorly with tracer particle data (Death in press).

Equations derived from hydrological relationships (e.g., Newbury 1984; Statzner *et al.* 1988; Duncan *et al.* 1999) attempt to relate stream slope, shear stress, and / or bed particle size distribution to bed movement. These methods are appealing as they require little time in the field and are not overly subjective. However, some studies (e.g., Death & Winterbourn 1994) have found that substrate movement, as predicted by these equations, may not correlate with observed bed movement. Problems with hydrologically derived equations can often be traced to the wide range of streams and flow conditions over which the equations are applied, and the poorly understood relationship between shear stress and bed movement (Downes *et al.* 1998).

Finally, the use of tracer particles is perhaps the most common method of measuring substrate movement. Tracer particles are stones marked *ex* or *in situ* (Downes *et al.* 1998), with potential movement surveyed at regular intervals. This method of measuring substrate movement has the advantage of directly measuring stone movement, rather than predicting or inferring it. While it may provide an accurate indication of bed stability (Townsend *et al.* 1997b) the surveying of tracer particles is a labour intensive process, particularly if a number of remote sites must be visited each month. In spite of this, the method has been widely used (e.g., Death & Winterbourn 1994, Townsend *et al.* 1997a, Death in press).

The aim of this study was to produce a predictive relationship by which channel and catchment characteristics such as stream slope, bankfull wetted perimeter, and stone

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size distribution, could be used to assess stream bed movement. Stepwise regression and neural network analyses of channel and catchment characteristics were used to produce models predicting previously measured tracer particle data in 42 streams in the Ruahine Forest Park, Urewera National Park, and Cass-Craigieburn region. It was hoped that the resulting equations would be more objective than qualitative indices, simpler to use than some equations derived from hydrological relationships, and require less time in the field than tracer particle use.

METHODS

Tracer Particle data

Ruahine Forest Park (see Chapter 3): 15 tracer particles were marked *in situ* at each of 12 sites. These particles were in five rows of three stones (one stone from each of the following three size classes - maximum linear planar dimension <60mm, 60-90mm, 90-180mm), with the rows randomly located between one and ten metres upstream of five consecutive riffle-run series in the study reach. Stone size order across the stream bed was random. Stones were marked using Fosroc Expocrete UA concrete fix, a two part, epoxy mortar which adheres and dries underwater and is clearly visible for up to a year after application.

Tracer particles were initially layed in July 2000. Every month, the sites were surveyed and the stones that were not displaced in the past month were located. When a stone was not found, another was marked in its place.

The number of stones from each size class that had not moved in successive surveys was summed for each site. These figures were adjusted according to the mean stone weight of each size class (Death, unpublished data) - stones with maximum linear planar dimension <60 mm were divided by 0.167, 60-90 mm by 0.327, and >90 mm by 1.128. Small particles that remain stationary were therefore more important in this scale of bed movement, accounting for the low relative frequency at which they are recovered. The result was converted to a percentage scale, with higher numbers indicating greater bed movement.

Urewera National Park (Death in press): The distance moved by five painted stones in each of three size categories (as above) was recorded in each of 21 streams at approximately three-monthly intervals between August 1996 and November 1997. When the sites were surveyed, stones were resettled, returned to the starting point, or replaced.

To convert distance data to a single measure of stream substrate movement, the distance travelled was multiplied by the mean weight of stones in that size class and summed for all painted stones at that site. If a stone was not found during a survey, a distance travelled of 50 m was assigned (this being the maximum distance at which any stone was recovered). The result was converted to a percentage scale as above.

Cass-Craigieburn region (Death & Winterbourn 1994): Five stones in each of three size classes (as above) were marked with fluorescent paint and placed at a specific point within a riffle in each of 10 streams. They were arranged in a line perpendicular to the shore and extended across at least half the width of the stream. Every month from December 1987 to May 1989, the distance travelled by each stone was recorded. Each month, all stones were resettled, returned to the starting point, or replaced.

Distance data was converted to a single measure of stream substrate movement as above.

Channel and catchment characteristics

A number of channel and catchment characteristics were measured over the periods of tracer particle data collection. These were: stream width and depth (at base flow and estimated bankfull) measured at five equidistant points in the Thalweg along the study reach, base and bankfull R (the hydraulic radius measured in metres, see Duncan *et al.* 1999), percentage of the bankfull stream bed cross-section which was dry at base flow, channel slope (measured with an Abney level over 10m), and Thalweg current velocity at base flow (measured with a Marsh McBirney velocity meter 10cm above the stream bed). Stream length (measured from the study site to the most distant upstream point of the stream that was marked on the map), catchment area, catchment perimeter, and mean stream slope (from the site to the most distant upstream point), were later measured from New Zealand Map Service 260 series 1:50 000 topographical maps.

In the Ruahine Forest Park sites, size distribution of the stream bed particles was examined by sampling the surface stones in fifteen $0.1m^2$ quadrats. These were located in the middle, mid-left and mid-right side of the stream on five transects randomly placed across the bed. The longest axis of all the surface stones lying within each

quadrat were measured and recorded. In the Urewera sites, stone size distribution was estimated by measuring the longest axis of 100 stones which were randomly chosen using a cross-sectional transect. In the Cass-Craigieburn sites, stone size distribution was assessed through the sampling of fifty stones from each of ten 0.1m² quadrats and a 50 stone survey using a cross-sectional transect. For all sites, substrate composition was converted to a single substrate size index (SI) by summing the mid-point values of the size classes weighted by their proportional abundance (Quinn & Hickey 1990), and mean substrate size (d50) was also calculated.

Each stream was also scored according to the fifteen criteria in the Pfankuch index (Pfankuch 1975). This is a subjective measure of channel stability based on a series of observations including the degree of bank undercutting and debris jam potential. Only the bottom component of the index was used in this study as this relates to a scale of bed stability more appropriate for measuring substrate stability (Winterbourn & Collier 1987).

Stepwise regression of channel and catchment characteristics

The stepwise regression procedure of SAS (2000) was used to produce an equation predicting bed movement from channel and catchment characteristics in the 42 streams. Variables which were strongly correlated with each other were removed, and those with significance below the 0.15 level were excluded from the model. All correlations were checked by eye for non-linearity.

Downes *et al.* (1998) found that human-placed tracer particles moved half as often as those marked *in situ*, suggesting that different particle marking methods produce significantly different estimates of bed movement. This may make it difficult to compare results from the two methods. While most data were collected using humanplaced particles, the Ruahine set was not; this data was excluded from a second stepwise regression to eliminate any possible confounding influence.

Neural network analysis of channel and catchment characteristics

The data from the 42 streams were also analysed using Easy NN 7.5 (Wolstenholme 2001), a three-layered artificial neural network. There were 17 input neurons to code the 17 independent variables, four neurons in the hidden layer (configured so as to minimise error during model training and testing), and a single output neuron predicting tracer particle movement.

Model training was performed with the complete data set, with cross-validation then tested using the 'leave-one-out' bootstrap method (Efron 1983). This method has been found to be appropriate for use in models involving small data sets (Guégan *et al.* 1998), and tests the robustness of the model.

Easy NN allows the relative importance of each input variable to be assessed. After training of the model, the input variable with the lowest connection weight was removed and training then performed on the reduced data set. This was repeated until only those variables with relative importance values of greater than 10 remained.

As with the stepwise regression, the Ruahine data set was excluded and a second neural network analysis performed.

RESULTS

Stepwise regression of channel and catchment characteristics

None of the measured channel and catchment characteristics were non-linearly related to measured tracer particle movement. Only two of the measured variables were correlated with tracer particle movement at r > 0.15 (Table 2.1); these were stream slope (r = 0.27), and percentage change in R between base and bankfull flow (r = 0.31).

The stepwise regression produced a significant fit to predict tracer particle movement, although only 17% of the variation in the data was explained ($F_{1,41} = 8.42$, P < 0.01, $r^2 = 0.17$) (Fig. 2.1). This yielded the equation :

Tracer particle movement = 38.4 - (0.3 change in R) - (42.8 stream slope)

When the Ruahine data were excluded from the stepwise regression, two of the channel and catchment characteristics were strongly correlated with particle movement. These were change in hydraulic radius (R) (r = 0.52), and base flow width (r = 0.30).

The stepwise regression once again produced a significant fit to predict tracer particle movement, with 24% of the variation in the data explained ($F_{1,41} = 12.38$, P < 0.05, $r^2 = 0.24$) (Fig. 2.2). This yielded the equation :

Tracer particle movement = 30.6 - (0.4 change in R) + (0.1 base flow width)

Table 2.1 Correlation (r) of measured channel and catchment characteristics with tracer particle movement in 42 streams in the Urewera, Cass-Craigieburn, and Ruahine regions. Note that none of these correlations are significant at P < 0.05.

	Measured tracer
	particle movement
Mean velocity	0.00
Mean base flow width	0.02
Mean bankfull width	0.03
Mean base flow depth	0.01
Mean bankfull depth increase	0.23
Mean base flow width:depth	0.00
Mean bankfull width:depth	0.00
Mean width:depth % change	0.01
Mean base flow hydraulic radius (R)	0.01
Mean bankfull hydraulic radius (R)	0.10
R % change from base flow to bankfull	0.31
% bed dry at base flow	0.03
Stream slope	0.27
Catchment area	0.01
Catchment length	0.02
Catchment perimeter	0.05
Catchment shape	0.05
SI	0.03
Mean stone size (d50)	0.00
% bedrock	0.00
% boulder	0.01
% cobble	0.00
% gravel	0.02
Pfankuch bottom component	0.01



Figure 2.1 Stone movement, as predicted by a multiple regression equation, as a function of measured stone movement in 42 streams in the Urewera, Cass-Craigieburn, and Ruahine regions. Solid points represent Urewera and Cass-Craigieburn sites, hollow points represent Ruahine sites. Note that the 12 Ruahine sites had tracer particle movement measured with particles marked *in situ*.

Tracer particle movement = $38.4 - (0.3 \text{ change in R}) - (42.8 \text{ stream slope}); r^2 = 0.17$



Figure 2.2 Stone movement, as predicted by a multiple regression equation, as a function of measured stone movement in 30 streams from the Urewera and Cass-Craigieburn regions.

Tracer particle movement = $30.6 - (0.4 \text{ change in R}) + (0.1 \text{ base flow width}); r^2 = 0.24$

Artificial neural network analysis of channel and catchment characteristics

Results in training of the artificial neural network were highly significant, with r^2 values of up to 0.99 when all 17 input variables were used. As variables were removed, the correlation between predicted and observed values declined, but remained above 0.80. Once the less important variables had been eliminated from the analysis, 'leave-one-out' testing was performed on the remaining six variables. These results were highly significant (0.75 < r^2 < 0.91). While it is not possible to extract the resulting model equation from Easy NN, the model produced by the neural network had the following six key variables (listed in order of relative importance) :

% stream bed dry at base flow	(relative importance = 50.7)	
base flow to bankfull depth increase	(37.0)	
SI	(36.6)	
stream slope	(36.1)	
bankfull hydraulic radius (R)	(28.1)	
stream length	(19.7)	

When these values were used to predict tracer particle movement in the original data set, predicted values were strongly linked to actual tracer particle movement data $(F_{1,41} = 268.99, P < 0.0001, r^2 = 0.87)$ (Fig. 2.3).



Figure 2.3 Stone movement, as predicted by an artificial neural network, as a function of measured stone movement in 42 streams in the Urewera, Cass-Craigieburn, and Ruahine regions. Solid points represent Urewera and Cass-Craigieburn sites, hollow points represent Ruahine sites. Note that the 12 Ruahine sites had tracer particle movement measured with particles marked *in situ*.

Predicted stone movement = $1 + (3.2 \text{ tracer particle movement}); r^2 = 0.87$

As with the stepwise regression, the Ruahine data set was then excluded from data analysis. Results in training were again highly significant, with r^2 values comparable to those achieved with the complete data set (i.e., up to 0.99). When the less important variables were removed the relationship between predicted and observed values weakened slightly, but remained above 0.82. 'Leave-one-out' testing was then performed on the remaining variables, with highly significant results (0.81 < r^2 < 0.94).

With the Ruahine data excluded, the artificial neural network produced a model with the following six key variables (listed in order of relative importance) :

base flow width	(relative importance $= 53.9$)	
SI	(35.4)	
base flow current velocity	(31.9)	
base flow depth	(24.6)	
% stream bed dry at base flow	(24.3)	
stream slope	(23.9)	

When these values were used to predict tracer particle movement in the original data set (less the Ruahine data), predicted values increased with measured tracer particle movement data ($F_{1, 41} = 343.51$, P < 0.0001, $r^2 = 0.92$) (Fig. 2.4).



Figure 2.4 Stone movement, as predicted by an artificial neural network, as a function of measured stone movement in 30 streams in the Urewera and Cass-Craigieburn regions.

Predicted stone movement = $0.9 + (4.3 \text{ tracer particle movement}); r^2 = 0.92$

DISCUSSION

Stepwise regression of channel and catchment characteristics produced a relatively poor model of measured tracer particle movement. The combination of change in hydraulic radius (R) and stream slope produced an equation that poorly predicted ($r^2 = 0.17$) tracer particle movement data from the 42 streams. The artificial neural network achieved an r^2 of 0.87 when applied to the same data set, suggesting that neural networks provide a more powerful tool for predicting substrate movement.

When the Ruahine data (i.e., the data gathered with tracer particles marked *in situ*) were removed, the stepwise regression produced an equation which gave a better fit with tracer particle data ($r^2 = 0.24$) than the previous, full data set equation ($r^2 = 0.17$). The artificial neural network was also able to predict tracer particle movement slightly more effectively in this reduced data set, with an r^2 of 0.92 (as opposed to $r^2 = 0.87$). These increases are slight, suggesting that the different methods did not have a large influence on the results. This may be due to the conversion of all data into a percentage scale - particles marked *in situ* may move twice as often as those placed by hand, but this difference is eliminated when the two sets of data are compared on a single scale.

The two stepwise regression procedures found that change in hydraulic radius (R) between base flow and bankfull flow was important in predicting tracer particle movement. R is related to stream depth, and as depth is important in determining shear stress one would expect that streams which have a large increase would have high bed movement. Change in depth could be more important than absolute depth at bankfull as the shear stresses in streams with continuously deep water will likely produce a bed

which is relatively immobile when compared to that of a stream which is shallow at base flow. Stream slope may be important for a similar reason, as steeper streams will have faster flowing water, and faster water results in higher shear stresses. As has been noted above, while these two theoretically important factors were used in the equation produced by the stepwise regression it remained a poor predictor of bed movement.

The artificial neural network analysis did not find change in R to be significant, but used the percentage of the bankfull stream bed which was dry at base flow (a measure of base to bankfull width increase) and base flow width - measures of width were more important than those of depth. It is likely that this link between width and tracer particle movement is the result of larger streams having more frequent or pronounced high flow events. SI (an index of substrate size) was also found to be important, which makes intuitive sense as smaller substrates are more readily disturbed. Stream slope, current velocity, and several measures of stream depth were also significant.

The artificial neural network produced quite a different group of key variables when used to analyse the full data set and the set with Ruahine data removed. Exactly why this should be so is difficult to explain, but is perhaps due to the chance combination of a number of factors at the Ruahine sites.

In conclusion, it appears that while stepwise regression of channel and catchment characteristics did allow tracer particle movement to be predicted, the artificial neural network analysis was far more effective. The equations derived by both methods seem to make sense inasmuch as the individual factors will be important in the determination of stream bed shear stresses and hence bed movement.

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Chapter 3:

SPATIAL AND TEMPORAL CHANGE IN THE MACROINVERTEBRATE COMMUNITIES OF NEW ZEALAND FOREST STREAMS



ABSTRACT

The macroinvertebrate communities of 43 streams in the Ruahine and Tararua Forest Parks were sampled during the summers of 1996 and 2001. At most sites, fewer taxa were collected in 2001. Change in community structure between the two years was not related to bed movement, change in periphyton level, or any other measured environmental characteristic. Persistence of taxon abundance was greater at sites with more periphyton in 2001. On average, MCI score changed by 12.8 points between 1996 and 2001, and the number of sites attaining an MCI of greater than 120 (indicative of a 'pristine' stream) dropped from 40 of the 43 sites to only 29. Streams which were cooler in 2001 than 1996 tended to increase in MCI, while those which were warmer showed a decrease. Biomonitoring programmes based on reference sites similar to these should take natural variation in pristine streams into account, or risk inaccurate assessment of test sites. Despite differences in taxon richness, invertebrate density and periphyton level between 1996 and 2001, richness and periphyton level were strongly linked in both years. More taxa occur at sites with higher periphyton biomass, with richness reaching an asymptote at chlorophyll *a* concentrations greater than 5 μ g/cm².

INTRODUCTION

Change in macroinvertebrate community structure is often used as an indicator of waterway degradation, but it is not clear how much change occurs in the communities of pristine streams with minimal anthropogenic impacts (Townsend *et al.* 1987). This is

an important issue, as changes in the communities of reference sites may influence the accuracy of environmental monitoring programmes (Scarsbrook 2002).

Few studies have reported the long-term variation in macroinvertebrate communities. Townsend et al. (1987) sampled 27 streams in southern England in 1976 and 1984, and found that community persistence was higher at sites with low discharge, stable temperature and constant pH - that is, sites with greater environmental stability showed higher community stability. This study also found that a core group of taxa (including Baetis sp., Hydropsyche siltalai, Simuliidae, and Pentaneurini) tended to persist at each site. A study of 18 upland streams in Wales (Weatherley & Ormerod 1990) yielded similar findings, with communities highly consistent across the five study years. Richards & Minshall (1992) looked at ten streams in Idaho, sampling annually from 1980 to 1984. The relative abundance of common taxa was stable through the five years of study, and was attributed to the predictable environmental conditions (in particular the seasonal hydrological regime) of the study streams. More recently, an annual study of 26 northern New Zealand river sites (Scarsbrook 2002) has revealed some interesting trends. Mean annual community change was greatest at sites with more variable flow conditions, with sites showing similar changes between years. Scarsbrook suggests that communities may fluctuate around a 'relatively stable state' but, given the degree of variation seen, predictive models based on reference site conditions should be used with caution.

In the current study, I investigated the changes in the macroinvertebrate communities in 43 streams in the lower North Island of New Zealand between 1996 and 2001. Unlike most previous studies of this type, all of the sites were within the boundaries of relatively pristine State Forest Parks, with 22 in the northern Ruahine
Ranges (half on the western side and half on the east), and 21 in the southern Tararua Ranges (ten on the west and 11 on the east). The study sites ranged from stable streamfed streams to larger, frequently disturbed streams draining steep hill country, with the expectation that disturbance by spates in an otherwise quite stable and pristine environment would be a major driving factor in community change. I predicted that communities at sites with less bed movement would show less change between surveys (Death & Winterbourn 1994). Given that the study sites are all within Forest Park boundaries, I expected to find that all sites had MCI scores in excess of 120, with little difference between years.

STUDY SITES

The 43 study sites were on 1st- to 3rd-order streams flowing from the Ruahine and Tararua Ranges in the North Island of New Zealand (see Fig. 3.1 and Table 3.1). They were within protected State Forest Parks and had varying degrees of predominantly beech, kamahi, rimu and tawa dominated native canopy cover (see Plate 3.1).

In 1996, 44 sites were sampled in four regions: 22 in the Ruahines (11 on the western side, and 11 on the eastern), and 22 in the Tararuas (11 on either side). When sampling was performed in 2001, site number 23 (a tributary of Baber Creek, on the western side of the Tararua Ranges) was dry and therefore was not sampled.



Figure 3.1 Locations of the 44 study sites in the Ruahine and Tararua Ranges in the lower North Island of New Zealand.

Site #	Site name	Coordinates	Ranges	Side
1	Mangatuatou Stream	175°53.308'E 40°09.525'S	Ruahine	West
2	Tamaki River West Branch	176°01.746'E 40°07.188'S	Ruahine	East
3	Mangapuaka Stream	175°58.712'E 40°10.275'S	Ruahine	East
4	A tributary of Matanganui Stream	175°51.252'E 40°11.896'S	Ruahine	West
5	Matanganui Stream	175°52.101'E 40°11.156'S	Ruahine	West
6	Reef Creek	175°36.176'E 40°28.218'S	Tararua	East
7	A tributary of Reef Creek	175°36.176'E 40°28.199'S	Tararua	East
8	A tributary of the Akiuhakatu Stream	175°28.866'E 40°36.827'S	Tararua	East
9	A tributary of Mangateretere Stream	175°26.543'E 40°42.410'S	Tararua	East
10	Coppermine Stream	175°13.107'E 40°53.205'S	Ruahine	East
11	A tributary of Coppermine Stream	175°13.107'E 40°50.205'S	Ruahine	East
12	Manawatu River	176°08.587'E 39°59.057'S	Ruahine	East
13	A tributary of Panatewaewae Stream	175°16.054'E 39°47.054'S	Tararua	West
14	Panatewaewae Stream	176°11.739'E 39°47.056'S	Tararua	West
15	Coal Creek	175°53.701'E 40°14.215'S	Ruahine	West
16	Cone Creek	175°53.701'E 40°14.566'S	Ruahine	West
17	Limestone Creek	175°36.701'E 40°18.837'S	Ruahine	West
18	A tributary of Kahuterawa Stream	175°36.716'E 40°28.218'S	Tararua	East
19	Otangane Stream	175°36.866'E 40°28.275'S	Tararua	West
20	Mangatainoka River	175°32.608'E 40°41.820'S	Tararua	East
21	A tributary of Mangatainoka River	175°32.819'E 40°41.605'S	Tararua	East
22	Mangaroa Stream	175°36.716'E 40°28.218'S	Tararua	East
23	A tributary of Baber Creek	175°29.480'E 40°28.172'S	Tararua	West
24	A stream flowing into Mangahoa No.2	175°29.512'E 40°28.222'S	Tararua	West
25	Sheridan Creek	175°13.107'E 40°53.203'S	Tararua	West
26	A tributary of the Waiotauru River	175°13.107'E 40°53.205'S	Tararua	West
27	Waikanae River	175°12.856'E 40°53.205'S	Tararua	West
28	Ngatiawa River	175°13.107'E 40°54.192'S	Tararua	West
29	A tributary of Kawhatau River	176°00.804'E 39°53.840'S	Ruahine	West
30	Mangakukeke Stream	176°00.804'E 39°54.121'S	Ruahine	West
31	Coal Stream	172°85.125'E 41°00.000'S	Tararua	East
32	Devil Creek	176°01.341'E 39°49.210'S	Tararua	East
33	Mikimiki Stream	175°36.716'E 40°28.218'S	Tararua	East
34	Rangiwahia Stream	176°00.803'E 39°53.870'S	Ruahine	West
35	Mangiore Stream	175°53.701'E 40°14.837'S	Ruahine	West
36	Ngamoko Stream	176°08.103'E 40°02.572'S	Ruahine	East
37	Waipawa River	176°11.656'E 39°48.391'S	Ruahine	East
38	Triplex Creek	176°11.739'E 39°47.521'S	Ruahine	East
39	Sentry Box Creek	175°23.174'E 40°38.772'S	Ruahine	East
40	A tributary of Ohara Stream	176°18.632'E 39°38.495'S	Ruahine	East
41	Raparapawai Stream	175°13.107'E 40°53.205'S	Ruahine	East
42	Te Ekaou Stream	175°54.290'E 40°06.650'S	Ruahine	West
43	A tributary of Kahuterawa Stream	175°35.278'E 40°29.389'S	Tararua	West
44	Waiti Stream	175°16.048'E 40°43.607'S	Tararua	West

Table 3.1 Names, coordinates, and locations of the 44 study sites. Note that as site 23 was dry in 2001, it was surveyed in 1996 only.



Plate 3.1 Site 11, a tributary of Coppermine Stream (top) and site 25, Sheridan Creek (bottom), two contrasting streams which were sampled in the summers of 1996 and 2001.

METHODS

Macroinvertebrate sampling protocol

Five randomly selected stones from each of three size classes (maximum linear planar dimension <60mm, 60-90mm, >90mm) were removed from the stream bed at each of 43 sites on two occasions: summer 1996 (January 29 to April 3), and summer 2001 (February 19 to March 3). On both occasions, sampling was carried out after a period of at least three weeks at base flow.

Stones were sampled as the collector moved progressively upstream. The invertebrates on each stone were collected by scooping the stone into a net of 250µm mesh, along with any fine sediment or detritus immediately below the collected stone. The stone was thoroughly washed in the net to ensure all invertebrates were removed. Death (1991) found this method to yield more precise estimates per unit effort for both macroinvertebrate density and diversity than Surber sampling. Invertebrates were stored in 10% formalin and later identified and enumerated using the keys of Winterbourn & Gregson (1989) and Boothroyd (2000).

After the invertebrates had been removed, the three axes of the sampled stones were measured to the nearest centimetre. The macroinvertebrate data was later converted to number of individuals per square metre of stone surface by dividing the density of invertebrates collected on each stone by the estimated surface area of that stone:

(1.15 (height x depth + height x width + width x depth)) / 100

Periphyton sampling protocol

Periphyton biomass was estimated by collecting five randomly selected stones (45-70mm maximum linear planar dimension) from the stream bed at each site on each sampling occasion. Pigments were extracted and analysed following the methods of Steinman & Lamberti (1996), with values corrected for surface area by weighing aluminium foil of known mass per unit area that was cut to snugly cover the stones. As chlorophyll *a* concentration has been found to correlate strongly with periphyton biomass in New Zealand streams (Clausen & Biggs 1997), this is taken to be an indicator of periphyton biomass in the study streams.

At some sites chlorophyll *a* concentrations were several orders of magnitude greater in 2001 than was seen in 1996. When calculating the percent change in periphyton level from 1996 to 2001, an arbitrary maximum value of 500% was imposed.

Measurement of bed movement

Bed movement was assessed using 15 tracer particles marked *in situ* at each site. These particles were in five rows of three stones (one stone from each of the following three size classes - maximum linear planar dimension <60mm, 60-90mm, >90mm), with the rows randomly located between one and ten metres upstream of five consecutive riffle-run series in the study reach. Stone size order across the stream bed was random. Stones

were marked using Fosroc Expocrete UA concrete fix, a two part, epoxy mortar which adheres and dries underwater and is clearly visible for up to a year after application.

Tracer particles were initially layed in July 2000. Every month, 12 of the sites (site numbers 1, 2, 3, 4, 5, 10, 11, 12, 15, 17, 34, and 36, see Chapter 4) were surveyed and the stones that were not displaced in the past month were located. When a stone was not found, another was marked in its place. At the remaining 31 sites, tracer particle movement was surveyed every three months, for 12 months.

For the 12 sites which were surveyed monthly, the number of stones from each size class that had not moved in three successive surveys (from July to October, October to January, January to April, and April to July 2001) was summed for each site. For the 31 which were surveyed every three months, the number of stones which had not moved in successive surveys were summed for each site. These figures were adjusted according to the mean stone weight of each size class (Death, unpublished data) - stones with maximum linear planar dimension <60mm were divided by 0.167, 60-90mm by 0.327, and >90mm by 1.128. This made the small particles which remain stationary more important in assessing bed movement. The resulting value was converted to a percentage scale with higher numbers indicating greater bed movement.

Bed movement at the 43 study sites was also predicted using a model created with an artificial neural network analysis of environmental variables from 42 streams in the Ruahine, Urewera, and Cass-Craigieburn regions. The model used the proportion of the bankfull stream bed which was dry at base flow, base flow to bankfull depth increase, stone size distribution, stream slope, and bankfull hydraulic radius (R) to predict stone movement (see Chapter 2).

Measurement of environmental variables

Temperature and conductivity were measured using an Orion 122 conductivity meter adjusted automatically to 25°C. pH was measured with an Orion Quickcheck model 106 meter. Slope was measured using an Abney level over 10 m. Stream width and Thalweg depth were measured at five equidistant points along the study reach. Velocity was measured at these same points in the Thalweg using a velocity head rod (in 1996) and a Marsh McBirney velocity meter 10 cm above the stream bed (in 2001). Canopy cover was visually estimated while standing in the stream centre.

The size distribution of the stream bed particles was examined in 2001 only. The maximum linear planar dimension of surface stones were measured in 15 0.1m² quadrats. These were located in the middle, mid-left and mid-right side of the stream on five transects randomly placed across the bed. Substrate composition was converted to a single substrate size index (SI) by summing the mid-point values of the size classes weighted by their proportional abundance (Quinn & Hickey 1990). The mean size of the stones collected from each quadrat was calculated, as was the standard deviation of stone size in each quadrat. Following Scarsbrook & Townsend (1993), Simpson's index was used to calculate substrate size diversity at each site (Simpson 1949).

Data analysis

Using Bray-Curtis distance measures in PC-ORD (McCune & Mefford 1997), the multivariate distance between 1996 and 2001 community structure and between taxon presence / absence were calculated.

At 40 of the sites, more individuals were collected in 1996 than in 2001. The number of individuals which were collected at a site in 2001 was randomly sub-sampled from that site's 1996 species pool to examine if community changes may be attributable to differences in overall diversity or merely sample size. This procedure was performed ten times for each site, with mean and standard deviation of the number of sub-sampled taxa calculated. The Bray-Curtis distance between each of the ten sub-sampled communities and its 2001 counterpart was calculated to examine whether the 2001 communities were distinctly different to those of 1996. Paired *t* tests were also performed to examine whether taxon richness was significantly different between years, and between each year and the sub-sampled community.

The taxa collected in each year were ranked according to density, with constancy of rank position from 1996 to 2001 then assessed with Kendell's coefficient of concordance (W) (Siegel & Castellan 1988). This is a technique of multiple rank correlation, and was carried out on both the ten most abundant taxa, and on all taxa collected regardless of abundance. Simpson's index was used to measure taxon evenness at each site, and Stark's (1985) Macroinvertebrate Community Index (MCI) was calculated for each site according to the scores given in Winterbourn *et al.* (2000).

The effect of sampling year and region on environmental variables, taxon richness, and taxon evenness were tested using the ANOVA procedure of SAS (2000). Taxon richness in 1996 and 2001 were compared using the paired *t*-test procedure of SAS (2000). Correlations and Bonferroni *a posteri* means test procedures were also performed using SAS.

RESULTS

Environmental characteristics

The range and mean of environmental characteristics in the streams of the four regions are presented in Table 3.2. Individual site details are provided in Appendix 1.

The streams had mean depths (measured in midstream) between 7 and 40cm. Stream depth did not change significantly between 1996 and 2001 ($F_{4,81} = 0.83$, P = 0.36), and were not significantly different between the four regions ($F_{4,81} = 0.98$, P = 0.41). Current velocities were between 5 and 70cm/s; these were not significantly different between years ($F_{4,81} = 0.02$, P = 0.90), but showed variation between regions ($F_{4,81} = 16.19$, P < 0.0001). Mean current velocity was significantly higher in the Ruahines than on either side of the Tararua ranges.

All sites were cool (10.2 to 17.4°C), with no significant temperature difference between regions ($F_{4,81} = 1.09$, P = 0.36) but a small increase from 1996 to 2001 (mean temperature change = 0.9°C, $F_{4,81} = 4.85$, P < 0.05). Stream conductivity was between 50 and 151µS/cm. There was no significant change in conductivity between years ($F_{4,81}$ = 2.26, P = 0.14), and no difference between regions ($F_{4,81} = 2.37$, P = 0.08).

Chlorophyll *a* concentrations were between 0.0 and 5.0 µg/cm² in 1996, and between 0.0 and 6.9μ g/cm² in 2001 - a significant increase in periphyton biomass between surveys ($F_{4,81} = 4.56$, P = 0.04). There was, however, no difference between the regions ($F_{4,81} = 1.60$, P = 0.20). pH (measured in 2001 only) ranged between 4.2 and 10.1, with a difference between regions ($F_{3,42} = 3.07$, P < 0.05); streams in the western Ruahines and eastern Tararuas had higher pH than the eastern Ruahines and western Tararuas.

Table 3.2 The range and mean values of environmental characteristics in the 43 streams in four regions of the Ruahine and Tararua Ranges. Depth, stream velocity, and conductivity were not significantly different between years, so only 2001 values are shown. Temperature increased slightly from 1996 to 2001, but as this change was less than 1°C only the latter values are shown.

	Western	Eastern Western		Eastern	
	Ruahines	Ruahines	Tararuas	lararuas	
Bed movement	36.0 - 99.3 (83.4)	66.8 - 99.3 (91.3)	66.8 - 99.3 (91.3) 79.7 - 99.3 (96.5)		
Predicted bed movement	17.4 - 64.0	17.2 - 63.6	17.2 - 81.6	18.4 - 85.4	
	(27.6)	(33.8)	(41.2)	(40.4)	
Slope (m/m)	0.01 - 0.08	0.00 - 0.08	0.01 - 0.32	0.01 - 0.08	
	(0.03)	(0.03)	(0.06)	(0.03)	
Mean stone size (m)	0.04 - 0.09	0.05 - 0.09	0.05 - 0.09	0.05 - 0.10	
	(0.05)	(0.06)	(0.06)	(0.06)	
% bedrock	0.3 - 2.9	0.4 - 4.1	0.3 - 5.4	0.3 - 7.3	
	(0.9)	(1.3)	(1.4)	(1.3)	
% boulder	2.7 - 14.5	3.6 - 14.8	4.1 - 15.9	1.7 - 22.4	
	(6.7)	(7.3)	(8.2)	(8.5)	
% cobble	24.6 - 58.3	34.4 - 60.0	30.9 - 64.9	24.6 - 61.8	
	(42.4)	(46.7)	(44.7)	(46.1)	
% gravel	0.3 - 5.0	0.0 - 5.2	0.0 - 2.3	0.1 - 4.4	
	(1.9)	(1.6)	(0.9)	(1.0)	
Canopy cover (%)	0 - 70	0 - 90	0 - 95	30 - 90	
	(28)	(31)	(51)	(61)	
2001 stream depth (m)	0.12 - 0.34	0.10 - 0.30	0.07 - 0.33	0.09 - 0.27	
	(0.22)	(0.18)	(0.20)	(0.19)	
2001 stream velocity (m/s)	0.19 - 0.63	0.19 - 0.79	0.07 - 0.47	0.09 - 0.32	
	(0.38)	(0.47)	(0.24)	(0.20)	
2001 water temp (°C)	12 - 17	11 - 17	12 - 18	10 - 16	
	(14.3)	(14)	(15)	(13)	
2001 conductivity (µS/cm)	60 - 181	73 - 116	65 - 116	50 - 95	
	(89)	(90)	(88)	(73)	
2001 pH	8.3 - 9.0	4.3 - 8.9	4.2 - 9.7	8.4 - 10.1	
	(8.6)	(7.9)	(8.0)	(8.9)	
1996 chlorophyll a (μg/cm ²)	0.3 - 5.0	0.0 - 5.2	0.0 - 2.3	0.1 - 4.4	
	(1.9)	(1.6)	(0.9)	(1.0)	
2001 chlorophyll a (μg/cm ²)	0.0 - 6.9	0.0 - 6.5	0.3 - 5.8	0.1 - 3.5	
	(2.3)	(2.3)	(2.2)	(1.3)	
1996 number of individuals	456 - 3376	29 - 3790	282 - 1985	217 - 2123	
	(1600)	(1479)	(914)	(727)	
2001 number of individuals	150 - 1234	15 - 1234	73 - 610	53 - 824	
	(357)	(406)	(357)	(251)	
1996 taxon richness	17 - 39	11 - 48	19 - 32	17 - 33	
	(30)	(31)	(25)	(26)	
2001 taxon richness	10 - 24	8 - 24	13 - 20	9 - 21	
	(16)	(15)	(15)	(15)	
1996 taxon evenness	0.12 - 0.26	0.03 - 0.27	0.13 - 0.66	0.16 - 0.34	
	(0.19)	(0.17)	(0.26)	(0.23)	
2001 taxon evenness	0.12 - 0.66	0.08 - 0.53	0.18 - 0.48	0.17 - 0.55	
	(0.35)	(0.28)	(0.26)	(0.35)	

Canopy cover was from 0 to 90% and was different between regions ($F_{3,42} = 6.46, P < 0.001$). The eastern Tararua region had more canopy cover than either side of the Ruahine ranges, while the western Tararuas had intermediate values. Mean particle size was between 4.5 and 8.7cm, SI from 3.2 to 9.0, and stone size diversity from 0.12 to 0.21; none of these showed a significant difference between regions ($F_{3,42} = 1.60, P = 0.20; F_{3,42} = 1.21, P = 0.31; F_{3,42} = 1.35, P = 0.26$ respectively). Stream slope ranged from 1 to 8 percent and did not differ between regions.

Measured bed movement ranged between 36.0 and 99.3 of a possible 99.3. This showed a significant difference between regions ($F_{3,42} = 6.73$, P < 0.0005), with bed movement lower in the western Ruahines than in any other region. Movement was also estimated using the artificial neural network model derived in Chapter 2. This gave bed movement scores of between 8.6 and 42.7 of a possible 100, with a mean of 17.8. There was no significant difference between regions ($F_{3,42} = 2.20$, P = 0.09).

The macroinvertebrate community

Densities of the taxa collected at each site are provided in Appendix 2.1 (1996 data) and Appendix 2.2 (2001 data). In 1996, the number of taxa found at a site ranged between 11 and 48, with a mean of 28. An average of 1186 individuals were collected from each site. The five most common taxa were *Deleatidium* sp. (770 m⁻²), *Beraeoptera roria*, *Helichopsyche albescens*, *Zelandoperla* sp., and Orthocladiinae. For the 43 sites, the Simpson's index of evenness was between 0.03 and 0.66, and had a mean of 0.21. In 2001, between 8 and 24 taxa were found at a site, with a mean of 15. At most sites far fewer individuals were collected in 2001, with a mean of 343 per site. The five most common taxa were *Deleatidium* sp. (270 m⁻²), *Beraeoptera roria*, Eukiefferulus, Polypedilum, and *Zelandoperla* sp. In 2001, the Simpson's index of evenness was between 0.08 and 0.66, with a mean of 0.31.

In 1996, the number of individuals collected differed between regions ($F_{3,42} = 3.59, P > 0.05$), with more invertebrates collected in the western Ruahines than the eastern Tararuas; the eastern Ruahine and western Tararua sites had intermediate values. There was, however, no difference in the number of taxa collected in each region ($F_{3,42} = 2.33, P = 0.09$). In 2001, there was no regional difference in either the number of invertebrates collected ($F_{3,42} = 0.50, P = 0.68$) or the number of taxa ($F_{3,42} = 0.15, P = 0.93$).

In 1996, the 43 sites had MCI scores of between 116 and 146, with a mean of 131; in 2001, scores were between 90 and 144 (mean 124).

Change in macroinvertebrate community structure

Paired *t* tests indicate that the number of taxa found in 1996 was greater than in 2001 $(t_{1,84} = 14.65, P < 0.0001)$. When sub-sampled, the resulting number of taxa was still greater than that found in 2001 $(t_{1,78} = 9.03, P < 0.0001)$. These results suggest that the higher number of taxa found in 1996 was not simply the result of the larger number of individuals collected.

The change in number of taxa between 1996 and 2001 correlated with 1996 periphyton biomass (Table 3.3). While this was only significant at the 10% level, the trend was quite strong (r = 0.48). The number of taxa persisting from 1996 to 2001 increased with 2001 periphyton level (Table 3.3). Once again, this was significant at the 10% level and had an r of 0.48.

The mean multivariate community change of the complete communities at the 43 sites was 0.52 (relative Sorensen), and 0.44 (Euclidian). The mean multivariate change of presence / absence data was 0.57 (relative Sorensen), and 0.23 (Euclidian). For the ten most common taxa, mean multivariate change was 0.44 (relative Sorensen), and 0.44 (Euclidian).

Regardless of ordination method, multivariate distance between the communities collected in 1996 and 2001 did not appear to be related to any of the environmental variables measured, or the change in an environmental variable between the two surveys (see Fig. 3.2, Table 3.3, and Appendix 1). Contrary to my hypothesis, none of the above measures of multivariate distance were related to either measured stream bed movement (Fig. 3.3) or predicted stream bed movement (Table 3.4).

Kendells coefficient of concordance (W) increased significantly with periphyton biomass in 2001 ($F_{1,42} = 6.26$, P < 0.005, $r^2 = 0.24$, Fig. 3.4). This was the strongest relationship found between any measure of community change and any environmental variable, or change in an environmental variable.

Change in the Simpson's index from 1996 to 2001 was between 0.00 and 0.43, with a mean of 0.13. This increase indicates that taxon evenness has decreased, ($F_{1,42} = 15.50$, P < 0.0005). There was no difference between regions ($F_{1,42} = 1.14$, P = 0.34).

Table 3.3 Correlation (r) of measures of community change with environmental change. Only those environmental variables which changed significantly between 1996 and 2001 are shown (note that mean stream temperature was higher in 2001, but was excluded from this table as the 0.9°C change was considered trivial).

* indicates significance at the 10% level, ** at the 5% level.

	Measured bed movement	Neural network prediction of bed movement	% change in periphyton biomass	1996 periphyton biomass	2001 periphyton biomass
Change in number of taxa	-0.22	0.15	-0.44	0.48*	0.04
Number of taxa persisting	0.19	0.23	0.07	0.34	0.48*
Proportion of taxa persisting	0.30	0.14	0.33	-0.09	0.29
Kendell's W (all taxa)	0.17	0.21	0.00	0.41	0.51**
Kendell's W (top ten taxa)	0.18	-0.30	-0.06	-0.01	-0.18
Community change (relative Sorensen)	-0.30	0.22	-0.02	0.16	0.20
Community change (Euclidian)	0.10	0.04	0.19	-0.36	-0.18
Change in presence / absence (relative Sorensen)	-0.24	0.08	-0.40	0.07	-0.31
Change in presence / absence (Euclidian)	-0.15	0.01	-0.44	0.38	-0.07
Change in top ten taxa (relative Sorensen)	-0.30	0.19	0.00	0.16	0.24
Change in top ten taxa (Euclidian)	0.09	0.02	0.21	-0.38	-0.18
Community change (sub- sample of 1996 data)	0.42	-0.16	0.13	-0.23	-0.07
Change in taxon evenness	0.43	0.10	0.09	0.10	0.31



Figure 3.2 Bray-Curtis ordination of the macroinvertebrate communities at 43 sites in the Ruahine and Tararua Ranges, sampled in the summers of 1996 (triangular points) and 2001 (circular points). Numbers within each triangle or circle indicate site number. It is clear that many of the communities have changed dramatically between surveys, indicated by the large distance between points with the same site number. Note that no measured environmental variable correlated with the ordination of the communities in multivariate space.



Figure 3.3 Change in community structure at 43 sites in the Ruahine and Tararua Ranges (relative Sorensen distance measure) between 1996 and 2001 as a function of measured bed movement. A higher score on the Bed movement indicates greater bed movement.

Between three and 16 taxa which were present at a site in 1996 were collected again at that site in 2001; this was 13 to 58% of the collected taxa. Neither the number or proportion of taxa which persisted was related to region ($F_{1,42} = 0.24$, P = 0.87; $F_{1,42} = 1.81$, P = 0.15, respectively). The change in number of taxa found at a site was between two and 27, with a mean of 12.7; this change differed between regions ($F_{1,42} = 6.51$, P < 0.001). The eastern Ruahines had a greater change in number of taxa than the sites from either side of the Tararuas, while the western Ruahine sites showed intermediate change.

The change in number of taxa, number of taxa persisting, and proportion of taxa persisting at a site, were not linked to measured bed movement ($F_{1,42} = 0.44$, P = 0.51; $F_{1,42} = 0.03$, P = 0.96; $F_{1,42} = 0.09$, P = 0.76 respectively); neither were these three factors related to predicted bed movement ($F_{1,42} = 0.19$, P = 0.67; $F_{1,42} = 2.61$, P = 0.11; $F_{1,42} = 1.50$, P = 0.23 respectively), or percent change in periphyton level ($F_{1,42} = 1.31$, P = 0.26; $F_{1,42} = 0.92$, P = 0.62; $F_{1,42} = 2.54$, P = 0.12 respectively).

Change in number of taxa was strongly linked with the number of taxa collected in 1996 ($F_{1,42} = 63.17$, P < 0.0001, $r^2 = 0.61$), as was the number of taxa persisting ($F_{1,42} = 34.16$, P < 0.0001, $r^2 = 0.45$). The proportion of taxa persisting was unrelated to the number of taxa collected in 1996, however ($F_{1,42} = 0.04$, P = 0.84). Change in number of taxa between 1996 and 2001 was not related to the number of taxa collected in 2001 ($F_{1,42} = 0.11$, P = 0.74). Both the number of taxa collected in 1996 and the proportion of taxa persisting at a site were higher at sites with a greater number of taxa in 2001 ($F_{1,42} = 187.20$, P < 0.001, $r^2 = 0.82$; $F_{1,42} = 36.34$, P < 0.001, $r^2 = 0.47$ respectively) (Fig. 3.5). In both 1996 and 2001, the number of taxa found at a site increased with

periphyton level ($F_{1,42} = 10.82$, P < 0.005, $r^2 = 0.35$; $F_{1,42} = 9.95$, P < 0.005, $r^2 = 0.33$ respectively) (Fig. 3.6).

Table 3.4 Correlation (r) of measures of community change against measured and predicted stream bed movement at 43 sites in the Ruahine and Tararua Ranges. Note that none of these correlations are significant at P < 0.05.

	All taxa (relative Sorensen)	All taxa (Euclidian)	Presence / absence (relative Sorensen)	Presence / absence (Euclidian)	Top ten taxa (relative Sorensen)	Top ten taxa (Euclidian)
Measured stream bed movement	0.28	0.00	0.08	0.10	0.33	0.00
Predicted stream bed movement	0.28	0.00	0.08	0.10	0.33	0.00



Figure 3.4 Kendell's coefficient of concordance (W) as a function of chlorophyll *a* concentration in 2001 for 43 sites in the Ruahine and Tararua Ranges.

W = 0.3 + (0.05 (2001 chl *a* concentration)) - (0.0005 (2001 chl *a* concentration)²); $r^2 = 0.24$



Figure 3.5 Taxon persistence from 1996 to 2001 as a function of taxon richness in 2001 at 43 sites in the Ruahine and Tararua Ranges.

Proportion of taxa persisting = (0.74 (2001 taxon richness)) - 1.69; $r^2 = 0.47$



Figure 3.6 Taxon richness as a function of chlorophyll *a* concentration at 43 sites in the Ruahine and Tararua Ranges in both 1996 (solid points) and 2001 (hollow points).

1996 taxon richness = $22.7 + (4.9 \text{ (chl } a \text{ concentration})) - (0.4 \text{ (chl } a \text{ concentration})^2); r^2 = 0.35$ 2001 taxon richness = $10.9 + (3.4 \text{ (chl } a \text{ concentration})) - (0.4 \text{ (chl } a \text{ concentration})^2); r^2 = 0.35$ A site's MCI score in 1996 was a poor predictor of MCI in 2001 ($F_{1,42} = 1.27$, P = 0.27) (Fig. 3.7). The mean change between 1996 and 2001 was 12.8 points, with 26 sites showing an increase in MCI while the score decreased at 17 sites; on average, MCI dropped by 7.2 (Fig. 3.8). There was a significant difference between years ($t_{1,42} = 3.32$, P > 0.002).

Change in MCI was not related to either measured bed movement ($F_{1,42} = 1.90$, P = 0.18) or predicted bed movement ($F_{1,42} = 2.99$, P = 0.09), and despite being an indicator of water enrichment, was not linked with change in conductivity ($F_{1,42} = 2.76$, P = 0.10). MCI tended to increase from 1996 to 2001 at sites which had become cooler, and decreased at sites which were warmer in 2001 ($F_{1,42} = 16.69$, P > 0.0005, $r^2 = 0.29$) (Fig. 3.9).



Figure 3.7 2001 MCI score as a function of 1996 MCI score at 43 sites in the Ruahine and Tararua Ranges.



Figure 3.8 Box-plot showing the range of MCI scores at 43 sites in the Ruahine and Tararua Ranges in the summers of 1996 (mean = 130.7; SD = 7.3) and 2001 (mean = 123.5; SD = 13.5). Streams with an MCI score greater than 120 are considered to be 'pristine'.



Figure 3.9 Change in MCI score between 1996 and 2001 as a function of the change in temperature between the two surveys at 43 sites in the Ruahine and Tararua Ranges.

Change in MCI = 4.1 - (3.4 (Change in temperature)); $r^2 = 0.29$

DISCUSSION

It is clear that the majority of the sampled communities have undergone considerable change between the summers of 1996 and 2001. At site 21 (a tributary of the Mangatainoka River) for example, only three of the 17 taxa present in 1996 were collected again in 2001, and the maximum proportion of taxa persisting at any site was 58% (15 of 26 taxa at site 18, a tributary of Kahuterawa Stream). These changes have occurred in spite of the sites' pristine surroundings, which has been suggested promotes persistence (Robinson *et al.* 2000).

Scarsbrook (2002) found that the average level of inter-annual variability of study communities was high enough to suggest it may be inappropriate to assess community stability or persistence from two points in time, as was done in the current study. It is quite possible that the degree of community change seen at my 43 study sites may have been different had samples been taken in other years, with stochastic factors influencing results to an unknown degree.

It has been proposed that a site's macroinvertebrate community will be characterised by that site's environmental conditions, which acts as a filter through which colonising taxa must pass (Scarsbrook & Townsend 1993; Townsend & Hildrew 1994; Poff 1997; Townsend *et al.* 1997). If the environment of a site changes little with time, one would expect community composition to remain relatively constant, while a significant change in conditions may result in the loss of some taxa and the colonisation of others. Stochastic events such as large disturbances or the arrival of a new predator may also cause fluctuations in the community, and it is the relative influence of these stochastic and deterministic events which will influence our ability to predict changes in the community over time.

The communities at sites with greater bed movement and / or a large difference in periphyton level between the two surveys were predicted to change more than those at more 'stable' sites. Townsend *et al.* (1987) and Weatherly & Ormerod (1990) found that environmental stability (such as change in pH or temperature) influenced the abundance of certain taxa in sampled communities, while Scarsbrook (2002) concluded that mean community change was greater at sites with variable flow conditions. I anticipated that bed movement would be a key factor in community structuring in the current study as many streams in the Ruahine and Tararua Ranges appear to be quite unstable. However, bed movement (both measured with tracer particles and predicted by the neural network model) was not associated with any measure of community change.

This may be due to the use of an inappropriate measurement of bed movement. The bed movement data produced from three-monthly surveys of tracer particle recovery does not show a great deal of variation between sites. Very few particles were recovered at most of the sites, including some which appeared to be quite stable. The artificial neural network gave estimated bed movement values that covered a far greater range than our field data, but it was not possible to test the accuracy of these figures against more frequently surveyed tracer particle data. Although the artificial neural network analysis appears to have produced a good model for predicting bed movement this lack of data verification means that any interpretation must err on the side of caution. The percent change in periphyton level between surveys was not related to community change, which was surprising given the increase in macroinvertebrate taxon richness at higher periphyton levels seen in both 1996 and 2001 surveys.

Kendell's coefficient of concordance was higher at sites with more periphyton in 2001, indicating that taxon rank had changed less at these sites. It is not clear why these sites should have greater stability of rank abundance, but this may be due to the higher density and taxon richness of macroinvertebrates found there, with a predictable subset of taxa becoming dominant under these conditions. Nevertheless, a mean value of 0.34 for the complete communities indicates that rank abundances tended to change a great deal between 1996 and 2001. This contrasts with a number of previous studies (Meffe & Minckley 1987; Weatherley & Ormerod 1990; Richards & Minshall 1992) which found that ranking stability remained high over a multi-year period despite the sometimes large fluctuations in absolute population size (but see Townsend *et al.* 1987).

Periphyton level was one of the few environmental factors that did change between years, but this was not associated with change in community structure. It is possible that a factor which I failed to take into account (such as CPOM or FPOM) was responsible for the observed changes.

While sites with more periphyton tend to have more macroinvertebrate taxa (e.g., Death & Winterbourn 1995; Minchin & Death in press), significantly *more* taxa were collected in 1996 than 2001, despite the lower periphyton levels found in this survey. Many of the study streams were hit by a 50 year flood in October of 2000 (horizons.mw records), and it is possible that the macroinvertebrate communities were still in a state of recovery when sampled four to five months later. Two of the five most common taxa collected in 2001 were Chironomidae, a family of predominantly fast colonising taxa. Proportionally fewer Chironomids were collected in 1996. This may indicate that the slower colonising taxa had yet to recover to pre-disturbance levels when sampling was performed in 2001. Periphyton levels may have been able to bounce back quickly while macroinvertebrate recovery lagged behind, which could explain the high periphyton level and low macroinvertebrate density and richness.

This may in part account for the marked decrease in MCI seen at some sites. An increase in the proportion of the Chironomidae and other 'weedy' taxa at a site could lower that site's MCI score. On average, MCI fell by over 7 points, and while 40 of the 43 sites had an MCI of greater than 120 and were therefore considered 'pristine' in 1996, only 29 sites reached this threshold in 2001. This change does not appear to have been the result of any loss of 'pristine-ness' in either the streams or the surrounding Forest Parks, but could be linked to the observed change in water temperature.

It has been suggested that fluctuations in macroinvertebrate communities over time could impact on studies that utilise reference sites as predictors of unimpacted conditions (Scarsbrook 2002). In the current study, MCI scores in these pristine streams changed by as much as 38 points between 1996 and 2001. If a subset of these streams were used as reference sites, changes such as these could have dramatic implications - a test site could appear either significantly closer or more distant from the reference condition, depending on when the reference site had been sampled. This suggests that reference sites (and perhaps test sites as well) should be sampled a number of times to allow for any natural fluctuations in community structure. If this sampling were carried out over an extended period it may also be possible to identify any trends or cycles which occur. The differences in pH, current velocity, canopy cover and bed movement between study regions did not appear to be of great importance in community structuring, despite previous work suggesting links between canopy cover, periphyton level, and invertebrate taxon richness (e.g., Robinson & Minshall 1986; Minchin & Death in press) or biomass (Tait *et al.* 1994). There was no distinct east / west division in factors such as bed movement or taxon richness, and a Ruahine / Tararua split was not found either.

Despite the differences between the 1996 and 2001 samples, they do show some interesting similarities. In both years taxon richness increased with periphyton level, with the number of taxa reaching an asymptote at approximately $5\mu g/cm^2$ chlorophyll *a*. This result agrees with data collected elsewhere in New Zealand, including the Taranaki (Zimmermann 2000) and Urewera (Death in press) National Parks.

This periphyton - taxon richness relationship appears to persist in spite of large changes in community structure and significant differences in periphyton level. It is difficult to explain why this relationship is seen in the 2001 samples when there is more periphyton and fewer taxa than in 1996 - two factors which should act to *reduce* competition. Taxon evenness (as measured with the Simpson's index) has increased, indicating that the 2001 communities have proportionally more rare taxa. This may be indicative of competitive dominance, and suggests that competition in macroinvertebrate communities may occur at low densities and in spite of relatively high primary production.

In conclusion, it appears that while large changes have occurred in the sampled macroinvertebrate communities, these are not directly related to any of the environmental factors which were measured. Significantly fewer taxa were collected in 2001 than 1996, and a higher proportion of these taxa had low MCI scores; in 2001, fewer sites attained a 'pristine' ranking in the MCI scale. This shift in the community may have been caused at least in part by changes in stream temperature. This suggests that the communities found at reference sites (which are often to be similar to the 43 Forest Park streams in the current study) do fluctuate over time and could be affected by natural changes in the stream environment, a finding which should be taken into account in the application of biomonitoring programmes. Despite the changes seen, a similar periphyton level - taxon richness relationship occurred in both 1996 and 2001.

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Chapter 4:

INTRA-ANNUAL VARIATION IN NEW ZEALAND STREAM INVERTEBRATE COMMUNITIES



ABSTRACT

The macroinvertebrate communities of 12 streams within the Ruahine Forest Park were sampled every three months between June 2000 and May 2001. Periphyton biomass and macroinvertebrate taxon richness were both lower in more disturbed streams, but the magnitude of seasonal change in community structure was not linked to either bed movement or change in periphyton level. Seasonal changes in community structure and evenness were not significantly different to the changes that occurred in these streams between 1996 and 2001. Community structure was no more stable between two summers separated by five years than it was between the seasons of a single year.

INTRODUCTION

In many parts of the world, marked seasonal patterns of both stream hydrology and macroinvertebrate community composition occur (e.g., Robinson & Minshall 1986; Resh *et al.* 1988; Melo & Froehlich 2001), but it may be difficult to tell whether changes in the community are the result of hydrology or simply a life-history induced fluctuation in taxon abundance (Doisy & Rabeni 2001). New Zealand streams may be particularly useful in studies of the effects of hydrological disturbances on macro-invertebrate communities, as hydrological regimes are often unpredictable - spates occur throughout the year, preventing the coordination of invertebrate lifecycles with hydrology (Winterbourn *et al.* 1981). Monitoring community composition in a number of streams with different disturbance regimes may allow the effects of hydrology to be studied independently of confounding factors.

Few studies of intra-annual change in the New Zealand macroinvertebrate fauna have been published. Collier & Winterbourn (1987) investigated the community dynamics of five streams in South Westland. No seasonal patterns in taxon abundance were recorded, but temporal variability of invertebrate densities was greater at unstable sites. Scarsbrook & Townsend (1993) studied two streams in central Otago, and found that the less stable of the pair showed greater variation in taxon richness over the course of their year-long study. Death & Winterbourn (1994) sampled a group of ten Southern Alp streams five times over a year, and found that the more stable sites had higher faunal persistence. Working in these same streams, Death & Winterbourn (1995) concluded that although taxon richness was lower at unstable sites, the relationship between stability and taxon richness did not change with season.

The current study follows the fluctuations of 12 macroinvertebrate communities in the winter and spring of 2000 and the summer and autumn of 2001, and attempts to identify the factors responsible for the changes seen. I hypothesised that the communities at sites with greater bed movement would change more than those at sites with stable beds, with these changes linked to bed movement induced fluctuations in periphyton biomass - following Minchin & Death (in press) I expected community composition to be strongly linked to periphyton biomass, with more taxa occurring at sites with more periphyton, and greater community change at sites with large fluctuations in periphyton level. Community structure was expected to change more between seasons than between the summers of 1996 and 2001.

STUDY SITES

All of the study sites were on first- to third-order streams flowing from the southern Ruahine State Forest Park into the Manawatu River, in the lower North Island of New Zealand (Table 4.1). Sites had varying degrees of predominantly beech, kamahi, rimu and tawa dominated native canopy cover, with six on the western and six on the eastern side of the Ranges.

METHODS

Macroinvertebrate sampling protocol

Macroinvertebrate samples were collected from 21 June - 17 July 2000 (winter), 10 - 14 October 2000 (spring), 21 - 28 February 2001 (summer), 28 - 30 May 2001 (autumn). In winter, spring, and summer, sampling was carried out after a period of at least three weeks' base flow. The autumn samples were collected only one week after a spate as this was the only 'window' available.

Five stones from each of three size classes (maximum linear planar dimension <60mm, 60-90mm, >90mm) were removed from the stream bed. Stones were sampled as the collector moved progressively upstream. The invertebrates on each stone were collected by scooping the stone into a net of 250μ m mesh, along with any fine sediment or detritus immediately below the collected stone. The stone was thoroughly washed in

the net to ensure all invertebrates were removed. Death (1991) found this method to yield more precise estimates per unit effort for both macroinvertebrate density and diversity than Surber sampling. Invertebrates were stored in 10% formalin and later identified and enumerated using the keys of Winterbourn & Gregson (1989) and Boothroyd (2000).

After the invertebrates had been removed, the three axes of the sampled stones were measured to the nearest centimetre. The macroinvertebrate data was later converted to number of individuals per square metre of stone surface by dividing the density of invertebrates collected on each stone by the estimated surface area of that stone:

(1.15 (height x depth + height x width + width x depth)) / 100

Measurement of habitat characteristics

Periphyton biomass was estimated by collecting five randomly selected stones (45-70mm maximum linear planar dimension) from the stream bed concurrent with invertebrate sampling. Pigments were extracted and analysed following the methods of Steinman & Lamberti (1996), with values corrected for surface area by weighing aluminium foil of known mass per unit area that was cut to snugly cover the stones. As chlorophyll *a* concentration has been found to correlate strongly with periphyton biomass in New Zealand streams (Clausen & Biggs 1997), it is taken to be an indicator of periphyton biomass in the study streams. Several habitat characteristics were also measured concurrently with invertebrate sampling: Temperature and conductivity were measured using an Orion 122 conductivity meter adjusted automatically to 25°C. pH was measured with an Orion Quickcheck model 106 meter. Stream width and Thalweg depth were measured at five equidistant points along the study reach. Velocity was measured at these same points in the Thalweg using a Marsh McBirney velocity meter 10cm above the stream bed.

Other habitat variables were measured in the summer of 2001 only: Slope was measured using an Abney level over 10m. Canopy cover was visually estimated while standing in the stream centre. The size distribution of the stream bed particles was examined by measuring the maximum linear planar dimension of surface stones in fifteen $0.1m^2$ quadrats. These were located in the middle, mid-left and mid-right side of the stream on five transects randomly placed across the bed. The mean size (d50) of the stones collected from each stream was then calculated. Substrate composition was converted to a single substrate size index (SI) by summing the mid-point values of the size classes weighted by their proportional abundance (Quinn & Hickey 1990).

Bed movement was assessed using 15 tracer particles marked *in situ* at each site. These particles were in five rows of three stones (one stone from each of the following three size classes - maximum linear planar dimension <60mm, 60-90mm, >90mm), with the rows randomly located between one and ten metres upstream of five consecutive riffle-run series in the study reach. Stone size order across the stream bed was random. Stones were marked using Fosroc Expocrete UA concrete fix, a two part, epoxy mortar which adheres and dries underwater and is clearly visible for up to a year after application.
Tracer particles were initially layed in July 2000. Every month, the sites were surveyed and the stones that were not displaced in the past month were located. When a stone was not found, another was marked in its place.

The number of stones from each size class that had not moved in successive surveys was summed for each site. These figures were adjusted according to the mean stone weight of each size class (Death, unpublished data) - stones with maximum linear planar dimension <60mm were divided by 0.167, 60-90mm by 0.327, and >90mm by 1.128. This made the small particles which remain stationary more important in assessing bed movement. The result was converted to a percentage scale, with a score of 0 indicating no bed movement while a score of 100 suggests that a large proportion of the stream bed is frequently moved.

Data analysis

Multivariate distance between communities was calculated using the Bray-Curtis distance measure in PC-ORD (McCune & Mefford 1997). This distance measure ranges from 0.0 (no community changed) to 1.0 (no overlap of taxon occurrence).

Simpson's index, a measure of taxon evenness, was calculated for each site in each season (Simpson 1949).

The effect of season on environmental variables, taxon richness, and taxon evenness were tested using the ANOVA procedure of SAS (2000). Community change between 1996 and 2001 was compared with the current study's intra-annual community change using the paired *t*-test procedure of SAS (2000). Bonferroni *a posteri* means test procedures were also performed using SAS.

Chapter T.	Chanter 4.
Inna-amnai	Intra_annual
Vallation	Variation
00	23

Site name	Site #	Coordinates	Bed movement	Mean velocity (m/s)	Mean width (m)	Mean depth (m)	Slope (m/m)	d50 (m)	SI	Mea n pH	Mean cond. (µs/cm)	Mean temp. (°C)	Canopy cover (%)
Mangatuatou Stream	1	175°53.308' E 40°09.525' S	71.2	0.56	3.3	0.22	0.03	.05	4.2	8.5	82	10	0
Tamaki River West Branch	2	176°01.746' E 40°07.188' S	75.1	0.57	3.9	0.19	0.01	.06	4.9	8.2	76	12	0
Mangapuaka Stream	3	175°58.712' E 40°10.275' S	74.9	0.38	3.1	0.10	0.03	.05	4.2	8.4	75	11	60
A tributary of Matanganui Stream	4	175°51.252' E 40°11.896' S	61.8	0.20	1.2	0.15	0.07	.04	3.2	8.6	79	11	0
Matanganui Stream	5	175°52.101' E 40°11.156' S	48.2	0.23	2.5	0.30	0.03	.09	7.4	8.3	78	12	10
Coppermine Stream	10	175°13.107' E 40°53.205' S	41.3	0.19	2.5	0.17	0.08	.09	7.5	8.8	82	11	90
A tributary of Coppermine Stream	11	175°13.107' E 40°50.205' S	56.1	0.75	2.0	0.21	0.06	.06	4.8	8.8	91	12	20
Manawatu River	12	176°08.587' E 39°59.057' S	39.7	0.31	2.2	0.15	0.01	.05	4.4	4.1	87	11	40
Coal Creek	15	175°53.701' E 40°14.837' S	78.6	0.42	3.7	0.17	0.02	.05	4.5	9.1	66	12	70
Limestone Creek	17	175°36.701' E 40°18.837' S	34.1	0.30	2.4	0.21	0.01	.05	4.0	8.5	174	10	70
Rangiwahia Stream	34	176°00.803' E 39°53.870' S	86.5	0.26	4.4	0.20	0.04	.06	4.1	8.6	71	9	10
Ngamoko Stream	36	176°08.103' E 40°02.572' S	50.6	0.33	1.2	0.10	0.03	.05	4.0	8.5	92	11	10

 Table 4.1 Habitat characteristics (measured in the summer of 2001, or the mean of measurements taken in the winter and spring of 2000, and summer and autumn of 2001) of 12 streams in the Ruahine State Forest Park.

RESULTS

In autumn there was little periphyton in many of the streams, and the communities sampled had few taxa. An ordination showed that the 12 communities collected in autumn differed from those collected in other seasons; Simpson's index of taxon evenness was also significantly higher in autumn than in any other season ($F_{3,45} = 6.29$, P = 0.001), indicating that the community was dominated by few taxa. As the autumn samples were collected only one week after high flows, it was suspected that the communities were therefore excluded from the remainder of the analysis.

Habitat characteristics

At the 12 study sites canopy cover ranged from 0 to 90%, mean particle size from 4.5 to 8.7 cm, SI from 3.2 to 9.0, and slope from one to eight percent. Sites were small forest streams with mean depth, width, and current velocity which ranged between eight and 32 cm, 1.0 to 5.3 metres, and 0.2 and 0.8 m / s, respectively, with no significant difference between seasons ($F_{2,33} = 0.02$, P = 0.98; $F_{2,33} = 0.20$, P = 0.82; $F_{2,33} = 0.01$, P = 0.99, respectively). The 12 sites differed somewhat in both pH (mean of 4.1 to 9.2) and conductivity (mean of 63 to 181μ S/cm), but there was no significant difference between seasons for these characteristics ($F_{2,33} < 0.01$, P > 0.99; $F_{2,33} = 0.04$, P = 0.96, respectively).

Of the habitat characteristics which were surveyed in each season, only temperature showed significant change ($F_{2,33} = 130.77$, P < 0.0001) with lower temperatures in winter.

Bed movement ranged from 34.1 of a possible 100 (Limestone Creek) to 86.5 (Rangiwahia Stream) (Table 4.1).

Chlorophyll *a* concentration at the 12 sites was not related to bed movement in winter ($F_{1,11} = 0.83$, P = 0.38), spring ($F_{1,11} = 4.06$, P = 0.06), or summer ($F_{1,11} = 3.43$, P = 0.09); likewise, mean chlorophyll *a* concentration over the three seasons was not related to bed movement ($F_{1,11} = 0.27$, P = 0.61) (Fig. 4.1).



Figure 4.1 Mean $(\pm 1SE)$ chlorophyll *a* concentration in the winter and spring of 2000 and summer of 2001, as a function of stream bed movement at 12 sites in the Ruahine Forest Park. A high score on the Bed movement axis indicates greater bed movement.

Macroinvertebrate community structure

Densities of the taxa collected at each site are provided in Appendix 3.1 (winter and spring 2000 data) and Appendix 3.2 (summer and autumn 2001 data).

Between four and 27 taxa were found at a site in any given season, with no significant difference in richness between seasons ($F_{2,33} = 0.55$, P = 0.58). The most common taxa were *Deleatidium* sp. (mean of 385 / m²), Orthocladiinae, *Beraeoptera* roria, *Helichopsyche* sp., and *Austrosimulium australense*.

The mean number of taxa collected over the three seasons was higher at sites with less bed movement ($F_{1, 11} = 11.06$, P < 0.01, $r^2 = 0.53$) (Fig. 4.2) and sites with more periphyton ($F_{1, 11} = 7.65$, P < 0.05, $r^2 = 0.43$) (Fig. 4.3). Variation in taxon richness over the study period (measured as coefficient of variation over the three seasons) was not related to bed movement ($F_{1, 11} = 0.51$, P = 0.49) (Fig. 4.4).



Figure 4.2 Mean number of macroinvertebrate taxa ($\pm 1SE$) collected in the winter and spring of 2000 and summer of 2001, as a function of stream bed movement at 12 sites in the Ruahine Forest Park. A high score on the Bed movement axis indicates greater bed movement.

Number of taxa = $26.6 - (0.2 \text{ x Bed movement}); r^2 = 0.53$



Figure 4.3 Mean number of macroinvertebrate taxa (± 1 SE) collected in the winter and spring of 2000 and summer of 2001, as a function of mean chlorophyll *a* concentration at 12 sites in the Ruahine Forest Park.

Number of taxa = $9.8 + (2.4 \text{ x Chlorophyll } a (\mu g / cm^2)); r^2 = 0.43$



Figure 4.4 Coefficient of variation of taxon richness from samples collected in the winter and spring of 2000 and summer of 2001, as a function of stream bed movement at 12 sites in the Ruahine Forest Park.

A Bray-Curtis ordination of the winter, spring, and summer macroinvertebrate communities indicated that none of the environmental variables measured were significantly correlated with community structuring (Fig. 4.5). Only one taxa (*Bereaoptera roria*) was strongly correlated with the axes of more than one season's ordination; this taxa was correlated with axis 1 in both spring and summer, with these corresponding to bed movement in spring and canopy cover in summer.





Figure 4.5 Bray-Curtis ordination of the macroinvertebrate communities collected in the winter and spring of 2000 and summer of 2001 at 12 sites in the Ruahine Forest Park. Winter samples are indicated by circles, spring by squares, summer by triangles, and autumn by diamonds. Numbers within each point indicate the study site number (see Table 1).

The mean change in community structure over the three seasons was not associated with stream bed movement ($F_{1, 11} = 0.34$, P = 0.57) (Fig. 4.5). Mean seasonal community change was also unrelated to mean chlorophyll *a* concentration ($F_{1, 11} = 0.21$, P = 0.65) and the coefficient of variation in chlorophyll *a* concentration ($F_{1, 11} = 1.71$, P = 0.22).



Figure 4.5 Mean seasonal change (\pm 1SE) of communities collected in the winter and spring of 2000 and summer of 2001, as a function of stream bed movement at 12 sites in the Ruahine Forest Park. A high score on the Bed movement axis indicates greater bed movement.

Across the 12 sites mean values for the Simpson's index of taxon evenness were 0.47, 0.38, and 0.35 for winter, spring, and summer samples, respectively. There was no significant difference between seasons ($F_{2,33} = 1.16$, P = 0.32).

To examine whether community change was greater between seasons or between years, the change in evenness at each site between the summers of 1996 and 2001 was compared with a) the mean change in taxon evenness at each site from one season to the next, and b) the maximum change in taxon evenness at each site from one season to the next. There was no significant difference between mean seasonal change and mean change from 1996 to 2001 ($t_{1,11} = -0.41$, P = 0.69), or between mean maximum seasonal change and mean change from 1996 to 2001 ($t_{1,11} = 0.74$, P = 0.48).

The mean multivariate distance between community structure at each site in each season was compared with the mean distance between community structure at each site in 1996 and 2001. The mean community change between seasons was 0.51, while the mean change between 1996 and 2001 was 0.56; there was no significant difference between the two ($t_{1,11} = -0.59$, P = 0.57). Seasonal change was not related to change between 1996 and 2001 ($F_{1,11} = 1.11$, P = 0.29).

DISCUSSION

Periphyton biomass, seasonal community change, and the coefficient of variation of macroinvertebrate taxon richness were all unrelated to bed movement in the 12 streams sampled in this study. These results were unexpected as bed movement was thought to be a major factor driving community change and would produce distinctly different communities at sites with stable and unstable beds. That the communities at sites with stable beds fluctuated as widely as those found at unstable sites suggests that either the communities change independantly of bed movement, or that the level of movement required to initiate change is quite low.

Previous work in Ruahine Forest Park streams (Minchin & Death in press) has suggested that taxon richness was more strongly linked to periphyton biomass than bed movement, but the current study found the opposite. The Habitat Templet hypothesis (Southwood 1977) predicts that the communities of unstable streams will be characterised by taxa able to recover quickly from disturbances (Scarsbrook & Townsend 1993; Townsend & Hildrew 1994; Poff 1997; Townsend *et al.* 1997a), as those unable to persist would be 'filtered out'. Death (1995) found that while the communities at unstable sites were similar and dominated by taxa presumably well adapted to harsh conditions, those at stable sites were quite different from both each other and the communities at unstable sites. In the present study there is no trend towards similarity of communities at unstable sites. Neither bed movement nor periphyton biomass were linked with community structure at these sites, suggesting that community composition was not greatly affected by these factors.

A very different picture may have emerged had sampling been more frequent and / or carried out without ensuring a three-week period of base-flow prior to sampling. This period of base-flow was intended to ensure that communities had recovered after spates so that any influence of season would not be confused with the influence of disturbances, as the length of time between sampling and the last disturbance has been found to influence the structure of the sampled community (Matthaei *et al.* 1996). Implicit in this is the assumption that disturbance effects are not the only factor changing with season and driving community change. The current study suggests that this assumption may in fact be false.

A large storm occurred in the Manawatu-Wanganui region in October of 2000, with return times on the flows in some rivers estimated to be 50 years (horizons.mw records). This major event may have been of a magnitude greater than tracer particle movement data would indicate as tracer particles give no indication of the size of a spate once all particles have been lost. The use of more tracer particles in each stream, or perhaps the marking of stones larger than those used in this study, may have allowed particularly large spates to be distinguished from smaller bed moving events. Studies have found that some taxa are disturbed by variations in flow or increases in shear stress that may not result in bed movement (Townsend *et al.* 1997b; Bond & Downes 2000; but see Holomuzki & Biggs 2000); flow data may be useful in studies such as this, so as to complement bed movement data. When the changes observed in these 12 streams over the course of a year are compared to those found between the summers of 1996 and 2001, it appears that year to year changes are of similar magnitude to intra-annual changes. This result was unexpected as it was assumed that the relatively stable summer months would produce a predictable community, while other seasons would bring more frequent spates, and changes in temperature, light levels and other environmental conditions which would result in a relatively stochastically formed community. It appears that the sampled communities fluctuate considerably both between years and within a single year, and that neither the direction nor magnitude of these changes may be predictable.

In conclusion, bed movement appears to have had little influence on periphyton level at the 12 study sites, while both periphyton biomass and bed movement are related to macroinvertebrate taxon richness. Variability in the macroinvertebrate community did not appear to be related to either bed movement or changes in periphyton level, and seasonal change was not significantly different to the changes seen between the summers of 1996 and 2001. This study was unable to ascertain exactly what it is that drives macroinvertebrate community change or affects community structure.

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Chapter 5:

THE INFLUENCE OF PERIPHYTON BIOMASS ON MACROINVERTEBRATE DRIFT AND COLONISATION



ABSTRACT

Eight 3m long channels were set in the bed of the Turitea Stream, a small, lowland tributary of the Manawatu River. Half of the channels began the experiment containing periphyton covered stones while the other half had stones with no periphyton; all channels began with no invertebrates on the substrate. Over the 14 day study period approximately one quarter of all drifting invertebrates settled in the channels, with colonisation rates similar between channels with and without periphyton. Benthic taxon richness peaked at four days and then declined slightly. Initial colonists were dominated by weedy taxa that were not dependent on periphyton. One third of the taxa that were caught in the drift had not colonised the substrate within 14 days.

INTRODUCTION

While several recent studies indicate that macroinvertebrate abundance and taxon richness are often influenced by stream bed periphyton density (e.g., Zimmermann 2000; Death in press; Minchin & Death in press), it is unclear what processes lead to this relationship. Death (in press) suggests that streams with more periphyton will support a higher number of taxa than streams with less periphyton. While this may be true when one compares a number of contrasting streams, it is not clear whether a patch with more periphyton would have more taxa than an adjacent, low periphyton patch.

If this were the case then macroinvertebrates must be able to assess patch quality and move from low- to high-resource patches. It has been suggested that individuals move between patches at rates dependant on periphyton abundance (Kohler 1985; Hinterleitner-Anderson *et al.* 1992) or the level of competition for resources (Hart 1981). Dudgeon & Chan (1992) shaded patches of a Hong Kong stream and allowed periphyton and invertebrates to colonise tiles. Both invertebrate abundance and richness were higher in unshaded, high periphyton conditions, although the response of individual taxa to shading varied greatly. In contrast to this, a Canadian study (Bourassa & Cattaneo 2000) using light reduction and nutrient addition to influence periphyton growth showed that invertebrate biomass was unaffected by periphyton biomass, but did not report any influence on invertebrate diversity.

While macroinvertebrate taxon richness and abundance within a patch may give a measure of patch preference, movement between patches may be equally important. Drift in the water column has been shown to be an important means of invertebrate dispersal (e.g., Elliot 2002). Rates of invertebrate drift into and out of patches may therefore relate to patch quality.

In the current study, I investigated macroinvertebrate colonisation of stream bed patches in a small lowland stream. I was interested in whether patches with more periphyton would be colonised more quickly than those with less periphyton, and whether a greater number of macroinvertebrate taxa would colonise periphyton rich patches. It was hypothesised that patches with more periphyton would have higher invertebrate abundances and more invertebrate taxa than patches with less periphyton. It was also hypothesised that the density of invertebrates entering the channels via drift would be relatively constant while drift out of a patch would decline with increasing periphyton density - that is, patches with more periphyton would retain a greater proportion of drifting invertebrates.

METHODS

Channel arrangement

Eight channels (each three metres long, and constructed of 35cm diameter half-round PVC tubing) were set in the bed of the Turitea Stream, on the Massey University Large Animal Teaching Unit five kilometres south of Palmerston North (175° 37.122 E 40° 25.218 N). This is a third order, regulated lowland stream draining native forest and farmland. The reach in which the experiment was performed had a mean depth of 19 cm, and mean flow velocity of 0.24 m/s. The stream was shaded by riparian willow trees. The experiment was run during a period of base flow, from 27 February to 12 March 2002.

Channels were laid on the stream bed in four pairs, with the channels of each pair set side by side and anchored with steel rods driven into the substrate. Each channel was placed in a shallow trench so that stones placed within them would be contiguous with the bed. The pairs were arranged in a shaded reach composed of a single run. There was a minimum of five metres between each pair, and neighbouring pairs were not directly in line with each other. Stones collected from the stream bed downstream of the experiment were placed in one channel of each pair, and the other was filled with stones collected from the bank of the stream; the former had a layer of periphyton (primarily diatoms) and will be referred to as 'P' channels, the latter were bare and will be referred to as '0' channels. All stones were between four and 22 centimetres maximum planar dimension. Before being placed in the channels all stones were sprayed with Black Flag Natural, a biodegradable, pyrethrum based insecticide which quickly killed any attached invertebrates and ensured that none would be present in the channels before the experiment began. Stones were checked as they were placed in the channels, and no invertebrates were found attached. Using this method, one channel from each pair contained stones with periphyton cover and no macroinvertebrates, while the other had no periphyton and no macroinvertebrates.

Drift sampling protocol

A 250µm mesh net (70cm long, with an 11 by 5.5cm mouth) was attached at the side of the upper end of each pair of channels to catch invertebrates as they drifted past, and a net was attached immediately below each channel to catch invertebrates as they drifted out (see Plate 5.1). The nets were emptied every 24 hours, with the collected invertebrates stored in 10% formalin and later identified and enumerated using the keys of Winterbourn & Gregson (1989).



Plate 5.1 One of four paired channels used for the drift and colonisation experiment conducted in the Turitea Stream in February and March 2002. The three drift sampling nets are visible alongside and below the channels.

Benthic sampling protocol

On days four and 14, invertebrates were collected from three randomly selected stones in each channel. Stones were sampled as the collector moved progressively upstream. The invertebrates on each stone were collected by scooping the stone into a hand net of 250µm mesh, along with any fine sediment or detritus immediately below the collected stone. The stone was thoroughly washed in the net to ensure all invertebrates were removed. The invertebrates were stored in 10% formalin and later identified and enumerated as above.

Periphyton sampling protocol

On days one, four, and 14, five periphyton samples were collected from each channel; on day one, these were taken from three randomly selected stones in each channel, while on days four and 14 they were taken from the three stones taken for invertebrate sampling, once all invertebrates had been removed. Samples were collected by firmly rubbing a 30mm diameter absorbent abrasive pad (cut from Scotch-Brite Doodlebug White Cleansing Pad) in a single position on the upper side of the stone. Pigments were extracted and analysed following the methods of Steinman & Lamberti (1996), with values then converted to $\mu g / cm^2$ chlorophyll *a*. As chlorophyll *a* concentration has been found to correlate strongly with periphyton biomass in New Zealand streams (Clausen & Biggs 1997), it is taken to be an indicator of periphyton biomass in the channels.

Data analysis

Bray-Curtis ordinations of drift and stone samples were performed using PC-ORD (McCune & Mefford 1997), and ordination axes correlated with the measured environmental variables to investigate whether these were related to the arrangement of communities in multivariate space.

The effects of channel type ('0' or 'P') and sampling date on periphyton biomass and number of drifting and colonising invertebrates were tested using the ANOVA procedure of SAS (2000) with channel type as a fixed factor and day as a random factor. Bonferroni *a posteri* means test procedures were also performed using SAS (2000).

RESULTS

Channel periphyton

Mean chlorophyll *a* concentrations are provided in Appendix 4.1. Mean chlorophyll *a* concentrations on day 1 of the experiment were $< 0.1 \ \mu\text{g} / \text{cm}^2$ in the '0' channels, and $1.9 \ \mu\text{g} / \text{cm}^2$ in the 'P' channels. On day 4 mean concentrations were $1.6 \ \mu\text{g} / \text{cm}^2$ in the '0' channels, and $1.7 \ \mu\text{g} / \text{cm}^2$ in the 'P' channels, and on day 14 mean concentration was $1.5 \ \mu\text{g} / \text{cm}^2$ in '0' channels while the 'P' channels had a mean of $2.3 \ \mu\text{g} / \text{cm}^2$. There was no difference in mean channel chlorophyll *a* concentrations on different sampling days $(F_{2,22} = 2.49, P = 0.17)$, but more chlorophyll was present in 'P' channels than '0' $(F_{1,23} = 0.17)$.

18.88, P > 0.05); the effect of day on chlorophyll *a* concentration differed according to channel type ($F_{6,18} = 10.63$, P > 0.01), with higher chlorophyll levels in 'P' channels (Fig. 5.1).



Figure 5.1 Mean $(\pm 1$ SE) chlorophyll *a* concentration as a function of time since the experiment began. Solid points indicate '0' channels (channels which began the experiment with no periphyton), while hollow points indicate 'P' channels (those which began the experiment with periphyton).

Drift samples

The number of invertebrates collected in drift nets are provided in Appendix 5.1. Between 13 and 253 individuals (mean 62.2) and between two and 11 taxa (mean 6.5) were collected in a single drift net in any one day. Overall, 19 taxa were collected in drift nets, the five most abundant being *Potampyrgus antipodarum*, *Austrosimulium australense*, Elmidae, *Deleatidium* sp., and *Pycnocentrodes* sp. More individuals and more taxa were caught in inflow nets than in outflow nets ($F_{1,111} = 15.00$, P > 0.001; $F_{1,111} = 18.32$, P > 0.0001 respectively).

A Bray-Curtis ordination of the number of individuals caught in drift samples indicated that neither time since the experiment began nor chlorophyll *a* concentration were significantly correlated with the structuring of the drift 'community' (Fig. 5.2).





Figure 5.2 Bray-Curtis ordination of the invertebrate drift 'community' caught over 14 days in the Turitea Stream. The samples collected from channel pair 1 are indicated by circles, pair 2 by triangles, pair 3 by squares, and channel pair 4 by diamonds; numbers within each point indicate the number of days since the experiment began.

Benthic samples

The numbers of invertebrates collected in benthic samples are provided in Appendix

5.2. Between 11 and 182 invertebrates were collected from a single stone, with a mean

of 58.9 in the '0' channels and 70.6 in the 'P' channels - this difference was not

statistically significant ($F_{1, 23} = 1.37$, P = 0.29). From each stone between three and 10 taxa were collected, with a mean of 5.2 in the '0' channels and 6.4 in the 'P' channels. Once again, this was not statistically significant ($F_{1, 23} = 1.54$, P = 0.26).

A total of 13 taxa were collected from benthic samples over the study period, with '0' and 'P' channels having the same rank order for the five most common taxa: the most abundant taxa was Austrosimulium australense (mean of 30.2 per sampled stone), followed by *Potampyrgus antipodarum*, *Pycnocentrodes* sp, *Deleatidium* sp., and Elmidae.

A mean of 81.2 invertebrates from 5.5 taxa had colonised each sampled stone in the experimental channels by day four; on day 14, these figures were 48.2 and 6.0, respectively. There was a significant change in number of individuals between days one, 10, and 14 ($F_{2,23} = 48.90$, P > 0.001); number of taxa increased significantly from day one to 10 ($F_{2,23} = 95.26$, P > 0.0001), but not between days 10 and 14 (Fig. 5.3).

The number of individual invertebrates collected in each channel on day four was not related to chlorophyll *a* concentration ($F_{1,7} = 1.20$, P = 0.32), but total number of taxa was ($F_{1,7} = 13.74$, P = 0.01, $r^2 = 0.70$). On day 14 the number of invertebrates and number of taxa collected were both unrelated to chlorophyll *a* concentration ($F_{1,11}$ = 3.06, P = 0.13; $F_{1,11} = 0.76$, P = 0.42 respectively). A Bray-Curtis ordination of the number of individuals collected from the benthos indicated that neither time since the experiment began nor chlorophyll *a* concentration were significantly correlated with community structuring.



Figure 5.3 Mean (\pm 1SE) number of taxa collected from the channel substrate as a function of time since the experiment began. Solid points indicate '0' channels (channels which began the experiment with no periphyton), while hollow points indicate 'P' channels (those which began the experiment with periphyton)s.

DISCUSSION

Approximately one quarter of the invertebrates drifting into the channels did not drift out of them, indicating that significant numbers left the water column and colonised the channel substrate. However, colonisation appeared to be unrelated to benthic periphyton density.

The vast majority of invertebrates collected in the current study were fast colonising 'weedy' taxa (Scarsbrook & Townsend 1993). *Deleatidium* was the most abundant grazing taxa, and appears to have rapidly colonised the substrate even when periphyton levels were quite low. Over the time scale of the current study *Deleatidium* did not appear to have been displaced by other taxa. *Potamopyrgus* was another common grazer, but one which is not considered to be weedy (Death, pers. comm.). This occurred in large numbers in drift samples, suggesting that a large source population with considerable emigration occurs upstream of the experimental site.

While peak taxon richness may have been achieved in four days, only two thirds of the taxa collected in drift samples were found on the channel substrate. It appears that a number of less abundant and perhaps slower colonising taxa require a longer period of time to reach densities sufficient to ensure their collection in benthic samples. Given figures published on the time required for full community recolonisation (e.g., Death 1996; Matthaei *et al.* 1996), it appears that the 14 day study period may have given a bias towards weedy taxa colonisation. If the experiment had been allowed to run for longer a relationship between periphyton density and taxon richness may have been found, but this was not possible in the time available.

Daily variation in the number of invertebrates caught in drift nets was of more than an order of magnitude and, given the quite open nature of the experiment, it is possible that some of the invertebrates caught in outflow nets had in fact swum or crawled perpendicular to the current as opposed to drifting straight down it. If this occurred, then some of the collected invertebrates may have entered the channel as little as a few centimetres above the outflow net. If this occurred too frequently it may have added considerable 'noise'; it may be prudent to use channels with walls protruding above the water level in future experiments of this type.

Also, the channels used in the current study may have been too short to allow adequate time for the colonisation of less common taxa. Elliot (2002) found that the mean time spent in the water column by drifting invertebrates was as high as 33 seconds for some taxa, with only two taxa spending an average of less than five seconds drifting. In the current study, water flowed the length of the channels in three to 20 seconds, a period of time that may have been insufficient to allow colonisation by large numbers of invertebrates, particularly by less common or long-drifting taxa. Of course, colonisation densities (that is, the number of invertebrates on a given area of stream bed) will not increase with channel size, but a longer channel would allow more benthic samples to be taken and so improve the chance of sampling rare taxa.

In conclusion, it appears that while a significant proportion of drifting invertebrates did colonise the channels, the number of individuals and taxon richness was unaffected by benthic periphyton level. The community was dominated by weedy taxa, and even at the end of the 14 day study period there had been no significant change in the benthic community. A longer study, possibly involving larger channels, may allow slower colonising taxa to appear, and perhaps a periphyton - taxon richness relationship to develop.

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Chapter 6:

Synthesis



While a stepwise regression model was unsuccessful in the prediction of stream bed movement from channel and catchment characteristics, an artificial neural network analysis produced a model which had good predictive power. It was not possible to verify the neural network model against an external data set, but the available testing procedures indicated that bed movement was predicted with a high level of accuracy.

When the macroinvertebrate communities of 43 forest streams were sampled in the summers of 1996 and 2001 it was found that change in community structure did not correlate with bed movement, change in periphyton level, or any other measured environmental variable. MCI score changed by an average of 12.8 points between the two surveys, and the number of sites with an MCI score of greater than 120 (i.e., a 'pristine' stream) dropped from 40 to only 29. Those streams which were cooler in 2001 than 1996 tended to increase in MCI, whereas a drop in MCI occurred at sites that were warmer. Community changes such as these could have dramatic implications if they occurred at the reference sites in a biomonitoring programme.

A subset of the 43 streams were sampled every three months between June 2000 and May 2001. Sites with greater bed movement tended to have less periphyton and lower macroinvertebrate taxon richness, but the degree of change in macro-invertebrate community structure between sampling events did not appear to be linked to bed movement or change in periphyton level. When the results of this study were compared with the changes seen at the same sites between 1996 and 2001, it was found that the intra- and inter-annual changes in community structure were similar - community structure was no more stable between summers separated by five years than it was between the seasons of a single year.

No periphyton level - macroinvertebrate taxon richness relationship was found when eight artificial channels, half with periphyton and half without, were set on a stream bed and allowed to be colonised. Approximately one quarter of the invertebrates that drifted through the channels colonised the substrate but this was not related to benthic periphyton level. Stream bed taxon richness peaked after only four days, although these represented only two thirds of all taxa collected from the drift. The experiment was run for 14 days which may not have allowed sufficient time for rare, slow colonising, or high periphyton density dependent taxa to appear on the channel substrate.

APPENDICES



APPENDIX 1: Environmental variables, macroinvertebrate community data, and measures of community change as measured at 43 streams in the Ruahine and Tararua Ranges in the summers of 1996 and 2001.

Site	Measured	Predicted bed	Stream	Mean	Canopy	Substrate	Substrate	SI
	bed	movement	slope	stone size	cover	diversity	diversity	
	movement	0.7	(m/m)	(m)	(%)	0.404	0.40	4.0
1	96.6	9.7	0.025	0.05	0	0.181	0.18	4.2
2	99.3	9.1	0.013	0.06	0	0.156	0.15	4.9
3	92.7	9.6	0.026	0.05	60	0.168	0.17	4.2
4	82.8	9.0	0.068	0.04	0	0.199	0.20	3.2
5	83.9	12.8	0.030	0.09	10	0.165	0.16	7.4
6	99.2	17.0	0.011	0.06	80	0.211	0.21	4.8
7	99.2	42.7	0.016	0.05	90	0.167	0.17	4.2
8	99.2	33.6	0.024	0.05	70	0.183	0.18	4.1
9	99.1	17.8	0.015	0.05	30	0.172	0.17	4.3
10	66.8	27.4	0.083	0.09	90	0.151	0.15	7.5
11	88.8	14.4	0.064	0.06	20	0.156	0.15	4.8
12	70.9	27.5	0.009	0.05	40	0.159	0.16	4.4
13	99.3	16.2	0.024	0.06	20	0.150	0.15	5.1
14	95.4	27.5	0.320	0.07	95	0.197	0.19	5.9
15	95.4	9.4	0.022	0.05	70	0.156	0.15	4.5
16	79.7	9.3	0.018	0.05	60	0.159	0.16	4.2
17	51.1	32.0	0.014	0.05	70	0.165	0.16	4.0
18	99.3	11.3	0.031	0.09	30	0.151	0.15	7.6
19	99.3	15.6	0.027	0.06	30	0.148	0.15	4.8
20	99.3	10.8	0.076	0.06	90	0.151	0.15	5.2
21	98.4	9.2	0.019	0.10	35	0.124	0.12	9.0
22	96.6	24.6	0.082	0.05	50	0.191	0.19	3.9
24	95.8	15.7	0.068	0.05	80	0.173	0.17	4.2
25	99.3	8.6	0.014	0.05	0	0.162	0.16	4.2
26	79.7	8.8	0.110	0.06	80	0.163	0.16	4.9
27	99.3	12.2	0.010	0.06	80	0.189	0.19	5.3
28	99.3	33.8	0.011	0.09	60	0.147	0.14	8.1
29	36.0	31.7	0.048	0.06	50	0.142	0.14	5.3
30	96.6	10.7	0.030	0.05	0	0.168	0.17	4.2
31	98.4	10.0	0.032	0.05	30	0.157	0.15	4.6
32	99.3	13.8	0.045	0.06	80	0.156	0.15	5.4
33	98.4	31.7	0.026	0.06	90	0.165	0.16	4.8
34	96.6	8.8	0.041	0.05	10	0.165	0.16	4.1
35	99.3	8.7	0.075	0.07	40	0.158	0.16	5.5
36	94.0	27.9	0.027	0.05	10	0.164	0.16	4.0
37	99.3	11.0	0.004	0.05	0	0.163	0.16	4.6
38	99.3	8.9	0.016	0.07	20	0.174	0.17	6.2
39	99.3	31.8	0.034	0.05	60	0.166	0.16	4.4
40	99.3	8.6	0.029	0.08	40	0.150	0.14	7.1
41	94.5	9.9	0.005	0.05	0	0.167	0.17	4.0
42	99.3	9.6	0.014	0.06	0	0.147	0.14	4.7
43	98.4	27.1	0.020	0.06	10	0.156	0.15	4.7
44	99.3	40.8	0.011	0.05	50	0.195	0.19	4.4

Site	%	%	%	%	1996	2001	1996	2001	1996	2001
	bedrock	boulder	cobble	gravel	mean	mean	mean	mean	temp	temp
					depth	depth	velocity	velocity	(°C)	(°C)
					(m)	(m)	(m/s)	(m/s)		
1	0.7	2.7	47.4	49.2	0.29	0.19	0.62	0.55	13.0	16.1
2	0.8	7.1	52.3	39.8	0.35	0.18	0.58	0.57	12.5	17.3
3	0.9	5.3	34.5	59.3	0.25	0.1	0.42	0.39	15.1	14.2
4	0.2	3.5	24.6	71.7	0.14	0.15	0.16	0.19	12.9	15.3
5	2.9	14.5	58.3	24.4	0.31	0.32	0.22	0.25	16.8	15.6
6	0.3	5.7	61.8	32.2	0.15	0.21	0.12	0.16	13.6	11.5
7	0.6	1.7	50.4	47.4	0.21	0.18	0.13	0.14	13.7	11.4
8	0.8	3.8	42.3	53.1	0.17	0.14	0.2	0.22	14.1	13.3
9	0.6	4.6	48.2	46.7	0.21	0.19	0.21	0.24	15.9	14.0
10	4.1	10.0	60.0	25.9	0.09	0.15	0.12	0.19	13.5	14.8
11	0.7	6.4	50.1	42.7	0.21	0.2	0.65	0.79	17.4	16.5
12	1.0	4.2	39.1	55.7	0.16	0.15	0.27	0.29	12.9	14.5
13	0.8	8.1	49.5	41.5	0.23	0.31	0.15	0.18	14.8	15.0
14	1.9	6.9	64.9	26.3	0.08	0.07	0.1	0.08	13.3	11.7
15	0.5	6.4	45.3	47.8	0.28	0.17	0.48	0.47	12.2	13.5
16	0.8	5.9	37.8	55.5	0.23	0.25	0.31	0.28	13.8	14.3
17	0.4	5.3	39.7	54.5	0.13	0.19	0.22	0.3	12.0	12.3
18	1.6	22.4	53.7	22.4	0.26	0.27	0.29	0.32	16.5	12.6
19	0.5	9.8	40.4	49.4	0.13	0.1	0.41	0.38	15.7	15.1
20	0.9	9.2	42.6	47.2	0.23	0.22	0.09	0.09	12.7	14.3
21	7.3	15.3	46.0	31.5	0.32	0.26	0.28	0.22	14.7	15.6
22	0.6	5.8	24.5	69.0	0.14	0.09	0.25	0.23	13.2	11.8
24	0.9	4.2	42.7	52.2	0.15	0.2	0.3	0.31	12.1	12.1
25	0.7	4.0	43.6	51.7	0.22	0.33	0.4	0.47	13.5	17.5
26	1.0	8.2	39.3	51.5	0.09	0.15	0.12	0.17	13.2	15.0
27	1.9	9.4	38.7	50.0	0.16	0.21	0.2	0.24	16.4	14.4
28	5.5	15.8	39.3	39.3	0.19	0.17	0.3	0.28	13.9	14.4
29	0.8	9.2	47.3	42.7	0.09	0.12	0.28	0.29	9.8	11.9
30	0.7	4.4	42.0	52.9	0.27	0.2	0.35	0.38	11.5	14.3
31	0.9	7.0	41.0	51.1	0.18	0.18	0.25	0.26	11.4	14.7
32	0.8	11.7	45.3	42.2	0.2	0.13	0.21	0.2	14.4	14.2
33	0.5	6.8	51.5	41.2	0.27	0.2	0.14	0.15	12.3	10.2
34	0.9	5.8	33.2	60.2	0.24	0.21	0.28	0.25	9.9	11.8
35	1.4	8.5	50.1	39.9	0.22	0.34	0.55	0.63	11.9	15.5
36	0.4	4.9	42.3	52.4	0.15	0.11	0.34	0.33	10.4	15.3
37	1.2	5.8	42.6	50.5	0.25	0.21	0.65	0.55	11.6	12.2
38	0.6	14.8	56.3	28.3	0.23	0.2	0.5	0.42	9.9	11.1
39	1.1	5.1	43.2	50.5	0.15	0.18	0.45	0.5	10.0	11.0
40	3.0	12.9	59.1	25.0	0.32	0.3	0.4	0.34	11.4	11.0
41	0.9	3.6	34.4	61.1	0.26	0.23	0.68	0.74	11.0	15.7
42	0.8	7.5	40.4	51.2	0.27	0.23	0.64	0.56	12.0	16.7
43	0.5	10.5	30.9	58.1	0.24	0.19	0.32	0.24	12.0	13.1
44	0.3	5.0	57.7	37.0	0.25	0.23	0.1	0.07	12.5	17.0
Site	1996 conductivity (μS/cm)	2001 conductivity (μS/cm)	1996 chlorophyll a (μg/cm ²)	1996 invertebrate abundance	1996 taxon richness	Sub-sampled 1996 taxon richness	2001 chlorophyll a (μg/cm ²)	2001 invertebrate abundance	2001 taxon richness	
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1	54.0	77.7	1.62	2680	39	20.8	0.02	234	16	
2	27.6	72.7	0.90	1590	35	22.7	4.52	288	13	
3	69.7	79.8	0.00	29	11		0.56	46	9	
4	64.8	72.2	2.52	1286	31	21.0	2.70	180	17	
5	69.4	79.2	2.23	1130	27	23.5	1.27	290	10	
6	65.0	70.3	4.42	729	31	20.1	1.08	91	15	
7	59.8	75.0	1.92	645	24	22.9	0.64	169	15	
8	66.7	71.2	0.85	217	23	15.6	1.23	77	10	
9	62.3	69.1	2.08	2123	33	29.9	3.50	824	20	
10	82.9	82.4	2.03	626	29	18.6	0.00	96	12	
11	91.7	94.9	2.00	1149	27	12.3	1.75	48	10	
12	81.1	88.3	1.11	946	28		2.17	1234	21	
13	76.7	94.4	0.87	544	21	18.6	2.14	210	13	
14	103.8	116.4	0.82	655	24	16.9	0.28	120	13	
15	53.8	62.5	0.29	1376	28	22.0	1.22	273	13	
16	53.8	60.0	2.06	1630	33	19.1	1.70	240	13	
17	122.1	181.0	1.92	1194	38	31.1	3.35	278	21	
18	84.2	94.7	0.53	905	26	22.5	1.27	405	19	
19	90.8	102.1	0.05	282	21		3.01	568	17	
20	47.0	50.3	0.18	368	21	11.7	0.10	53	9	
21	53.3	61.2	0.16	482	17	12.9	0.88	121	10	
22	90.1	85.6	0.15	696	19	16.1	1.25	179	14	
24	59.5	65.1	0.02	671	27	13.3	0.51	73	13	
25	73.1	73.1	0.85	876	19	15.8	1.47	441	15	
26	71.5	68.5	0.23	558	20	19.8	0.27	170	13	
27	92.7	97.6	0.17	829	28	26.0	2.52	385	20	
28	98.5	101.6	1.37	813	26	24.8	4.69	576	15	
29	61.9	68.6	4.97	1389	31	23.5	6.91	196	19	
30	66.6	76.1	0.66	1275	24	23.0	2.03	460	16	
31	77.7	84.9	0.06	405	28	28.0	2.78	359	13	
32	71.2	71.0	0.16	882	33	26.1	1.65	311	21	
33	64.9	73.7	0.31	541	31	25.9	0.21	175	16	
34	63.8	66.2	0.55	456	17	13.1	1.50	150	10	
35	69.2	74.8	1.34	1811	24	16.7	1.57	395	17	
36	93.4	95.8	5.19	2104	48	40.3	4.69	733	21	
37	106.9	116.4	1.04	1487	30	8.0	0.00	15	8	
38	77.2	77.1	0.97	3790	37	21.9	6.54	430	20	
39	98.9	103.2	1.95	1649	38	37.1	2.40	496	22	
40	101.0	99.4	1.61	1912	34	33.1	1.85	1037	24	
41		85.1	0.24	983	28	11.6	0.23	42	8	
42		155.2	2.58	3376	34	32.2	2.83	1234	24	
43	104.7	76.8	2.32	1924	32	27.5	5.75	610	16	
44	68.9	84.4	1.91	1985	28	18.5	1.63	421	16	

Site	Change in chlorophyll a concentration from 1996 to 2001	Change in number of taxa from 1996 to 2001	Number of taxa persisting from 1996 to 2001	Proportion of taxa persisting from 1996 to 2001	Kendell's W (complete communities)	Kendell's W (top ten taxa)	1996 MCI score	2001 MCI score
1	-99%	23.0	11.0	0.28	0.377	0.709	132	113
2	+401%	22.0	9.0	0.26	0.352	0.794	132	98
3	+500%	2.0	4.0	0.36	0.184	0.976	124	107
4	+7%	14.0	10.0	0.32	0.363	0.691	128	118
5	-43%	17.0	6.0	0.22	0.282	0.758	144	138
6	-76%	16.0	10.0	0.32	0.358	0.673	123	136
7	-67%	9.0	9.0	0.38	0.320	0.818	134	141
8	+44%	13.0	7.0	0.30	0.273	0.636	131	144
9	+68%	13.0	14.0	0.42	0.414	0.406	123	120
10	-100%	17.0	8.0	0.28	0.308	0.594	127	132
11	-13%	17.0	7.0	0.26	0.291	0.788	116	124
12	+95%	7.0	13.0	0.46	0.402	0.630	139	127
13	+147%	8.0	7.0	0.33	0.280	0.648	137	118
14	-65%	11.0	7.0	0.29	0.288	0.509	125	129
15	+320%	15.0	10.0	0.36	0.344	0.733	131	120
16	-17%	20.0	7.0	0.21	0.324	0.667	128	129
17	+74%	17.0	16.0	0.42	0.484	0.418	128	138
18	+137%	7.0	15.0	0.58	0.431	0.897	138	142
19	+500%	4.0	7.0	0.33	0.291	0.430	139	141
20	-46%	12.0	6.0	0.29	0.251	0.558	128	136
21	+438%	7.0	3.0	0.18	0.198	0.612	135	122
22	+500%	5.0	7.0	0.37	0.286	0.685	127	133
24	+500%	14.0	10.0	0.37	0.345	0.630	134	125
25	+74%	4.0	8.0	0.42	0.290	0.594	123	105
26	+13%	7.0	8.0	0.40	0.290	0.524	123	131
27	+500%	8.0	12.0	0.43	0.393	0.918	138	126
28	+243%	11.0	12.0	0.46	0.363	0.624	139	141
29	+39%	12.0	10.0	0.32	0.355	0.588	124	122
30	+208%	8.0	11.0	0.46	0.347	0.558	146	129
31	+500%	15.0	8.0	0.29	0.311	0.339	127	143
32	+500%	12.0	14.0	0.42	0.423	0.352	128	122
33	-34%	15.0	13.0	0.42	0.416	0.842	135	128
34	+171%	7.0	5.0	0.29	0.228	0.855	145	124
35	+17%	7.0	8.0	0.33	0.320	0.733	141	113
36	-10%	27.0	14.0	0.29	0.450	0.455	125	101
37	-100%	22.0	4.0	0.13	0.273	0.788	128	90
38	+500%	17.0	14.0	0.38	0.454	0.955	128	124
39	+23%	16.0	16.0	0.42	0.481	0.703	119	121
40	+15%	10.0	15.0	0.44	0.459	0.885	116	128
41	-2%	20.0	4.0	0.14	0.244	0.885	134	105
42	+10%	10.0	16.0	0.47	0.468	0.733	134	111
43	+148%	16.0	9.0	0.28	0.342	0.667	126	95
44	+15%	12.0	11.0	0.39	0.396	0.624	139	121

Site	Relative Sorensen distance (1996 to 2001complete communities)	Euclidian distance (1996 to 2001 complete communities)	Relative Sorensen distance (1996 to 2001 species presence/ absence)	Euclidian distance (1996 to 2001 species presence/absence)	Relative Sorensen distance (1996 to 2001 top ten taxa)	Euclidian distance (1996 to 2001 top ten taxa)	Relative Sorensen distance (sub-sampled 1996 community to 2001 community)	1996 taxon evenness	2001 taxon evenness
1	0.756	0.165	0.636	0.283	0.643	0.122	0.253	0.14	0.57
2	0.499	0.155	0.625	0.245	0.443	0.153	0.595	0.26	0.22
3	0.467	0.707	0.500	0.173	0.431	0.677		0.03	0.14
4	0.410	0.101	0.727	0.316	0.349	0.100	0.647	0.21	0.30
5	0.462	0.744	0.667	0.200	0.361	0.724	0.523	0.23	0.66
6	0.449	0.525	0.625	0.245	0.156	0.458	0.501	0.17	0.46
7	0.408	0.486	0.714	0.265	0.227	0.476	0.606	0.31	0.25
8	0.362	0.167	0.833	0.245	0.345	0.159	0.606	0.24	0.45
9	0.691	0.230	0.545	0.245	0.607	0.123	0.316	0.16	0.25
10	0.510	0.547	0.778	0.300	0.452	0.529	0.564	0.14	0.21
11	0.470	0.118	0.714	0.245	0.349	0.112	0.548	0.17	0.43
12	0.727	0.357	0.429	0.200	0.701	0.353		0.15	0.53
13	0.571	0.557	0.600	0.173	0.519	0.554	0.499	0.27	0.25
14	0.767	0.682	0.750	0.200	0.789	0.656	0.363	0.21	0.20
15	0.585	0.134	0.571	0.200	0.536	0.131	0.393	0.19	0.44
16	0.455	0.121	0.778	0.283	0.624	0.120	0.328	0.19	0.29
17	0.672	0.897	0.600	0.245	0.637	0.862	0.381	0.12	0.14
18	0.403	0.631	0.333	0.200	0.354	0.608	0.608	0.22	0.24
19	0.770	0.667	0.667	0.224	0.733	0.632		0.26	0.22
20	0.450	0.346	0.833	0.245	0.381	0.341	0.523	0.22	0.40
21	0.233	0.586	0.100	0.200	0.151	0.583	0.765	0.32	0.49
22	0.270	0.550	0.600	0.200	0.173	0.537	0.701	0.34	0.55
24	0.570	0.531	0.625	0.245	0.516	0.524	0.426	0.22	0.22
25	0.301	0.763	0.600	0.224	0.178	0.745	0.748	0.66	0.48
20	0.564	0.331	0.500	0.173	0.474	0.226	0.466	0.13	0.30
21	0.425	0.410	0.500	0.245	0.232	0.309	0.682	0.14	0.18
20	0.524	0.742	0.500	0.200	0.401	0.733	0.527	0.29	0.34
30	0.733	0.152	0.500	0.224	0.075	0.137	0.440	0.10	0.12
31	0.510	0.713	0.000	0.224	0.330	0.315	0.300	0.17	0.40
32	0.607	0.665	0.429	0.224	0.570	0.513	0.458	0.17	0.37
33	0.360	0.552	0.444	0.224	0.254	0.543	0.430	0.10	0.25
34	0.446	0.418	0.100	0.224	0.394	0.402	0.591	0.26	0.40
35	0.384	0.162	0.500	0.200	0.273	0.155	0.728	0.25	0.40
36	0.652	0.166	0.545	0.265	0.609	0.163	0.396	0.17	0.14
37	0.590	0.176	0.818	0.300	0.443	0.163	0.469	0.14	0.08
38	0.345	0.368	0.250	0.173	0.213	0.368	0.717	0.27	0.24
39	0.419	0.119	0.333	0.173	0.350	0.117	0.568	0.17	0.29
40	0.344	0.851	0.444	0.245	0.296	0.822	0.744	0.22	0.34
41	0.673	0.811	0.889	0.316	0.562	0.745	0.445	0.14	0.49
42	0.711	0.404	0.500	0.265	0.698	0.380	0.334	0.25	0.21
43	0.911	0.239	0.600	0.265	0.794	0.219	0.055	0.21	0.19
44	0.383	0.367	0.429	0.200	0.347	0.144	0.768	0.23	0.22

Austrosimulium tillyardianum	Austroperla cyrene	Austroclima sepia	Archicauliodes diversus	Aphrophila neozelandica	Aoteapsyche colonica	Amphipoda	Ameletopsis perscitus	Acari sp.	Acanthophlebia cruentata	Site
0.000669	0.009845	0.000403	0.006575	0.001498	0.0	0.000101	0.000303	0.000468	0.0	
0.019046	0.003672	0.0	0.000595	0.001294	0.0	0.0	0.0	0.000135	0.0	N
0.000961	0.000077	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ω
0.000206	0.000104	0.002890	0.003110	0.001944	0.0	0.000209	0.000105	0.001414	0.0	4
0.0	0.000385	0.0	0.004153	0.0	0.0	0.0	0.000136	0.0	0.0	UT
0.0	0.004491	0.0	0.000641	0.000914	0.000430	0.0	0.000696	0.0	0.0	თ
0.0	0.004517	0.0	0.000750	0.0	0.0	0.0	0.0	0.000129	0.0	7
0.0	0.000210	0.0	0.000920	0.000138	0.0	0,0	0.000375	0.0	0.0	8
0.001682	0.003682	0.0	0.004474	0.001506	0.000076	0.0	0.000233	0.0	0.0	ø
0.0	0.000151	0.005219	0.000442	0.0	0.000141	0.000141	0.000341	0.000151	0.0	0-
0.000414	0.000556	0.0	0.005336	0.0	0.001303	0.0	0.0	0.0	0.0	
0.0	0.002997	0.000499	0.000461	0.0	0.0	0.0	0.000673	0.0	0.0	N-
0.0	0.0	0.0	0.000261	0.0	0.000228	0.0	0.0	0.000296	0.0	ω -
0.0	0.0	0.000941	0.0	0.0	0.002660	0.0	0.0	0.0	0.0	4 4
0.0	0.001521	0.0	0.000170	0.000842	0.004719	0.0	0.0	0.0	0.0	0n
0.0	0.003886	0.0	0.003146	0.001973	0.014396	0.0	0.000340	0.0	0.0	o →
0.0	0.000627	0.0	0.001336	0.000064	0.002461	0.0	0.000433	0.0	0.0	71
0.0	0.000181	0.0	0.001342	0.001765	0.007630	0.0	0.0	0.0	0.0	∞ →
0.0	0.0	0.0	0.000170	0.0	0.000632	0.0	0.000120	0.0	0.0	ω →
0.000485	0.0	0.0	0.0	0.0	0.000108	0.0	0.0	0.000108	0.0	ON
0.0	0.000347	0.0	0.0	0.0	0.0	0.0	0.0	0.001074	0.0	-N
0.0	0.000287	0.0	0.0	0.0	0.001218	0.0	0.000265	0.0	0.0	NN
0.0	0.000811	0.0	0.001172	0.0	0.000710	0.0	0.000428	0.000296	0.0	4 N
0.0	0.0	0.0	0.000251	0.001354	0.0	0.0	0.0	0.0	0.0	UN
0.0	0.0	0.0	0.0	0.0	0.001601	0.0	0.0	0.000641	0.0	ON
0.000790	0.0	0.000100	0.000869	0.000370	0.002766	0.0	0.001208	0.0	0.0	NN
0.0	0.000398	0.0	0.000502	0.000828	0.0	0.0	0.0	0.0	0.0	00 N
0.0	0.000618	0.015044	0.0	0.000815	0.0	0.049979	0.0	0.0	0.0	(ON
0.0	0.001135	0.0	0.0	0.003759	0.0	0.0	0.0	0.0	0.0	0ω
0.0	0.000093	0.0	0.000203	0.0	0.0	0.0	0.0	0.0	0.0	w
0.000206	0.000660	0.0	0.002193	0.000722	0.001294	0.0	0.0	0.0	0.0	Nω
0.0	0.002232	0.0	0.001649	0.001358	0.000392	0.0	0.000901	0.000155	0.0	ωω
0.0	0.0	0.0	0.0	0.000419	0.0	0.0	0.0	0.000493	0.0	4ω
0.0	0.000567	0.0	0.000347	0.002663	0.000220	0.0	0.0	0.0	0.0	σω
0.0	0.001668	0.004805	0.002127	0.009397	0.000590	0.0	0.0	0.000069	0.0	ດພ
0.008291	0.002622	0.0	0.001632	0.033958	0.000687	0.0	0.0	0.000138	0.0	73
0.000290	0.001500	0.0	0.007558	0.0	0.003718	0.0	0.0	0.0	0.000315	ω ω
0.0	0.000315	0.0	0.001380	0.005241	0.001079	0.0	0.0	0.0	0.0	မမ
0.0	0.000884	0.0	0.008427	0.005648	0.024731	0.0	0.0	0.0	0.0	40
0.0	0.001568	0.0	0.000635	0.000833	0.002885	0.0	0.000342	0.0	0.0	4 4
0.0	0.000436	0.000269	0.011241	0.002067	0.023395	0.0	0.001418	0.0	0.0	N4
0.0	0.000119	0.000218	0.001087	0.003561	0.004189	0.000324	0.0	0.000380	0.0	4 ω
0.0	0.000516	0.0	0.000208	0.000824	0.005231	0.0	0.0	0.0	0.0	4 4
		the second se			the second se				and the second se	

Chironomidae Polypedellum	Chironomidae Pirara sp.	Chironomidae Naonella sp.	Chironomidae Maoridiamesa	Chironomidae Kaniwhaniwhas sp.	Chironomidae Eukkieferulus sp.	Chironomidae Cricotopus sp.	Chironomidae //Claspers sp.	Ceratopogionidae	Beraeoptera roria	Site
0.0	0.0	0.0	0.008439	0.0	0.047540	0.0	0.0	0.0	0.016155	-
0.0	0.0	0.003613	0.016244	0.0	0.003954	0.0	0.0	0.0	0.006070	N
0.0	0.0	0.0	0.001057	0.0	0.000343	0.0	0.0	0.0	0.0	ω
0.0	0.0	0.003954	0.037227	0.0	0.015466	0.0	0.0	0.000101	0.0	4
0.0	0.0	0.010611	0.002002	0.0	0.003613	0.0	0.0	0.0	0.056800	ۍ ا
0.000274	0.0	0.011390	0.005500	0.0	0.001341	0.0	0.0	0.0	0.004025	თ
0.0	0.0	0.003436	0.001682	0.0	0.001893	0.0	0.0	0.000262	0.001719	7
0.0	0.0	0.003871	0.001017	0.0	0.003720	0.0	0.0	0.0	0.0	8
0.0	0.0	0.190866	0.050671	0.0	0.000325	0.002600	0.0	0.002468	0.019830	9
0.0	0.0	0.001824	0.007022	0.0	0.007353	0.0	0.0	0.0	0.0	0-
0.0	0.0	0.033754	0.019398	0.0	0.002780	0.0	0.0	0.0	0.033232	
0.0	0.0	0.004219	0.006506	0.0	0.000801	0.0	0.0	0.0	0.033436	N -
0.0	0.0	0.002959	0.000685	0.0	0.0	0.0	0.0	0.0	0.005131	ω →
0.0	0.0	0.001004	0.012667	0.0	0.006036	0.0	0.0	0.0	0.0	- 4
0.0	0.001230	0.0	0.0	0.0	0.001894	0.000170	0.0	0.0	0.123052	07 - 1
0.0	0.000094	0.0	0.000072	0.0	0.000841	0.000132	0.0	0.0	0.098055	o →
0.0	0.0	0.0	0.0	0.000564	0.004900	0.000239	0.001702	0.0	0.069437	~ -
0.0	0.0	0.000362	0.000650	0.0	0.0	0.0	0.0	0.0	0.013210	∞ →
0.0	0.0	0.0	0.0	0.000174	0.001660	0.0	0.0	0.0	0.000170	- Q
0.0	0.0	0.001254	0.000618	0.0	0.000233	0.0	0.0	0.0	0.000161	ON
0.0	0.0	0.001999	0.0	0.0	0.0	0.0	0.0	0.0	0.0	- N
0.0	0.0	0.001155	0.006502	0.0	0.005730	0.0	0.0	0.0	0.0	NN
0.0	0.0	0.000105	0.001073	0.0	0.000919	0.0	0.0	0.0	0.000370	4 N
0.0	0.0	0.000737	0.003416	0.0	0.001566	0.0	0.0	0.0	0.0	σN
0.0	0.0	0.001492	0.012273	0.0	0.004460	0.0	0.0	0.0	0.0	σN
0.0	0.0	0.000737	0.002419	0.0	0.0	0.0	0.0	0.0	0.004741	2
0.0	0.0	0.000562	0.007459	0.0	0.000984	0.0	0.0	0.0	0.000719	00 N
0.0	0.0	0.004366	0.093602	0.0	0.011822	0.0	0.0	0.0	0.0	ØN
0.0	0.0	0.000230	0.012173	0.0	0.0	0.0	0.0	0.0	0.011771	03
0.0	0.0	0.000360	0.004521	0.0	0.002558	0.0	0.0	0.0	0.0	w
0.0	0.0	0.000357	0.011954	0.0	0.003847	0.0	0.0	0.0	0.0	Nω
0.0	0.0	0.0	0.002618	0.0	0.004513	0.0	0.0	0.0	0.000302	ωω
0.0	0.0	0.0	0.002808	0.0	0.0	0.0	0.0	0.0	0.001183	ω 4
0.0	0.0	0.000250	0.011883	0.0	0.0	0.0	0.0	0.0	0.152176	onω
0.0	0.000175	0.004621	0.0	0.000254	0.002379	0.000891	0.000305	0.0	0.026147	ດພ
0.0	0.001663	0.0	0.0	0.006929	0.117151	0.003550	0.005620	0.0	0.009545	73
0.0	0.000689	0.0	0.0	0.0	0.009324	0.012014	0.0	0.0	0.343223	8 3
0.0	0.000419	0.000433	0.0	0.002605	0.020308	0.016287	0.001346	0.0	0.033789	ωw
0.0	0.001653	0.000159	0.0	0.000180	0.005779	0.008150	0.000428	0.0	0.184714	40
0.0	0.006764	0.0	0.0	0.0	0.011139	0.000358	0.000716	0.0	0.028238	4 4
0.0	0.0	0.0	0.0	0.002069	0.017319	0.0	0.002237	0.0	0.070558	4 4
0.0	0.001006	0.0	0.0	0.0	0.000582	0.000099	0.0	0.0	0.014227	4 ω
0.0	0.000199	0.0	0.0	0.0	0.001876	0.001660	0.0	0.0	0.111356	44

Elmidae larvae	Emlidae adults	Deleatidium sp.	Cryptobiosalla ptomasi	Cristaperla fimbria	Costachorema xanthoptera	Costachorema callista	Coloburiscus humeralis	Collembola sp.	Chironomidae Tanypodini sp.	Site
0.024526	0.0	0.093166	0.0	0.0	0.0	0.0	0.017372	0.000714	0.0	
0.006958	0.0	0.148359	0.0	0.0	0.000925	0.0	0.001291	0.0	0.0	N
0.000431	0.0	0.001099	0.0	0.0	0.0	0.0	0.0	0.000226	0.0	ω
0.006108	0.004005	0.117738	0.0	0.0	0.0	0.0	0.039337	0.0	0.0	4
0.006766	0.003168	0.120246	0.0	0.0	0.0	0.0	0.005862	0.000101	0.0	Ch
0.004023	0.005203	0.057787	0.0	0.0	0.0	0.0	0.005896	0.0	0.0	თ
0.001615	0.000591	0.063383	0.0	0.0	0.0	0.0	0.003792	0.0	0.0	7
0.002139	0.000426	0.031769	0.0	0.0	0.0	0.0	0.000428	0.0	0.0	8
0.010880	0.004548	0.121972	0.0	0.0	0.0	0.000408	0.020757	0.0	0.0	ø
0.003814	0.000190	0.054186	0.0	0.0	0.0	0.0	0.003284	0.000233	0.0	0-1
0.014087	0.000380	0.095748	0.0	0.0	0.0	0.0	0.005569	0.0	0.0	
0.000315	0.003093	0.080036	0.0	0.0	0.0	0.0	0.028925	0.0	0.0	N ->
0.002017	0.0	0.051695	0.0	0.0	0.0	0.0	0.002192	0.0	0.0	ω →
0.003405	0.0	0.012476	0.0	0.0	0.0	0.0	0.004578	0.000411	0.0	- 4
0.005547	0.0	0.088155	0.000207	0.0	0.0	0.0	0.001220	0.0	0.0	0n ->
0.003310	0.0	0.079082	0.000298	0.0	0.0	0.0	0.013014	0.0	0.0	σ <u>→</u>
0.001356	0.0	0.041360	0.0	0.0	0.0	0.000758	0.014130	0.0	0.0	71
0.000579	0.000181	0.075121	0.0	0.0	0.0	0.0	0.011328	0.0	0.0	co -+
0.0	0.0	0.030873	0.000167	0.0	0.0	0.000466	0.006445	0.0	0.0	9 1
0.000810	0.0	0.035720	0.0	0.0	0.0	0.0	0.000317	0.000210	0.0	ON
0.003953	0.0	0.079728	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-N
0.002712	0.0	0.092245	0.0	0.0	0.0	0.0	0.002978	0.0	0.0	NN
0.001087	0.000105	0.053383	0.0	0.0	0.000843	0.0	0.028349	0.0	0.0	4 N
0.002694	0.0	0.149292	0.0	0.0	0.000107	0.0	0.0	0.0	0.0	υN
0.004519	0.0	0.030725	0.0	0.0	0.0	0.0	0.0	0.000133	0.0	ON
0.010561	0.0	0.048621	0.0	0.0	0.0	0.0	0.024448	0.0	0.0	72
0.005891	0.000264	0.082256	0.0	0.0	0.0	0.000456	0.001840	0.0	0.0	00 N
0.004036	0.000317	0.043031	0.0	0.0	0.000260	0.0	0.082757	0.0	0.0	9 N
0.039904	0.000978	0.113917	0.0	0,0	0.0	0.0	0.000297	0.0	0.0	0ω
0.005682	0.000338	0.038158	0.0	0.0	0.000457	0.0	0.006750	0.000097	0.0	÷ω
0.001949	0.000764	0.073026	0.0	0.0	0.000191	0.0	0.023204	0.000140	0.0	Nω
0.002290	0.000104	0.059623	0.0	0.0	0.0	0.0	0.007414	0.0	0.0	ωω
0.008002	0.0	0.051523	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ω 4
0.024041	0.000672	0.110463	0.0	0.0	0.0	0.0	0.000360	0.000110	0.0	υω
0.000751	0.0	0.142506	0.0	0.0	0.0	0.001007	0.062074	0.0	0.0	ດພ
0.056294	0.0	0.037904	0.0	0.0	0.0	0.002832	0.000250	0.0	0.0	73
0.000838	0.0	0.224986	0.0	0.0	0.0	0.000404	0.001223	0.0	0.000813	ထယ
0.004899	0.0	0.124406	0.000084	0.0	0.000105	0.000304	0.002664	0.0	0.000388	ωw
0.013088	0.0	0.103179	0.0	0.0	0.000462	0.0	0.001031	0.0	0.000231	40
0.011593	0.0	0.063935	0.0	0.000175	0.0	0.001394	0.002193	0.0	0.0	4 4
0.010241	0.0	0.034170	0.0	0.0	0.0	0.000123	0.034343	0.0	0.0	4 M
0.005143	0.0	0.069856	0.0	0.0	0.000260	0.0	0.025736	0.0	0.0	4 ω
0.010213	0.0	0.090210	0.0	0.0	0.000199	0.0	0.001270	0.0	0.0	44

Hydrobiosis clavigera	Hydrochorema crassicaudatum	Hydrometra risbeci	Hydraenidae adults	Hydrobiosidae (early instar)	Hudsonema amabilis	Hexatomini sp.	Helichopsyche sp.	Eriopterini sp.	Empididae sp.	Site
0.0	0.0	0.000406	0.000405	0.0	0.0	0.0	0.088647	0.0	0.0	-
0.0	0.0	0.000085	0.000270	0.0	0.0	0.0	0.0	0.000376	0.0	N
0.0	0.0	0.0	0.000077	0.0	0.0	0.0	0.0	0.000077	0.0	ω
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.020568	0.0	0.0	4
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.006976	0.0	0.0	UT
0.0	0.0	0.0	0.0	0.0	0.000092	0.0	0.002334	0.0	0.000183	o
0.0	0.0	0.0	0.0	0.0	0.000495	0.0	0.003454	0.0	0.0	7
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000151	0.0	0.0	00
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001828	0.0	0.0	φ
0.0	0.0	0.001106	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0-1
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001067	
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.027397	0.0	0.0	N -
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000131	0.0	0.0	ω -
0.0	0.0	0.000574	0.0	0,0	0.0	0.0	0.000423	0.0	0.000245	← 4
0.0	0.0	0.0	0.000721	0.0	0.0	0.0	0.007247	0.000286	0.0	07 - 1
0.0	0.000220	0.000165	0.0	0.001827	0.0	0.0	0.038614	0.000183	0.0	o →
0.0	0.0	0.000272	0.006118	0.000988	0.0	0.0	0.022848	0.001917	0.000340	7 1
0.0	0.0	0.0	0.000741	0.0	0.0	0.0	0.052302	0.0	0.0	∞ →
0.0	0.0	0.000232	0.0	0.0	0.0	0.0	0.000914	0.0	0.0	- Q
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000350	0.0	0.0	ON
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	→ N
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	NN
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.008895	0.0	0.000118	AN
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000107	0.000122	0.0	UN
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000723	0.0	0.0	ON
0.001832323	0.0	0.000580	0.001369	0.0	0.0	0.0	0.008004	0.0	0.0	N
0.0	0.0	0.0	0.000735	0.0	0.0	0.0	0.000967	0.0	0.0	00 N
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.008338	0.001854	0.002026	9N
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.007057	0.000736	0.0	00
0.0	0.0	0.000314	0.0	0.0	0.0	0.0	0.002250	0.000250	0.0	ω
0.0	0.0	0.000140	0.0	0.0	0.0	0.000290	0.001833	0.0	0.0	Nω
0.0	0.0	0.0	0.000608	0.0	0.000309	0.0	0.004860	0.0	0.0	ωω
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ω 4
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000148	0.0	0.0	σω
0.0	0.0	0.0	0.001863	0.001373	0.0	0.000753	0.024858	0.0	0.0	ດພ
0.0	0.0	0.000137	0.0	0.002309	0.0	0.0	0.0	0.001726	0.0	73
0.000122856	0.000358	0.0	0.005467	0.001954	0.0	0.0	0.028964	0.000206	0.000133	ωω
0.0	0.0	0.0	0.000512	0.001526	0.0	0.0	0.000617	0.000541	0.0	မမ
0.0	0.0	0.0	0.000356	0.000818	0.0	0.0	0.015804	0.0	0.0	40
0.0	0.0	0.0	0.000216	0.0	0.0	0.0	0.001117	0.0	0.0	4 ~
0.0	0.0	0.0	0.007645	0.0	0.0	0.0	0.374515	0.0	0.0	A VA
0.0	0.0	0.0	0.002165	0.000218	0.0	0.0	0.208548	0.0	0.0	4 60
0.0	0.000103	0.000271	0.000566	0.001228	0.0	0.0	0.114026	0.0	0.0	44

Limonia nigrescens	Limnophora sp.	Latia sp.	lchthybotus hudsoni	Hygraula nitens	Hydrophilidae	Hydrochorema tenuicaudatum	Hydrobiosis spatulata	Hydrobiosis parsumpripennis	Hydrobiosis frater	Site
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-
0.0	0.000481	0.0	0.0	0.0	0.0	0.0	0.0	0.000293	0.0	N
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ω
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000604	0.0	4
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000148	0.0	0.0	UN
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	Ø
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7
0.0	0.0	0.0	0.0	0.0	0.000151	0.0	0.0	0.000138	0.0	00
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0-1
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000157	0.0	0.0	N -
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000586	0.0	0.0	ω
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000836	0.0	0.0	- 4
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000340	0.0	Un →
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	on →
0.0	0.0	0.0	0.0	0.000422	0.0	0.0	0.0	0.0	0.0	71
0.0	0.0	0.000106	0.0	0.0	0.0	0.0	0.0	0.0	0.0	00 - -
0.0	0.0	0.0	0.0	0.000270	0.0	0.0	0.0	0.0	0.0	<u>د</u> و
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ON
0.000162	0.0	0.0	0.0	0.0	0.0	0.0	0.000325	0.000284	0.0	- N
0.0	0.0	0.0	0.0	0.0	0.000171	0.0	0.000400	0.0	0.0	NN
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4 N
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000149	0.000120	UN
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	σN
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000141	0.0	42
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	00 N
0.000217	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ØN
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	00
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	- w
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.002114	0.0	23
0.0	0.0	0.0	0.0	0.0	0.000302	0.0	0.0	0.0	0.0	ωω
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001070	ω 4
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	σιω
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ია
0.0	0.0	0.0	0.0	0.0	0.0	0.000186	0.0	0.000548	0.0	73
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000819	0.0	0.0	ω ω
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000084	0.0	မမ
0.0	0.000090	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	40
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000342	0.0	4 4
0.0	0.0	0.001129	0.000121	0.0	0.0	0.0	0.0	0.002262	0.0	N A
0.0	0.0	0.050622	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4 ω
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	44

Oeconesus sp.	Nothodixa sp.	Neucorema confusum	Nesameletus sp.	Neozephlebia scita	Neocurupira hudsoni	Neocurupira chiltoni	Molophilus sp.	Megaloptoperla grandis	Megaloptoperla diminuta	Site
0.0	0.0	0.003165	0.001500	0.001072	0.0	0.000096	0.0	0.000096	0.000101	-
0.0	0.0	0.004554	0.009443	0.000135	0.0	0.0	0.000546	0.000241	0.001424	N
0.0	0.0	0.0	0.0	0.0	0.0	0.000075	0.0	0.0	0.0	ω
0.0	0.0	0.000147	0.004939	0.001391	0.0	0.0	0.000701	0.0	0.0	4
0.0	0.0	0.000796	0.003797	0.001293	0.0	0.000287	0.0	0.000148	0.000237	CT .
0.0	0.0	0.001421	0.002652	0.000119	0.0	0.0	0.0	0.0	0.0	თ
0.0	0.0	0.002592	0.001018	0.001305	0.0	0.0	0.0	0.0	0.0	7
0.0	0.0	0.000285	0.0	0.001591	0.0	0.0	0.0	0.0	0.0	00
0.0	0.0	0.012188	0.041742	0.000212	0.0	0.0	0.0	0.000111	0.0	9
0.0	0.0	0.000769	0.001266	0.000760	0.0	0.0	0.000136	0.0	0.0	0 -
0.0	0.0	0.004023	0.051147	0.0	0.0	0.0	0.0	0.0	0.0	
0.0	0.0	0.001067	0.003518	0.0	0.0	0.0	0.0	0.0	0.0	N -
0.0	0.0	0.000801	0.002470	0.0	0.0	0.0	0.0	0.000629	0.0	ω
0.0	0.0	0.000141	0.000768	0.0	0.0	0.000828	0.0	0.0	0.0	4 -
0.0	0.0	0.0	0.006524	0.0	0.0	0.0	0.0	0.0	0.001380	01 -
0.0	0.0	0.000166	0.001331	0.0	0.000166	0.0	0.0	0.0	0.000466	6 -
0.0	0.0	0.000496	0.005680	0.0	0.0	0.0	0.0	0.0	0.000858	1
0.0	0.0	0.000377	0.005016	0.0	0.0	0.001639	0.0	0.000537	0.0	∞ →
0.0	0.0	0.0	0.003311	0.0	0.0	0.0	0.0	0.000406	0.0	é 0
0.0	0.0	0.001008	0.008135	0.0	0.0	0.000547	0.0	0.0	0.0	ON
0.0	0.0	0.001851	0.036033	0.0	0.0	0.0	0.000294	0.0	0.0	- N
0.0	0.0	0.002263	0.006758	0.0	0.0	0.000433	0.0	0.0	0.0	NN
0.0	0.0	0.001052	0.009740	0.0	0.0	0.000485	0.0	0.0	0.000105	4 N
0.0	0.0	0.000509	0.006086	0.0	0.0	0.0	0.0	0.0	0.0	U N
0.0	0.0	0.000107	0.010682	0.0	0.0	0.0	0.0	0.0	0.0	ON
0.0	0.0	0.000933	0.0	0.0	0.0	0.000244	0.0	0.0	0.0	72
0.0	0.0	0.001715	0.000619	0.0	0.0	0.001330	0.0	0.0	0.001072	00 N
0.000997	0.0	0.000179	0.001175	0.0	0.0	0.0	0.0	0.0	0.000378	ØN
0.0	0.0	0.001636	0.006746	0.0	0.0	0.0	0.0	0.000186	0.002928	0ω
0.0	0.000157	0.000203	0.000662	0.000585	0.0	0.0	0.0	0.0	0.0	ω
0.0	0.0	0.002712	0.000810	0.000290	0.0	0.000206	0.0	0.0	0.0	Nω
0.0	0.0	0.000693	0.001865	0.0	0.0	0.0	0.0	0.0	0.0	ωω
0.0	0.0	0.0	0.009452	0.0	0.0	0.000301	0.0	0.0	0.0	ω 4
0.0	0.0	0.000221	0.005968	0.0	0.0	0.000213	0.0	0.0	0.000110	σω
0.0	0.0	0.000124	0.009263	0.0	0.0	0.0	0.0	0.0	0.001176	တယ
0.0	0.0	0.000997	0.0	0.0	0.0	0.0	0.0	0.0	0.000207	73
0.0	0.000167	0.003123	0.0	0.0	0.0	0.0	0.0	0.0	0.000843	ထမ
0.0	0.0	0.000084	0.002884	0.0	0.001004	0.0	0.000231	0.0	0.004441	မမ
0.0	0.0	0.001486	0.005215	0.0	0.0	0.0	0.0	0.0	0.0	40
0.0	0.0	0.000300	0.010237	0.0	0.0	0.0	0.0	0.0	0.0	4 4
0.0	0.0	0.003168	0.016009	0,0	0.000123	0.0	0.0	0.0	0.0	N A
0.0	0.000212	0.0	0.008078	0.0	0.0	0.0	0.0	0.0	0.0	ω 4
0.0	0.0	0.000106	0.001536	0.0	0.000104	0.0	0.0	0.0	0.0	44

Platyhelminthe	Paralimnophila skusei	Oxythyra albiceps	Ostracoda	Ortopsyche thomasi	Onigaster wakefieldii	Olinga feredayi	Olilrgochaeta (small)	Olilrgochaeta (medium)	Olilrgochaeta (large)	Site
0.002201	0.000963	0.0	0.0	0.006916	0.0	0.011399	0.000917	0.0	0.000758	-
0.0	0.000226	0.0	0.0	0.002562	0.0	0.004368	0.000085	0.0	0.0	N
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ω
0.0	0.0	0.0	0.0	0.004043	0.0	0.0	0.0	0.0	0.0	4
0.0	0.001708	0.0	0.0	0.006037	0.0	0.001035	0.0	0.0	0.0	UT .
0.0	0.000756	0.0	0.0	0.002782	0.0	0.004130	0.000183	0.0	0.0	07
0.0	0.0	0.0	0.0	0.004037	0.0	0.002450	0.000205	0.0	0.0	7
0.0	0.0	0.0	0.0	0.0	0.0	0.000242	0.0	0.0	0.0	00
0.000233	0.0	0.001934	0.0	0.033512	0.0	0.016923	0.000636	0.0	0.0	9
0.0	0.0	0.0	0.0	0.022946	0.0	0.0	0.000151	0.0	0.0	0-1
0.0	0.001387	0.000261	0.0	0.015452	0.0	0.000989	0.000261	0.0	0.0	
0.000853	0.000212	0.0	0.0	0.020235	0.0	0.002875	0.0	0.0	0.0	N-
0.0	0.0	0.000131	0.0	0.006944	0.0	0.000392	0.0	0.0	0.0	ω
0.0	0.0	0.0	0.0	0.063664	0.0	0.0	0.000225	0.0	0.0	- 4
0.000116	0.0	0.0	0.0	0.002739	0.0	0.005640	0.0	0.0	0.0	01 ->
0.004089	0.0	0.0	0.0	0.0	0.0	0.012618	0.000466	0.0	0.0	on →
0.001053	0.0	0.0	0.0	0.033296	0.0	0.000268	0.000367	0.0	0.000257	~ 4
0.0	0.0	0.0	0.0	0.002468	0.0	0.000962	0.0	0.0	0.0	∞ →
0.0	0.0	0.0	0.0	0.008764	0.0	0.0	0.0	0.0	0.0	<u>د</u> ص
0.0	0.0	0.0	0.0	0.016592	0.0	0.0	0.0	0.0	0.0	ON
0.0	0.000487	0.0	0.0	0.001871	0.0	0.0	0.0	0.0	0.0	-N
0.0	0.0	0.0	0.0	0.012604	0.0	0.0	0.000213	0.0	0.0	NN
0.000160	0.0	0.0	0.0	0.004818	0.0	0.0	0.0	0.0	0.0	A A
0.0	0.0	0.000149	0.0	0.000400	0.0	0.0	0.0	0.0	0.0	UN
0.0	0.0	0.0	0.0	0.009357	0.0	0.0	0.0	0.0	0.0	σN
0.0	0.0	0.0	0.0	0.003119	0.0	0.011970	0.0	0.0	0.0	NN
0.0	0.0	0.0	0.0	0.000974	0.0	0.002207	0.0	0.0	0.0	00 N
0.001374	0.0	0.0	0.0	0.056677	0.0	0.0	0.003590	0.0	0.000434	ØN
0.000423	0.0	0.0	0.0	0.031811	0.0	0.000099	0.0	0.0	0.0	00
0.001016	0.0	0.0	0.0	0.019715	0.0	0.000345	0.000453	0.0	0.0	μ
0.000351	0.0	0.0	0.0	0.018853	0.0	0.002655	0.0	0.0	0.0	Nω
0.000933	0.0	0.0	0.0	0.002623	0.0	0.022350	0.000592	0.0	0.0	ωω
0.0	0.0	0.0	0.0	0.000082	0.000506	0.0	0.0	0.0	0.0	ω 4
0.0	0.0	0.0	0.0	0.007396	0.000583	0.0	0.0	0.0	0.0	σω
0.000137	0.0	0.0	0.000106	0.055540	0.0	0.007479	0.0	0.0	0.0	ດພ
0.0	0.0	0.0	0.0	0.002015	0.0	0.001984	0.0	0.0	0.0	7 W
0.000358	0.0	0.0	0.0	0.000506	0.0	0.050528	0.0	0.000206	0.0	ω ω
0.003709	0.0	0.0	0.0	0.092483	0.0	0.001784	0.0	0.000757	0.0	ωω
0.002463	0.0	0.0	0.0	0.000159	0.0	0.018656	0.0	0.0	0.0	40
0.0	0.0	0.0	0.0	0.0	0.0	0.006345	0.0	0.0	0.0	4 -
0.000376	0.0	0.0	0.0	0.0	0.0	0.026209	0.0	0.0	0.0	A VA
0.000661	0.0	0.0	0.0	0.0	0.0	0.009031	0.000411	0.0	0.0	40
0.0	0.0	0.0	0.0	0.000106	0.0	0.015043	0.0	0.0	0.0	44

Stenoperla prasina	Pycnocentrodes sp.	Pycnocentria evecta	Pycnocentrella eruensis	Ptylodactylidae	Psilochorema nemorale	Psilochorema bidens	Potamamopyrgus sp.	Polyplectropus sp.	Podaena sp.	Site
0.000307	0.0	0.108168	0.0	0.000967	0.000704	0.0	0.003861	0.001329	0.0	-
0.000208	0.001275	0.006519	0.0	0.000208	0.0	0.0	0.0	0.000331	0.0	N
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ω
0.0	0.0	0.003143	0.0	0.000101	0.0	0.0	0.000435	0.000158	0.0	4
0.000252	0.0	0.009496	0.0	0.0	0.0	0.0	0.0	0.0	0.0	Ch
0.000600	0.0	0.021274	0.0	0.000090	0.0	0.0	0.000183	0.0	0.0	Ø
0.001215	0.0	0.004272	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7
0.000295	0.0	0.000634	0.0	0.000143	0.0	0.0	0.000141	0.0	0.0	8
0.000787	0.0	0.031350	0.0	0.000287	0.0	0.0	0.000262	0.0	0.0	9
0.000982	0.0	0.0	0.0	0.000416	0.0	0.0	0.0	0.0	0.0	0 -1
0.000977	0.0	0.011940	0.0	0.0	0.0	0.0	0.0	0.000104	0.0	
0.001202	0.0	0.013722	0.0	0.000212	0.0	0.0	0.000563	0.0	0.0	N -
0.000131	0.0	0.001677	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ω -
0.000104	0.0	0.000141	0.0	0.0	0.0	0.0	0.0	0.0	0.0	- 4
0.001364	0.000196	0.0	0.000250	0.0	0.0	0.0	0.000517	0.0	0.0	Un →
0.001135	0.000193	0.0	0.0	0.0	0.0	0.0	0.000469	0.0	0.0	6 1
0.001697	0.000422	0.0	0.004142	0.0	0.000119	0.0	0.000414	0.0	0.000119	1
0.000109	0.004124	0.0	0.015310	0.0	0.000654	0.0	0.0	0.0	0.0	∞ →
0.0	0.0	0.0	0.001008	0.0	0.0	0.0	0.0	0.0	0.0	9 -
0.000108	0.0	0.001032	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ON
0.0	0.0	0.003267	0.0	0.0	0.0	0.0	0.0	0.0	0.0	- N
0.000573	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	NN
0.000518	0.0	0.000119	0.0	0.000118	0.0	0.0	0.0	0.0	0.0	0 4 N
0.0	0.0	0.0	0.010127	0.0	0.000509	0.0	0.0	0.0	0.0	UN
0.000430	0.0	0.0	0.000133	0.000214	0.000557	0.0	0.0	0.0	0.0	σN
0.000311	0.0	0.0	0.024447	0.0	0.0	0.000368	0.000200	0.0	0.0	NN
0.000241	0.0	0.0	0.003851	0.0	0.0	0.000815	0.0	0.0	0.0	00 N
0.001522	0.0	0.038877	0.010887	0.007981	0.000790	0.0	0.0	0.0	0.0	9 2
0.001056	0.0	0.023532	0.0	0.006965	0.0	0.000540	0.0	0.0	0.0	03
0.000781	0.0	0.0	0.000921	0.0	0.0	0.000381	0.000093	0.0	0.0	<i>→</i> ω
0.000582	0.0	0.0	0.024905	0.0	0.0	0.000713	0.000238	0.0	0.0	Nω
0.001259	0.0	0.0	0.008496	0.0	0.002216	0.0	0.0	0.0	0.0	ယယ
0.000331	0.0	0.0	0.003923	0.0	0.000853	0.0	0.0	0.0	0.0	ω 4
0.000213	0.0	0.0	0.038965	0.0	0.000859	0.0	0.0	0.0	0.0	σω
0.000778	0.0	0.0	0.001121	0.000434	0.001796	0.0	0.000771	0.0	0.0	σω
0.0	0.0	0.0	0.0	0.0	0.001289	0.000275	0.0	0.0	0.000186	73
0.000614	0.000123	0.000206	0.0	0.0	0.001184	0.000067	0.0	0.0	0.000067	ထမ
0.000693	0.0	0.0	0.001561	0.0	0.001004	0.0	0.0	0.0	0.0	မမ
0.0	0.003169	0.0	0.0	0.0	0.001377	0.0	0.001360	0.0	0.0	40
0.000460	0.028611	0.0	0.0	0.0	0.0	0.000175	0.0	0.0	0.0	4 -
0.000683	0.046250	0.0	0.000635	0.0	0.000242	0.0	0.001106	0.0	0.000274	A M
0.000199	0.003795	0.0	0.0	0.0	0.0	0.0	0.001992	0.0	0.000099	4 60
0.000826	0.001769	0.0	0.0	0.0	0.0	0.000103	0.000207	0.0	0.0	44

Zephlebia dentata	Zephlebia borealis	Zelolessia cheira	Zelandoperla fenestrata	Zelandobius furcillatus	Zelandobius confusus	Trogiidae	Tanypodinae	Tabanidae	Plecoptera (early instar)	Site
0.0	0.0	0.0	0.001984	0.0	0.000839	0.0	0.0	0.000109	0.0	-
0.0	0.0	0.0	0.095293	0.0	0.004384	0.0	0.0	0.0	0.0	N
0.0	0.0	0.0	0.001952	0.0	0.0	0.0	0.0	0.0	0.0	ω
0.003240	0.0	0.0	0.003759	0.0	0.0	0.000527	0.0	0.0	0.0	4
0.0	0.0	0.0	0.014871	0.0	0.002877	0.0	0.0	0.0	0.0	Ch
0.0	0.0	0.0	0.002445	0.0	0.001190	0.0	0.0	0.0	0.0	თ
0.001462	0.0	0.0	0.000666	0.0	0.0	0.0	0.0	0.0	0.0	7
0.000789	0.0	0.0	0.0	0.0	0.000482	0.0	0.0	0.0	0.0	œ
0.000212	0.0	0.0	0.014554	0.0	0.0	0.0	0.0	0.0	0.0	ω
0.001320	0.0	0.0	0.005094	0.0	0.012575	0.000583	0.0	0.0	0.0	0-
0.0	0.0	0.0	0.015270	0.0	0.000498	0.001358	0.000355	0.0	0.0	
0.000250	0.0	0.0	0.012905	0.0	0.003078	0.000212	0.0	0.0	0.0	N -
0.0	0.0	0.0	0.043251	0.0	0.0	0.0	0.000164	0.0	0.0	ω→
0.0	0.0	0.0	0.006100	0.0	0.011043	0.0	0.000413	0.0	0.0	~ 4
0.000196	0.0	0.0	0.016690	0.0	0.0	0.0	0.0	0.0	0.010754	Un →
0.0	0.001106	0.0	0.015748	0.001980	0.0	0.0	0.0	0.0	0.000466	o →
0.000894	0.0	0.0	0.003198	0.017160	0.0	0.0	0.0	0.0	0.0	1
0.0	0.0	0.0	0.002881	0.0	0.000449	0.0	0.0	0.0	0.0	∞ →
0.000210	0.0	0.0	0.000083	0.0	0.000170	0.0	0.0	0.0	0.000412	<u>د م</u>
0.000210	0.0	0.0	0.001919	0.0	0.005096	0.0	0.0	0.0	0.0	ON
0.0	0.0	0.0	0.011511	0.0	0.000325	0.0	0.000265	0.0	0.0	-N
0.0	0.0	0.0	0.002998	0.0	0.011762	0.0	0.0	0.0	0.0	NN
0.0	0.0	0.0	0.002300	0.0	0.008508	0.0	0.0	0.0	0.0	4 N
0.0	0.0	0.0	0.001954	0.0	0.0	0.0	0.0	0.0	0.0	UN
0.004860	0.0	0.0	0.005338	0.0	0.025656	0.0	0.0	0.0	0.0	ON
0.0	0.000100	0.0	0.009954	0.0	0.000158	0.0	0.0	0.0	0.0	42
0.0	0.0	0.0	0.039452	0.0	0.002570	0.0	0.0	0.0	0.0	00 N
0.000892	0.0	0.0	0.0	0.0	0.004423	0.0	0.0	0.0	0.0	9 N
0.0	0.0	0.0	0.020557	0.0	0.010401	0.0	0.0	0.0	0.0	00
0.001136	0.0	0.0	0.0	0.0	0.004317	0.0	0.0	0.0	0.0	w
0.000346	0.0	0.0	0.006253	0.0	0.000424	0.0	0.0	0.0	0.0	Nω
0.001114	0.0	0.0	0.018862	0.0	0.001023	0.0	0.0	0.0	0.0	ωω
0.0	0.0	0.0	0.017234	0.0	0.006416	0.0	0.0	0.0	0.0	ω 4
0.0	0.0	0.0	0.038081	0.0	0.002417	0.0	0.0	0.0	0.0	σιω
0.002514	0.0	0.000430	0.021331	0.007206	0.0	0.0	0.0	0.0	0.000305	တယ
0.0	0.0	0.0	0.107429	0.000186	0.0	0.0	0.0	0.0	0.0	73
0.0	0.0	0.0	0.102744	0.000866	0.0	0.0	0.0	0.0	0.0	ω ω
0.0	0.0	0.0	0.012514	0.003499	0.0	0.0	0.0	0.0	0.002662	ωω
0.0	0.000503	0.0	0.026539	0.000183	0.0	0.0	0.0	0.000108	0.000198	40
0.000230	0.0	0.0	0.046351	0.001540	0.001248	0.0	0.0	0.0	0.0	4 ~
0.003315	0.0	0.0	0.005759	0.0	0.0	0.0	0.0	0.0	0.0	N4
0.003566	0.0	0.000819	0.001797	0.0	0.0	0.0	0.0	0.0	0.0	4ω
0.0	0.0	0.0	0.021823	0.001183	0.0	0.0	0.0	0.0	0.0	44

Site	1	2	3	4	5	6	7	8	9	1 0	1	1 2	13	1 4	1 5	1 6	17	1 8	1 9	20	2	22	2 4	25	2 6	27	2 8	2 9	3 0	3	32	33	3 4	3 5	36	3 7	3 8	39	4 0	4	42	43	4 4
Zephlebia spectabilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001998	0.0	0.0
Zephlebia versicolor	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001680	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000154	0.0

Austroperla cyrene	Archicauliodes diversus	Arachnocolus phillipsi	Aphrophila neozelandica	Aoteapsyche colonica	Anisops sp.	Amphipoda	Ameletopsis perscitus	Acari sp.	Acanthophlebia cruentata	Site
0.0	0.000105	0.0	0.001209	0.0	0.0	0.0	0.0	0.0	0.0	-
0.0	0.0	0.0	0.000072	0.000086	0.0	0.0	0.0	0.0	0.0	N
0.0	0.000165	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ω
0.0	0.000368	0.0	0.001385	0.000411	0.0	0.0	0.0	0.0	0.0	4
0.0	7.72E-05	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	CT
0.0	0.000464	0.0	0.0	0.000681	0.0	0.0	0.0	0.0	0.000614	Ø
0.0	0.000731	0.0	0.0	0.001003	0.0	0.0	0.0	0.0	0.000408	7
0.0	0.000146	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000131	00
0.0	0.000254	0.0	0.0	0.007260	0.0	0.0	0.0	0.0	0.0	ø
0.0	0.0	0.0	0.0	0.001823	0.0	0.0	0.000053	0.0	0.000053	0-
0.0	0.000060	0.0	0.000112	0.0	0.0	0.0	0.0	0.0	0.0	
0.000691	0.000343	0.0	0.0	0.001399	0.0	0.0	0.0	0.0	0.0	N -
0.0	0.0	0.0	0.0	0.00011	0.0	0.0	0.0	0.0	0.0	ω
0.0	0.0	0.0	0.0	0.018211	0.0	0.0	0.0	0.0	0.0	- 4
0.0	0.0	0.0	0.000171	0.000347	0.0	0.0	0.0	0.0	0.0	U1
0.0	0.000103	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000538	o →
0.00436	0.0	0.0	0.0	0.018441	0.0	0.0	0.0	0.0	0.0	71
0.0	0.000104	0.000472	0.000501	0.001696	0.0	0.0	0.0	0.0	0.0	00 -
0.0	0.0	0.0	0.0	0.003367	0.0	0.0	0.0	0.0	0.0	· 0
0.0	0.0	0.0	0.0	0.000913	0.0	0.0	0.0	0.0	0.000887	ON
0.0	0.000369	0.0	0.0	0.000153	0.0	0.0	0.0	0.0	0.0	- N
0.0	0.0	0.0	0.0	0.001865	0.0	0.0	0.0	0.0	0.0	NN
0.000652	0.0	0.0	0.0	0.002895	0.0	0.0	0.0	0.0	0.0	4 N
0.0	0.0	0.0	0.000959	0.0	0.0	0.0	0.0	0.0	0.0	(IN N
0.0	0.0	0.0	0.0	0.006344	0.0	0.0	0.0	0.0	0.000216	σN
0.0	0.000312	0.0	0.000156	0.006705	0.0	0.0	0.0	0.0	0.000156	NN
0.0	0.0	0.0	0.005892	0.005755	0.0	0.0	0.0	0.0	0.0	00 N
0.0	0.0	0.0	0.000979	0.001639	0.0	0.002795	0.0	0.0	0.0	ØN
0.0	0.000616	0.0	0.001575	0.0	0.0	0.0	0.0	0.0	0.0	00
0.0	0.000134	0.0	0.0	0.002165	0.0	0.0	0.0	0.0	0.0	<u>→</u> ω
0.000274	0.0	0.0	0.0	0.005577	0.0	0.0	0.0	0.0	0.000151	Nω
0.000348	0.000484	0.0	8.69E-05	0.00269	0.0	0.0	0.0	0.0	0.0	ယယ
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4ω
0.0	0.0	0.0	0.006248	0.001953	0.0	0.0	0.0	0.0	0.0	σω
0.0	0.0	0.0	0.004339	0.000244	0.0	0.0	0.0	0.0	0.0	ດພ
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	73
0.000228	0.000437	0.0	0.000668	0.000228	0.0	0.0	0.0	0.0	0.0	ထယ
0.0	0.000700	0.0	0.002499	0.006785	0.0	0.0	0.0	0.0	0.0	ဖမ
0.0	0.000139	0.0	0.000121	0.01784	0.0	0.0	0.0	0.0	0.000662	40
0.0	0.0	0.0	0.0	0.0	0.000429	0.0	0.0	0.000072	0.0	4
0.0	0.000831	0.0	0.004657	0.008375	0.0	0.0	0.0	0.0	0.0	N A
0.0	0.0	0.0	0.008495	0.0	0.0	0.0	0.0	0.0	0.0	ω 4
0.0	0.0	0.0	0.000662	0.001962	0.0	0.0	0.0	0.0	0.0	44

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Empididae sp.	Elmidae larvae	Deleatidium sp.	Coloburiscus humeralis	Chironomidae Polypedellum	Chironomidae Pirara sp.	Chironomidae Maoridiamesa	Chironomidae Eukkieferulus	Chironomidae Cricotopus sp.	Beraeoptera roria	Austrosimulium tillyardianum	Site
0.0	0.000105	0.030828	0.000113	0.000584	0.0	0.0	0.001029	0.000376	0.0	0.001029	
0.0	0.000559	0.014949	0.0	0.005577	0.002125	0.0	0.034774	0.0	0.0	0.003578	N
0.0	0.000819	0.007186	0.0	0.001137	0.0	0.0	0.002804	0.0	0.0	0.002307	ω
0.0	0.000403	0.034671	0.001008	0.003798	0.000568	0.0	0.002456	0.001142	0.0	0.0	4
0.0	0.0	0.076863	0.000386	0.0	0.0	0.0	0.0	0.0	0.000655	0.0	Ch
0.0	0.0	0.013056	0.001059	0.0	0.0	0.0	0.0	0.0	0.000574	0.0	თ
0.0	0.000425	0.016133	0.001668	0.0	0.0	0.0	0.0	0.0	0.000753	0.0	7
0.0	7.26E-05	0.019058	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8
0.0	0.000585	0.035882	0.001022	0.001666	0.001040	0.0	0.001928	0.0	0.054477	0.000339	9
0.0	0.000459	0.008054	0.0	0.0	0.0	0.0	0.0	0.002104	0.0	0.0	0 ->
0.0	0.0	0.005739	0.0	0.0	0.0	0.0	0.000460	0.0	0.0	0.0	
0.0	0.048805	0.048805	0.000383	0.013215	0.008971	0.0	0.002244	0.0	0.382033	0.0	N -1
0.0	0.0	0.021096	0.0	0.001036	0.003017	0.0	0.0	0.0	0.021977	0.0	ω -
0.0	0.000185	0.011112	0.000805	0.0	0.0	0.0	0.0	0.005217	0.0	0.0	4 4
0.0	0.000177	0.044819	0.0	0.001194	0.0	0.0	0.000082	0.0	0.0	0.0	v →
0.0	0.0	0.026310	0.0	0.000382	0.0	0.0	0.000384	0.0	0.0	0.0	o →
0.0	0.000947	0.020758	0.001722	0.0	0.0	0.0	0.008745	0.0	0.001498	0.0	1
0.0	0.001588	0.015560	0.000963	0.0	0.0	0.0	0.0	0.0	0.013024	0.000188	∞ →
0.0	0.000463	0.029677	0.000105	0.0	0.0	0.0	0.0	0.0	0.049671	0.001526	9 -
0.0	0.0	0.006988	0.000609	0.000191	0.0	0.0	0.0	0.0	0.0	0.0	ON
0.0	0.001845	0.029338	0.0	0.000111	0.0	0.0	0.0	0.0	0.0	0.0	- N
0.0	7.82E-05	0.040744	0.000886	0.0	0.0	0.0	0.001174	0.0	0.000469	0.0	NN
0.0	0.000171	0.011396	0.000130	0.0	0.0	0.0	0.000326	0.000856	0.0	0.0	4 N
0.0	0.001771	0.075995	0.0	0.000834	0.0	0.001356	0.012311	0.012626	0.001135	0.000363	σN
0.0	0.001748	0.019067	0.001667	0.000105	0.0	0.0	0.001543	0.0	0.0	0.0	ON
0.0	0.004587	0.028425	0.001945	0.000078	0.0	0.0	0.0	0.000312	0.005301	0.0	72
0.0	0.000621	0.048914	0.000262	0.0	0.0	0.0	0.000679	0.0	0.059289	0.0	68 N
0.0	0.0	0.019431	0.003893	0.005096	0.0	0.0	0.002807	0.004525	0.0	0.0	9 N
0.0	0.002303	0.089107	0.0	0.0	0.0	0.0	0.001114	0.0	0.035106	0.000537	0 3
0.0	0.0	0.036034	0.001125	0.001458	0.0	0.0	0.0	0.0	0.022775	0.0	$\rightarrow \omega$
0.0	0.000420	0.030499	0.000274	0.001816	0.0	0.001362	0.004087	0.0	0.021889	0.000835	Nω
0.0	0.0	0.012722	0.002335	0.000151	0.0	0.0	0.0	0.000331	0.000425	0.0	ωω
0.0	0.001682	0.015692	0.0	0.000279	0.0	0.0	0.000735	0.0	0.0	0.0	4ω
0.0	0.002684	0.029346	0.0	8.73E-05	0.000310	0.0	0.001997	0.0	0.021318	0.0	σω
0.0	0.000182	0.039310	0.0	0.025584	0.012070	0.004025	0.092844	0.000809	0.040871	0.001080	თω
0.0	0.0	0.000800	0.0	0.000140	0.0	0.000143	0.000391	0.0	0.000739	0.0	7
0.0	0.0	0.025825	0.000228	0.009437	0.0	0.006787	0.020367	0.0	0.055157	0.004328	ထယ
0.0	0.000265	0.055026	0.003187	0.002768	0.0	0.0	0.008157	0.000812	0.043977	0.0	မမ
0.0	0.002990	0.031625	0.005793	0.003506	0.0	0.0	0.001894	0.0	0.211477	0.000060	40
0.0	0.003046	0.015014	0.0	0.0	0.0	0.0	0.000429	0.0	0.0	0.0	4 4
0.0	0.000693	0.033549	0.002573	0.128102	0.000571	0.002698	0.069305	0.031969	0.080455	0.002196	N A
0.000094	0.0	0.002268	0.0	0.050432	0.062631	0.0	0.036933	0.003561	0.001250	0.004288	4 ω
0.0	0.000280	0.022927	0.000330	0.000878	0.0	0.0	0.001639	0.0	0.050509	0.004779	44

Neocurupira hudsoni	Megaloptoperla grandis	Megaloptera dimunita	Liodessus plicatus	Limonia nigrescens	Hydrobiosis parsumbripenn	Hydrobiosidae (early instar)	Hydraenidae adults	Hudsonema amabilis	Helichopsyche sp.	Eriopterini sp.	Site
0.0	0.0	0.0	0.0	0.0	0.0	0.000320	0.000207	0.0	0.0	0.0	
0.0	0.0	0.0	0.0	0.0	0.001912	0.0	0.0	0.0	0.0	0.0	N
0.0	0.0	0.0	0.0	0.0	0.000112	0.0	0.0	0.0	0.0	0.0	ω
0.0	0.0	0.0	0.0	0.0	0.000174	0.0	0.000513	0.0	0.011746	0.0	4
0.0	0.0	0.0	0.0	0.0	0.0	0.000758	0.000216	0.0	0.0	0.0	Ch
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000102	0.0	0.000553	0.0	σ
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000356	0.0	0.005503	0.0	7
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.008781	0.0	8
0.0	0.0	0.0	0.0	0.000693	0.001537	0.0	0.000472	0.0	0.010895	0.0	Q
0.0	0.0	0.0	0.0	0.0	0.0	0.000186	0.0	0.0	0.0	0.0	0-1
0.0	0.0	0.0	0.0	0.0	0.0	0.000060	0.0	0.0	0.0	0.0	
0.0	0.0	0.0	0.0	0.004014	0.001300	0.003107	0.001917	0.0	0.007907	0.0	N-
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000077	0.0	0.000200	0.0	ω
0.0	0.0	0.0	0.0	0.0	0.0	0.001325	0.0	0.0	0.000549	0.000970	- 4
0.0	0.0	0.0	0.0	0.0	0.0	0.002160	0.001026	0.0	0.0	0.0	()1
0.0	0.0	0.0	0.0	0.0	0.001944	0.000868	0.002459	0.0	0.000492	0.0	o →
0.0	0.0	0.000670	0.0	0.0	0.0	0.003137	0.001979	0.0	0.002115	0.000181	~ 4
0.0	0.000104	0.0	0.0	0.0	0.000062	0.000597	0.000466	0.0	0.046708	0.0	∞ →
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000066	0.0	0.038231	0.000386	- Q
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000384	0.0	0.001972	0.0	ON
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000998	- N
0.000486	0.0	0.0	0.0	0.0	0.000688	0.000071	0.0	0.0	7.82E-05	0.0	NN
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.016700	0.0	N4
0.0	0.0	0.0	0.0	0.0	0.000264	0.0	0.0	0.0	0.000131	0.0	UN
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001526	0.0	σN
0.000119	0.0	0.0	0.000094	0.0	0.0	0.0	0.001934	0.0	0.007524	0.0	NN
0.000240	0.0	0.0	0.0	0.0	0.000064	0.0	0.000102	0.0	0.000086	0.0	00 N
0.0	0.0	0.0	0.0	0.0	0.0	0.000341	0.000522	0.001432	0.005707	0.0	ØN
0.0	0.0	0.0	0.0	0.0	0.0	0.001710	0.000469	0.0	0.0	0.000078	00
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000066	0.0	0.001199	0.0	ω
0.000274	0.0	0.0	0.0	0.0	0.0	0.000910	0.0	0.0	0.021928	0.0	Nω
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000636	0.0	ωω
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000153	0.0	0.0	0.000118	4 6
0.000238	0.0	0.0	0.0	0.0	0.001243	0.000238	0.000277	0.0	0.0	0.0	υυ
0.0	0.0	0.0	0.0	0.0	0.000713	0.002309	0.003987	0.0	0.013345	0.0	ດພ
0.0	0.0	0.0	0.0	0.0	0.0	0.000362	0.0	0.0	0.0	0.0	73
0.0	0.0	0.0	0.0	0.0	0.002834	0.002825	0.003061	0.0	0.000725	0.0	ထမ
0.0	0.0	0.0	0.0	0.0	0.001006	0.000707	0.000909	0.0	0.000497	0.0	မမ
0.0	0.0	0.0	0.0	0.0	0.001797	0.000268	0.000520	0.0	0.001042	0.000006	40
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000429	0.0	0.0	0.0	4 -
0.0	0.0	0.0	0.0	0.0	0.003064	0.002716	0.0	0.001758	0.000364	0.0	A M
0.0	0.0	0.0	0.0	0.0	0.000226	0.0	0.0	0.0	0.005401	0.0	4ω
0.0	0.0	0.0	0.0	0.0	0.000382	0.000330	0.0	0.0	0.003180	0.0	44

Pycnocentria funeria	Ptilodactylidae	Psilochorema nemoralis	Psilochorema bidens	Potamopyrgus sp.	Platyhelminthe	Oxythira albiceps	Olinga feredayi	Nothodixa sp.	Nesameletus sp.	Neozephlebia scita	Site
6	0.0	0.0	0.0	0.0	0.0	0.0	0.000204	0.0	0.0	0.0	-
0	0.0	0.0	0.0	0.0	0.0	0.0	0.002905	0.0	0.001496	0.0	N
0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ω
0	0.0	0.0	0.0	0.00098	0.0	0.0	0.002925	0.0	0.003138	0.0	4
0	0.0	0.0	0.0	0.0	0.000122	0.0	0.0	0.0	0.008341	0.0	Ch.
8.01E-05	0.0	0.0	0.0	0.0	0.000318	0.0	0.000262	0.0	0.000748	0.0	თ
0	0.0	0.0	0.0	0.0	0.000791	0.0	0.001265	0.0	0.0	0.000214	7
0	0.0	0.0	0.0	0.0	0.000797	0.0	0.000306	0.0	0.0	0.000131	œ
0	0.0	0.0	0.0	0.0	0.000800	0.0	0.003025	0.0	0.001488	0.0	9
0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000523	0.000945	0 -
0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001798	0.0	
0	0.0	0.0	0.0	0.0	0.001074	0.0	0.023489	0.0	0.002100	0.0	N -
0	0.0	0.0	0.0	0.000077	0.0	0.0	0.009615	0.0	0.001116	0.0	ω →
0	0.0	0.0	0.0	0.0	0.000306	0.0	0.0	0.0	0.0	0.003588	4 4
0	0.0	0.0	0.0	0.0	0.0	0.0	0.001297	0.0	0.003595	0.0	01 - A
0.000898	0.0	0.0	0.0	0.0	0.0	0.0	0.008579	0.0	0.000421	0.0	o →
0	0.0	0.0	0.0	0.000192	0.0	0.0	0.026256	0.0	0.004444	0.001096	1
0	0.0	0.0	0.0	0.0	0.0	0.0	0.001300	0.0	0.003178	0.0	00 -
0	0.0	0.00066	0.0	0.000386	0.0	0.0	0.000207	0.000746	0.000257	0.0	<u>د</u> و
0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000511	0.0	ON
0	0.0	0.0	0.0	0.0	0.000111	0.0	0.001142	0.0	0.009200	0.0	→ N
0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.004731	0.000071	NN
0	0.0	0.0	0.0	0.0	0.002994	0.0	0.001034	0.0	0.000225	0.000065	4 N
0	0.0	0.0	0.0	0.0	0.0	0.0	0.002990	0.0	0.000344	0.0	σN
0	0.000148	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000928	0.002714	σN
0	0.0	0.0	0.000095	0.002177	0.0	0.0	0.008873	0.0	0.000440	0.0	27
0	0.0	0.0	0.0	0.0	0.0	0.0	0.000783	0.0	0.000261	0.0	ØN
0.004109	0.000346	0.0	0.0	0.0	0.000427	0.0	0.002025	0.0	0.001452	0.003244	9 2
0	0.0	0.0	0.0	0.0	0.000078	0.0	0.012066	0.0	0.002576	0.0	00
0	0.0	0.0	0.0	0.0	0.0	0.0	0.001141	0.0	0.000465	0.0	÷ω
0	0.0	0.0	0.0	0.0	0.0	0.000151	0.002422	0.0	0.003474	0.0	NW
0	0.0	0.0	0.0	0.0	0.000922	0.0	0.000532	0.0	0.000075	0.0	ωω
0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.015864	0.0	4 ω
0	0.0	0.0	0.0	0.0	0.0	0.0	0.002163	0.000087	0.000958	0.0	თ ω
0	0.0	0.0	0.0	0.000074	0.001579	0.0	0.001416	0.0	0.001131	0.0	ດພ
0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3
0	0.0	0.0	0.0	0.0	0.000948	0.0	0.005982	0.0	0.001858	0.0	ω ω
8.84E-05	0.0	0.0	0.0	0.0	0.000613	0.0	0.009218	0.000265	0.001454	0.0	ဖမ
0	0.0	0.0	0.0	0.000164	0.0	0.0	0.011697	0.000078	0.002778	0.000164	40
0	0.0	0.0	0.0	0.000336	0.0	0.0	0.0	0.0	0.0	0.0	4 4
0	0.0	0.0	0.0	0.0	0.000057	0.0	0.012712	0.0	0.005079	0.001729	N A
0	0.0	0.0	0.0	0.0	0.0	0.005333	0.0	0.0	0.004418	0.0	4ω
0	0.0	0.0	0.0	0.0	0.0	0.0	0.004522	0.0	0.001350	0.0	4.4

Zephlebia spectabilis	Zephlebia borealis	Zelandoperla fenestrata	Zelandobius confusus	Stratiomyidae	Stenoperla prasina	Pycnocentrodes sp.	Pycnocentria sylvestris	Site
0.0	0.0	0.009055	0.000105	0.0	0.00099	0.000783	0.0	-
0.0	0.0	0.029604	0.0	0.0	0	0.004456	0.0	N
0.0	0.0	0.003236	0.0	0.0	0.000278	0.0	0.0	ω
0.0	0.0	0.0	0.0	0.0	0.000104	0.0	0.0	4
0.0	0.0	0.007946	0.0	0.0	0	0.002617	0.0	UT
0.0	0.0	0.000928	0.000107	0.0	0	0.000107	0.0	თ
0.0	0.0	0.0	0.005266	0.0	5.79E-05	0.000151	0.0	7
0.0	0.0	0.001439	0.0	0.0	0.000146	0.0	0.0	00
0.0	0.0	0.039328	0.0	0.0	0.000522	0.002946	0.0	ω
0.0	0.0	0.0	0.000874	0.0	0.000542	0.000443	0.0	0-
0.0	0.0	0.002200	0.000060	0.0	0.000131	0.000112	0.0	
0.0	0.0	0.000491	0.0	0.0	9.16E-05	0.000183	0.0	N-
0.0	0.0	0.001879	0.000607	0.0	0	0.002384	0.0	ω <u></u>
0.0	0.0	0.000611	0.004282	0.0	0.001376	0.0	0.0	- 4
0.0	0.0	0.004017	0.0	0.0	0.001546	0.019977	0.0	01 - ¥
0.0	0.0	0.0	0.0	0.0	0	0.006400	0.0	o -
0.0	0.0	0.001932	0.000158	0.000112	0.001507	0.001860	0.0	71
0.0	0.0	0.000501	0.0	0.0	0.000198	0.003589	0.0	∞ <u>→</u>
0.0	0.0	0.004754	0.0	0.000066	0.021087	0.0	0.0	- Q
0.0	0.0	0.0	0.000304	0.0	0	0.0	0.0	ON
0.0	0.0	0.0	0.000531	0.0	0	0.0	0.0	-N
0.0	0.0	0.001982	0.000513	0.0	0	0.0	0.0	NN
0.0	0.0	0.0	0.000970	0.0	0	0.0	0.0	4 N
0.0	0.0	0.002569	0.0	0.0	0	0.000998	0.0	UN
0.0	0.0	0.0	0.003121	0.0	0.000242	0.0	0.0	ON
0.0	0.0	0.006360	0.0	0.0	0	0.004004	0.0	NN
0.0	0.0	0.011693	0.0	0.0	0.000772	0.0	0.0	00 N
0.0	0.0	0.0	0.0	0.0	0.000228	0.0	0.0	ØN
0.0	0.0	0.004459	0.000078	0.0	0.000246	0.0	0.0	00
0.0	0.0	0.004718	0.001950	0.0	0.000763	0.0	0.0	<i>→</i> ω
0.0	0.000148	0.000274	0.0	0.0	0.000269	0.000931	0.0	Nω
0.0	0.0	0.005169	0.000897	0.0	0	0.0	0.0	ωω
0.0	0.0	0.000355	0.000160	0.0	0.000153	0.0	0.0	ω 4
0.0	0.0	0.025970	0.000072	0.0	0	0.0	0.0	σω
0.0	0.0	0.004874	0.0	0.0	0	0.0	0.000259	σω
0.0	0.0	0.000573	0.000131	0.0	0	0.0	0.0	~ W
0.0	0.0	0.004341	0.0	0.0	0.000469	0.0	0.0	ωω
0.0	0.0	0.001681	0.001228	0.0	0.000984	0.0	0.0	ωw
0.0	0.0	0.001736	0.0	0.0	0.000707	0.009956	0.0	40
0.0	0.0	0.000552	0.0	0.0	0	0.0	0.0	4
0.0	0.0	0.001310	0.0	0.0	5.71E-05	0.011370	0.0	N A
0.000978	0.0	0.000651	0.0	0.0	0	0.003124	0.0	4 40
0.0	0.0	0.029991	0.0	0.0	0	0.005732	0.0	4.4

Chironomidae Orthocladiinae	Chironomidae Maoridiamesa sp.	Beraeoptera roria	Austrosimulium tillyardianum	Austropería cyrene	Archicauliodes diversus	Aphrophila neozelandica	Aoteapsyche colonica	Acanthophlebia cruentata	Site
0.004990	0.001955	0.0	0.0	0.0	0.0	0.0	0.000171	0.0	1 (winter)
0.003044	0.0	0.0	0.0	0.0	0.0	0.000093	0.0	0.0	2 (winter)
0.000455	0.003909	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3 (winter)
0.005759	0.001750	0.0	0.0	0.0	0.002488	0.0	0.001943	0.001064	4 (winter)
0.001894	0.000930	0.001433	0.0	0.0	0.0	0.000079	0.001070	0.0	5 (winter)
0.003985	0.002226	0.0	0.0	0.0	0.0	0.0	0.001819	0.000194	10 (winter)
0.007010	0.003811	0.001041	0.0	0.0	0.0	0.0	0.002467	0.0	11 (winter)
0.008289	0.011185	0.011872	0.0	0.000702	0.000974	0.0	0.005203	0.000525	12 (winter)
0.000104	0.000082	0.0	0.0	0.0	0.0	0.0	0.0	0.008168	15 (winter)
0.000505	0.000427	0.000127	0.0	0.000396	0.0	0.0	0.003548	0.0	17 (winter)
0.000561	0.000104	0.002006	0.0	0.0	0.0	0.000179	0.0	0.0	34 (winter)
0.002867	0.004274	0.009955	0.0	0.000366	0.000354	0.002000	0.009917	0.002249	36 (winter)
0.000712	0.001865	0.0	0.000606	0.0	0.0	0.0	0.0	0.0	1 (spring)
0.060202	0.015968	0.0	0.078967	0.0	0.0	0.0	0.0	0.000708	2 (spring)
0.181082	0.008675	0.0	0.012954	0.0	0.0	0.0	0.0	0.0	3 (spring)
0.006604	0.001768	0.0	0.0	0.0	0.004063	0.0	0.001959	0.001465	4 (spring)
0.005624	0.005029	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5 (spring)
0.008007	0.005343	0.0	0.000232	0.0	0.0	0.0	0.001933	0.000120	10 (spring)
0.037247	0.001922	0.004275	0.006679	0.0	0.001196	0.0	0.0	0.000185	11 (spring)
0.016852	0.012195	0.000474	0.001099	0.0	0.0	0.0	0.0	0.0	12 (spring)
0.015959	0.001131	0.0	0.000516	0.0	0.0	0.0	0.0	0.000121	15 (spring)
0.013665	0.000825	0.000306	0.000727	0.0	0.0	0.0	0.002464	0.0	17 (spring)
0.000625	0.000178	0.000618	0.0	0.0	0.0	0.0	0.0	0.0	34 (spring)
0.008227	0.000302	0.002426	0.016139	0.0	0.000443	0.0	0.000270	0.000198	36 (spring)

APPENDIX 3.1: Mean macroinvertebrate densities (invertebrates $/ m^2$) from 15 single-stone samples collected in the winter and spring of 2000 at 12 sites in the Ruahine Ranges.

	lchthybotus hudsoni	Hydrobiosis parumbripennis	Hydrobiosidae (early instar)	Hydraenidae adults	Helichopsyche sp.	Eriopterini sp.	Elmidae Larvae	Emlidae adults	Deleatidium sp.	Coloburiscus humeralis	Site
	0.0	0.0	0.001452	0.001140	0.0	0.000059	0.0	0.0	0.075579	0.000077	1 (winter)
	0.0	0.0	0.002320	0.000217	0.0	0.0	0.0	0.000124	0.106900	0.0	2 (winter)
	0.0	0.0	0.0	0.000079	0.0	0.0	0.0	0.0	0.005326	0.0	3 (winter)
	0.0	0.0	0.001554	0.000923	0.010858	0.000079	0.000925	0.0	0.098425	0.003285	4 (winter)
	0.0	0.000537	0.000633	0.000641	0.0	0.0	0.000146	0.0	0.122367	0.001032	5 (winter)
	0.0	0.000170	0.000085	0.000936	0.0	0.000621	0.001127	0.0	0.023281	0.0	10 (winter)
	0.0	0.0	0.001768	0.0	0.0	0.0	0.000634	0.0	0.065919	0.001654	11 (winter)
	0.000273	0.0	0.001043	0.003432	0.005847	0.0	0.002065	0.0	0.075969	0.009654	12 (winter)
	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15 (winter)
	0.0	0.0	0.000769	0.000814	0.002010	0.000255	0.002868	0.0	0.020312	0.002093	17 (winter)
	0.0	0.0	0.000075	0.0	0.0	0.0	0.000548	0.0	0.020038	0.0	34 (winter)
	0.0	0.000347	0.002561	0.003290	0.016757	0.000119	0.000919	0.0	0.110585	0.007905	36 (winter)
8	0.0	0.0	0.000295	0.004543	0.0	0.0	0.000295	0.0	0.038780	0.0	1 (spring)
	0.0	0.0	0.000451	0.000451	0.0	0.0	0.000941	0.0	0.011397	0.0	2 (spring)
	0.0	0.0	0.0	0.000148	0.0	0.0	0.0	0.0	0.002118	0.0	3 (spring)
	0.0	0.0	0.0	0.000094	0.004086	0.0	0.000823	0.0	0.128295	0.003755	4 (spring)
	0.0	0.0	0.000447	0.000893	0.000268	0.0	0.000447	0.0	0.037821	0.000161	5 (spring)
	0.0	0.0	0.0	0.0	0.0	0.0	0.000788	0.0	0.010851	0.0	10 (spring)
	0.0	0.0	0.000787	0.002380	0.018981	0.0	0.000383	0.0	0.055069	0.001016	11 (spring)
	0.0	0.0	0.000259	0.000263	0.000941	0.0	0.000458	0.0	0.019178	0.0	12 (spring)
	0.0	0.0	0.000104	0.0	0.002461	0.0	0.000281	0.0	0.010449	0.0	15 (spring)
	0.0	0.0	0.001121	0.003429	0.000532	0.0	0.001254	0.0	0.006448	0.001286	17 (spring)
	0.0	0.0	0.000432	0.000106	0.000432	0.0	0.002620	0.0	0.009384	0.0	34 (spring)
	0.0	0.0	0.001896	0.005472	0.046021	0.0	0.001264	0.0	0.032599	0.000703	36 (spring)

Platyhelminthe	Oligochaeta (small)	Oligochaeta (medium)	Neurocorema confusum	Nesameletus sp.	Neocurupira hudsoni	Megaloptoperla grandis	Megaloptoperla diminuta	Limonia nigrescens	Site
0.0	0.000414	0.0	0.0	0.000519	0.000112	0.0	0.0	0.000112	1 (winter)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2 (winter)
0.0	0.0	0.000670	0.0	0.0	0.0	0.0	0.0	0.0	3 (winter)
0.0	0.0	0.000326	0.000079	0.023804	0.0	0.0	0.0	0.0	4 (winter)
0.000146	0.000112	0.000239	0.0	0.001005	0.0	0.000112	0.0	0.0	5 (winter)
0.0	0.0	0.002461	0.0	0.002071	0.0	0.0	0.0	0.000707	10 (winter)
0.0	0.000103	0.0	0.0	0.002188	0.0	0.0	0.0	0.000121	11 (winter)
0.000333	0.002291	0.000352	0.0	0.000386	0.0	0.0	0.0	0.003358	12 (winter)
0.000141	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15 (winter)
0.000970	0.002907	0.000123	0.0	0.000258	0.0	0.0	0.0	0.0	17 (winter)
0.0	0.000075	0.0	0.0	0.011472	0.0	0.0	0.0	0.0	34 (winter)
0.001270	0.000282	0.0	0.0	0.000535	0.0	0.0	0.0	0.000119	36 (winter)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1 (spring)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2 (spring)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3 (spring)
0.0	0.000309	0.0	0.0	0.006054	0.0	0.0	0.0	0.0	4 (spring)
0.0	0.000161	0.0	0.0	0.000613	0.0	0.0	0.0	0.0	5 (spring)
0.0	0.0	0.0	0.0	0.000167	0.0	0.0	0.0	0.0	10 (spring)
0.001090	0.006255	0.0	0.000482	0.001275	0.0	0.0	0.0	0.001719	11 (spring)
0.0	0.000163	0.0	0.006794	0.0	0.0	0.0	0.0	0.0	12 (spring)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000225	15 (spring)
0.0	0.002190	0.0	0.0	0.000556	0.0	0.0	0.000100	0.0	17 (spring)
0.0	0.000269	0.0	0.0	0.003449	0.0	0.0	0.0	0.000090	34 (spring)
0.0	0.006604	0.0	0.0	0.001087	0.0	0.0	0.0	0.0	36 (spring)

Zephlebia versicolor	Zephlebia dentata	Zelandoperta fenestrata	Zelandobius confusus	Stenoperla prasina	Pycnocentria sp.	Pycnocentria evecta	Psilochorema nemorale	Potamamopyrgus sp.	Site
0.000059	0.0	0.004911	0.0	0.0	0.0	0.0	0.0	0.000059	1 (winter)
0.0	0.0	0.007129	0.0	0.001263	0.0	0.0	0.0	0.0	2 (winter)
0.0	0.0	0.001517	0.0	0.0	0.0	0.0	0.0	0.0	3 (winter)
0.000503	0.005373	0.002706	0.0	0.0	0.0	0.0	0.0	0.000550	4 (winter)
0.0	0.0	0.020895	0.000450	0.0	0.0	0.0	0.0	0.0	5 (winter)
0.0	0.003637	0.001329	0.000901	0.0	0.0	0.0	0.0	0.0	10 (winter)
0.0	0.0	0.004644	0.0	0.0	0.0	0.0	0.0	0.0	11 (winter)
0.000365	0.000273	0.000513	0.003576	0.000488	0.000187	0.002248	0.0	0.000284	12 (winter)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15 (winter)
0.0	0.0	0.0	0.0	0.003000	0.0	0.0	0.0	0.000127	17 (winter)
0.0	0.0	0.000754	0.0	0.0	0.0	0.0	0.0	0.0	34 (winter)
0.0	0.000119	0.002644	0.002803	0.000467	0.0	0.000101	0.0	0.000192	36 (winter)
0.0	0.0	0.0	0.0	0.000076	0.0	0.0	0.000280	0.0	1 (spring)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2 (spring)
0.0	0.0	0.000105	0.0	0.0	0.0	0.0	0.0	0.0	3 (spring)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000277	0.001480	4 (spring)
0.0	0.0	0.000322	0.0	0.0	0.000109	0.0	0.0	0.0	5 (spring)
0.0	0.000083	0.000081	0.0	0.0	0.0	0.0	0.000161	0.0	10 (spring)
0.0	0.0	0.000545	0.0	0.0	0.000650	0.0	0.0	0.000280	11 (spring)
0.0	0.0	0.000210	0.0	0.0	0.0	0.0	0.000178	0.0	12 (spring)
0.0	0.0	0.000211	0.0	0.0	0.0	0.0	0.0	0.0	15 (spring)
0.0	0.0	0.000665	0.0	0.000727	0.0	0.0	0.0	0.000107	17 (spring)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	34 (spring)
0.0	0.0	0.0	0.0	0.0	0.004933	0.000198	0.0	0.000602	36 (spring)

Chironomidae Orthocladiinae	Beraeoptera roria	Austrosimulium tillyardianum	Austroperta cyrene	Archicauliodes diversus	Aphrophila neozelandica	Aoteapsyche colonica	Ameletopsis perscitus	Acanthophlebia cruentata	Site
0.001405	0.0	0.001029	0.0	0.000105	0.001209	0.0	0.0	0.0	1 (summer)
0.034774	0.0	0.003578	0.0	0.0	0.000073	0.000086	0.0	0.0	2 (summer)
0.002804	0.0	0.002307	0.0	0.000165	0.0	0.0	0.0	0.0	3 (summer)
0.003598	0.0	0.0	0.0	0.000368	0.001385	0.000411	0.0	0.0	4 (summer)
0.0	0.000655	0.0	0.0	0.000077	0.0	0.0	0.0	0.0	5 (summer)
0.002104	0.0	0.0	0.0	0.0	0.0	0.001823	0.000053	0.000053	10 (summer)
0.0	0.0	0.0	0.0	0.000060	0.000112	0.0	0.0	0.0	11 (summer)
0.002244	0.382033	0.0	0.000691	0.000343	0.0	0.001399	0.0	0.0	12 (summer)
0.000083	0.0	0.0	0.0	0.0	0.000171	0.000347	0.0	0.0	15 (summer)
0.008745	0.001498	0.0	0.004360	0.0	0.0	0.018441	0.0	0.0	17 (summer)
0.000735	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	34 (summer)
0.097678	0.040871	0.001080	0.0	0.0	0.004339	0.000244	0.0	0.0	36 (summer)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1 (autumn)
0.0	0.0	0.0	0.000305	0.0	0.001294	0.000752	0.0	0.0	2 (autumn)
0.0	0.001396	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3 (autumn)
0.0	0.0	0.0	0.0	0.002248	0.0	0.001670	0.0	0.000977	4 (autumn)
0.0	0.000087	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5 (autumn)
0.0	0.000159	0.0	0.0	0.0	0.000177	0.000102	0.0	0.0	10 (autumn)
0.0	0.000137	0.0	0.0	0.0	0.000120	0.0	0.0	0.0	11 (autumn)
0.000246	0.005153	0.003265	0.0	0.002286	0.0	0.006700	0.0	0.0	12 (autumn)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15 (autumn)
0.0	0.000157	0.0	0.0	0.0	0.0	0.000247	0.0	0.0	17 (autumn)
0.0	0.0	0.0	0.000965	0.0	0.0	0.0	0.0	0.0	34 (autumn)
0.000207	0.000779	0.001642	0.0	0.000079	0.0	0.0	0.0	0.0	36 (autumn)

APPENDIX 3.2: Mean macroinvertebrate densities (invertebrates $/ m^2$) from 15 single-stone samples collected in the summer and autumn of 2001 at 12 sites in the Ruahine Ranges.

Hydraenidae adults	Helichopsyche sp.	<i>Eriopterini</i> sp.	Elmidae Iarvae	Elmidae adults	Deleatidium sp.	Coloburiscus humeralis	Chironomida <i>e</i> Tanypodiane	Chironomidae Chironominae	Site
0.000207	0.0	0.0	0.000105	0.0	0.030828	0.000113	0.0	0.000584	1 (summer)
0.0	0.0	0.0	0.000559	0.0	0.014949	0.0	0.002125	0.005577	2 (summer)
0.0	0.0	0.0	0.000819	0.0	0.007186	0.0	0.0	0.001137	3 (summer)
0.000513	0.011746	0.0	0.000403	0.0	0.034671	0.001008	0.000568	0.003798	4 (summer)
0.000216	0.0	0.0	0.0	0.0	0.076863	0.000386	0.0	0.0	5 (summer)
0.0	0.0	0.0	0.000459	0.0	0.008054	0.0	0.0	0.0	10 (summer)
0.0	0.0	0.0	0.0	0.0	0.005739	0.0	0.0	0.000460	11 (summer)
0.001917	0.007907	0.0	0.0	0.0	0.048805	0.000383	0.008971	0.013215	12 (summer)
0.001026	0.0	0.0	0.000177	0.0	0.044819	0.0	0.0	0.001194	15 (summer)
0.001979	0.002115	0.000181	0.000947	0.0	0.020758	0.001722	0.0	0.0	17 (summer)
0.000153	0.0	0.000118	0.001682	0.0	0.015692	0.0	0.0	0.000279	34 (summer)
0.003987	0.013345	0.0	0.000182	0.0	0.039310	0.0	0.012070	0.025584	36 (summer)
0.0	0.0	0.0	0.0	0.0	0.015770	0.0	0.0	0.0	1 (autumn)
0.0	0.0	0.0	0.000216	0.0	0.029997	0.000384	0.0	0.0	2 (autumn)
0.0	0.0	0.0	0.0	0.0	0.013465	0.0	0.0	0.0	3 (autumn)
0.0	0.0	0.0	0.0	0.0	0.096571	0.003465	0.0	0.0	4 (autumn)
0.0	0.000087	0.0	0.000090	0.0	0.012726	0.0	0.0	0.0	5 (autumn)
0.0	0.0	0.0	0.001378	0.0	0.035135	0.000102	0.0	0.0	10 (autumn)
0.0	0.0	0.0	0.000109	0.0	0.019018	0.000378	0.0	0.000120	11 (autumn)
0.0	0.018195	0.0	0.004612	0.000296	0.087672	0.018185	0.0	0.0	12 (autumn)
0.0	0.0	0.0	0.0	0.0	0.002823	0.0	0.0	0.0	15 (autumn)
0.0	0.0	0.0	0.0	0.0	0.074998	0.000232	0.0	0.0	17 (autumn)
0.0	0.0	0.0	0.0	0.0	0.015261	0.0	0.0	0.0	34 (autumn)
0.0	0.000094	0.000103	0.000336	0.001266	0.053723	0.005723	0.0	0.0	36 (autumn)

Oligochaeta (medium)	Oligochaeta (large)	Neurocorema confusum	Nesameletus sp.	Neozephlebia scita	Megaloptoperla diminuta	Limonia nigrescens	Hydrobiosis parumbripennis	Hydrobiosidae (early instar)	Site
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000320	1 (summer)
0.0	0.0	0.0	0.001496	0.0	0.0	0.0	0.001912	0.0	2 (summer)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000112	0.0	3 (summer)
0.0	0.0	0.0	0.003138	0.0	0.0	0.0	0.000174	0.0	4 (summer)
0.0	0.0	0.0	0.008341	0.0	0.0	0.0	0.0	0.000758	5 (summer)
0.0	0.0	0.0	0.000523	0.000945	0.0	0.0	0.0	0.000186	10 (summer)
0.0	0.0	0.0	0.001798	0.0	0.0	0.0	0.0	0.000060	11 (summer)
0.0	0.0	0.0	0.002100	0.0	0.0	0.004014	0.001300	0.003107	12 (summer)
0.0	0.0	0.0	0.003595	0.0	0.0	0.0	0.0	0.002160	15 (summer)
0.0	0.0	0.0	0.004444	0.001096	0.000670	0.0	0.0	0.003137	17 (summer)
0.0	0.0	0.0	0.015864	0.0	0.0	0.0	0.0	0.0	34 (summer)
0.0	0.0	0.0	0.001131	0.0	0.0	0.0	0.000713	0.002309	36 (summer)
0.0	0.0	0.0	0.000353	0.0	0.0	0.0	0.0	0.000353	1 (autumn)
0.0	0.0	0.0	0.000111	0.0	0.0	0.0	0.0	0.000781	2 (autumn)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3 (autumn)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4 (autumn)
0.0	0.0	0.0	0.000634	0.0	0.0	0.0	0.0	0.0	5 (autumn)
0.0	0.0	0.000159	0.000534	0.0	0.0	0.0	0.0	0.0	10 (autumn)
0.0	0.0	0.000640	0.000600	0.0	0.0	0.0	0.0	0.0	11 (autumn)
0.000211	0.0	0.001837	0.000634	0.0	0.0	0.0	0.0	0.0	12 (autumn)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15 (autumn)
0.0	0.0	0.0	0.001893	0.0	0.0	0.0	0.000288	0.001449	17 (autumn)
0.0	0.0	0.0	0.000182	0.0	0.0	0.0	0.0	0.0	34 (autumn)
0.0	0.000094	0.0	0.000389	0.0	0.0	0.0	0.0	0.001225	36 (autumn)

Stenoperla prasina	Pycnocentria sp.	Pycnocentria sylvestris	Pycnocentria evecta	Psilochorema nemorale	Potamamopyrgus sp.	Platyhelminthe	Onigaster wakefieldii ∤	Oligochaeta (small)	Site
0.000990	0.000783	0.0	0.0	0.0	0.0	0.0	0.0	0.000204	1 (summer)
0.0	0.004456	0.0	0.0	0.0	0.0	0.0	0.0	0.002905	2 (summer)
0.000278	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3 (summer)
0.000104	0.0	0.0	0.0	0.0	0.000980	0.0	0.0	0.002925	4 (summer)
0.0	0.002617	0.0	0.0	0.0	0.0	0.000122	0.0	0.0	5 (summer)
0.000542	0.000443	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10 (summer)
0.000131	0.000112	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11 (summer)
0.000092	0.000183	0.0	0.0	0.0	0.0	0.001074	0.0	0.023489	12 (summer)
0.001546	0.019977	0.0	0.0	0.0	0.0	0.0	0.0	0.001297	15 (summer)
0.001507	0.001860	0.0	0.0	0.0	0.000192	0.0	0.0	0.026256	17 (summer)
0.000153	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	34 (summer)
0.0	0.0	0.000259	0.0	0.0	0.000074	0.001579	0.0	0.001416	36 (summer)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1 (autumn)
0.000519	0.0	0.0	0.0	0.000432	0.0	0.0	0.0	0.000425	2 (autumn)
0.000092	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3 (autumn)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4 (autumn)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5 (autumn)
0.0	0.0	0.0	0.0	0.000191	0.0	0.000070	0.0	0.0	10 (autumn)
0.000120	0.0	0.0	0.0	0.000217	0.0	0.0	0.0	0.0	11 (autumn)
0.0	0.0	0.0	0.001361	0.0	0.006041	0.0	0.0	0.005074	12 (autumn)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15 (autumn)
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17 (autumn)
0.000079	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000677	34 (autumn)
0.000374	0.000094	0.0	0.0	0.001054	0.0	0.0	0.000103	0.007459	36 (autumn)

Zelandoperta fenestrata	Zelandobius confusus	Stratiomyidae	Site
0.009055	0.000105	0.0	1 (summer)
0.029604	0.0	0.0	2 (summer)
0.003236	0.0	0.0	3 (summer)
0.0	0.0	0.0	4 (summer)
0.007946	0.0	0.0	5 (summer)
0.0	0.000874	0.0	10 (summer)
0.002200	0.000060	0.0	11 (summer)
0.000491	0.0	0.0	12 (summer)
0.004017	0.0	0.0	15 (summer)
0.001932	0.000158	0.000112	17 (summer)
0.000355	0.000160	0.0	34 (summer)
0.004874	0.0	0.0	36 (summer)
0.000829	0.0	0.0	1 (autumn)
0.001618	0.002037	0.0	2 (autumn)
0.001470	0.0	0.0	3 (autumn)
0.000922	0.0	0.0	4 (autumn)
0.000090	0.0	0.0	5 (autumn)
0.001492	0.0	0.0	10 (autumn)
0.000874	0.0	0.0	11 (autumn)
0.004477	0.0	0.0	12 (autumn)
0.0	0.0	0.0	15 (autumn)
0.002216	0.0	0.0	17 (autumn)
0.001081	0.0	0.0	34 (autumn)
0.005449	0.000104	0.0	36 (autumn)

APPENDIX 4.1: Mean periphyton concentration (μ g / cm²) in each of eight experimental channels, as measured on days 1, 4, and 14 of the colonisation experiment.

				Char	nnel			
Day	1 '0'	1 'P'	2 '0'	2 'P'	3 '0'	3 'P'	4 '0'	4 'P'
1	0	4.6	0	1.2	0.1	2.1	0	1.7
4	1.7	2.7	2.2	1.1	0.9	1.6	1.6	1.3
14	0.6	1.2	0.2	0.4	4.1	6.0	1.1	1.4

APPENDIX 5.1: Number of macroinvertebrates caught in 24 hours drift samples over the 14 day period of the colonisation experiment. 'In' indicates that the net was set to catch invertebrates as the passed by the entrance to the channel, 'Out '0" indicates that the net caught invertebrates exiting the '0' channel, and 'Out 'P" indicates that the net caught invertebrates exiting the 'P' channel.

			Aoteapsyche colonica	Arthropoda	Austrosimulium australense	Chironomidae	Deleatidium sp.	Elmidae adult	Elmidae larvae	Platyhelminthe	Hudsonema amabilis	Hydrobiosis patumbripennis	Oxythira albiceps	Latia	Potamopyrgus sp.	Psilochorema bidens	Ptilodactilidae	Pycnocentria evecta	Zephlebia dentata
Day 1	Channel 1	In	0	0	2	0	2	1	22	0	1	1	0	1	13	0	0	0	0
		Out '0'	1	0	14	1	9	2	66	2	0	4	0	0	1	0	0	0	0
		Out 'P'	0	0	3	0	3	0	34	0	0	0	0	1	2	0	0	0	0
	Channel 2	In	1	2	2	0	8	3	28	2	2	0	0	0	133	0	0	5	0
		Out '0'	0	0	4	0	0	2	18	1	0	0	0	0	2	0	0	0	0
		Out 'P'	0	1	1	0	3	0	15	0	0	0	0	0	16	0	0	2	0
	Channel 3	In	1	0	5	0	1	0	44	0	0	1	0	0	50	1	0	10	0
		Out '0'	0	0	2	0	4	0	12	0	0	0	0	0	39	0	0	0	0
		Out 'P'	1	0	1	0	0	0	14	3	0	0	0	0	77	0	0	0	0
	Channel 4	In	1	0	5	0	1	0	26	1	0	0	0	0	0	0	0	2	0
		Out '0'	2	0	3	5	11	0	57	1	0	4	0	0	2	0	0	0	0
		Out 'P'	1	0	7	5	0	0	34	0	0	0	0	0	2	0	0	0	0
Day 2	Channel 1	In	0	0	9	1	6	0	11	7	0	2	1	0	22	0	0	5	0
		Out '0'	1	0	30	0	6	0	9	2	1	0	0	0	5	0	0	0	0
		Out 'P'	5	2	16	1	0	1	5	1	0	1	0	0	5	0	0	0	1
	Channel 2	In	6	2	22	0	12	1	20	4	0	5	0	0	82	0	0	4	0
		Out '0'	1	0	10	1	1	0	8	0	0	0	0	0	9	0	0	1	0
		Out 'P'	1	0	1	0	7	12	0	1	0	4	0	0	70	0	0	1	0
	Channel 3	In	4	4	25	3	8	29	0	13	1	6	0	0	105	0	0	4	0
		Out '0'	1	0	27	0	3	4	0	3	0	1	0	0	0	45	0	0	0
		Out 'P'	0	2	0	0	1	0	3	0	0	0	0	0	247	0	0	0	0
	Channel 4	In	1	0	49	12	4	2	23	1	0	5	0	0	2	0	0	5	0
		Out '0'	0	1	70	5	2	1	21	2	0	4	0	0	1	0	0	4	0
		Out 'P'	1	5	50	1	3	0	31	1	0	7	0	0	12	0	0	0	1

			Aoteapsyche colonica	Arthropoda 7	Austrosimulium australense	Chironomidae	Deleatidium sp.	Elmidae adult	Elmidae larvae	Platyhelminthe	Hudsonema amabilis	Hydrobiosis patumbripennis	Oxythira albiceps	Latia	Potamopyrgus sp.	Psilochorema bidens	Ptilodactilidae	Pycnocentria evecta	Zephlebia dentata
Day 3	Channel 1	In	0	0	19	0	4	1	5	8	0	2	0	0	8	0	0	3	0
		Out	0	0	34	1	0	0	3	1	0	0	0	0	5	0	0	0	0
		Out	1	1	8	0	6	1	3	0	0	2	0	0	78	0	0	0	0
	Channel 2	In	7	0	9	2	2	3	9	12	0	0	0	0	135	0	0	3	0
	~	Out '0'	0	0	28	1	2	0	2	1	0	0	0	0	23	0	0	0	0
		Out 'P'	1	1	21	4	1	1	6	2	0	1	0	0	15	0	0	0	0
	Channel 3	In	5	0	18	1	4	0	17	20	0	1	0	0	52	0	0	3	0
		Out '0'	1	0	9	0	1	0	6	2	0	0	0	0	67	0	0	0	0
		Out 'P'	0	5	0	0	0	0	3	2	0	0	0	0	105	0	0	0	0
	Channel 4	In	2	1	46	2	5	0	13	1	0	2	0	0	3	0	0	1	0
		Out '0'	0	0	27	1	3	3	5	3	0	3	0	0	22	0	0	2	0
		Out	0	0	25	2	5	1	11	0	0	0	0	0	11	0	0	0	0
Day 4	Channel 1	In	0	1	23	0	3	0	4	1	0	1	1	0	14	0	0	0	0
		Out '0'	0	0	17	0	2	0	7	2	0	1	0	0	3	0	0	0	0
		Out 'P'	0	0	21	0	2	3	9	0	1	1	0	0	1	0	0	0	0
	Channel 2	In	2	2	20	0	3	0	8	3	0	2	0	0	108	0	0	0	0
		Out '0'	0	0	28	2	5	0	9	2	1	1	0	0	22	0	0	0	0
		Out 'P'	1	0	14	0	2	0	12	3	2	0	0	0	17	0	0	0	0
	Channel 3	In	0	0	27	2	3	0	13	4	0	3	2	0	36	0	0	1	0
		Out '0'	0	0	20	0	0	0	3	5	2	0	0	0	46	0	0	0	0
		Out 'P'	1	1	13	0	0	0	10	5	0	0	0	0	112	0	0	1	0
	Channel 4	In	0	0	30	0	1	1	6	0	0	3	0	0	1	0	0	0	0
		Out '0'	0	0	41	0	3	1	14	1	0	3	0	0	23	0	0	2	0
		Out 'P'	0	0	36	0	3	1	14	0	0	0	0	0	7	0	0	1	0

			Aoteapsyche colonica	Arthropoda	Austrosimulium australense	Chironomidae	Deleatidium sp.	Elmidae adult	Elmidae larvae	Platyhelminthe	Hudsonema amabilis	Hydrobiosis patumbripennis	Oxythira albiceps	Latia	Potamopyrgus sp.	Psilochorema bidens	Ptilodactilidae	Pycnocentria evecta	Zephlebia dentata
Day 5	Channel 1	In	0	0	14	1	7	1	10	0	0	0	0	0	9	0	0	0	0
		Out '0'	1	1	12	0	3	1	4	0	0	2	0	0	4	0	0	1	0
		Out 'P'	0	0	24	0	5	0	23	0	0	0	0	0	0	0	0	0	0
	Channel 2	In	0	0	5	0	6	0	22	1	0	0	0	0	60	0	0	1	0
		Out '0'	0	0	25	0	5	0	12	3	0	2	0	0	32	0	0	0	0
		Out 'P'	1	0	7	0	6	1	9	2	0	0	0	0	3	0	0	0	0
	Channel 3	In	0	0	9	1	6	0	46	8	0	0	0	0	54	0	0	0	0
		Out '0'	1	0	94	2	3	0	17	5	0	1	0	0	22	0	0	0	0
		Out 'P'	0	0	16	0	2	0	20	1	0	2	0	0	5	0	0	1	0
	Channel 4	In	0	0	32	0	0	2	10	0	0	1	1	0	0	0	0	0	0
		Out '0'	0	0	48	1	9	1	20	0	0	5	0	0	2	0	0	2	1
		Out 'P'	0	0	22	0	1	0	17	0	0	2	0	0	1	0	0	0	0
Day 6	Channel 1	In	0	2	28	0	4	0	8	0	0	1	0	0	10	0	0	0	0
		Out '0'	0	0	17	1	9	1	25	5	0	4	0	0	0	0	0	0	0
		Out 'P'	0	2	21	0	8	0	11	2	0	1	0	0	1	0	0	0	0
	Channel 2	In	2	1	11	1	16	0	14	9	0	1	0	0	46	0	0	0	0
		Out '0'	1	0	15	1	6	0	21	2	0	1	0	0	52	0	0	0	0
		Out 'P'	0	3	21	0	12	1	18	7	1	0	0	0	13	0	0	0	0
	Channel 3	In	1	0	23	0	12	0	17	3	0	3	0	0	45	0	0	1	0
		Out '0'	2	1	24	1	3	0	17	5	0	1	0	0	22	0	0	0	0
		Out 'P'	0	0	14	0	1	0	26	4	0	2	2	0	21	0	0	0	0
	Channel 4	In	0	0	25	3	4	0	12	0	0	1	0	0	5	0	0	0	0
		Out '0'	0	0	46	0	4	0	18	1	0	0	1	0	6	0	0	0	0
		Out 'P'	1	1	34	1	3	0	27	2	0	1	1	0	3	0	0	0	0

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			Aoteapsyche colonica	Arthropoda	Austrosimulium australense	Chironomidae	Deleatidium sp.	Elmidae adult	Elmidae larvae	Platyhelminthe	Hudsonema amabilis	Hydrobiosis patumbripennis	Oxythira albiceps	Latia	Potamopyrgus sp.	Psilochorema bidens	Ptilodactilidae	Pycnocentria evecta	Zephlebia dentata
Day 7	Channel	In	0	1	12	0	5	0	9	2	0	1	0	0	7	0	0	1	0
-		Out	0	0	42	8	2	0	0	1	0	2	0	0	4	0	0	0	0
		Out	0	0	12	1	1	0	13	2	0	0	0	0	5	0	0	0	0
	Channel 2	In	0	0	4	0	5	0	6	1	0	0	0	0	46	0	0	0	0
	~	Out '0'	0	0	16	2	0	0	9	5	0	2	0	0	18	0	0	1	0
		Out 'P'	0	0	9	3	2	0	10	2	0	1	0	0	1	0	0	0	0
	Channel 3	In	0	0	14	0	2	0	14	3	0	0	0	0	23	0	0	0	0
		Out '0'	0	1	20	0	0	0	3	2	0	0	0	0	55	0	0	0	0
		Out 'P'	0	3	19	1	0	0	4	4	0	1	0	0	99	0	0	0	0
	Channel 4	In	0	1	15	1	4	0	6	0	0	2	0	0	0	0	0	0	0
		Out '0'	0	0	8	0	4	0	8	0	0	0	0	0	0	0	0	0	0
		Out 'P'	0	0	19	0	0	0	10	0	0	0	0	0	0	0	0	0	0
Day 8	Channel 1	In	0	0	11	0	3	1	1	2	0	1	0	0	6	0	0	0	0
		Out '0'	0	0	18	0	3	0	4	1	0	1	0	0	0	0	0	0	0
		Out 'P'	1	0	28	7	1	1	6	1	0	1	0	0	0	0	0	1	0
	Channel 2	In	0	0	3	0	4	0	14	6	0	0	0	0	19	0	0	0	0
		Out '0'	0	0	37	0	3	0	13	0	0	0	0	0	10	0	0	0	0
		Out 'P'	0	0	26	0	3	0	14	1	0	1	0	0	5	0	0	0	0
	Channel 3	In	0	1	18	0	0	0	14	5	0	1	0	0	23	0	0	1	0
		Out '0'	0	0	26	1	1	0	15	5	0	3	0	0	14	0	0	1	0
		Out 'P'	0	1	8	0	1	0	9	2	0	0	0	0	45	0	0	0	0
	Channel 4	In	0	1	18	3	3	0	12	0	0	1	0	0	2	0	0	0	0
		Out '0'	0	0	15	0	2	0	17	2	0	0	0	0	1	0	0	0	0
		Out 'P'	1	0	5	1	0	1	7	1	0	0	0	0	5	0	0	0	0

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			Aoteapsyche colonica	Arthropoda	Austrosimulium australense	Chironomidae	Deleatidium sp.	Elmidae adult	Elmidae larvae	Platyhelminthe	Hudsonema amabilis	Hydrobiosis patumbripennis	Oxythira albiceps	Latia	Potamopyrgus sp.	Psilochorema bidens	Ptilodactilidae	Pycnocentria evecta	Zephlebia dentata
Day 9	Channel 1	In	1	24	13	0	6	0	6	3	0	0	0	0	18	0	0	0	0
		Out '0'	0	0	47	0	3	1	10	1	0	1	0	0	0	0	0	0	0
		Out 'P'	1	1	32	2	3	0	7	3	0	0	0	0	2	0	0	0	0
	Channel 2	In	1	3	5	0	5	0	2	6	0	1	0	0	55	0	0	1	0
		Out '0'	0	0	38	1	3	0	7	1	0	5	0	0	15	0	0	0	0
		Out 'P'	0	1	11	1	3	0	4	3	0	1	0	0	9	0	0	0	0
	Channel 3	In	0	1	16	0	3	0	9	2	0	1	0	0	36	0	0	1	0
		Out '0'	0	1	5	0	1	0	6	0	0	1	0	0	40	0	0	0	0
		Out 'P'	0	1	5	0	0	0	1	0	0	0	0	0	14	0	0	0	0
	Channel 4	In	0	0	12	1	1	1	5	1	0	1	0	0	2	0	0	1	0
		Out '0'	0	0	14	0	2	0	5	0	0	1	0	0	5	0	0	1	0
		Out 'P'	0	0	10	0	1	1	7	3	0	0	0	0	6	0	0	0	0
Day 10	Channel 1	In	0	3	17	0	3	0	4	1	0	0	0	0	28	0	0	0	0
		Out '0'	0	0	32	0	0	0	2	0	0	2	0	0	3	0	0	0	0
		Out 'P'	0	0	8	0	0	0	4	7	0	0	0	0	5	0	0	0	0
	Channel 2	In	0	0	1	0	7	0	8	4	0	0	0	0	46	0	0	0	0
		Out '0'	0	0	25	0	4	0	2	2	0	0	0	0	31	0	0	0	0
		Out 'P'	0	0	6	0	2	0	0	1	0	1	0	0	23	0	0	0	0
	Channel 3	In	0	3	4	2	8	0	5	6	0	0	0	0	72	0	0	0	0
		Out '0'	0	3	13	0	2	0	2	0	0	0	0	0	37	0	0	0	0
		Out 'P'	0	3	7	1	0	0	2	0	0	0	0	0	95	0	0	0	0
	Channel 4	In	0	41	13	2	1	0	7	0	0	0	0	0	10	0	0	0	0
		Out '0'	0	0	29	1	3	0	13	0	0	1	1	0	4	0	0	0	0
		Out 'P'	0	1	18	1	1	0	8	1	0	0	0	0	16	0	0	3	0

			Aoteapsyche colonica	Arthropoda	Austrosimulium australense	Chironomidae	Deleatidium sp.	Elmidae adult	Elmidae larvae	Platyhelminthe	Hudsonema amabilis	Hydrobiosis patumbripennis	Oxythira albiceps	Latia	Potamopyrgus sp.	Psilochorema bidens	Ptilodactilidae	Pycnocentria evecta	Zephlebia dentata
Day 11	Channel 1	In	0	2	11	0	0	0	6	0	0	3	0	0	22	0	0	0	1
		Out	0	0	27	0	1	0	2	1	0	0	0	0	18	0	0	0	0
		Out	0	0	12	0	4	0	3	2	0	1	0	0	5	0	0	0	0
	Channel 2	In	0	0	7	0	4	0	5	1	0	2	0	0	58	0	0	3	0
		Out '0'	0	1	30	1	2	0	1	4	0	1	0	0	34	0	0	0	0
		Out 'P'	0	0	9	0	1	0	0	2	0	1	0	0	15	0	0	0	0
	Channel 3	In	0	3	9	0	0	0	4	4	0	1	0	0	0	0	0	59	0
		Out '0'	0	0	15	0	0	0	1	0	0	0	0	0	0	0	0	34	0
		Out 'P'	0	5	1	0	0	0	1	5	0	0	0	0	0	0	0	110	0
	Channel 4	In	0	0	19	1	1	0	8	1	0	0	0	0	4	0	1	0	0
		Out '0'	0	0	7	0	2	0	3	3	0	0	0	0	5	0	0	1	0
		Out 'P'	0	0	15	6	4	0	6	0	0	0	0	0	9	0	0	0	0
Day 12	Channel 1	In	0	0	12	0	9	0	2	1	0	3	0	0	15	0	0	0	0
		Out '0'	0	0	10	0	2	0	4	0	0	1	0	0	9	0	0	0	0
		Out 'P'	0	1	10	0	1	0	4	1	0	1	0	0	3	0	0	0	1
	Channel 2	In	1	2	11	1	4	0	3	4	0	1	0	0	54	0	0	0	0
		Out '0'	0	0	12	0	2	1	0	1	0	1	0	0	13	0	0	0	0
		Out 'P'	0	0	11	0	0	0	1	1	0	4	0	0	11	0	0	0	0
	Channel 3	In	0	0	14	0	2	0	8	4	0	1	0	0	0	2	0	36	0
		Out '0'	0	0	18	0	0	0	4	5	0	0	0	0	0	0	0	25	0
		Out 'P'	0	2	5	0	0	0	0	0	0	0	0	0	0	0	0	52	0
	Channel 4	In	0	14	12	0	2	0	5	0	0	1	0	0	4	0	0	0	0
		Out '0'	0	0	6	2	2	0	4	1	0	1	0	0	0	0	0	5	0
		Out 'P'	0	1	10	0	3	0	7	1	0	0	0	0	0	0	0	15	0

			Aoteapsyche colonica	Arthropoda	Austrosimulium australense	Chironomidae	Deleatidium sp.	Elmidae adult	Elmidae larvae	Platyhelminthe	Hudsonema amabilis	Hydrobiosis patumbripennis	Oxythira albiceps	Latia	Potamopyrgus sp.	Psilochorema bidens	Ptilodactilidae	Pycnocentria evecta	Zephlebia dentata
Day 13	Channel 1	In	0	0	9	0	1	0	1	2	0	1	0	0	12	0	0	0	0
		Out '0'	0	1	7	1	0	0	5	2	0	0	0	0	15	0	0	0	0
		Out 'P'	0	0	10	1	0	0	5	2	0	0	0	0	2	0	0	0	0
	Channel 2	In	0	2	0	1	4	0	5	4	0	1	0	0	116	0	0	0	0
		Out '0'	0	0	4	0	2	0	2	0	0	0	0	0	70	0	0	0	0
		Out 'P'	0	1	5	0	2	0	2	1	0	0	0	0	44	0	0	0	0
	Channel 3	In	0	0	4	0	2	0	5	2	1	0	0	0	23	0	0	3	0
		Out '0'	0	0	3	1	0	0	2	4	0	0	0	0	12	0	0	0	0
		Out 'P'	0	2	0	0	0	0	1	1	0	0	0	0	76	0	0	0	0
	Channel 4	In	1	0	0	2	4	0	7	0	0	0	0	0	16	0	0	0	0
		Out '0'	0	1	2	1	0	0	5	2	0	0	0	0	6	0	0	0	0
		Out 'P'	0	1	6	0	2	0	5	1	0	0	0	0	9	0	0	0	0
Day 14	Channel 1	In	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Out '0'	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Out 'P'	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Channel 2	In	0	1	2	0	2	0	10	8	2	0	0	0	39	0	0	0	0
		Out '0'	0	0	6	0	0	0	2	1	0	2	0	0	8	0	0	0	0
		Out 'P'	0	0	3	0	0	0	3	1	0	0	0	0	17	0	0	0	0
	Channel 3	In	0	0	1	0	0	0	6	3	0	0	0	0	27	0	0	1	0
		Out '0'	0	0	3	0	0	0	7	0	0	0	0	0	3	0	0	0	0
		Out 'P'	0	0	1	0	0	0	2	6	0	0	0	0	58	0	0	0	0
	Channel 4	In	0	0	2	0	1	0	11	0	0	1	0	0	0	0	0	0	0
		Out '0'	0	1	0	6	3	0	4	1	0	0	0	0	1	0	0	1	0
		Out 'P'	0	2	3	0	1	0	8	1	0	1	1	0	8	0	0	0	0

APPENDIX 5.2: Mean number of macroinvertebrates sampled from the channel benthos on days 4 and 14 of the colonisation experiment. '0' indicates that the samples were collected in the '0' channel, and 'P' indicates that the samples were collected in the 'P' channel.

		Aoteapsyche colonica	Arthropoda 🕈	Austrosimulium australense	Chironomidae	Deleatidium sp.	Elmidae larvae	Platyhelminthe	Hudsonema amabilis	Hydrobiosis amabilis	Latia	Oxythira albiceps	Potamopyrgus sp.	Pycnocentrodes evecta
Channel 1	'P' A	1	1	82	0	84	1	0	0	2	0	0	4	2
	'P' B	1	2	48	1	4	0	0	0	1	0	0	3	9
	'P' C	0	1	161	0	1	0	2	0	0	0	0	5	12
	'0' A	0	0	112	0	2	0	0	0	0	0	0	1	0
	'O' B	0	0	29	0	0	1	0	0	0	0	0	1	0
	'O' C	0	0	55	0	4	0	0	0	2	0	0	8	15
Channel 2	'P' A	0	0	5	0	0	0	0	1	0	0	0	5	8
	'P' B	1	0	49	0	1	2	0	0	2	0	0	23	3
	'P' C	0	0	29	0	1	0	0	0	0	0	0	7	2
	'0' A	0	0	70	0	3	0	0	0	0	0	0	12	4
	'O' B	0	0	17	0	3	0	0	0	0	0	0	14	2
	'0' C	0	2	104	2	3	0	1	0	3	0	0	8	1
Channel 3	'P' A	0	0	13	0	3	1	0	0	0	0	0	34	8
	'P' B	0	0	11	0	0	2	0	0	0	0	0	16	2
	'P' C	0	0	99	0	6	4	2	0	0	0	0	14	23
	'0' A	0	0	78	0	0	0	1	0	0	0	0	29	3
	'O' B	0	0	39	0	2	0	0	0	1	0	0	15	5
	'0' C	0	0	12	0	0	1	0	0	0	0	0	19	12
Channel 4	'P' A	1	0	28	0	2	13	0	0	2	6	0	22	31
	'P' B	2	0	54	0	3	7	0	0	1	0	0	4	6
	'P' C	0	0	10	1	3	0	0	0	4	0	0	12	19
	'0' A	1	0	61	1	6	6	0	0	3	0	0	14	20
	'O' B	0	1	16	0	4	0	0	0	1	0	0	17	9
	'0' C	0	0	29	0	5	4	0	0	1	0	0	10	8
Channel 1	'P' A	1	0	32	0	11	5	0	0	0	0	0	0	17
	'P' B	1	0	1	0	1	1	0	0	0	0	0	3	4
	'P' C	0	2	4	3	3	3	0	0	0	0	0	9	6
	'0' A	0	0	6	0	4	0	0	0	1	0	0	1	1
	'O' B	1	0	2	0	3	1	0	0	0	0	0	8	8
	'0' C	0	0	2	0	2	0	0	0	0	0	0	9	7
Channel 2	'P' A	0	0	0	1	2	2	0	0	0	0	0	18	3
	'P' B	0	0	15	0	4	0	0	0	0	0	0	15	0
	'P'C	0	0	26	0	4	1	0	0	0	0	0	5	0
	10' A	0	1	13	0	5	1	1	0	0	0	0	14	0
	0.B	0	0	4	0		4	0	0	0	0	0	14	
Obanas 10	10.0	0	0	5	0	4	8	0	0	0	0	0	20	
Channel 3	PA			5	3	1	0		0	0	0	0	51	0
	PB			0	0	3	1	0	0		0	0	52	0
	PC			10	0	3	4	0	0		0		40	
	10'A	0	0	1	2	1	0	0	0	0	0	0	39	0
	10'C	0	0	21	0		4	0	0	0	0	0	23	4
Channel 4	'D' A	2	0	24	1	11	4	0	0	2	2	0	15	22
Channel 4	PA	1	0	7	10	0	4	2	0	2	3	0	17	22
	PC	5	0	10	2	0	14	4	0	5	4	0	27	20
	10' 4	1	1	10	2	5	8	0	0	1	0	0	22	42
	'0' B	0	0	8	1	5	1	0	0	0	0	0	4	12
	10' C	0	3	1	0	13	3	0	0	0	0	0	11	11
				<u> </u>		1.0								
APPENDIX 6: Invertebrate species richness in New Zealand forest streams

ABSTRACT

Invertebrate communities in 44 headwater streams in the lower North Island of New Zealand were assessed in the Austral summer of 1996. Half of the streams were in the Ruahine Ranges, the other half were in the Tararua Ranges. Substrate stability did not differ between the two ranges, but Tararua streams have greater canopy cover. Stability influenced periphyton biomass and invertebrate species richness at the Ruahine sites, but did not at the Tararua sites. Periphyton biomass was the best predictor of species richness in both areas. We conclude that stability influences invertebrate communities through the removal of periphyton.

INTRODUCTION

Stability is believed to have a profound influence on species richness (Death & Winterbourn 1995, Townsend *et al.* 1997, McCabe & Gottelli 2000), but the nature of this relationship has proven elusive. Studies have found a variety of stability - richness relationships, including a quadratic curve peaking at intermediate levels of disturbance (Connell 1978, Townsend *et al.* 1997), and a linear decline in species richness as stability decreases (Death & Winterbourn 1995, Death in press). It is therefore difficult to predict, based on stability alone, the number of species that will be found at a site.

Stability, however, is not the only factor that will influence the number of macroinvertebrate species occurring at a site. In-stream primary production may also be of importance, but there is some debate as to whether higher productivity will support a greater or lesser number of species (Rosenzweig 1993). Exactly how the effects of primary production and stability interact, and which of the two is more important to macroinvertebrate communities, remains unresolved (but see Robinson & Minshall 1986).

In the current study, we investigated the links between stability, periphyton biomass, and macroinvertebrate species richness in 44 streams in the lower North Island of New Zealand. All of these were within pristine forest parks, with 22 in the northern Ruahine Ranges and 22 in the southern Tararua Ranges. We were particularly interested in identifying whether stability or periphyton biomass provided a better predictor of species richness at these sites.

METHODS

Five randomly selected stones from each of three size classes (maximum linear planar dimension <60mm, 60-90mm, >90mm) were removed from the stream bed at each of 44 sites between January 29 and April 3, 1996. The invertebrates on each stone were collected by scooping the stone into a net of 250 μ m mesh, along with any fine sediment or detritus immediately below the collected stone. The stone was thoroughly washed in the net to ensure all invertebrates were removed. Invertebrate samples were stored in

10% formalin and were later identified and enumerated using the keys of Winterbourn & Gregson (1989).

Periphyton biomass was estimated by collecting four randomly selected stones from the stream bed at each site. Pigments were extracted and analysed following the methods of Steinman & Lamberti (1996), with values corrected for surface area by weighing aluminium foil of known mass per unit area which was cut to snugly cover the stones.

Stream stability was determined at each site using the bottom component of the Pfankuch index (Pfankuch 1975). This is a subjective measure of channel stability based on a series of observations including the degree of bank undercutting and debris jam potential.

Data were analysed with regression, ANOVA, and ANCOVA procedures of SAS (1996).

RESULTS

The streams surveyed in the Ruahines and Tararuas did not differ significantly in stability ($F_{1,42}$ =1.29, P=0.26). However, at a given level of stability the Ruahine sites tended to have more periphyton ($F_{1,40}$ =8.14, P=0.08) and greater macroinvertebrate species richness ($F_{1,40}$ =10.07, P=0.003).

In the Ruahines, there was a linear decrease in species richness as stability decreased ($F_{1,21}$ =7.93, P=0.01, r^2 =0.28) with a similar, but weaker trend in the Tararuas ($F_{1,21}$ =4.80, P=0.04, r^2 =0.19) (Fig. 1). Less stable sites also showed a linear reduction in chlorophyll *a* levels in the Ruahines ($F_{1,21}$ =28.57, P<0.001, r^2 =0.59). This was not the

case at the Tararua sites, where chlorophyll *a* levels did not appear to be influenced by stability ($F_{1,21}$ =0.72, P=0.41) (Fig. 2).



Figure 1: Total number of macroinvertebrate species collected from 15 stones at each of 44 study sites (between January 29 and April 3, 1996), as a function of stream stability. Solid points represent Ruahine sites (species richness = 54.15 - 0.55 stability), hollow points represent Tararua sites (species richness = 37.81 - 0.27 stability).



Figure 2: Mean chlorophyll a levels from four stones collected at each of 44 study sites (between January 29 and April 3, 1996), as a function of stream stability. The regression equation for the Ruahine sites (solid points) is (chlorophyll a = 5.25 - 0.10 stability). No line is plotted for the Tararua sites (hollow points) as these show no significant correlation.

In both the Ruahines and Tararuas, streams with higher chlorophyll *a* levels had more macroinvertebrate species ($F_{2,43}$ =24.37, P<0.001, r^2 =0.37) (Fig. 3), with the number of species collected increasing most rapidly at lower periphyton levels. Of the variables measured, r^2 values indicate that chlorophyll *a* levels were the best predictor of species richness at the study sites.



Figure 3: Total number of macroinvertebrate species collected from 15 stones at each of 44 study sites (between January 29 and April 3, 1996), as a function of mean chlorophyll *a* level. Solid points represent Ruahine sites, hollow points represent Tararua sites. The line plotted is fitted to the complete data set (species richness = 35.68 (chlorophyll $a^{0.10}$)).

DISCUSSION

There was a linear increase in species richness with higher stability (Fig. 1), similar to that found in a number of other New Zealand streams (e.g., Death & Winterbourn 1995, Death in press). Stability and chlorophyll *a* concentration were also strongly correlated

in the Ruahines, but not in the Tararuas because of greater stream shading at the latter sites (Fig. 2). Light attenuation from canopy cover appears to be more important in controlling periphyton growth in the Tararuas, and thus reduces the impact of disturbances on periphyton levels as streams with little periphyton will not suffer much periphyton loss during high flows.

This strong link between chlorophyll *a* concentrations and species richness (Fig. 3) appears to support the Productivity Disturbance Model (Death in press). Death has suggested that invertebrate species richness will increase as primary productivity increases, with species richness reaching an asymptote at high levels of productivity. Similar results have also been found in Taranaki streams on the west coast of the North Island (Zimmermann and Death unpublished data), suggesting that the importance of primary productivity in predicting macroinvertebrate species richness may be widespread, at least within New Zealand.

Chlorophyll *a* concentration appears to be a better predictor of species richness than stability in our study streams. We suggest that the correlation between stability and species richness (Fig. 1) is in fact a by-product of the influence of stability on chlorophyll *a* levels (Fig. 2). Disturbances reduce periphyton biomass, with a lower periphyton biomass allowing few macroinvertebrate species to coexist in a patch.

Thus the macroinvertebrate community of a stream with little canopy cover will show greater variation as a result of disturbances, as the periphyton of an open stream will be more influenced by the disturbance regime, with subsequently greater effects on the invertebrate community. A stream with dense canopy cover will have little periphyton regardless of the disturbance regime. Disturbances may have little effect on

the macroinvertebrate community in streams with a dense canopy as there will be little periphyton to remove, even after a period of stable flow.

Macroinvertebrates are also affected directly by disturbances, with individuals dislodged from the substrate as shear stresses and bed movement increase. We suggest that while this is an important process, recolonisation of the denuded substrate may be rapid (Death & Winterbourn 1995) but is controlled by the re-establishment of primary producers; disturbances reduce periphyton biomass and remove macroinvertebrates, and the rate of invertebrate recolonisation is determined by the rate of periphyton re-establishment and growth. Macroinvertebrates are influenced directly by disturbances, but, as their recolonisation may be more rapid than the re-establishment of their periphyton food, they will be tightly controlled by periphyton levels.

In summary, it appears that the macroinvertebrate community is strongly influenced by periphyton biomass, with more periphyton allowing a greater number of macroinvertebrate species to coexist in a patch. Periphyton levels are in turn determined by substrate stability and light levels. While stability may correlate with macroinvertebrate species richness, we suggest that the influence of stability on the invertebrate community is primarily through disturbances controlling periphyton biomass.

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