# Spatial patterns of invertebrate communities in spring and runoff-fed streams

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## Abstract

Invertebrate spatial patterns were investigated in 36 and 12 spring and runoff-fed streams in New Zealand and in Northern Spain, respectively. Moss biomass and resource levels were more abundant in springbrooks than in runoff-fed streams. Invertebrate densities were greater in spring habitats, but invertebrate richness was higher and lower at more stable sites in New Zealand and Spain, respectively. These differences in invertebrate diversity may be related to the larger diversity of invertebrate predators in New Zealand springbrooks, and the lack of temperature mediated life history cues in the New Zealand invertebrate fauna.

I carried out two experiments to look at the effect of local factors on the spatial distribution of invertebrate communities. The first experiment investigated the effect that algal biomass and habitat structure had on stream invertebrate communities. To do this I used artificial canopies to reduce algal growth and artificial substrates with different habitat complexities. Numbers of invertebrate taxa and individuals were both lower on bricks under the artificial canopies and on the simplest substrates. Algal productivity may enhance invertebrate richness by increasing the number of individuals in a given area, whereas habitat complexity may increase invertebrate richness by providing greater food and/or space resources.

The second experiment examined the effects of primary productivity and physical disturbance on stream invertebrates by using artificial canopies and by kicking and raking patches of the stream bed ($10 \ m^2$). We compared the effects of natural versus experimental disturbance on the benthic invertebrate fauna. Invertebrate fauna in high productivity patches recovered quicker than in low productivity patches after both experimental and natural disturbance. The experimental disturbance reduced number of invertebrate taxa and individuals to a greater extent than the spate. Primary productivity limited the recovery of the invertebrate fauna after the disturbances.

I also investigated temperature patterns in five runoff and seven spring-fed streams in the North and South Islands of New Zealand. The invertebrate fauna was sampled at 4 distances (0, 100, 500 and 1 km) from seven spring sources. Temperature variability was much larger for runoff-fed streams than for springs, and it increased with distance from the source. Flow, altitude, and the number and type (i.e., spring or runoff-

fed) of tributaries joining the springbrook channel determined the degree of temperature variability downstream of the spring sources. Moving downstream, invertebrate communities progressively incorporated taxa with higher mobility and those more common to runoff-fed streams. Changes in substrate composition, stability and invertebrate drift are more likely explanations of the observed longitudinal patterns in the invertebrate communities than changes in temperature regimes.

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**Note on text and authorship**

This thesis is a combination of five individual papers. This has resulted in some repetition in introductions, methods and site descriptions between chapters. Chapter 2 has been accepted for publication in Archiv für Hydrobiologie. Chapters 1 and 5 have been sent to the Journal of the North American Benthological Society and to Freshwater Biology, respectively, while chapters 3 and 4 have been sent to Oikos and to Oecologia, respectively. The only co-author is my principal supervisor Russell Death; this recognizes his contribution in developing the original project concept, editing manuscripts, overseeing project administration and discussing ongoing developments. For all chapters my input was the greatest. I planned the research, undertook all fieldwork, analyzed all data, and wrote all manuscripts.

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# General Introduction

Spatial patterns of stream invertebrate communities are determined by a variety of factors (e.g., current, substrate, temperature, resource levels) (Resh and Rosenberg 1984, Allan 1996), that interact at different scales (Fisher 1992, Raffaelli et al. 1992). In streams, substrate disturbance (i.e., floods) is considered to be one of the major forces structuring macroinvertebrate communities (Resh et al. 1988, Lake 2000, Death 2002b). Floods directly remove individuals, but they may also have indirect effects on invertebrate populations by changing the habitat. For example, higher discharges may reduce the amount of moss and macrophytes (Englund 1991, Suren 1993), or scour algae and wash detritus away (Biggs et al. 1999, Bond and Downes 2000), which will decrease the level of habitat complexity and the amount of resources.

Experimental work has shown that increased disturbance rates reduce the number of invertebrate individuals and species (Robinson and Minshall 1986, Death 1996, Bond and Downes 2000, McCabe and Gotelli 2000), although others have found low numbers of species in more stable streams (Townsend et al. 1997). Springs and springbrooks are remarkable habitats to examine the effects that flow disturbance has on the spatial patterns of stream invertebrates, as they are generally stable lotic habitats compared to streams (Odum 1957). A number of studies have compared spring and stream invertebrate communities (Davidson and Wilding 1943, Ward and Dufford 1979, Meffe and Marsh 1983, Anderson and Anderson 1995), and found that springs generally have lower numbers of macroinvertebrate taxa than similar downstream reaches or nearby runoff-fed streams. In contrast, a number of studies (Death 1995, Death and Winterbourn 1995, Death et al. 2004) have found the opposite pattern for New Zealand springs and streams.

Chapter one examines invertebrate spatial patterns in spring and runoff-fed streams in four regions of New Zealand. I was particularly interested in how streambed stability would affect invertebrate community structure, that is, are invertebrate communities more similar in streams with similar stability or from the same region?. Chapter two examines invertebrate spatial patterns in springs and streams of Northern Spain. This chapter complements chapter one, in that I examine invertebrate spatial patterns in habitats with similar physicochemical characteristics to the New Zealand sites,

but with a completely different pool of colonizers. Again, I wished to clarify whether streambed stability has similar effects on the invertebrate fauna of Northern and Southern Hemisphere springs.

Streambed stability was shown in chapters one and two to enhance moss growth (habitat complexity) and algal biomass (productivity), which in turn will affect invertebrate communities. Generally, it is accepted that diversity will increase with higher productivity rates, although a decrease in diversity with increasing productivity may occur because of competitive exclusion (Rosenzweig and Abramsky 1993, Huston 1994). However, several mechanisms other than competitive exclusion can be invoked to explain a decrease in species richness with higher productivity (Abrams 1995). A review by Waide et al. (1999) indicates that finding unimodal, positive linear, negative linear or non significant relationships depends on the type of organisms being studied and the scale of observation. Increases in habitat complexity may lead to a higher number of individuals because of increases in surface area, and thus more taxa through passive sampling. This is the sampling phenomenon hypothesis (SPH) (Dean and Connell 1987a). Alternatively, the number of taxa may increase because complexity increases resource quantity and diversity. This is the resource availability hypothesis (RAH) (Dean and Connell 1987b, O'Connor 1991, Douglas and Lake 1994). The SPH assumes that everything else being equal habitat complexity does not change species evenness, while the RAH predicts a larger number of taxa on more complex substrates through an increase in the number of available niches (Dean and Connell 1987a, b). Thus, chapter three examines how macroinvertebrate communities are affected by algal productivity and substrate complexity. In order to achieve this I used artificial canopies, which blocked the light, and artificial substrates, ranging from bare clay bricks to bricks with artificial grass or plastic fence twine interwoven in the artificial grass. I hypothesized that increases in both would lead to a higher number of taxa and animals.

Recent studies have identified the importance of food resource levels in the recovery of invertebrate faunas following disturbance, suggesting that invertebrate recovery only occurs following recovery of periphytic communities (Death 2002a, Minchin and Death 2002, Death 2003). There are few studies that have examined experimentally the combined effects of disturbance and productivity on the invertebrate

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fauna (Zimmermann 2001). Chapter four investigates the effects that resource levels and physical disturbance have on invertebrate communities. This chapter examines the recovery of stream invertebrate fauna following natural and experimental disturbances on ambient and reduced productivity, by using artificial canopies. The main objective of this chapter was to compare the rate of recovery of the invertebrate fauna in high and low productivity patches after natural and experimental disturbances.

Finally, the spatial composition and structure of stream biotic communities has been shown to change in response to the longitudinal modification of stream attributes (Hynes 1970, Fisher 1982, Allan 1996). In glacier-fed streams a distinct and predictable change in invertebrate faunal assemblage occurs (Milner and Petts 1994, Ward 1994, Milner et al. 2001), however, downstream invertebrate community patterns are not so distinctive in spring-fed streams. The thermal and flow constancy of spring sources have been shown to decrease invertebrate diversity compared with downstream reaches and nearby runoff-fed streams (Davidson and Wilding 1943, Ward and Dufford 1979, Meffe and Marsh 1983, Erman and Erman 1992, Barquín and Death in press). However, in chapter one spring communities were shown to be more diverse than those in nearby runoff-fed streams. Chapter five assesses the thermal variability of some of the runoff and spring-fed streams studied in chapter one. I investigated longitudinal changes in the invertebrate fauna in some of the spring-fed streams included in chapter one. Higher temperature variability may be associated with higher flow variability which has been shown to reduce invertebrate diversity (Death 1996, Vinson and Hawkins 1998). Thus, invertebrate diversity was hypothesised to be higher at sites with larger thermal ranges but without increased flow variability (i.e., springbrooks without any major runoff-fed streams entering the main channel).

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# 1

# Spatial patterns of macroinvertebrate diversity in New Zealand springbrooks and streams

# Abstract

Invertebrate spatial patterns were examined in five rheocrene springbrooks, and five nearby runoff-fed streams in four different regions of New Zealand. Physical attributes of the springbrooks did not differ from those of the runoff-fed streams, although their streambeds were more stable. Periphyton biomass, epilithic carbon and organic matter were more abundant and more patchily distributed in springbrooks than in runoff-fed streams. Invertebrate species richness and density were greater at more stable sites, counter to the predictions of the Intermediate disturbance hypothesis and the Dynamic equilibrium hypothesis. Altitude, habitat stability and food resource levels were the best predictors of invertebrate richness, whereas pH, phosphate concentration, habitat stability and food resource levels were the best predictors of total density. Differences in invertebrate diversity between northern hemisphere and New Zealand springbrooks may be related to the larger diversity of invertebrate predators in New Zealand springbrooks, and the lack of temperature-mediated life history cues in the New Zealand invertebrate fauna. Altitude, which limits the dispersal of invertebrates, may also play an important role in determining the maximum number of invertebrate taxa in a given stream. A dispersal- stability framework is proposed to explain the observed patterns of invertebrate diversity in these streams. The general pattern of non-insect dominance in lowland springs is believed to be the result of the interaction between dispersal ability and the effects of the last glaciation.

**Key words:** Altitude, diversity, habitat stability, invertebrate communities, invertebrate dispersal, spatial patterns, spring-fed streams.

## Introduction

Biological diversity can be influenced by a dynamic array of biotic and abiotic factors that interact at different spatial and temporal scales (Ricklefs and Schluter 1993, Ricklefs 2004). Disturbance is an important structuring force in many communities (Connell 1978, Sousa 1979, Pickett and White 1985) and is often postulated as a dominant factor in models of community diversity e.g., the intermediate disturbance hypothesis (IDH) (Connell 1978), the harsh-benign hypothesis (HBH) (Menge 1976) and Huston's dynamic equilibrium hypothesis (DEH) (Huston 1994). More recently, Hubbell's neutral theory of biodiversity also included disturbance as a key mechanism in generating ecological drift, which is a random process of species replacement (Hubbell 2001). Disturbance not only affects population sizes and diversity, but also the level of resources and the structure of the habitat, which in turn will influence diversity (McCoy and Bell 1991, Waide et al. 1999, Death 2002).

In streams, disturbance (i.e., floods) is considered to be one of the major forces structuring macroinvertebrate communities (Resh et al. 1988, Lake 2000, Death 2002). Floods directly remove individuals, but they may also have indirect effects on invertebrate populations by changing the habitat. For example, higher discharges may reduce the amount of moss and macrophytes (Englund 1991, Suren 1993, Barquín and Death 2004), or scour algae and wash detritus away, which will decrease the level of habitat complexity and the amount of resources (Biggs et al. 1999, Bond and Downes 2000). Moreover, high flows can also affect habitat heterogeneity by rearranging the substrate and providing different ranges of water depths and velocities, which in turn will affect invertebrate richness (Townsend 1989, Cooper et al. 1997, Palmer and Poff 1997). Experimental work has shown that increased disturbance rates reduce the number of invertebrate individuals and species (Robinson and Minshall 1986, Death 1996, Bond and Downes 2000, McCabe and Gotelli 2000), although some studies have found low numbers of species in more stable streams (Townsend et al. 1997, Barquín and Death 2004).

In the present study, we examine invertebrate diversity patterns in springbrooks and runoff-fed streams. Springs and springbrooks are generally stable lotic habitats compared to streams (Odum 1957). A number of studies have compared spring and

stream invertebrate communities (Davidson and Wilding 1943, Ward and Dufford 1979, Meffe and Marsh 1983, Anderson and Anderson 1995, Barquín and Death 2004), and found that springs generally have lower numbers of macroinvertebrate taxa than similar downstream reaches or nearby runoff-fed streams. In contrast, a number of studies (Death 1995, Death and Winterbourn 1995, Death et al. 2004) have found the opposite pattern for New Zealand springs and streams.

We also wanted to examine whether the effect of habitat stability on invertebrate richness is consistent across different regions of New Zealand. It may be that regional factors (i.e., altitude, geology, rainfall patterns) obscure the relationship between habitat stability and invertebrate richness. Regional attributes could constrain the pool of available colonizers and therefore change the response of stream invertebrate communities to disturbance. We hypothesized that less stable habitats would be physically more homogeneous and have lower resource levels. In contrast, more stable streams were expected to support more species, as a consequence of a greater habitat complexity and resource levels. We also expected to find differences in regional diversity with regions having higher annual rainfall or altitude, being expected to have lower invertebrate richness (Cornell and Lawton 1992, Heino et al. 2003, Ricklefs 2004).

## Materials and methods

### Study Sites

Study sites were first to third order streams in Waimakariri basin and Nelson in the South Island and Ruapehu and Taranaki in the North Island of New Zealand (Appendix 1). Five springbrooks and 5 streams were sampled in Waimakariri basin and Tongariro (Ruapehu) National Park while 4 springbrooks and 4 streams were sampled in Kahurangi (Nelson) and Mt Taranaki National Parks. All springbrooks were fed by rheocrene springs, where emerging water immediately forms a stream (Danks and Williams 1991). Sites were selected so that a spring-fed stream was paired with a similar sized nearby stream, which had a larger proportion of its annual flow as surface runoff water. Samples were taken in the austral autumn (April/May) of 2001. Streams ran through colluvium deposits (Waimakariri basin), karst regions (Kahurangi-Nelson), and volcanic areas (e.g., Ruapehu and Taranaki volcanoes). All sites were stony streams without any obvious anthropogenic

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impacts. There was no macrophyte growth at any site but substratum in springs was largely covered by moss. The vegetation in the lower part of these regions is typical southern beech forest, except for Taranaki where there is Podocarp-broadleaf forest. Stream altitude varied from 20 to 1100 m a.s.l with sites at higher altitudes located in subalpine scrub.

**Physicochemical measures**

A number of physicochemical variables were measured between April and May 2001, concurrently with invertebrate sampling (see below). Conductivity and temperature were measured with an Orion 122 meter and pH with a pHTestr 2 meter. Dissolved oxygen concentration and % saturation were measured with a YSI 58 in December 2001. Current velocity was measured with a Flo-mate Marsh-McBirney 2000, in each of five 0.1 m$^2$ Surber areas. Substrate composition was assessed by counting the number of stones in each of 10 size classes (maximum width; bedrock >300, 300-128, 128-90, 90-64, 64-45, 45-32, 32-14, <14 mm, gravel and sand) collected in each Surber area. Gravel (14-3mm) and sand (<3mm) classes were estimated visually as percentage coverage of the sampled area. These measures were converted to a single substrata size index (SI) by summing the mid-point values of the size classes weighted by the number of stones in each size class (bedrock was assigned a nominal size of 400 mm for use in the calculations) (Quinn and Hickey 1990). Substrate heterogeneity was estimated using Simpson's diversity index:

$$D = \Sigma \left( \frac{n_i(n_i-1)}{N(N-1)} \right)$$

where $n_i$ = the number of stones in the $i$th size class and $N$ = the total number of stones.

Riparian cover was visually assessed as percentage stream channel shaded, the reliability of the visual assessment was not assessed. We measured streambed stability using two methods. The first was an index of stability developed for New Zealand mountain streams (Duncan et al. 1999), which calculates the maximum substrata size moved at bankfull. Once this index was calculated we estimated the percentage of substrata moved at bankfull for each site. The second method involved marking five stones in situ with a blend of red dye and quick concrete mix in each of three different

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size classes (maximum linear dimension, <55 mm; 55-90 mm; 90-180 mm). One stone from each size class was marked at five random positions along the stream channel. Any movement of the stones was recorded after four months. A score of 15 indicated no stones moved during the 4 months and 0 that all moved. A 250 ml non-filtered water sample was analyzed in the laboratory within 24 hours of collection for free inorganic nitrate and orthophosphate using ion chromatography in a Hach DR2000 UV/visible spectrophotometer. Nitrate and orthophosphate concentration were estimated by Cadmium reduction and reaction with Molybdate, respectively.

**Biological collections**

Five 0.1 m$^2$ Surber samples (mesh = 250 μm) were collected at random from riffles in each stream during April and May 2001 along a 15 - 50 m reach. Samples were preserved in 10% formalin and returned to the laboratory for identification to the lowest possible taxonomic level using available keys (Winterboum et al. 2000). This sampling strategy is focused on spatial coverage at the expense of temporal coverage, however, New Zealand macroinvertebrate communities generally vary little throughout the year (Death and Winterboum 1994, Scarsbrook 2000). Fauna was separated into functional feeding groups (FFG) following Cowie (1990), Death (1995) and Winterboum (2000).

Coarse particulate organic matter (CPOM, >1 mm) and fine particulate organic matter (FPOM, 0.25-1 mm) remaining after invertebrates were removed were also dried to constant weight at 95 °C, weighed and ashed at 550 °C for 2 h to yield ash free dry weight. In this study, CPOM included mosses, leaves and twigs. A representative stone (maximum linear dimension: 150-50 mm) was collected from each Surber area to measure epilithic carbon content, using a modified version of the technique used by Sinsabaugh et al. (1991). Organic matter was scraped from the whole stone surface with a stiff brush into a bucket, filtered through a 250 μm sieve into a known volume of water and a 60 ml sample frozen. Any organic matter and animals remaining on the 250 μm sieve were added to the Surber sample. In the lab the 60 ml sample was filtered through a pre-ashed 45 μm glass fiber filter, dried to constant weight at 95 °C, weighed and ashed at 550 °C for 2 h to yield ash free dry weight. Estimates of epilithic carbon were corrected for stone surface area calculated following Graham et al. (1988) and divided in half as

only part of the stone is exposed to colonization. Five stones without moss (maximum width: 80-25 mm) were similarly collected for measuring periphyton biomass. Stones were kept frozen until pigments were extracted in 90% acetone at 5 °C for 24 h in the dark. Absorbancies were read on a Varian-CARY 50 Conc. UV/visible spectrophotometer and converted to pigment concentration (chlorophyll *a* and phaeophytins) following Steinman and Lamberti (1996). Pigment concentration was corrected for surface area calculated following Graham et al. (1988) and divided in half to allow for the fact that only the upper stone surface is exposed to light.

**Statistical analysis**

Data from the five Surber samples were pooled together to calculate number of invertebrate taxa and individuals, CPOM, FPOM, chlorophyll *a* and epilithic carbon concentration for each site. In order to compare taxa counts among habitats with different invertebrate densities it is preferable to use rarified number of species (number of species/number of individuals) rather than species richness (number of species/area) (McCabe and Gotelli 2000). We calculated the rarified diversity values for each site using the PRIMER statistical package (Clarke and Warwick 1994). The minimum number of individuals in our sites was 131, so species richness was corrected to this density. Differences in parameters were tested with two-way analysis of variance (ANOVA) with spring-stream and region as treatments. Both were treated as fixed factors (SAS Institute Inc. 1988). Variables were log-transformed to remove heteroscedasticity if necessary. Tukey's post hoc means test was used to determine where significant differences occurred if the ANOVA revealed they were present (SAS Institute Inc. 1988).

PCA multivariate analysis was used to combine the variables measuring stability (Duncan index of instability, number of marked stones recovered, percentage of substrata moved at bankfull and quantity of moss) and level of resources (FPOM, Chlorophyll *a*, Phaeophytin and Epilithic Carbon) into indices of stability and resource availability (explaining 55 and 70% of the variation, respectively), which will be referred to as stability and productivity hereafter. We investigated the relationship between both indices and invertebrate richness in order to test the predictions of the IDH and the DEH. Relationships between number of invertebrate taxa and individuals and environmental

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variables were examined with the Spearman rank correlation procedure (SAS Institute Inc. 1988). We also examined the relationship between densities of functional feeding groups and resource levels using Spearmen rank correlation. Coefficients of variance (CV = (Variance/mean)x100) for physical parameters and resources were also examined with the same ANOVA design to explore spatial variation (heterogeneity-patchiness) in both types of streams (Crowl et al. 1997).

Patterns in community composition were examined using non-metric multidimensional scaling (NMS) with the PC-ORD statistical package (McCune and Mefford 1995). The Sorensen distance measure was used to determine similarity between samples. Initial examination of stress patterns in the data suggested three dimensions were appropriate for the final ordination, which was established with 500 iterations of the data. Relationships between the ordination axes and the measured local and regional environmental variables were examined using simple correlation and stepwise regression (SAS Institute Inc. 1988).

To determine the significance of invertebrate community differences we performed an analysis of similarities (ANOSIM) on springbrook and runoff-fed stream communities using the PRIMER statistical package (Clarke and Warwick 1994). The mean density of taxa that contributed most ($\geq$ 90%) to the dissimilarity between springs and streams was evaluated using the SIMPER procedure in the PRIMER statistical package. Bray–Curtis similarity distances were also calculated with the SIMPER procedure to compare springbrook and stream communities within and between regions.

## Results

### Physicochemical characteristics

Springbrook and stream width ranged from 0.3 to 7 m, and mean depth and current velocity from 6 to 38 cm and from 0.01 to 0.7 m/s, respectively. Springbrooks and streams did not differ overall in their physicochemical measures, except for temperature and pH, which were both higher in streams (Table 1, Appendix 2). Environmental variables differed more often between regions than between springs and streams overall; Nelson sites had the highest conductivity (276 $\mu$S/cm) and nitrate concentration (0.14 mg/ml), while Taranaki and Ruapehu had the highest phosphate concentration (0.32 and

0.38 mg/ml, respectively). Substrate size was larger in Nelson and Taranaki, which averaged more than 80 mm (Table 1 and Appendix 2). Although dissolved oxygen may be expected to be lower in spring-fed streams, oxygen concentration was close to saturation at all sites. Canopy cover did not exceed 60% of channel shade at any site and was significantly higher in Taranaki than any other region. Overall stability and resource abundance indices were larger for springbrooks than for streams (Appendix 2). Coefficients of Variation (CVs) of physical attributes were not different between springbrook and stream habitats (Table 1). These results indicate that for the range of measures sampled, springbrooks and streams may be thought of as having similar habitat attributes and physical variation, the stability of the habitat being the only major difference.

**Periphyton, organic matter and epilithic carbon**

Overall, spring-fed streams had more than twice the periphyton biomass and epilithic carbon than runoff-fed streams and nearly 5 times more particulate organic matter (Fig. 1, Table 1 and Appendix 2). Nelson had 3 times more periphyton biomass than any other region (Fig. 1, Table 1 and Appendix 2), but there was no significant difference in organic matter and epilithic carbon between regions (Table 1). Habitat stability (PCA index) enhanced the amount of organic matter ($r_s$= 0.66), algal pigment concentration ($r_s$= 0.62) and epilithic carbon ($r_s$= 0.61). Organic matter, algal pigment concentration and epilithic carbon had larger coefficients of variance in springbrooks than in streams (Table 1). Habitat stability, thus, increased the amount of all food resource types, and created greater heterogeneity in the distribution of these food resources.

**Invertebrate abundance and diversity patterns**

Twelve non-insect and 96 insect taxa were collected in this study. We collected more taxa from springbrooks (102) than from streams (81), with 75 taxa common to both habitats. The number of taxa collected in each region was quite similar, 78 were collected in Nelson, 76 in Ruapehu and Taranaki and 75 in Waimakariri. Total number of macroinvertebrate taxa and individuals collected at each site were higher for springbrooks than for streams (Fig. 2, Table 1).

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**Table 1** Two way ANOVA results for region and spring/stream factors testing for differences in invertebrate community metrics, level of resources, physicochemical variables, and coefficients of variance of resource and physical parameters measured in New Zealand, in the autumn of 2001. Kendall rank correlation coefficients with axes one and two of NMDS, and Spearman rank correlations with number of invertebrate taxa (Tx) and individuals (Ind.) are also given. W= Waimakariri, N= Nelson, R= Ruapehu, T= Taranaki, Sp= Springs, St= Streams, *= p 0.05-0.01, **= p < 0.01, - separates significantly different means.

| | Region $F_{3,28}$ | Tukey's | Sp/St $F_{1,28}$ | Tukey's | Interaction $F_{3,28}$ | Axis 1 | Axis 2 | Tx | Ind. |
|---|---|---|---|---|---|---|---|---|---|
| er of Individuals | 3.93 * | WNR-NRT | 9.42 ** | Sp > St | 3.18 * | | | | |
| er of Taxa | 1.95 | | 4.08 * | Sp > St | 0.04 | | | | |
| ed number of taxa | 1.61 | | 1.43 | | 1.75 | | | | |
| on's index of diversity | 0.66 | | 0.12 | | 1.02 | | | | |
| ophyll *a* | 5 * | N-WRT | 9.82 * | Sp>St | 2.23 | 0.28 * | 0.16 | 0.4 * | 0.5 ** |
| ic Carbon | 1.38 | | 10.8 * | Sp>St | 2.52 | 0.3 * | 0.39 * | 0.36 * | 0.43 ** |
| 1 | 0.53 | | 16.55 ** | Sp>St | 0.53 | 0.18 | 0.44 * | 0.45 ** | 0.23 |
| I | 4.18 * | RNW-NWT | 13.76 ** | Sp>St | 1.71 | 0.02 | 0.41 * | 0.26 | 0.01 |
| | 6.25 * | RNT-TW | 4.62 * | Sp<St | 0.68 | -0.42 * | -0.03 | -0.18 | -0.44 ** |
| erature | 8.54 ** | WNR-T | 8.7 ** | Sp<St | 1.09 | 0.18 | -0.1 | 0.06 | 0.12 |
| ictivity | 16.13 ** | N-RT-TW | 0.02 | | 0.24 | 0.09 | -0.16 | 0.21 | 0.19 |
| es | 6.33 ** | NR-RWT | 1.99 | | 0.44 | 0.14 | -0.11 | -0.12 | 0.26 |
| hates | 18.26 ** | RT-NW | 0.34 | | 3.59 * | -0.4 * | -0.02 | -0.18 | -0.55 ** |
| ie | 20.96 ** | R-WT-N | 0.67 | | 0.1 | -0.03 | 0.14 | -0.44 ** | -0.23 |
| y Cover | 7.44 ** | TN-NRW | 0.32 | | 0.38 | -0.39 * | 0.26 * | 0.37 * | -0.33 |
| arge | 1.32 | | 0.1 | | 1.46 | 0.05 | -0.28 * | -0.06 | 0.03 |
| width | 1.3 | | 0.65 | | 1.12 | 0.08 | -0.22 | 0.24 | 0.1 |
| depth | 3 | | 0.02 | | 2.38 | -0.03 | -0.21 | -0.12 | 0.02 |
| velocity | 0.72 | | 0.32 | | 3.37 * | -0.01 | -0.14 | -0.26 | -0.13 |
| ate heterogeneity | 1.24 | | 0.24 | | 1.72 | 0.08 | 0.03 | 0.12 | 0.2 |
| ate size index | 5.57 * | TN-NW-WR | 0.02 | | 1.19 | -0.03 | -0.12 | 0.22 | 0.12 |
| ty | 5.41 * | WNT-NTR | 60.55 ** | Sp>St | 1.39 | 0.26 * | 0.46 * | 0.44 ** | 0.38 * |
| ctivity | 3.73 * | NWR-WRT | 13.91 ** | Sp>St | 1.32 | 0.31 * | 0.22 | 0.35 * | 0.49 ** |
| OM | 0.16 | | 7.49 * | Sp > St | 0.84 | | | | |
| OM | 1.73 | | 2.92 | | 0.26 | | | | |
| lorophyll *a* | 0.4 | | 14.45 ** | Sp > St | 1.44 | | | | |
| ilithic Carbon | 0.43 | | 5.37 * | Sp > St | 1.12 | | | | |
| 50 | 2.49 | | 0.08 | | 0.51 | | | | |
| idth | 0.77 | | 0.59 | | 1.16 | | | | |
| epth | 1.08 | | 1.61 | | 3.2 | | | | |
| elocity | 2.01 | | 0.29 | | 0.46 | | | | |

There were no significant differences in total number of taxa between regions, but Waimakariri and Nelson had significantly more individuals than Taranaki (Fig. 2, Table 1). Species evenness was not different between springbrooks and streams or between

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regions, as indicated by Simpson's index of diversity (Fig. 2, Table 1). Springbrooks and streams had similar relationships between invertebrate richness and number of individuals, as indicated by the rarefied number of taxa. Our results showed no evidence of a decrease in invertebrate richness with increasing stability, or unimodal relationships predicted by the IDH (Fig. 3). Invertebrate richness did not peak at intermediate levels of disturbance and resource availability, and thus provided no support for the DEH (Fig.3).
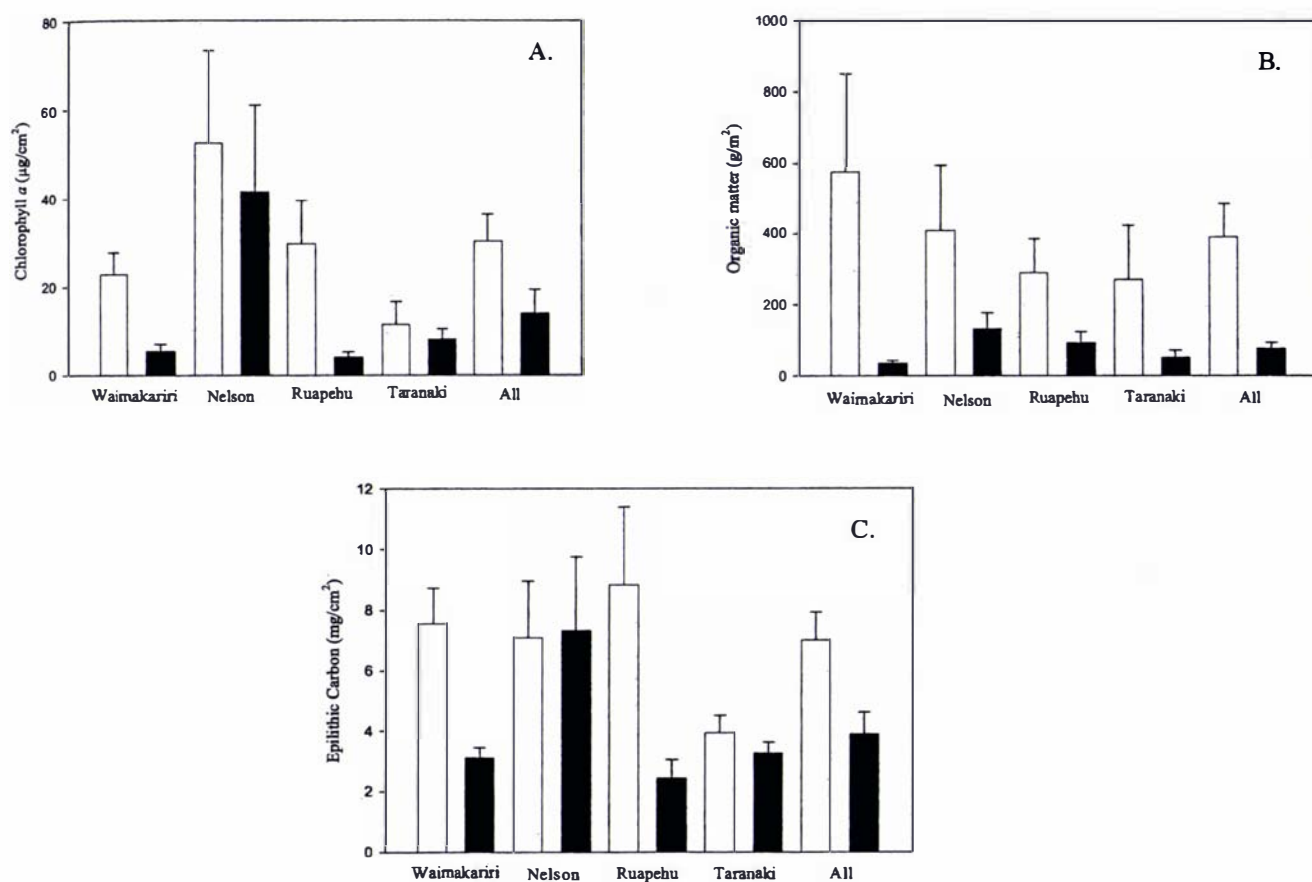


**Figure 1** Mean (± 1 SE) A. Chlorophyll *a* B. Organic matter C. Epilithon carbon collected in 5 Surber samples in springs (open bars) and streams (solid bars) in four regions of New Zealand, in the autumn of 2001.

Spearman rank correlations of habitat characteristics with community metrics revealed altitude, canopy cover, stability and productivity indices, periphyton biomass, organic matter and epilithic carbon were most strongly correlated with invertebrate

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richness (Table 1), whereas pH, phosphate concentration, stability and productivity indices, periphyton biomass and epilithic carbon were most strongly correlated with total density (Table 1).
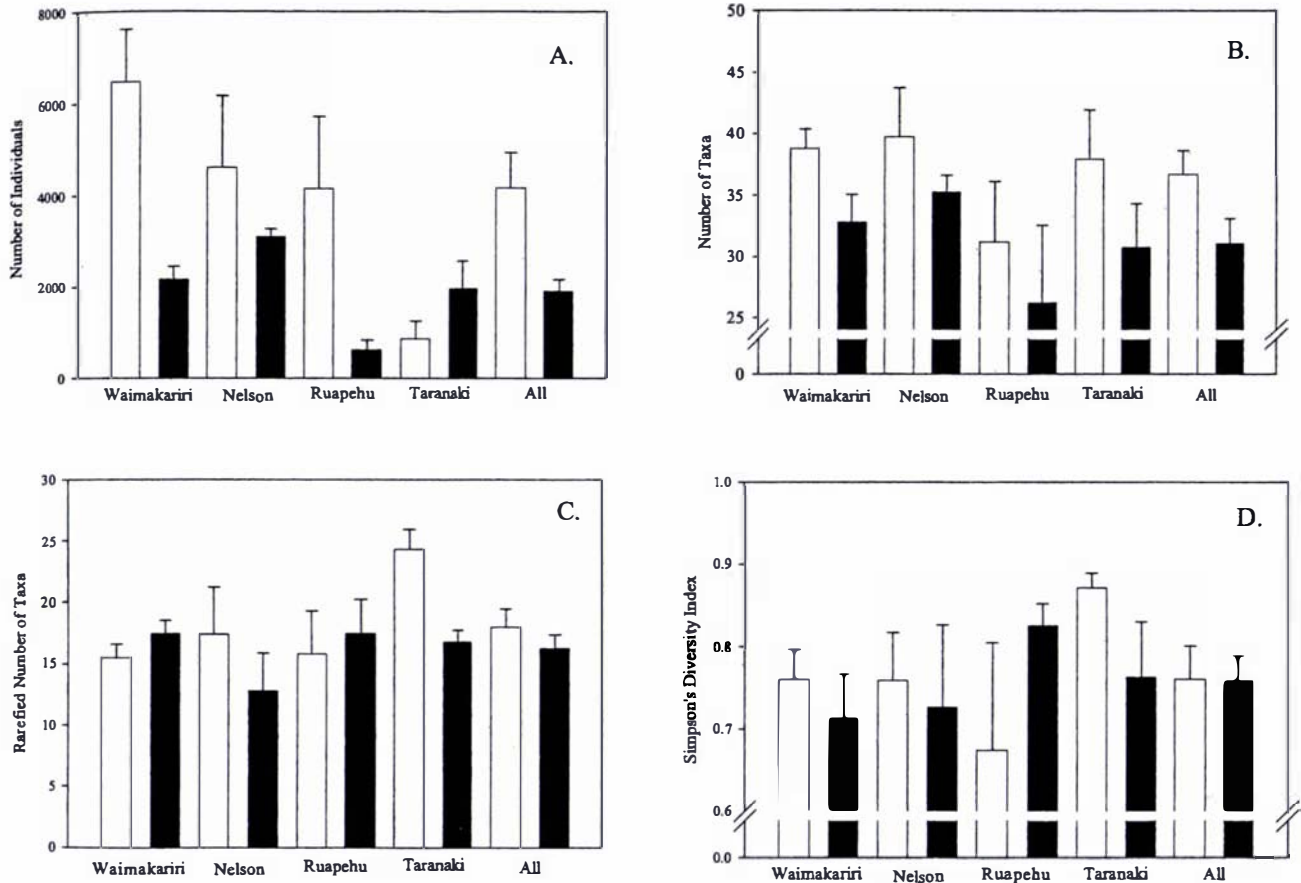


**Figure 2** Mean (± 1 SE) A. number of individuals, B. number of taxa, C. rarified taxa number and D. Simpson's diversity index for invertebrate communities in springs (open bars) and streams (solid bars) in four regions of New Zealand, in the autumn of 2001.

## Community structure

Taxonomic composition

Overall, Coleoptera, Diptera, Ephemeroptera and Plecoptera had similar richness in both springs and streams, although Trichoptera had a higher number of taxa ($F_{1,28}$ =3.44, p <0.07) in springbrooks (36) than in streams (27). There were twice as many non insect taxa in spring-fed (12) than runoff-fed streams (7) ($F_{1,28}$ =22.05, p <0.001).

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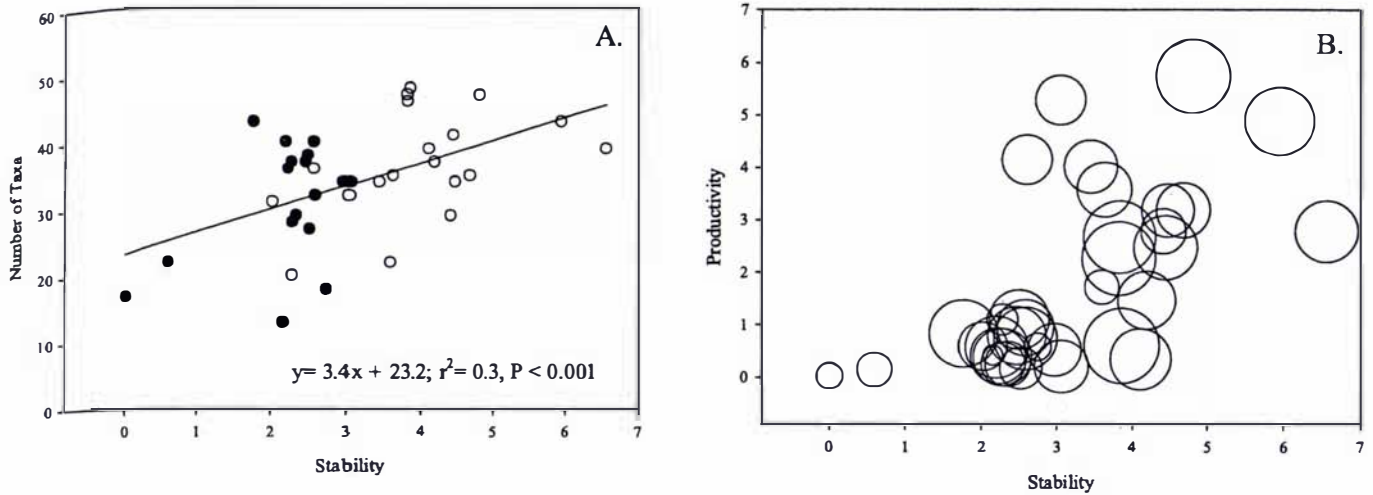
**Figure 3** Number of invertebrate taxa as a function of A. Habitat stability and B. Habitat stability and productivity collected in spring-fed (●) and runoff-fed (○) streams in four regions of New Zealand, in the autumn of 2001. The size of the circles in figure B. is a function of the number of invertebrate taxa.

Numerically, insects dominated both spring and stream communities. Few of the most abundant taxa presented a consistent abundance pattern between springs and streams. The mayfly *Deleatidium* spp., the caddis *Aoteapsyche* spp. and *Hydora* sp. were some of the few taxa which consistently had higher densities in streams, with *Deleatidium* spp. numerically dominating stream communities in all regions. Chironomid larvae comprised 29% overall of spring-fed stream communities, and 13% of runoff-fed stream communities (Fig.4, Table 2), but when we look at each region independently we find that they are only present at higher densities in springbrooks of the Waimakariri basin and Ruapehu (Fig. 4). Members of the cased caddisfly family Conoesucidae also had greater densities in springbrooks than in streams, although different species were found in different regions. The only members of the Conoesucidae, which had higher densities in runoff-fed streams were *Pycnocentrodes* spp. and *Beraeoptera roria* (Fig. 4, Table 2).

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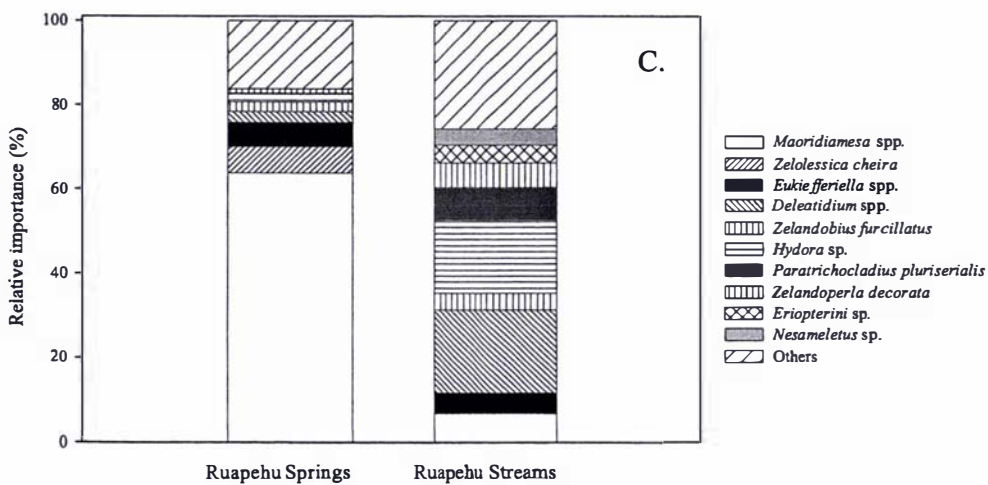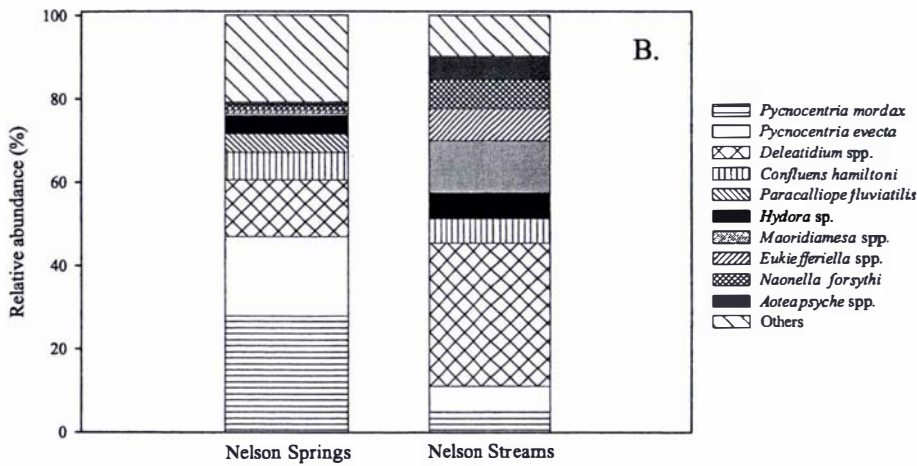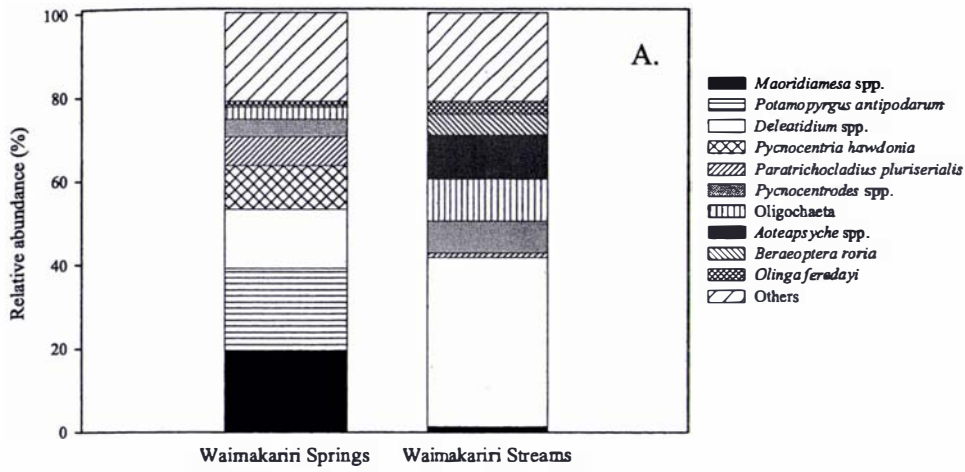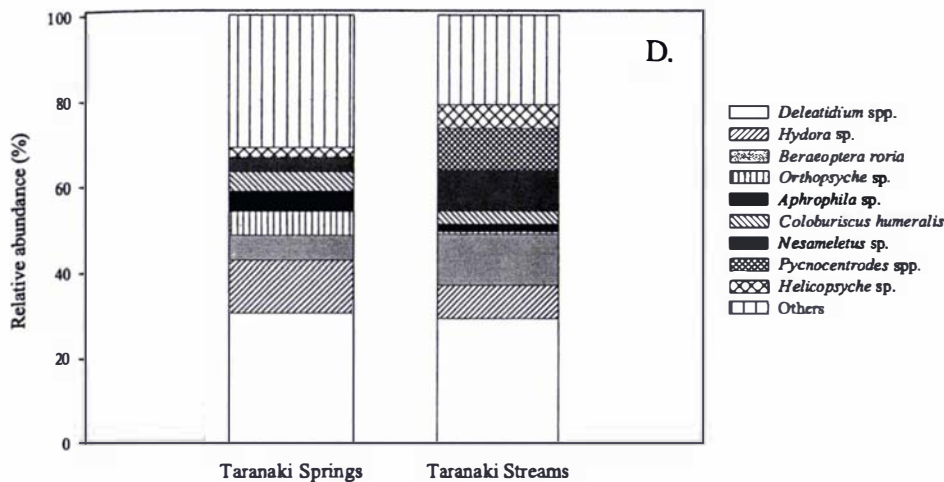
**Figure 4** Relative abundance of key taxa in A. Waimakariri, B. Nelson, C. Ruapehu, and D. Taranaki collected in New Zealand, in the autumn of 2001.

Some taxa exhibited high densities in springbrooks and very low densities in runoff-fed streams, independent of the region (Fig. 4). These included the mayfly genus _Austroclima_ spp., the caddis genera _Orthopsyche_, _Zelolessica_ and _Oxyethira_, the amphipods _Paracalliope fluviatilis_ and _Paraleptamphopus subterraneus_ and the snail _Potamopyrgus antipodarum_.

ANOSIM indicated that overall spring and stream communities were different from each other (R= 0.17, P < 0.01). Different regions also had different invertebrate communities (R= 0.22, P < 0.01), with North and South Island macroinvertebrate communities being significantly different from each other, although no differences were found between regions within either the North or South island regions (Table 3). Invertebrate composition was most similar between Taranaki sites and most dissimilar between Ruapehu sites (Table 4). Springbrook communities showed greater variability between sites than stream communities, within and between regions (Table 4). The reason for these differences may be that runoff-fed streams were generally dominated by chironomid larvae, the mayfly _Deleatidium_ spp., the trichopterans _Aoteapsyche_ spp., _B. roria_ and _Pycnocentrodes_ spp. and the beetle _Hydora_ spp. in most regions, whereas springbrooks accumulated a larger proportion of rare taxa and were dominated by different taxa depending on the region.

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**Table 2** Average abundance of taxa differentiating spring-fed and runoff-fed stream communities collected in New Zealand, in the autumn of 2001. ANOVA results testing for differences in abundance of these taxa between springs and streams, and Kendall rank correlation coefficients of these taxa with axes one and two of NMDS are also given. Taxa are listed in order of decreasing importance in differentiating spring and stream communities. Bold characters indicate significant differences and correlations, $p < 0.05$.

| | Mean Abundance (± 1 SE) | | | | | |
| | Springs | | Streams | | F | Axis 1 | Axis 2 |
|---|---|---|---|---|---|---|---|
| *Maoridiamesa* spp. | 1073.33 | ± 500.36 | 116.67 | ± 58.82 | 0.17 | **0.46** | **-0.38** |
| *Deleatidium* spp. | 481.28 | ± 158.75 | 642.83 | ± 127.8 | 0.63 | **0.22** | **-0.30** |
| *Potamopyrgus antipodarum* | 384.44 | ± 189.54 | 1.56 | ± 0.67 | 0.17 | **0.35** | **0.32** |
| *Pycnocentria mordax* | 287.50 | ± 198.21 | 0.28 | ± 0.28 | **14.47** | 0.17 | 0.02 |
| *Hydora* sp. | 89.33 | ± 28.68 | 119.00 | ± 40.00 | 0.21 | **-0.21** | -0.10 |
| *Pycnocentria hawdonia* | 187.00 | ± 131.6 | 0.39 | ± 0.27 | **13.48** | **0.36** | 0.13 |
| *Aoteapsyche* spp. | 14.33 | ± 8.39 | 124.61 | ± 37.67 | **10.11** | 0.04 | **-0.39** |
| Oligochaeta | 84.28 | ± 25.37 | 78.94 | ± 48.94 | 2.72 | **0.31** | **0.31** |
| *Confluens hamiltoni* | 68.61 | ± 60.31 | 42.22 | ± 30.72 | 0.43 | 0.01 | -0.10 |
| *Paratrichocladius pluriserialis* | 128.00 | ± 124.34 | 29.67 | ± 9.32 | 0.7 | 0.10 | -0.16 |
| *Pycnocentrodes* spp. | 74.94 | ± 54.62 | 88.33 | ± 43.92 | 0.01 | 0.14 | -0.06 |
| *Pycnocentria evecta* | 219.17 | ± 191.53 | 6.89 | ± 5.74 | 0.01 | **0.24** | **0.22** |
| *Eukiefferiella* spp. | 80.72 | ± 50.67 | 67.67 | ± 40.61 | 2.58 | **0.28** | **-0.28** |
| *Beraeoptera roria* | 27.89 | ± 12.8 | 90.56 | ± 50.73 | **5.4** | 0.07 | -0.08 |
| *Naonella forsythi* | 61.17 | ± 25.3 | 70.83 | ± 45.23 | 0.01 | 0.16 | 0.15 |

Stability and level of resources were positively correlated with axes one and two, while pH and phosphate concentration were negatively correlated with axis one (Table 1). The NMDS corroborates the importance of geography and habitat stability in differentiating invertebrate communities. Moreover, springbrook communities are more dispersed in the ordination than the runoff-fed stream communities, indicating larger differences between springbrook than stream communities.

NMDS graded spring and runoff-fed stream communities along axis 2 (Fig. 5). North Island sites occurred to the left of axis one and South Island sites to the right. Axes one and two explained 38% and 21% of the total variance, respectively. Final stress for

the NMDS analysis was 11.77, indicating a reliable ordination (McCune and Mefford 1995).

**Table 3** ANOSIM results testing differences between regions of macroinvertebrate communities collected in New Zealand, in the autumn of 2001. Bold characters indicate significant differences between regions, $p < 0.05$.

| Regional Comparisons | R-Statistic |
|---|---|
| Waimakariri / Nelson | 0.095 |
| Waimakariri / Ruapehu | **0.314** |
| Waimakariri / Taranaki | **0.277** |
| Nelson / Ruapehu | **0.308** |
| Nelson / Taranaki | **0.189** |
| Ruapehu / Taranaki | 0.139 |

**Table 4** Bray-Curtis similarity distances for spring-fed and runoff-fed stream invertebrate communities collected in New Zealand, in the autumn of 2001. The left part of the tabulation contains similarity distances calculated for all sites and for spring and runoff-fed streams in each region, whereas the right part includes similarity distances between spring or runoff-fed streams across regions. A= Waimakariri, N= Nelson, R= Ruapehu and T= Taranaki.

| Region | All Sites | Spring Communities | Stream Communities | W | N | R | T |
|---|---|---|---|---|---|---|---|
| W | 26 | 25.8 | 49.8 | Springs | 40.2 | 19.4 | 40.1 |
| N | 27.4 | 22.9 | 36.2 | 11.5 | | 16.8 | 32.5 |
| R | 18 | 20.9 | 26.2 | 15.6 | 10.6 | | 24 |
| T | 31.7 | 26.6 | 37.5 | 6.7 | 17.5 | 14.8 | Streams |
| Overall | | 15.1 | 30.1 | | | | |
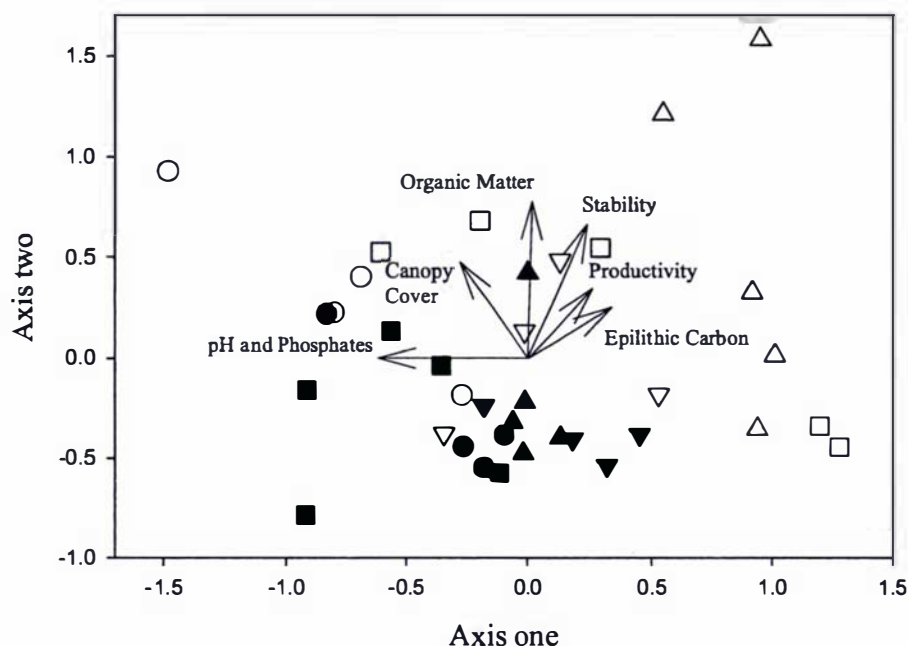
**Figure 5** Non metric multidimensional scaling (NMDS) plot of axis 1 against axis 2 for mean invertebrate communities collected in four regions of New Zealand, in the autumn of 2001. Regions are denoted as follows: Waimakariri (Springs: △; and Streams: ▲), Nelson (Springs: ▽; and Streams: ▼), Ruapehu (Springs: □; and Streams: ■) and Taranaki (Springs: ○; and Streams: ●).

Functional feeding group (FFG) composition

Diversity of FFGs was not different between regions or springbrooks and streams, except for predators which were more diverse in Nelson than in Ruapehu, and sessile browsers (SB) which were more diverse in springbrooks than in streams (Table 5). Mobile browsers (MB), SB and predators were less abundant in Taranaki than in other regions. Predators were two times more abundant in springbrooks, whereas filterers were two times more abundant in streams (Table 5). SB dominated springbrook communities in the Waimakariri basin and Ruapehu, while MB dominated springbrooks in Nelson, because of the large densities of chironomids and *Potamopyrgus*, and the trichopteran family Conoesucinae, respectively. SB were correlated with algal pigment concentration and epilithic carbon, while MB were correlated with algal pigment concentration (Table 5). Predator densities were best predicted by the total number of invertebrate individuals. We

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believe that the high correlation coefficients between level of resources and predator densities are a byproduct of the correlation between resources and total number of invertebrate individuals (Table 1).

**Table 5** Spearman rank correlations of level of resources with density of invertebrate functional feeding groups (FFG) collected in New Zealand, in the autumn of 2001. Two way ANOVA results testing for differences in region and spring/stream factors for density and diversity of FFG are also given. W= Waimakariri, N= Nelson, R= Ruapehu and T= Taranaki Sp = Springs, St = Streams, * = p 0.05-0.01, ** = p < 0.01.

| | CPOM | FPOM | Chlorophyll a | Phaeophytin | Epilithic Carbon | Individuals |
|---|---|---|---|---|---|---|
| Mobile Browser | 0.14 | 0.03 | 0.32* | 0.47** | 0.5** | |
| Sessile Browser | 0.21 | -0.1 | 0.41* | 0.45** | 0.26 | |
| Predator | 0.45* | 0.25 | 0.54* | 0.68** | 0.63** | 0.8** |
| Filterer | -0.24 | -0.33 | 0.07 | -0.01 | -0.11 | |
| Shredder | 0.09 | 0.05 | 0.21 | 0.22 | 0.1 | |

| | Region | | Spring/Stream | | Interaction | |
|---|---|---|---|---|---|---|
| | $F_{3,28}$ | Tukey's | $F_{1,28}$ | Tukey's | $F_{3,28}$ | |
| Diversity | | | | | | |
| Mobile Browser | 2.14 | | 0.02 | | 1.04 | |
| Sessile Browser | 2.42 | | 4.8* | Sp>St | 0.4 | |
| Predator | 3.77 | NWT-WTR | 3.06 | | 0.15 | |
| Filterer | 0.38 | | 3.28 | | 0.15 | |
| Shredder | 0.49 | | 3.05 | | 1.06 | |
| Density | | | | | | |
| Mobile Browser | 8.07** | WRN-T | 2.91 | | 4.86** | |
| Sessile Browser | 7.85** | NWT-WTR | 1.31 | | 2.42 | |
| Predator | 5.55** | WNR-NRT | 4.69* | Sp>St | 2.33 | |
| Filterer | 2.01 | | 4.94* | St>Sp | 0.82 | |
| Shredder | 0.33 | | 0.33 | | 0.83 | |

## Discussion

This study supports the hypothesis that more stable lotic habitats harbor higher invertebrate richness and densities. The springbrooks and runoff-fed streams in this study did not differ in their physicochemical characteristics or heterogeneity, but did differ in

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stream bed stability. Habitat productivity, complexity (moss growth and CPOM) and patchiness of food resources (higher CVs) were also greater in the springbrooks studied than in the streams. Several other studies have found habitat stability to be associated with high standing crops of moss, organic matter and algae (Englund 1991, Biggs et al. 1999, Barquín and Death 2004). Our results coincide with those of Beisel et al. (1998), who showed that at the reach level heterogeneity associated with organic habitat characteristics (i.e. algae, biofilms, moss) could be more important in influencing invertebrate diversity and abundance than physical heterogeneity.

Stable habitats were associated in the present study with high numbers of invertebrate taxa and individuals. Most of the experimental work relating to disturbance and invertebrate richness also supports the view that substrate stability enhances invertebrate diversity (Robinson and Minshall 1986, Death 1996, Vinson and Hawkins 1998, Bond and Downes 2000, McCabe and Gotelli 2000). This does not provide support for the intermediate disturbance hypothesis (Connell 1978) or the dynamic equilibrium hypothesis (Huston 1994), which predict a peak of diversity at intermediate levels of disturbance and productivity. We believe the higher levels of food resources and the greater levels of habitat complexity (moss) in springbrooks may be responsible for the higher invertebrate diversity and densities.

Our results are consistent with other studies carried out in New Zealand where invertebrate richness was higher in spring-fed streams than in nearby runoff-fed streams (Death 1995, Death and Winterboum 1995, Death et al. 2004) but contrasts with previous research comparing invertebrate communities from Northern Hemisphere springs and runoff-fed streams which found the reverse pattern (Davidson and Wilding 1943, Meffe and Marsh 1983, Anderson and Anderson 1995, Barquín and Death 2004). Two reasons have been given for lower invertebrate richness in Northem Hemisphere springs. Firstly, biotic interactions will be stronger as a result of flow constancy and may thus reduce diversity by predation on rarer taxa (Glazier 1991, Zollhöfer 1999, Barquín and Death 2004). Secondly, constant temperature regimes will reduce thermal niches and/or eliminate thermal cues for life history patterns, which may also eliminate some taxa (Lehmkuhl 1972, Van Gundy 1973). However, in the present study the more stable habitats harboured the higher numbers of invertebrate taxa.

Why then are New Zealand spring-fed streams, with similar physical attributes to Northern Hemisphere springs, more diverse than the runoff-fed streams? We believe that these differences may be partially explained if we examine the type of invertebrate communities found in Northern and Southern Hemisphere springbrooks. First, the predator community in Northern Hemisphere springs is essentially composed of large populations of amphipods (Glazier 1991, Zollhöfer 1999, Barquín and Death 2004), whereas in this study the spring predator community is much more diverse and composed of Diptera, Ephemeroptera, Plecoptera, Trichoptera, Megaloptera and other non-insect taxa. Predators in the present study did not reach such large densities as in Northern Hemisphere springs, but they still were twice as abundant in springbrooks as in runoff-fed streams (Table 5). Higher predator pressure in springs is consistent with the Harsh-benign hypothesis (Menge 1976), of higher predation pressure in more benign habitats. We hypothesize that the higher diversity of invertebrate predators in New Zealand springs than in Northern Hemisphere springs may be responsible for maintaining total invertebrate diversity, as predators may be regulating each others densities. Secondly, New Zealand stream insect life cycles in general are not synchronous or closely tied to thermal cues (Winterbourn 1997, Scarsbrook 2000). Thus, New Zealand insect life history patterns will be less affected by the thermal constancy of springs than the Northern Hemisphere insect fauna.

Finally, some may argue that the observed reverse pattern in invertebrate diversity between Northern and Southern Hemisphere spring and runoff-fed streams can be caused by higher rates of disturbance in runoff-fed streams in Southern than in Northern Hemisphere runoff-fed streams (Winterbourn et al. 1981, Lake et al. 1985). However, some studies have shown that Northern hemisphere streams can have as much rainfall and be as unpredictable as the New Zealand streams included in this study (Barquín and Death 2004). Moreover, the streams in the present study are located in four different regions and thus have distinct rainfall patterns (Appendix 1). The consistency of the invertebrate diversity patterns within the four New Zealand regions helps to support the view that the differences in invertebrate diversity patterns between Northern Hemisphere and New Zealand springbrooks are largely due to the different attributes of the invertebrate communities inhabiting these systems.

Both regional and spring/runoff-fed stream factors were important in differentiating invertebrate communities. Regions were more important in determining community composition in springbrooks, with replacements of chironomids and Conoesucidae taxa between regions, while runoff-fed streams had a core of chironomid larvae, the mayfly *Deleatidium* spp., the trichopterans *Aoteapsyche* spp., *B. roria* and *Pycnocentrodes* spp. and the beetle *Hydora sp*. Other studies in New Zealand have also found that stable streams present a more clearly site-specific faunal composition than unstable streams, which are usually dominated by chironomids and the mayfly *Deleatidium spp.* (Death 1995, Winterboum 1997). These results indicate that the selected regions may be covering different invertebrate distribution ranges, whereas bed stability selects taxa which are able to survive under more severe disturbance conditions.

The limestone geology of the Nelson region results in greater water conductivity and nitrate concentration and in turn higher periphyton biomass. Harding et al. (1997) argued that differences in number of invertebrate taxa between eco-regions in the South Island of New Zealand may be attributed to differences in climate, geomorphology, catchment vegetation and past biogeographical events. In the present study, Taranaki had the largest annual rainfall (more than 5000 mm in 2001, unpublished data), while the Ruapehu volcano erupted last in 1996 impacting streams on the east side of the mountain (Neall et al. 1999). However, we did not observe significant differences in invertebrate diversity between regions (Number of taxa =78 in Nelson, 76 in Ruapehu & Taranaki and 75 in Waimakariri) despite differences in rainfall patterns, geomorphology, glaciation and volcanism histories. These results suggest that invertebrate regional diversity mirrors variation in local species richness, and is expected when local habitat conditions are more important in determining patterns of invertebrate diversity than regional attributes (Heino et al. 2003).

One of the most striking results is the numeric dominance of insects in all the spring-fed streams included in this study. The literature on spring invertebrate faunas suggests non-insect dominate in lowland spring-fed streams with a change to insect-dominance at higher altitudes (Table 6). Our study sites ranged from 20 to 1100 m a.s.l., so it is surprising that non-insect taxa were not dominant in any of the lowland

springbrooks. However, other studies in New Zealand lowland springs (Table 6) demonstrate dominance of non-insect fauna.

**Table 6** Altitude, invertebrate richness and dominance of benthic communities in spring systems located in the Northern and Southern Hemispheres. Sampling effort was different between studies. *= altitude was estimated from a reference point given in the study paper, += number of families, ++ =just chironomids, n.g.= not given.

| Location | Spring Type | Geology | Altitude | Number of Taxa | Dominance | Reference |
|---|---|---|---|---|---|---|
| h hemisphere | | | | | | |
| rica | | | | | | |
| ut Basin, USA | Rheocrene | Granite /Limestone | <116 | n.g. | Non-Insect | (Myers and Resh 2002) |
| is, USA | Rheocrenes | Limestone | 107-134 | n.g. | Non-Insect | (Webb et al. 1995) |
| ucky, USA | Rheocrene | Limestone | <200 | 9-31 | Non-Insect | (Minshall 1968) |
| nto, Canada | Rheocrene | Limestone | 150 | 60 | Insects | (Williams and Hogg 1988) |
| , USA | Rheocrene | Dolomite | 280 | 12 | Non-Insect | (Butler 1984) |
| iessee, USA | Rheocrene | Limestone | 300* | 9-17 | Insects | (Wilhm 1970) |
| hington, USA | Mix | Igneous rock | 340 | 18-27 | Non-Insect | (Davidson and Wilding 1943) |
| ka, USA | Rheocrene | Alluvial | 350 | 1-14 | Insects | (Laperriere 1994) |
| omia, USA | Rheocrene | n.g. | 486 | 8-11 | Insects | (Resh 1983) |
| iessee, USA | Rheocrene | Limestone | 600* | 47 | Insects | (Stern and Stern 1969) |
| Appalachians, | Rheocrene | Limestone | <650 | 26 | Non-Insect | (Gooch and Glazier 1991) |
| na, USA | Rheocrene | Alluvial | 800 | 27-46 | Non-Insect | (Meffe and Marsh 1983) |
| rado, USA | Rheocrene | Limestone | 1597 | 36-43 | Insects | (Ward and Dufford 1979) |
| o, USA | Rheocrene | Alluvial | 2083 | n.g. | Insects | (Robinson and Minshall 1998) |
| omia, USA | Rheocrene | Igneous rock | 1963-2408 | 9-17 + | Insects | (Erman 1998) |
| ral Plains, USA | Mix | Varied | 990-2500 | 6-38 ++ | Insect | (Blackwood et al. 1995) |
| pe | | | | | | |
| nark | Helocrene | Limestone | <116 | >20 | Non-Insect | (Thorup 1970) |
| nark | Rheocrene | Limestone | <120 | n.g. | Non-Insect | (Iversen 1988) |
| den | Rheocrene | Glacial-fluvial | <200 | 12-17 | Insects | (Hoffsten and Malmqvist 2000) |
| and | Rheocrene | Limestone | 145-203 | 12-32 | Non-Insect | (Smith et al. 2003) |
| n | Rheocrenes | Limestone | 110-540 | 18-27 | Non-Insect/Insect | (Barquín and Death 2004) |
| zerland | Rheocrenes | Limestone | 362-905 | 10-30 | Non-Insect/Insect | (Zollhöfer 1999) |
| zerland | Rheocrenes | Glacial | >2000 | 24.6 | Insect | (Klein and Tockner 2000) |
| zerland | Rheocrenes | Glacial | 2280-2450 | 93 | Insect | (Fureder et al. 2001) |
| | Rheocrenes | Glacial | 2850 | 15-30 | Insect | (Kownacki 1991) |
| th hemisphere | | | | | | |
| Zealand | Rheocrene | Glacial-alluvial | <100 | 9 | Non-insect | (Marshall 1973) |
| Zealand | Limnocrene | Limestone | <100 | 4-34 | Non-insect | (Michaelis 1977) |
| Zealand | Rheocrene | Glacial-alluvial | 580-790 | 74-92 | Insects | (Death and Winterbourn 1995) |
| Zealand | Rheocrene | Greywacke | 850 | 33 | Insects | (Cowie and Winterbourn 1979) |
| Zealand | Rheocrene | Volcanic-glacial-karst | 20-1100 | 3-47 | Non-Insect/Insect | (Death et al. 2004) |

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This pattern is consistent across different continents and it may be a consequence of the convergence of two vectors: insects which are believed to have become aquatic in headwater streams and crustaceans and molluscs which have reached streams from the marine environment (Vannote et al. 1980, Statzner and Higler 1985). However, some studies in more northern countries have found higher insect dominance at low elevations (Williams and Hogg 1988, Laperriere 1994, Hoffsten and Malmqvist 2000), which may be a reflection of past glaciations (Death et al. 2004).

Altitude was one of the best predictors of invertebrate richness, with lower altitude sites having the richest communities (Fig. 6). Other studies have also reported lower invertebrate richness at higher altitude because of glaciation, climatic changes, isolation and the direct effect of temperature (Kownacka and Kownacki 1972, Ormerod et al. 1994, Ward 1994, Jacobsen et al. 1997). When we consider the combined effects of altitude and habitat stability simultaneously, we find that altitude sets the upper limit to invertebrate richness and habitat stability determines the number of invertebrate taxa for a given altitude (Fig. 6). We believe altitude acts by limiting invertebrate dispersal. For example, elevation has been shown to decrease wing length in some adult Plecoptera (Ward and Stanford 1982) and lower temperatures reduce Trichoptera adult activity (Ward et al. 1996). The main dispersal mechanism between streams for insects is flying adults (Ward 1992) while for non-insect taxa it is movement upstream (Minckley 1964, Hughes 1969, Butler IV and Hobbs III 1982). Non-insect taxa thus, will need stable flows to be able to colonize upper reaches, whereas flying insects will be highly dependent on temperature (Ward and Stanford 1982, Ward 1992). We observed in this study that springbrook invertebrate communities are more different from each other than from runoff-fed stream communities (see above). This result can be explained by a dispersal-stability framework. Springbrooks may harbour a bigger proportion of the pool of available species at a given altitude because flow constancy allows those taxa that reach the stream to remain. On the other hand, the flow variability of runoff-fed streams only allows for taxa which resist or recover quickly after a disturbance (e.g., chironomids, *Deleatidium* spp., *Aoteapsyche* spp., *B. roria*, *Pycnocentrodes* spp. and the beetle *Hydora* sp.). Thus, dispersal limits regional diversity and habitat stability limits local scale diversity.

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Limited dispersal of stream invertebrate fauna between New Zealand's North and South Islands (separated by Cook Strait) also explains the observed differences in invertebrate community composition between both islands. A similar dispersal-disturbance framework has already been suggested by other authors (Palmer et al. 1996) to explain local dynamics of marine and stream benthic invertebrate communities. Stochastic dispersal and ecological drift generated by disturbance also constitute the basis for the recent unified neutral theory of biodiversity (Hubbell 2001).
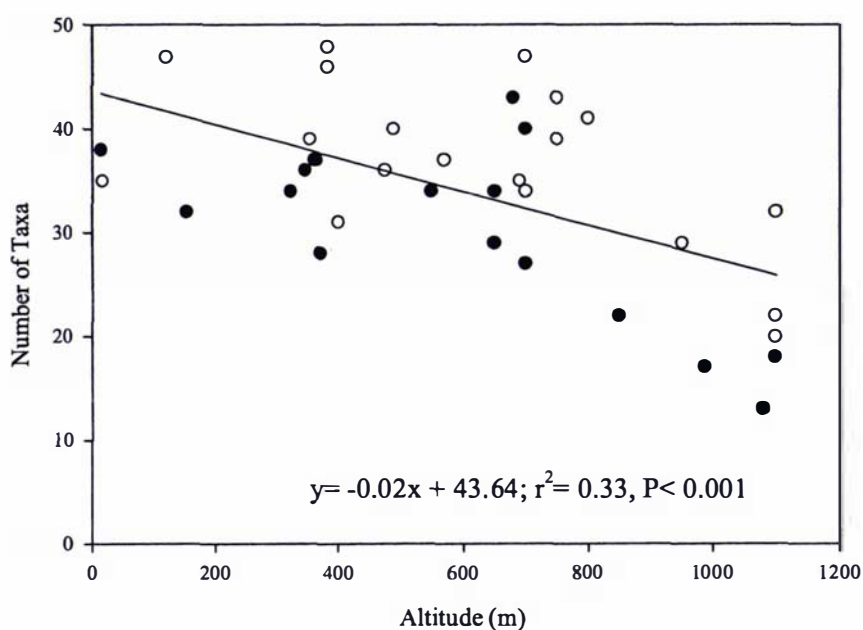


**Figure 6** Relationship between altitude and number of invertebrate taxa collected in spring-fed (O) and runoff-fed (●) streams in New Zealand, in the autumn of 2001.

In conclusion, invertebrate diversity seems to be controlled by a variety of factors that interact at different spatial scales. At the scale of the stream reach, stability seems to enhance levels of food resources, habitat complexity and heterogeneity and results in higher numbers of invertebrate taxa and individuals. At the reach scale predation pressure may also play an important role in controlling invertebrate diversity. At the regional scale altitude may restrict the dispersal of invertebrate taxa and limit the number of taxa that can reach a given stream. Finally, it seems there is a well established pattern across

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different continents of non-insect and insect dominance in lowland and upland springs, respectively, which may be the result of the different dispersal ability of insect and non-insect taxa.

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**Appendix 1** Study sites sampled in April and May 2001 in four National Parks in New Zealand. New Zealand map coordinates are given.

| National Park | Site | Spring/Stream | Name | Northing | Easting |
|---|---|---|---|---|---|
| **South Island** | | | | | |
| Waimakariri basin (W) | W1 | Spring | Slip Spring I | 5770929 | 2405121 |
| | W2 | Stream | Whitewater River | 5773036 | 2406311 |
| Geology | W3 | Spring | Slip Spring II | 5771026 | 2405377 |
| Alluvial Plains | W4 | Stream | Cave Stream | 5778442 | 2407797 |
| | W5 | Spring | Cass Spring | 5797000 | 2408531 |
| Rainfall (mm) | W6 | Stream | Manson Creek | 5785494 | 2409719 |
| 3812 | W7 | Spring | Hawdow Valley I | 5804000 | 2405378 |
| | W8 | Spring | Hawdow Valley II | 5804000 | 2405378 |
| | W9 | Stream | Andrew River | 5803000 | 2413412 |
| | W10 | Stream | Boundary Stream | 5795717 | 2421444 |
| Kahurangi - Nelson (N) | N1 | Spring | Blue Creek | 5969000 | 2474000 |
| | N2 | Stream | Nuggety River | 5970000 | 2473000 |
| Geology | N3 | Stream | Graham River | 6003500 | 2493600 |
| Karst | N4 | Spring | Pearse Resurgence | 5999555 | 2488200 |
| | N5 | Spring | Riwaka Resurgence | 6019094 | 2501572 |
| Rainfall (mm) | N6 | Stream | Riwaka River | 6015143 | 2500929 |
| 1310-2767 | N7 | Spring | Fish Creek | 6039770 | 2490604 |
| | N8 | Stream | Pariwhakaoho River | 6045794 | 2487763 |
| **North Island** | | | | | |
| Tongariro - Ruapehu (R) | R1 | Stream | Mangaeitoenui River | 6215254 | 2745775 |
| | R2 | Stream | Waikatu River | 6210002 | 2746612 |
| Geology | R3 | Spring | Waihohonu Spring I | 6220800 | 2740333 |
| Volcanic Andesite | R4 | Spring | Waihohonu Spring II | 6220252 | 2740725 |
| | R5 | Stream | Waihohonu River | 6218500 | 2740684 |
| Rainfall (mm) | R6 | Spring | Ohinepango Spring | 6217394 | 2741239 |
| 1015-2525 | R7 | Spring | Waitaiki Stream | 6199400 | 2727333 |
| | R8 | Stream | Omarae River | 6196000 | 2727000 |
| | R9 | Stream | Waihoruru River | 6196222 | 2725422 |
| | R10 | Spring | Unamed | 6196222 | 2725000 |
| Mt Egmont/Taranaki (T) | T1 | Spring | Cold Stream | 6202701 | 2597602 |
| | T2 | Stream | Punehu River | 6200791 | 2598369 |
| Geology | T3 | Spring | Taungatara Stream | 6202702 | 2597151 |
| Volcanic Andesite | T4 | Stream | Mangahume River | 6203458 | 2595814 |
| | T5 | Spring | Unamed | 6203030 | 2596351 |
| Rainfall (mm) | T6 | Stream | Kapoaiaia River | 6212155 | 2591437 |
| 884-5629 | T8 | Spring | Bubling Springs | 6209000 | 2605000 |
| | T10 | Stream | Te Popo Stream | 6210000 | 2608000 |

**Appendix 2** Physicochemical variables and level of resource ranges measured in streams and springbrooks in four regions of New Zealand, in autumn 2001, Sp= Spring and St= Stream.

| Region | | pH | Temperature ($^{\circ}$C) | Conductivity ($\mu$S/cm) | Nitrates (mg/ml) | Phosphates (mg/ml) | Altitude (m) | Canopy Cover (%) | Discharge ($m^3$/s) | Mean width (m) | Mean depth (m) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Waimakariri | Sp | (7.3-7.6) | (10.1-11.8) | (44-64) | (0.13-0.03) | (0.14-0.08) | (570-800) | (0-40) | (0.006-0.2) | (1.8-5.4) | (6-14) |
| | St | (7.3-8) | (10.2-13) | (18.4-110.6) | (0.10-0.04) | (0.24-0.05) | (490-700) | (0-20) | (0.05-0.5) | (2-8) | (8-21) |
| Nelson | Sp | (7.9-8.4) | (7-12.3) | (176.9-331) | (0.22-0.10) | (0.11-0.05) | (17-400) | (20-30) | (0.03-0.3) | (2.8-10.2) | (11-25) |
| | St | (6.5-8.3) | (6.9-19.4) | (91.8-530) | (0.21-0.8) | (0.22-0.05) | (17-360) | (0-40) | (0.03-0.3) | (2.5-6.3) | (8-27) |
| Ruapehu | Sp | (6.5-9) | (6.5-10.3) | (64-235) | (0.13-0.6) | (0.45-0.21) | (690-1100) | (0-40) | (0.09-0.9) | (2.4-9.1) | (21-38) |
| | St | (8.3-9.2) | (9.5-14.6) | (60-184) | (0.12-0.03) | (0.85-0.18) | (680-1100) | (0-40) | (0.05-0.8) | (2.7-9.2) | (8-30) |
| Taranaki | Sp | (7.6-8.3) | (4.5-7.7) | (39-124) | (0.07-0.05) | (0.57-0.33) | (353-950) | (40-60) | (0.06-0.3) | (1.6-5) | (11-24) |
| | St | (8-8.3) | (4.8-8.3) | (39-133) | (0.06-0.02) | (0.3-0.11) | (344-850) | (40-50) | (0.02-0.4) | (1.9-8.6) | (13-25) |

| Region | | Mean velocity (m/s) | Substrate heterogeneity | Substrate size index (mm) | Stability (PCA index) | Productivity (PCA index) | CPOM ($g/m^2$) | FPOM ($g/m^2$) | Chlorophyll *a* ($\mu g/cm^2$) | Epilithic Carbon ($mg/cm^2$) |
|---|---|---|---|---|---|---|---|---|---|---|
| imakariri | Sp | (0.07-0.7) | (0.13-0.18) | (34.6-64.3) | (4.18-6.56) | (1.46-4.88) | (9.4-286-8) | (3.4-13.7) | (2.6-7.8) | (0.9-2.3) |
| | St | (0.3-0.7) | (0.13-0.16) | (38.4-65.6) | (2.2-3.06) | (0.17-0.57) | (2.3-9.9) | (1.8-3.1) | (0.3-2.2) | (0.4-0.8) |
| son | Sp | (0.2-0.3) | (0.13-0.17) | (63.5-147.3) | (2.02-4.8) | (0.59-5.74) | (8.2-159.4) | (3.4-15.2) | (1.6-18.2) | (0.5-2.5) |
| | St | (0.2-0.5) | (0.13-0.18) | (116-89.9) | (2.15-3.44) | (0.42-4.15) | (5-38.6) | (3.4-10) | (0.4-19.8) | (0.3-2.6) |
| pehu | Sp | (0.4-0.7) | (0.12-0.15) | (24.1-84.6) | (2.28-4.68) | (1.1-5.28) | (16.1-113.6) | (4.18-11.7) | (1.6-12.5) | (0.6-3.7) |
| | St | (0.2-0.4) | (0.12-0.19) | (16-59.2) | (0-2.74) | (0-0.83) | (1.4-37.1) | (3.3-6.1) | (0.2-2.1) | (0.2-0.8) |
| anaki | Sp | (0.3-0.6) | (0.11-0.5) | (43.2-130) | (2.58-4.41) | (0.34-2.78) | (9.8-133.5) | (3.6-10.4) | (0.5-5.3) | (0.6-1.4) |
| | St | (0.01-4) | (0.11-0.17) | (62.6-113.8) | (0.59-2.29) | (0.11-0.28) | (4.9-20.6) | (0.7-1.80 | (0.6-2.6) | (0.5-0.8) |

# 2

# Patterns of invertebrate diversity in streams and freshwater springs in Northern Spain

# Abstract

Invertebrate diversity patterns were examined in six rheocrene springs and six nearby, runoff-fed streams in Cantabria, Northern Spain. Periphyton biomass, organic matter and biomass of moss were always higher in springs than streams. Species densities (number of species/area) and rarified species richness (number of species/number of individuals) were lower and invertebrate densities greater in spring habitats. Of 22 variables chlorophyll *a* was the best predictor of species richness, whereas total organic matter was the best predictor of invertebrate density, although neither relationship was strong. Spring habitats had invertebrate communities dominated by non-insect taxa (e.g., *Echinogammarus*, and Hydrobiidae and Neritidae snails), in contrast to the insect dominated communities in runoff-fed streams (e.g., *Baetis*, *Ecdyonurus*, *Elmis*, *Prosimulium*, *Scirtes* and Chironomidae). *Echinogammarus* had the highest densities in springs; an order of magnitude greater than any other taxa. The effects of biotic processes, such as predation from *Echinogammarus* on community structure may be more marked in springs because predated individuals cannot be as readily replaced by drifting animals from upstream reaches. The reduced diversity in springs compared to streams could be a result of several factors including increased predation from animals such as *Echinogammarus* or the unusually constant thermal characteristics.

**Key words**: Freshwater springs, streams, macroinvertebrate diversity, community structure, stability, Spain

## Introduction

The mechanisms underlying patterns of species diversity in biological communities are a dominant theme of research in ecology (Huston 1994). Biological diversity is influenced by a variety of historical and geographical circumstances as well as local ecological determinants (Ricklefs and Schluter 1993). At a local scale, diversity could be regarded as the outcome of the interaction between the physical conditions of the environment and biotic factors, such as competition and predation (Schluter and Ricklefs 1993). Attempts to explain patterns of diversity must integrate both abiotic and biotic factors, as for example, in the intermediate disturbance hypothesis (Connell 1978) and the harsh-benign hypothesis (Menge 1976),

Streams are habitats that have a high level of temporal and spatial variability and are therefore generally considered to be dominated by physical factors (e.g., variation in discharge) (Resh et al. 1988, Lake 2000). Streams that suffer from frequent disturbances or experience extremes of physical conditions (e.g., temperature) will be depauperate in species (Pritchard 1991). If such disturbance events or extremes are reduced, macroinvertebrate diversity and population sizes can be expected to increase (Williams 1991). Field experiments in streams have shown that increasing substrate disturbance reduces the number of species and individuals of macroinvertebrates (Rosser and Pearson 1995, Death 1996, Gayraud et al. 2000), although some studies have shown diversity may decline again in very stable sites (Meffe and Marsh 1983, Anderson and Anderson 1995, Townsend et al. 1997). This lower richness in stable streams is hypothesized to be the result of the effects of predation and/or competition on macroinvertebrate communities (Menge 1976, Connell 1978). Predation has been shown to have significant effects on macroinvertebrate assemblages, reducing diversity in stable habitats (Peckarsky et al. 1990, Lancaster 1996, Pringle and Hamazaki 1997, Nakano et al. 1999), but see Thomson et al. (2002). However, few studies have conclusively demonstrated that competitive exclusion can reduce macroinvertebrate diversity in streams (Townsend et al. 1997). The high spatial heterogeneity of stream habitats combined with the high mobility of most macroinvertebrate taxa between patches, is likely to override any effects of competition on overall macroinvertebrate diversity (Townsend 1989, Lake 2000, Death 2002).

Springs and springbrooks are generally stable lotic habitats compared to the majority of streams (Odum 1957). If any lotic invertebrate community is likely to be influenced by biotic interactions it would seem that the highly stable spring and spring brook communities are the most likely candidates. However, surprisingly few studies have compared invertebrate communities in spring habitats with nearby runoff-fed streams (Davidson and Wilding 1943, Ward and Dufford 1979, Meffe and Marsh 1983, Anderson and Anderson 1995). These studies, all in the USA, generally found that springs had lower numbers of macroinvertebrate taxa than similar downstream reaches or nearby runoff-fed streams. In contrast, a number of studies (Death 1995, Death and Winterbourn 1995, Death et al. 2004) have found the opposite pattern for New Zealand springs and streams.
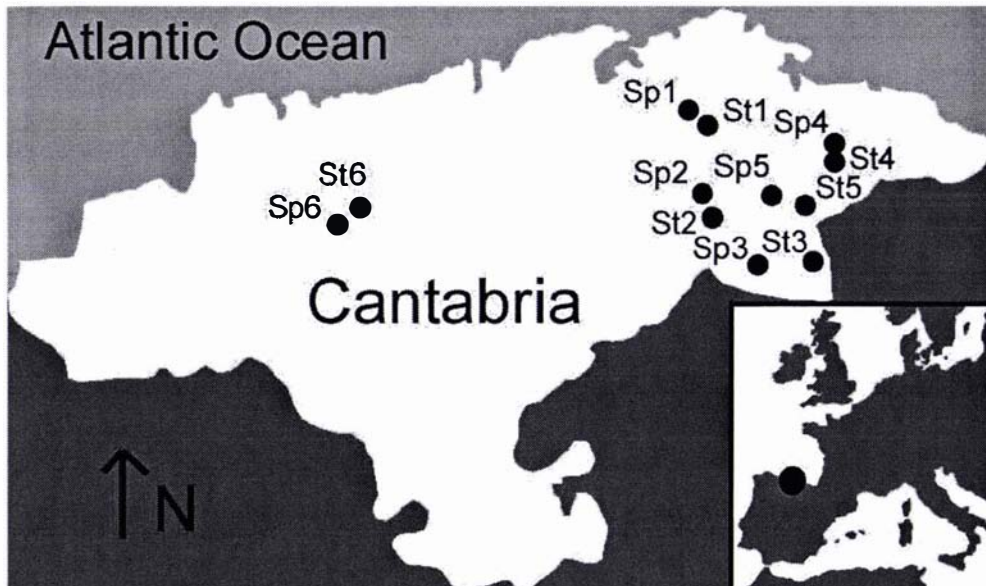


**Figure 1** Map showing spring and stream sites sampled in northern Spain, Europe, in July 2002.

Between the provinces of Basque Country, Cantabria and Asturias (Northern Spain, Fig. 1) there is a belt of Urgonian Limestone with a significant number of rheocrene springs (Mugnier 1969). Rheocrenes are springs where emerging water immediately forms a stream (Danks and Williams 1991), and are thus ideal habitats to compare with runoff-fed streams. Some of the springs and streams in this region are in semi-pristine conditions away from the more populated areas. Moreover, runoff-fed

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streams in this region are subject to frequent disturbance events because of unpredictable and frequent summer and autumn storms and long periods of rain in winter and spring in Northern Spain (Fig. 2). In this study, we investigated the hypothesis that the more physically stable springs will have reduced diversity compared to similar streams in the area.
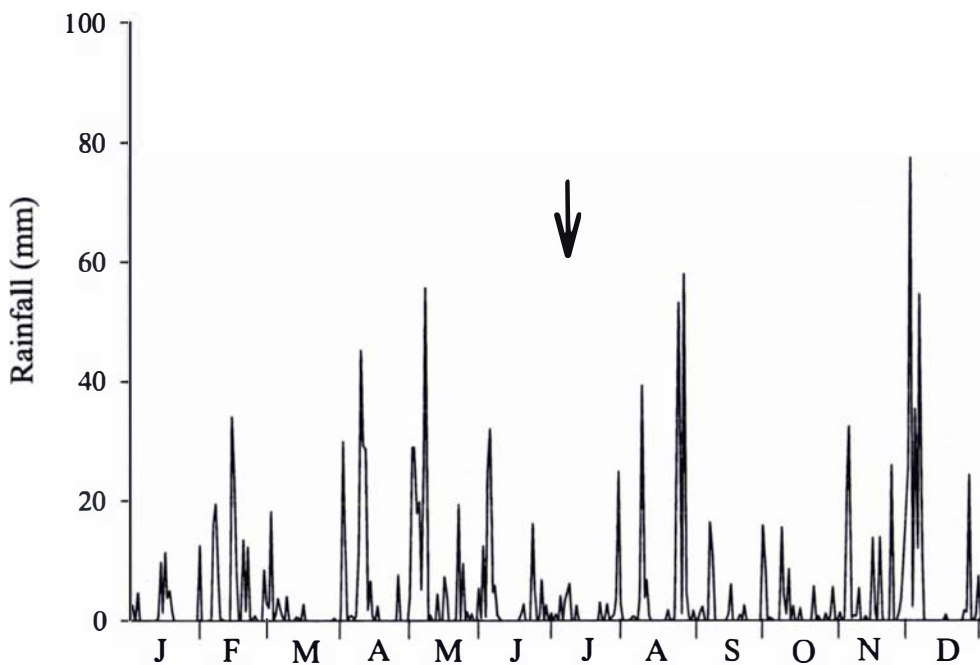


**Figure 2** Rainfall recorded during the year 2002 at Udalla station, Cantabria, Spain. Arrow indicates sampling date.

## Materials and methods

### Study Sites

Study sites comprised 12 first to third order streams in Saja and Ason Natural Parks, Cantabria, Northern Spain (Fig. 1). La Fuentona Spring (Sp6) and Bayones Stream (St6) are located in the Saja River watershed, whereas the others are all in the Ason River watershed. Both rivers drain into the Cantabrian Sea. Sites were selected so as to pair a spring-fed stream with a nearby runoff-fed stream, yielding six pairs of springs and streams. All sites were stony streams situated in the upper parts of the basins without any

obvious anthropogenic impacts. There was no macrophyte growth at any site but substratum in springs was largely covered by moss. Average channel width ranged from 3.1 to 13.7 m. Typical Atlantic deciduous forest mixed with pasture surrounded most study sites. Atlantic forest comprises largely a mixture of oaks (*Quercus* spp.) and northern beeches (*Fagus sylvatica*). Riparian forest comprised alders (*Alnus glutinosa*), ash trees (*Fraxinus excelsior*), elms (*Ulmus glabra*), oaks (*Quercus* spp.), willows (*Salix* spp.) and hazels (*Corylus avellanea*). Stream altitude varied from 110 to 540 m a.s.l.

**Physicochemical measures**

A number of physicochemical variables were measured concurrently with invertebrate sampling. Conductivity, dissolved oxygen concentration and saturation, temperature and pH were measured with a YSI 556 MPS meter. Current velocity was calculated from the time taken by corks to travel 10 m. Flow was estimated as the average of the product of depth, water velocity and width in at least five cross sections of stream. Substrate composition was assessed by counting the number of stones in each of seven size classes (maximum width; >300, 300-128, 128-90, 90-64, 64-45, 45-32, 32-14mm) found in each Surber area sampled for invertebrates (see below). Gravel (14-3mm) and sand (<3mm) classes were estimated visually as percentage coverage of the sampled area. These measures were converted to a single substrata size index (SI) by summing the mid-point values of the size classes weighted by the number of stones in each size class (bedrock was assigned a nominal size of 400 mm for use in the calculations) (Quinn and Hickey 1990). Substrate heterogeneity was estimated using Simpson's diversity index:

$$D = \Sigma \left( \frac{n_i(n_i-1)}{N(N-1)} \right)$$

where $n_i$ = the number of stones in the *i*th size class and $N$ = the total number of stones. Riparian cover was assessed visually as percentage shaded area over the stream channel.

**Biological collections**

Five 0.1 m$^2$ Surber samples (mesh = 250 µm) were collected from riffles in July 2002 along a 20 - 45 m reach on each stream. Spring-fed streams were sampled within the first

40 m from the source. Samples were preserved in 10% formalin and returned to the laboratory for identification, usually to genus level, using available keys (Tachet et al. 2002). This sampling protocol only provides a snapshot of the invertebrate community. However, because our study focused on spatial variation in macroinvertebrate assemblages between spring and streams not temporal variability, the sampling strategy was deemed appropriate. The study coincided with the annual maximum for macroinvertebrate diversity in this part of Spain (Riaño 1998, Barquín 2000, Gonzalez 2000), and therefore most taxa would have been present at the time of sampling.

Fauna were grouped into functional groups following Merrit and Cummins (1996) and studies in the north of Spain by Riaño (1998) and Barquín (2000). Coarse particulate organic matter (CPOM, >1 mm) and fine particulate organic matter (FPOM, 1-0.25 mm) remaining after invertebrates were removed were dried to constant weight at 95 °C, weighed and ashed at 550 °C for 2 h to yield ash free dry weight. CPOM included mosses, leaves and twigs.

Five stones without moss (maximum width: 30-90 mm) per site were also collected from each Surber sample area for measuring periphyton biomass. Stones were kept frozen prior to pigments being extracted in 90% acetone at 5 °C for 24 h in the dark. Absorbancy was measured with a Hach™ DR2000 UV-Visible spectrophotometer and pigment concentration (chlorophyll *a* and phaeophytins) calculated following Steinman and Lamberti (1996). Stone surface area was determined by measuring the three longest axes of the stone and using these in the equation developed by Graham et al. (1988). As only part of a stone is exposed to light (we assumed half the total surface area), estimates of pigment concentration were divided by two. Individual differences in stone shape, orientation and embeddedness will affect the accuracy of these estimates, but any errors introduced by such assumptions should be small in comparison with differences in biomass within and between sites.

**Statistical analysis**

Differences in the biological variables between springs and streams were examined with a nested three-way analysis of variance (ANOVA) with Habitat type (spring-stream) and Location treated as fixed factors and Surber sample as nested within Habitat type. As

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locations of the spring and stream pairs were quite widely dispersed in Cantabria, we also examined whether the effects of Habitat type differed between Location in the ANOVA design. ANOVAs were performed in SAS Institute Inc. (1988) with type III sums of squares and Tukey's post hoc means test when significant differences were found. Differences in physico-chemical measures between spring and stream habitat types were examined with a simple one-way ANOVA, with Habitat type treated as a fixed factor. Variables were transformed to remove heteroscedasticity when necessary. Relationships between number of taxa and individuals, and environmental variables were analyzed with simple linear regressions (SAS Institute Inc. 1988).

Patterns in community composition were examined using non-metric multidimensional scaling (NMDS) with the PC-ORD statistical package (McCune and Mefford 1995). The Sorensen distance measure was used to determine similarity between samples. Initial examination of stress patterns in the data suggested three dimensions were appropriate for the final ordination, which was established with 500 iterations of the data. Relationships between the ordination axes and the measured local and regional environmental variables were examined using simple correlation (SAS Institute Inc. 1988).

To determine the significance of differences in invertebrate community composition between springs and streams we performed an analysis of similarities (ANOSIM) using the PRIMER statistical package (Clarke and Warwick 1994). ANOSIM is a non-parametric procedure that evaluates whether the average similarities between samples within groups are closer than the average similarities of all pairs of replicates between groups (Clarke and Warwick 1994). The mean density of taxa that contributed most ($\geq 90\%$) to the dissimilarity between springs and streams was evaluated using the SIMPER procedure in the PRIMER statistical package. In order to compare species counts among habitats with different invertebrate densities it is preferable to use rarified species richness (number of species/number of individuals) rather than species richness (number of species/area) (McCabe and Gotelli 2000). We calculated the rarified diversity values for each of our Surber samples using the PRIMER statistical package (Clarke and Warwick 1994). The minimum number of individuals in our samples was 87, so species richness was corrected to this number of animals.

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**Table 1** Physicochemical characteristics of the study sites measured in July 2002. Sites are arranged in spring-stream pairs for each location: Aguanaz (Sp1, St1), Arredondo (Sp2, St2), Gandara (Sp3, St3), Rasines (Sp4, St4), Ogarrio (Sp5, St5) and Ruente (Sp6, St6). *F* and *P* values for ANOVA testing of differences in these measures between springs and streams are also given, Sp= spring, St= stream.

| | Conductivity ($\mu$S/cm) | Oxygen mg/l | pH | Temp-erature (°C) | Flow ($m^3$/s) | Mean Depth (cm) | Mean Velocity (m/s) | Hetero-geneity | Substrate Size Index (mm) |
|---|---|---|---|---|---|---|---|---|---|
| az Spring (Sp1) | 274 | 7.6 | 7.6 | 13 | 0.6 | 16 | 0.4 | 0.18 | 51 |
| do Stream (St1) | 339 | 7.87 | 8 | 14 | 0.5 | 12 | 0.2 | 0.23 | 47 |
| | | | | | | | | | |
| a Spring (Sp2) | 214 | 8.67 | 8. | 10 | 4.5 | 19 | 0.4 | 0.24 | 61 |
| lado Stream (St2) | 222 | 9.82 | 8.4 | 12 | 1.1 | 23 | 0.3 | 0.2 | 68 |
| | | | | | | | | | |
| ra Spring (Sp3) | 234 | 9.01 | 8 | 9 | 1 | 16 | 0.5 | 0.13 | 104 |
| te Stream (St3) | 262 | 7.54 | 8.3 | 14 | 0.2 | 13 | 0.2 | 0.18 | 65 |
| | | | | | | | | | |
| del Valle Spring (Sp4) | 280 | 8.47 | 7.8 | 13 | 0.1 | 13 | 0.2 | 0.14 | 67 |
| mosa Stream (St4) | 236 | 8.48 | 7.8 | 15 | 0.1 | 17 | 0.3 | 0.2 | 56 |
| | | | | | | | | | |
| o Spring (Sp5) | 309 | 8.79 | 7.8 | 13 | 0.1 | 12 | 0.2 | 0.29 | 47 |
| Stream (St5) | 131 | 7.36 | 7.5 | 14 | 0.2 | 15 | 0.2 | 0.2 | 90 |
| | | | | | | | | | |
| ntona Spring (Sp6) | 218 | 5.7 | 7.7 | 14 | 0.5 | 23 | 0.4 | 0.21 | 85 |
| es Stream (St6) | 62 | 6.45 | 7 | 14 | 0.9 | 19 | 0.6 | 0.18 | 57 |
| | | | | | | | | | |
| | 1.15 | 0.03 | 0.01 | 3.63 | 0.77 | 0.00 | 0.48 | 0.00 | 0.27 |
| es | 0.31 | 0.87 | 0.92 | 0.08 | 0.4 | 0.96 | 0.51 | 0.99 | 0.61 |

## Results

### Physicochemical characteristics

All sites had circumneutral pH (7-8.4) and riparian forest that did not exceed greater than 40% canopy of the stream. Conductivity, at 25 °C, ranged from 62 to 339 $\mu$S/cm and

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temperature from 9 to 15 °C. Mean depth and current velocity measured at each site ranged from 12 to 23 cm and from 0.19 to 0.52 m/s, respectively. Dissolved oxygen concentration was close to saturation at all sites except for Sp6 and St6. There were no significant differences overall between springs and streams for any physicochemical variable (Table 1).

**Periphyton and organic matter**

Overall, springs had almost 9 times more periphyton biomass and nearly 3 times more organic matter than streams (Fig. 3, Table 2). The Arredondo and Aguanaz spring and stream sites had higher levels of periphyton than the other localities (Table 2). There was no significant difference in total organic matter between localities (Table 2).
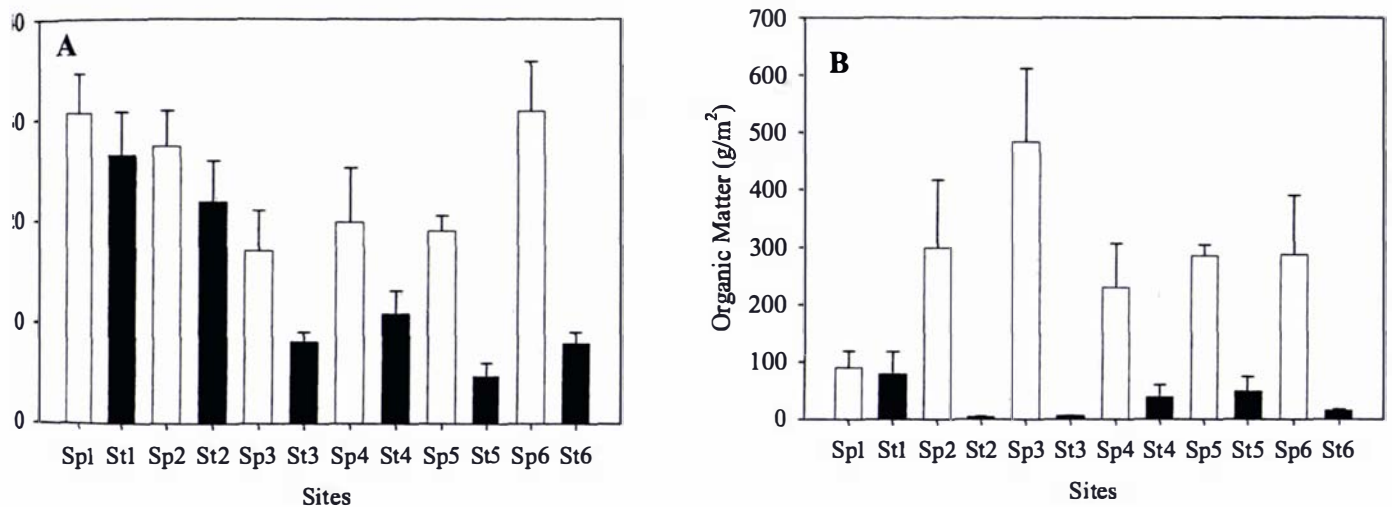


**Figure 3** Mean (± 1 SE) amounts of A, Chlorophyll *a*; and B, Organic matter including living bryophytes collected in 5 Surber samples in springs (open bars) and streams (solid bars) in Cantabria, Spain, July 2002.

**Invertebrate abundance and diversity patterns**

Ninety taxa were collected at the 12 study sites. Forty taxa were common to both habitats: 54 occurred in springs and 77 in runoff-fed streams. Streams had almost twice as many taxa as springs (Table 2, Fig. 4). Invertebrate density was two times greater in springs than in streams (Table 2, Fig. 4), with differences between springs and streams

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greatest at Sp3, Sp5 and Sp6. Simpson's index and rarified species richness were lower in springs than streams (Table 2). Simple regressions of potential predictor variables for number of taxa and individuals indicated total pigment concentration was the best predictor of invertebrate species richness ($r^2 = 0.24$) and total organic matter concentration was the best predictor of total density ($r^2 = 0.15$).

**Table 2** Results of nested ANOVA examining differences in biological data collected in Cantabria, Spain, in July 2002. Tukey's post hoc analysis results are also given. Asterisks indicate P values < 0.05, and lines join locations with no statistical differences. St=stream, Sp=spring, Ag= Aguanaz, Ar= Arredondo, Ga= Gandara, Ra= Rasines, Ru= Ruente and Og= Ogarrio.

| | Habitat $F_{37,1}$ | Locality $F_{37,5}$ | H*L $F_{37,5}$ | Replicates $F_{37,8}$ |
|---|---|---|---|---|
| Number of Taxa | 94.5* | 3.7** | 6.6* | 1 |
| | st>sp | Ru Og Ra Ga Ar Ag | | |
| Number of Individuals | 36.6* | 1.5 | 6.4* | 1.3 |
| | sp>st | | | |
| Number of Rarified Taxa | 276.1* | 7.9** | 11.7* | 0.88 |
| | st>sp | Ru Ra Og Ga Ag Ar | | |
| Simpson Index of Diversity | 9* | 0.8 | 4.9* | 0.79 |
| | st>sp | | | |
| | $F_{40,1}$ | $F_{40,5}$ | $F_{40,5}$ | $F_{40,8}$ |
| Chlorophyll *a* | 36.9* | 9.7** | 3.3* | 1.4 |
| | | Ag Ar Ru Rs Gd Og | | |
| Phaeophytin | 51.54* | 5.22** | 0.38 | 0.47 |
| | | Ar Ag Gd Og Rs Ru | | |
| Total Pigment Concentration | 60.4* | 7.8** | 1.58 | 1 |
| | | Ar Ag Ru Rs Gd Og | | |
| | $F_{34,1}$ | $F_{34,5}$ | $F_{34,5}$ | $F_{34,8}$ |
| CPOM | 70.18* | 1 | 4.8 | 1.1 |
| FPOM | 47.36* | 6.4** | 1.1 | 0.4 |
| | | Rs Og Ag Gd Ru Ar | | |
| Total Organic Matter | 95.18* | 1.9 | 5.4* | 1.2 |
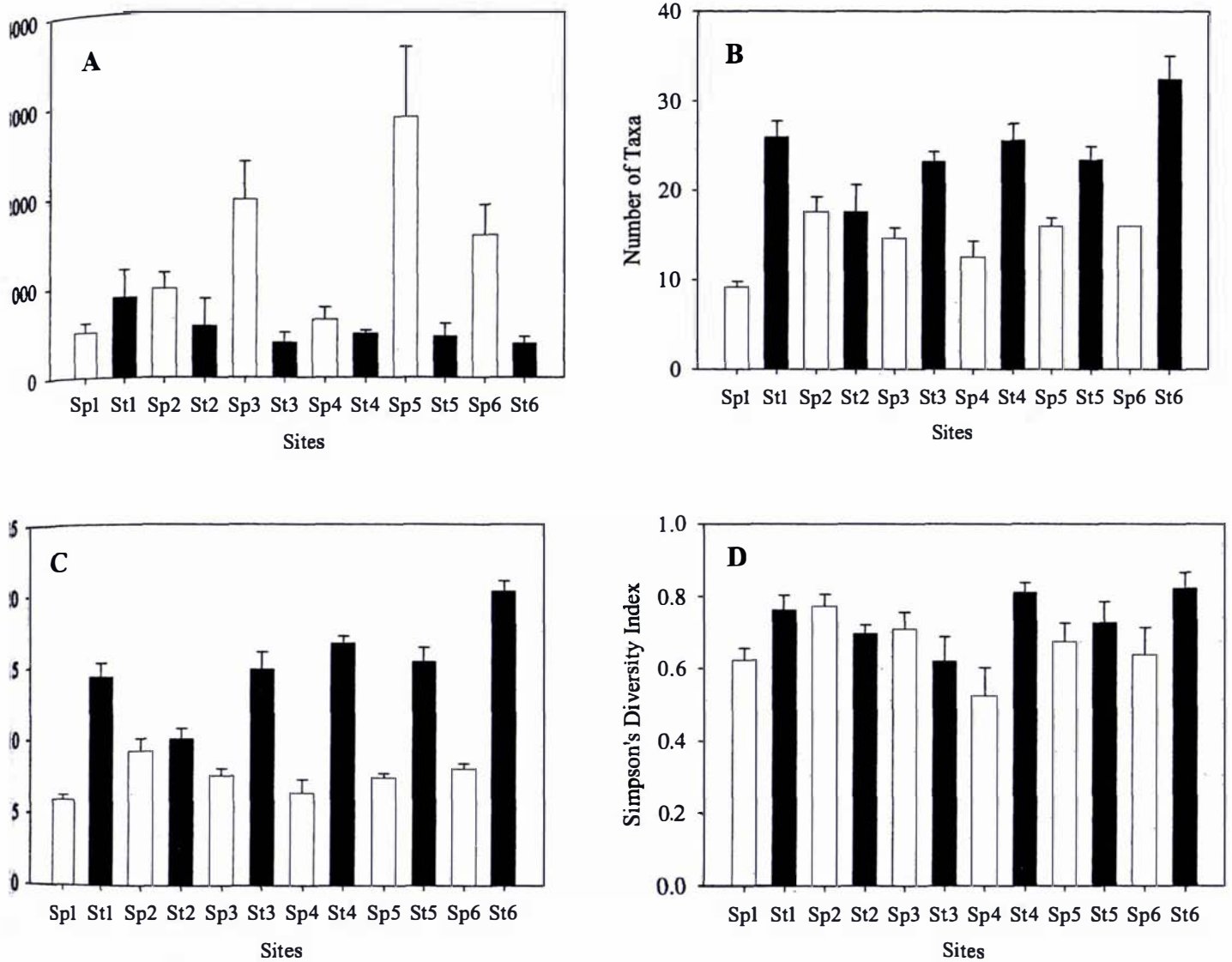
**Figure 4** Mean (± 1 SE) A, number of individuals; B, number of taxa; C, rarified taxa number standardized to 87 individuals per Surber sample, and D, Simpson diversity index for invertebrate communities in springs (open bars) and streams (solid bars) in Cantabria, Spain, July 2002.

**Community structure**

Taxonomic composition

Non-insect taxa had similar richness in both springs (16) and streams (14), but the insect fauna was markedly richer in streams (63) than in springs (38). Diptera, Coleoptera, Ephemeroptera, Plecoptera and Trichoptera were always taxonomically richer in streams.

Numerically, *Echinogammarus* spp. and snails in the families Hydrobiidae and Neritidae dominated springs. These taxa, along with *Baetis* spp., *Elmis* spp. and Chironomidae made up more than 94% of the individuals collected in all springs. *Baetis* spp., *Ecdyonurus* sp., *Elmis* spp., *Prosimulium* sp., *Scirtes* sp. and Chironomidae made up 79% of the individuals collected in streams, whereas *Echinogammarus* spp. represented 16% (Fig. 5A).

A.
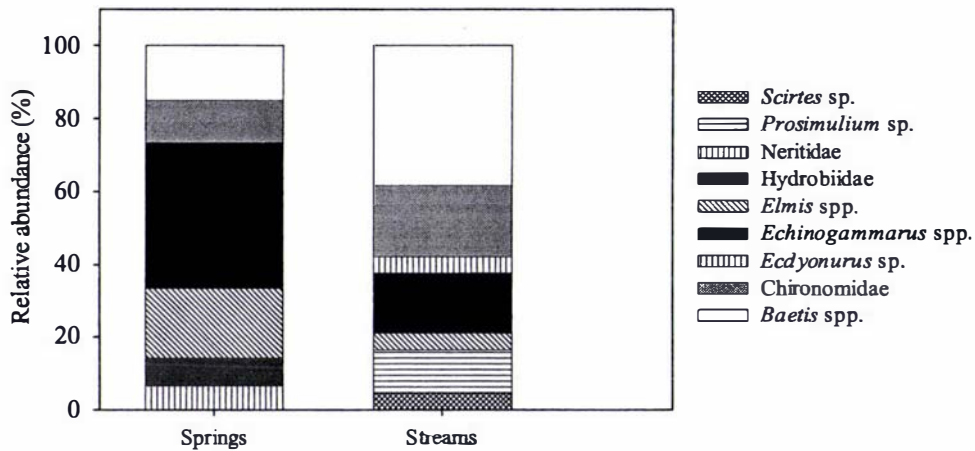


B.
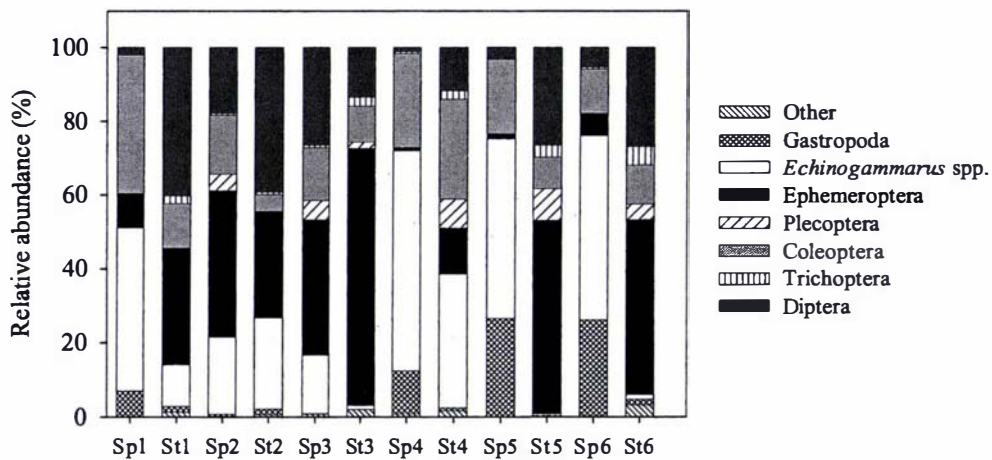


**Figure 5** A, relative abundance of 9 key taxa in pooled spring and stream communities, and B, relative abundance of all major taxa in individual springs and streams, collected in Cantabria, Spain, in July 2002.

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ANOSIM indicated that overall, spring and stream communities were different (R= 0.23, P< 0.02). *Echinogammarus* spp., *Baetis* spp., *Elmis* spp., Orthocladiinae and *Bythinella* sp. densities contributed 73% to the dissimilarity between spring and stream communities (Table 3), and were more numerous in springs. Final stress for the NMDS analysis was 7.9, indicating a reliable ordination (McCune and Mefford 1995). Axis 1 and axis 2 explained 58% and 32% of the total variance, respectively. Springs occurred to the left of axis one of the NMDS whereas streams were to the right (Fig. 6). Of the 22 habitat descriptors only algal pigment and organic matter concentration were negatively correlated with axis one (Table 4).

**Table 3** Mean abundance of the most important taxa differentiating spring and stream communities collected in Cantabria, Spain, in July 2002. Results of nested ANOVA testing for differences in abundance of taxa between habitat types (spring/streams) and locality, and Kendall rank correlation coefficients of taxa with axis one and two of the non metric multidimensional scaling analysis are also given. Taxa are listed in order of decreasing importance in differentiating spring and stream communities. Asterisks indicate significance at P< 0.05.

| Taxon | Mean abundance (±1 SE) | | | | Habitat type $F_{5,37}$ | Locality $F_{1,37}$ | H*L $F_{5,37}$ | Surber $F_{8,37}$ | Axis 1 | Axis 2 |
|---|---|---|---|---|---|---|---|---|---|---|
| | Springs | | Streams | | | | | | | |
| *Echinogammarus* spp. | 514.1 | ± 100.3 | 70.4 | ●15.4 | 182.5* | 3.7* | 23.9* | 0.8 | -0.67 | -0.52 |
| *Baetis* spp. | 190.5 | ●16.6 | 161.6 | ± 10.2 | 12.9* | 13.2* | 9.4* | 1.6 | 0.36 | 0.52 |
| *Elmis* spp. | 241.7 | ± 37.3 | 19.2 | ± 4.3 | 276.4* | 3.88* | 10.4* | 3.3* | -0.58 | -0.3 |
| Orthocladiinae | 142.7 | ± 48.4 | 72.3 | ± 39.8 | 3.4 | 3.4* | 12.9* | 2.2 | 0.09 | 0.18 |
| *Bythinella* sp. | 99.6 | ●41.9 | 0.6 | ± 0.3 | 84.2* | 12.9* | 14.8* | 0.5 | -0.64 | -0.39 |
| *Theodoxus fluviatilis* | 85.6 | ●36.6 | 2.9 | ± 1 | 131.5* | 20.6* | 28.4* | 0.9 | -0.41 | -0.6 |
| *Prosimulium* sp. | 0.3 | ●0.1 | 50.6 | ± 33.4 | 42.92* | 1 | 0.6 | 0.7 | 0.5 | 0.34 |
| *Ephemerella ignita* | 40.3 | ± 11.2 | 4.4 | ± 1.1 | 21.2* | 26* | 22.9* | 1.3 | -0.08 | 0.23 |
| *Scirtes* sp. | 0 | ± 0 | 19.3 | ± 4.6 | 141* | 7.1* | 7.1* | 0.3 | 0.49 | 0.28 |
| *Protonemura* sp. | 26.9 | ± 9 | 0.3 | ± 0.3 | 108.6* | 56.1* | 65.9* | 1 | 0.06 | 0.46 |
| *Ecdyonurus* sp. | 2.1 | ± 0.8 | 18.5 | ± 3.7 | 90.6* | 6.5* | 8.3* | 0.3 | 0.42 | -0.08 |
| *Esolus* sp. | 1.1 | ± 0.4 | 12.3 | ± 2.5 | 70.1* | 3.2* | 4.8* | 1 | 0.61 | 0.23 |

There appear to be two broad types of spring community (Fig 4 B); one dominated by *Echinogammarus* spp., *Elmis* spp. and snails (Sp1, Sp4, Sp5 and Sp6) and another where snails are less abundant and Ephemeroptera (*Baetis* sp. and *Ephemerella ignita* in Sp2 and *Baetis* sp. in Sp3), Chironomidae, *Echinogammarus* spp. and *Elmis* spp.

comprise most of the community. Communities from runoff-fed streams were quite different from spring communities in community composition, although there was considerable variability among communities from run-off fed streams (Fig. 6)
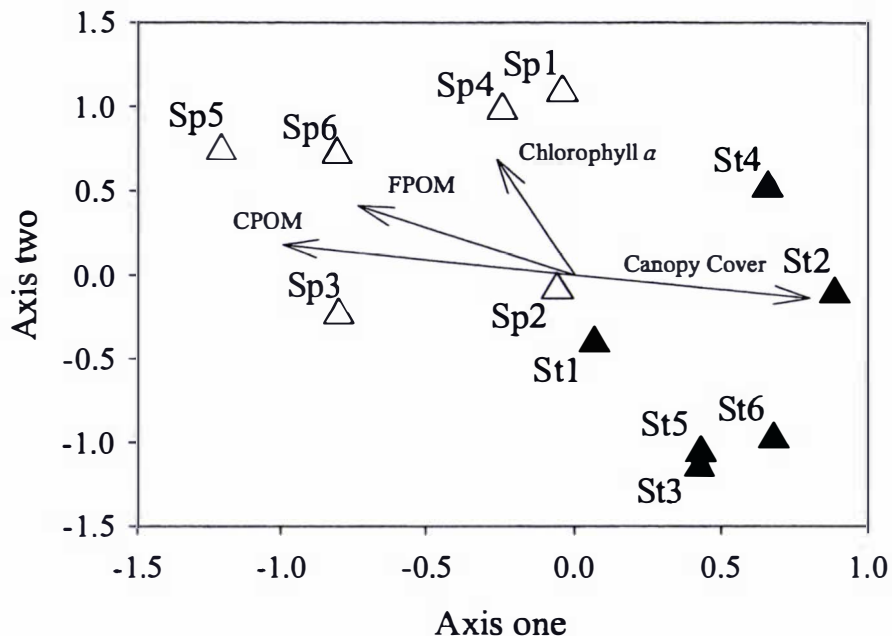


**Figure 6** Non-metric multidimensional scaling (NMDS) plot of axis 1 against axis 2 for mean invertebrate communities collected in Cantabria, Spain, in July 2002. Springs are open triangles and streams solid triangles. Arrows show relationships between environmental variables and axis one and two of the ordination (cutoff value =0.25).

Functional feeding group composition

Spring communities comprised largely collector-gatherer/scrapers (43%), shredders (40%) and scrapers (13%), with *Echinogammarus* spp. comprising 90% of the shredders. In streams, collector-gatherer/scrapers and shredders comprised 54% and 24%, respectively. Scrapers (1%) were less abundant, and predators (5%) and collector-filterers (10%) were more abundant (Table 5), in streams than springs. All functional groups, except scrapers, were more diverse in streams than springs (Table 5). Overall, predators and collector-gatherer/scrapers were the most taxon-rich diverse functional groups in streams.

**Table 4** Kendall rank correlations of physicochemical variables measured in July 2002 at 12 springs and streams in Northern Spain with axis one and two of the non metric multidimensional scaling analysis on invertebrate communities collected at the same time. Asterisks indicate significant correlation, P< 0.05.

| Variables | Axis 1 | Axis 2 |
| --- | --- | --- |
| pH | 0.12 | 0.09 |
| Temperature | 0.33 | 0 |
| Conductivity | -0.33 | -0.12 |
| Oxygen | -0.18 | -0.15 |
| Altitude | 0.25 | 0.34 |
| Canopy cover | 0.28 | 0.08 |
| Discharge | 0.06 | 0.15 |
| Mean width | 0.09 | 0.12 |
| Mean depth | 0.11 | -0.17 |
| Mean velocity | 0 | 0.12 |
| Substrate heterogeneity | 0 | -0.33 |
| Substrate size index | 0.06 | 0.15 |
| Bedrock, % | 0.33 | 0.26 |
| Boulder, % | -0.02 | 0.26 |
| Cobbles, % | 0.21 | -0.18 |
| Pebbles, % | 0.06 | -0.15 |
| Gravel, % | 0.17 | -0.17 |
| Sand, % | -0.4 | 0.28 |
| CPOM | -0.39 | -0.12 |
| FPOM | -0.55* | -0.15 |
| Chlorophyll *a* | -0.58* | -0.3 |
| Phaeophytin | -0.52* | -0.18 |

## Discussion

The habitat stability of springs and springbrooks has been linked to both low (Davidson and Wilding 1943, Ward and Dufford 1979, Meffe and Marsh 1983, Anderson and Anderson 1995) and high invertebrate diversity (Death 1995, Death and Winterbourn 1995, Death et al. 2004). We hypothesized that our spring-fed streams would have less diversity than the nearby runoff-fed streams, and this study clearly shows that the more stable spring-fed streams had lower invertebrate diversity and greater invertebrate

densities than the nearby runoff-fed streams. These patterns could be the result of a variety of determinants that we discuss below.

The Spanish springs we studied had greater periphyton biomass and benthic organic matter (mainly living moss) than the streams. A number of studies on spring habitats have attributed the presence of mats of moss and watercress to the stability of the spring substrate (Lindegaard and Thorup 1975, Gaines et al. 1992, Erman and Erman 1995). The presence of moss could explain the higher levels of algae and organic matter in spring habitats, since moss increases surface area for algal attachment and enhances trapping of detrital food particles (Stem and Stem 1969, Englund 1991, Suren and Duncan 1999).

**Table 5** Mean abundance and taxon richness of macroinvertebrate functional feeding groups collected in 5 Surber samples in springs and streams in Cantabria, Spain, in July 2002. Results of nested ANOVA testing for differences between springs and streams and locations are also given. Asterisks indicate P values < 0.05.

| Functional Group | Mean abundance (±1 SE) | | | | Habitat type $F_{1,37}$ | Locality $F_{5,37}$ | H*L $F_{5,37}$ | Surber $F_{8,37}$ |
|---|---|---|---|---|---|---|---|---|
| | Springs | | Streams | | | | | |
| Collector-Filterer | 0.52 | ± 0.2 | 54.1 | ± 33.5 | 9.7* | 0.7 | 0.5 | 1 |
| Collector-Gatherer | 11 | ± 2.58 | 30.2 | ± 4.7 | 49.9* | 4.8* | 18.4* | 2.7* |
| Collector-Gatherer/Scraper | 629.9 | ± 122 | 304.8 | ± 54.7 | 14.1* | 4.2* | 5.3* | 1.5 |
| Predator | 11.9 | ± 3 | 26.6 | ± 2.9 | 35.7* | 3.5* | 4.6* | 1.9 |
| Scraper | 191.6 | ± 68.5 | 6.8 | ± 1.3 | 51.5* | 11.8* | 14.3* | 0.7 |
| Shredder | 568.5 | ± 96.8 | 140.7 | ± 21.2 | 78.2* | 5.1* | 10.8* | 0.8 |
| **Mean diversity (±1 SE)** | | | | | | | | |
| Functional Group | Springs | | Streams | | | | | |
| Collector-Filterer | 0.3 | ± 0.1 | 1.7 | ± 0.2 | 42.1* | 0.3 | 1.9 | 0.8 |
| Collector-Gatherer | 1.6 | ± 0.2 | 3.2 | ± 0.3 | 52.1* | 4.2* | 12* | 1.8 |
| Collector-Gatherer/Scraper | 5.4 | ± 0.3 | 8.3 | ± 0.3 | 59.1* | 1.7 | 3.9* | 0.9 |
| Predator | 2.5 | ± 0.3 | 6.3 | ± 0.5 | 55.6* | 1.3 | 2.5* | 0.7 |
| Scraper | 2.7 | ± 0.3 | 1.7 | ± 0.3 | 15.1* | 5.7* | 4.8* | 0.6 |
| Shredder | 1.6 | ± 0.2 | 3.3 | ± 0.2 | 55.69* | 4.9* | 4.9* | 1.1 |

Invertebrate community composition was markedly different between streams and springs, although differences were also found within spring and stream communities. The

dominance of the non-insect fauna, especially *Echinogammarus* spp. and snails, at Sp1, Sp4, Sp5 and Sp6 contrasted with the absence of snails and dominance of ephemeropterans and chironomids in Sp2 and Sp3 springs. Communities dominated by amphipods and snails have also been found in limestone springs elsewhere in Europe (Thorup and Lindegaard 1977, Iversen 1988, Smith et al. 2003) and in the USA (Glazier and Gooch 1987). The lack of crustaceans and molluscs in some streams has been attributed to low pH, alkalinity and calcium concentration (Sutcliffe and Carrick 1973, Dillon and Benfield 1982, Griffith and Perry 1994). In the present study, however, springs and streams were physically and chemically similar, so presence/absence of amphipods or snails cannot be accounted for by differences in water chemistry. Communities at Sp2 and Sp3 were more similar to those in runoff-fed streams, particularly St1, mainly because of the high densities of Orthocladiinae. Both Sp2 and Sp3 springs have higher conduit flow than Sp1, Sp4, Sp5 and Sp6 and thus greater flow variability in periods of heavy rain (Martin Zalama, pers. comm.). Increases in flow velocity could adversely affect snail (Richards et al. 2001) and Gammaridae (Gayraud et al. 2000) populations by removing individuals. The inability of these taxa to cope with high velocity flows may explain why they do not dominate in Sp2 and Sp3 springs. If these springs do experience more flow disturbances than the other springs then this could also explain the dominance of mayflies and chironomids which are good colonizers following disturbance (Robinson et al. 1993). Dominance of insect taxa could also be a consequence of a longer term disturbance such as glaciation (Williams and Danks 1991, Williams and Williams 1998). Insect faunas dominate Swedish springs (Hoffsten and Malmqvist 2000), while springs in more southern European countries which were deglaciated several years after, such as England (Smith et al. 2003) or Denmark (Lindegaard et al. 1998), are dominated by *Gammarus pulex*. In our study Sp2 and Sp3 are the springs at higher elevation, and thus insect dominance may also be attributed to the greater effects of glaciation that these sites may have experienced. Evaluating whether short term flow disturbance or longer term glaciation disturbance has led to these differences in the spring faunas will be difficult.

Springs had higher numbers of invertebrates but a lower number of taxa than the streams. These results contrast with the findings of a majority of disturbance experiments

with stream macroinvertebrates, which indicate diversity declines monotonically with increasing disturbance (Death 1996, Vinson and Hawkins 1998, McCabe and Gotelli 2000). Higher macroinvertebrate densities and lower taxa richness in stable rheocrene springs than nearby streams have also been found in other Northern Hemisphere regions (Ward and Dufford 1979, Meffe and Marsh 1983, McCabe 1998) and have generally been attributed to thermal and flow constancy. However, a number of studies in New Zealand (Death 1995, Death and Winterbourn 1995, Death et al. 2004) found higher richness and densities in spring-fed streams than in similar sized runoff-fed streams in their vicinity. When comparing studies from different evolutionary regions we have to take into account that although we may be comparing habitats with similar physicochemical characteristics the biota that establish in these habitats could have different attributes (Ricklefs 2004). The presence-absence of predators, and/or competitors that have different responses to disturbances, may explain the differences in results of the Northern and Southern Hemisphere studies (Wootton 1998). Temperate rheocrene springs are habitats with similar physical characteristics, but the biological communities that establish will be highly dependent on the pool of colonists available in a region. We therefore hypothesize that, for a given stream, macroinvertebrate diversity will be the result of the interaction between the pool of available colonizers, which will resolve the biotic interactions that may be established, and the level of habitat stability.

Species densities and rarified number of species were both higher at more unstable stream sites, indicating that higher macroinvertebrate densities do not always yield larger numbers of taxa. These results contrast with the results of McCabe and Gotelli (2000), who found that macroinvertebrate species densities declined with higher levels of disturbance, whereas rarified species diversity increased.

Flow constancy of the Cantabrian springs enhances macroinvertebrate densities by reducing downstream losses of individuals and food. Greater densities could increase biotic interactions by increasing the number of encounters between individuals (Yount 1956). This is in line with the predictions of the intermediate disturbance hypothesis (Townsend et al. 1997) and the harsh-benign hypothesis (Peckarsky et al. 1990) that a greater level of biotic interactions will occur in macroinvertebrate communities at more stable sites. One possible candidate is *Echinogammarus* spp. that may reduce densities of

other invertebrates via predation and lead to low macroinvertebrate diversity in the Cantabrian springs. Other studies in Central Oregon springs (Anderson and Anderson 1995) and Washington State springs (Cushing 1996), found that absence of amphipods was correlated with greater macroinvertebrate diversity. In a review of temperate coldwater springs of North America, Glazier (1991) suggested that non-insect fauna may prey intensely on unprotected insect eggs, dormant larvae and prepupae of insect fauna, and as a consequence decrease overall diversity. Moreover, Macan (1977) found that predation by amphipods reduced the number of macroinvertebrate taxa in invertebrate communities of stones in English lakes. *Echinogammarus* spp. gut contents (Barquín, unpublished data) from the Cantabrian study springs indicate that a high proportion of the amphipod diet comprises insect larvae as well as detritus. In Ireland, *Gammarus pulex*, another member of the Gammaridae family, actively preys on insect larvae as well as consuming detritus (Kelly et al. 2002a). They also found that amphipods might have further negative impacts on insect larvae as they chase them out of shelter and therefore enhance the probability of capture by trout (Kelly et al. 2002b). Zollhöfer (1999) proposed competition and predation by *Gammarus fossarum* as important factors lowering diversity in some Swiss rheocrenes. It seems possible that habitat stability enhances *Echinogammarus* spp. densities and this in turn reduces macroinvertebrate diversity in our Cantabrian study springs. Testing whether flow reduces *Echinogammarus* populations and whether *Echinogammarus* spp. is an active predator could be a rewarding objective for future research.

Differences between spring and stream communities could also be a result of lower macroinvertebrate immigration rates into spring habitats. Cooper et al. (1990) found that immigration/emigration rates had an overwhelming influence on the effects of biotic processes on macroinvertebrate populations. Spring habitats lack upstream reaches, thus drift, the main source of recolonization and redistribution of the benthic fauna in lotic systems (Williams and Hynes 1976) is missing from springs. Therefore, any effect of predation on macroinvertebrate populations will not be equally buffered in spring and stream habitats.

Reduced temperature variation and modification of the annual temperature regime may also alter macroinvertebrate diversity. This has been suggested as one of the main

factors reducing macroinvertebrate diversity below reservoirs (Lehmkuhl 1974, Ward 1976). Van Gundy (1973) also proposed temperature constancy was the main factor reducing diversity in some Utah springs. Water temperature data from Sp1, Sp2, Sp3 and Sp4 between May 1997 and 1998 indicated temperatures were ± 2-3.5 °C of the mean (MARTIN ZALAMA, unpublished data). This thermal constancy may reduce macroinvertebrate diversity by removing the thermal cues necessary for synchronizing invertebrate life histories (Vannote and Sweeney 1980, Stanford and Ward 1983) or stimulating development of critical life stages (Lehmkuhl 1972). Amphipods and snails, dominant taxa in the studied springs, lack flying adults and thus will not be as adversely affected as insects by a reduction in temperature variation.

In conclusion, flow variability seems to play an important role in determining invertebrate community structure in Cantabrian springs and streams although the exact mechanisms are unclear. Constant thermal regime, increased numbers of predators, and reduced invertebrate immigration into springs may all contribute to the lower diversity in springs compared to runoff-fed streams. Larger scale disturbances such as glaciation may also contribute to the observed patterns and the differences between our findings and those in other studies.

## Acknowledgements

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# 3

**The effect of resource levels and habitat complexity on stream invertebrates**

## Abstract

The effect of algal biomass and habitat structure on stream invertebrate communities was investigated in the Taungatara stream, New Zealand. Artificial canopies that blocked light were used to reduce algal growth. Artificial substrates, ranging from bare clay bricks to bricks with artificial grass or plastic fence twine interwoven with the artificial grass, provided habitats of differing complexity. Numbers of invertebrate taxa and individuals were both lower on bricks under the artificial canopies and on the simplest substrates. The relationship between food resource levels (i.e., algal biomass and organic matter) and invertebrate richness was best described by a power function. The amount of organic matter was the best predictor of invertebrate richness. Algal productivity may enhance invertebrate richness by increasing the number of individuals in a given area, whereas habitat complexity may increase invertebrate richness by providing greater food and/or space resources. The increase in invertebrate diversity with increasing habitat complexity can not be explained by an increase in area alone. Our results fit the predictions of the resource availability hypothesis, and support the view that stream invertebrate communities are physically regulated at local scales.

Keywords: Artificial substrates, habitat structure, macroinvertebrate colonization, productivity, species-area relationships, species richness

## Introduction

The relationship between ecosystem productivity and species richness has been, and still is, a central topic in the study of natural communities (Rosenzweig and Abramsky 1993, Huston 1994, Abrams 1995). Generally, diversity will increase with higher productivity rates, although a decrease in diversity with increasing productivity may occur because of a loss in resource diversity, and thus, an increased opportunity for competitive exclusion (Rosenzweig and Abramsky 1993, Huston 1994). However, the applicability of the hump-shaped curve to describe the relationship between productivity and diversity in all ecosystems has been challenged (Abrams 1995) and several mechanisms can be invoked to explain a decrease in species richness with higher productivity. A review by Waide et al. (1999) indicates that we are a considerable way from accepting a universal relationship between ecosystem productivity and diversity, and they concluded that finding of unimodal, positive linear, negative linear or non significant relationships depends on the type of organisms being studied and the scale of observation.

In pristine stream systems, invertebrate abundance (Hawkins and Sedell 1981, Behmer and Hawkins 1986, Lester et al. 1994) and richness (Hawkins et al. 1982, Friberg et al. 1997, Quinn et al. 1997, Death 2002) have been shown to be greater in streams with higher algal productivity outside densely forested canopies. Experimental reduction of light in streams to decrease algal productivity has revealed both reduction (Quinn et al. 1997) and no effect (Towns 1981, Zimmermann and Death 2002) on invertebrate richness. The few studies describing the shape of the relationship between invertebrate richness and algal biomass have shown both power (Death 2002, Minchin and Death 2002) and quadratic (Zimmermann 2001) models to best fit the data.

The form of the relationship between productivity and species richness may also be complicated by environmental variability (Cardinale et al. 2000). For example, habitat structure can affect species richness by changing the availability of resources (Dean and Connell 1987a, b, Taniguchi and Tokeshi 2004) and disturbance may interact with productivity, resulting in species richness peaking at intermediate levels of both parameters (Connell 1978, Huston 1994). A recent survey of 36 lotic systems in New Zealand (Chapter one, Death et al. 2004) found that high algal biomass, and the presence of moss resulted in increased density and diversity of invertebrates in more stable streams

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compared to nearby unstable ones. However, a similar study in Spain showed invertebrate richness to be lower in the more stable streams, where moss growth and algal biomass were higher (Chapter two, Barquín and Death 2004). Moss in streams provides shelter for invertebrates, a surface for algal attachment and a detritus trap, all resulting in greater invertebrate densities than those found on nearby stony substrates(Maurer and Brusven 1983, Englund 1991, Suren and Winterbourn 1992, Bowden 1999). The structural complexity created by moss fits the definition of habitat complexity given by McCoy and Bell (1991) as the absolute abundance of different structural components per unit of area.

In the present study, we examine how macroinvertebrate communities are affected by algal productivity and substrate complexity, and hypothesize that increases in both will lead to a higher number of taxa and individual invertebrates. High productivity is expected to increase the number of animals because of increased quantities of resources (i.e., algal biomass). However, it is unclear whether invertebrate richness will decrease or increase with increases in the same resource. Increases in habitat complexity may lead to a higher number of individuals because of increases in surface area, and thus more taxa through passive sampling. This is the sampling phenomenon hypothesis (SPH) (Dean and Connell 1987a). Alternatively, the number of taxa may increase because complexity increases resource quantity and diversity. This is the resource availability hypothesis (RAH) (Dean and Connell 1987b, O'Connor 1991, Douglas and Lake 1994). The SPH assumes that everything else being equal habitat complexity does not change species evenness, while the RAH predicts a larger number of taxa on more complex substrates through an increase in the number of available niches (Dean and Connell 1987a, b). In this study, artificial canopies are used to reduce light intensity and therefore decrease algal productivity (Towns 1981, Zimmermann and Death 2002). Artificial substrates, ranging from bare clay bricks to bricks with artificial grass and plastic fence twine interwoven in the artificial grass, are used to examine the effect of increasing habitat complexity on invertebrate communities.

## Materials and methods

### Study Site

The experiment was conducted along a 200 m stretch of Taungatara Stream, a spring-fed stream draining Mt Taranaki in the North Island of New Zealand. The study stretch of stream runs through pasture, however the stream runs for 2.5 km through native broadleaf-Podocarp forest prior to this. Channel width averaged 4.4 m and the streambed was dominated by cobbles and pebbles, with no macrophytes or bryophytes growing in the channel. Base flow in the selected riffles averaged 0.45 $m^3$/s, with water depths ranging from 12 to 28 cm and velocities from 0.4 to 0.8 m/s. Water temperature during the experiment was between 10 and 15 °C, pH between 8.2 and 8.4 and conductivity between 101 and 129 $\mu$S/cm. Nitrate and phosphate concentrations were moderately low, 0.3 mg/ml and 0.5 mg/ml, respectively. Further information on this study site and the invertebrate communities is given in chapter one.

### Experimental design

On 28 March 2003 three riffle sections were conditioned for the experiment by removing any large boulders and flattening the stream bed as much as possible. These "uniform" riffle sections (approximately 60 $m^2$) were divided into high (no canopy) and low (canopy) productivity treatments. Canopies were approximately 5 m long by 7 m wide and were constructed from black polythene sandwiched between two layers of 5 $cm^2$ wire mesh, and supported by wooden beams secured on each bank. Each canopy covered the whole width of the stream with both upstream and downstream ends being covered by black polythene skirts. The canopies rested 0.75 to 2 m above the water level.

Light intensity was measured with a portable quantum sensor LI-COR (LI-250) meter at 5 different points inside and outside the experimental canopy. Light concentration was reduced from 1132.5 $\mu$mol $s^{-1}$ $m^{-2}$ outside the three canopies to 1.7 $\mu$mol $s^{-1}$ $m^{-2}$ inside ($F_{1,27} = 2811.3$; p < 0.001).

Experiment I – Effects of Algal Productivity on Invertebrate Communities

Fifteen days after the canopies were constructed, one (0.1 $m^2$) Surber sample (mesh = 250 $\mu$m) was collected from each of the 3 high and low productivity treatment replicates. This

was repeated every 7 days for four weeks. Samples were preserved in 10% formalin and returned to the laboratory for identification to the lowest possible taxonomic level using available keys (Winterbourn et al. 2000). Fauna was separated into functional feeding groups (FFG) following Cowie (1990), Death (1995) and Winterbourn (2000). After the removal of invertebrates, coarse particulate organic matter (CPOM, >1 mm) and fine particulate organic matter (FPOM, 1-0.45 mm) were dried to constant weight at 95 °C, weighed and ashed at 550 °C for 2 h to yield ash free dry weight. Three stones (maximum length: 40-80 mm) were collected from each replicate for analysis of periphyton biomass. Stones were kept frozen until pigments were extracted using 90% acetone at 5 °C for 24 h in darkness. Absorbancies were read on a Varian-CARY 50 Conc. UV/visible spectrophotometer and converted to pigment concentration (chlorophyll *a* and phaeophytins) following Steinman and Lamberti (1996). Total stone surface area was calculated using the equation of Graham et al. (1988). As only part of a stone is exposed to light (we assumed half the total surface area), estimates of algal pigment concentration were corrected for stone surface area by dividing the total stone surface area in half.

Experiment II - Effects of Algal Productivity and Habitat Structure on Invertebrates
On 11 April 2003 we placed 72 clay bricks (0.23 x 0.11 x 0.05 m) in each of the three riffle sections, 12 in each of the high and low productivity treatments. The bricks consisted of three different levels of habitat complexity: bare bricks (B); bricks with artificial grass glued to the upper surface (G); bricks with plastic fence twine interwoven with the artificial grass (T). Every 7 days for 4 consecutive weeks 18 bricks were collected by lifting them into a net (250 μm mesh) held immediately downstream. Bricks were placed into plastic containers and kept on ice before returning to the laboratory.

In the laboratory, each brick was washed in a set of two sieves (1 mm, and 45 μm). Invertebrates and any organic matter were removed and preserved in 10% formalin. Invertebrates were identified to the lowest possible taxonomic level using available taxonomic keys (Winterbourn et al. 2000). Remaining coarse particulate organic matter (CPOM, >1 mm) and fine particulate organic matter (FPOM, 1-0.45 mm) were quantified as described above. After invertebrate and organic matter removal, algal pigment

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concentration was estimated by placing bricks, grass or twine-grass patches into 90% acetone at 5 °C for 24 h in darkness as described above.

**Statistical analysis**

We calculated Shannon's, Simpson's and rarified diversity values for each of our Surber samples and bricks using the PRIMER statistical package (Clarke and Warwick 1994). The minimum number of individuals in our Surber samples was 59, so species richness was corrected to this number of animals, whereas for brick treatments rarified number of species was corrected to the lowest number of individuals found in each week. As number of individuals increases with sampling area (Hart and Horwitz 1991), and G and T treatments have larger surface areas than the B treatment, we used rarified number of species to compare invertebrate richness between treatments. We also calculated densities of invertebrates (individuals/m$^2$) by estimating the total surface area provided by artificial grass and twine patches. This gave surface areas of 0.025, 0.1 and 0.18 m$^2$ for B, G and T substrates, respectively. Habitat complexity was quantified by dividing the total surface area by the brick surface area. The SPH assumes that given increased surface area but similar resources species diversity will occur in the same relative proportions in both simple and complex habitats (O'Connor 1991). In order to test this assumption we computed an evenness index, E5. This index is not affected by sample size and is known as the "modified Hill's ratio", it is calculated by the equation:

$$E5 = \frac{(1/\lambda)}{e^{H'}-1}$$

where $\lambda$ is Simpson's Index and H' is the Shannon-Weaver Index, both defined in (Ludwig and Reynolds 1988). E5 ranges from 0 (less diverse community) to 1 (more diverse community). Finally, a single value of chlorophyll *a* and phaeophytin per productivity treatment and week was obtained by averaging the values obtained from the three collected stones in each canopy.

Split-plot analysis of variance (ANOVA) was used to test for effects of productivity on invertebrate and resource level measures. Each stream riffle (section) was regarded as a block and productivity as the treatment on the main plot, whereas week of

sampling was regarded as the treatment on the split-plot. Block and productivity effects were tested with the error term Section*Productivity, while the effects of week and the interaction of productivity and week were tested with the error term Section*Week(Productivity).

To test for differences in measures of community structure and resource levels from the effect of productivity, habitat type (Brick, Grass and Twine) and week of sampling factors we performed a 3-factorial analysis of variance (ANOVA) with blocking. Riffle section was regarded as the block while productivity and habitat type were treated as fixed factors, and week as a random factor. ANOVAs were performed in (SAS Institute Inc. 1988) with type III sums of squares and Tukey's post hoc means test when significant differences were found. Variables were transformed to remove heteroscedasticity when necessary. Differences in the density and diversity of functional feeding groups and in the densities of the 12 most abundant taxa were examined with the above ANOVA designs. Spearman rank correlations were performed using (SAS Institute Inc. 1988) to investigate the relationships between resource levels and number of invertebrate taxa and individuals, functional feeding group density and densities of the two most common taxa in each functional feeding group. In order to determine the shape of the relationship between the level of resources (R) and number of taxa (S) we applied linear ($S = C+zR$), exponential ($S = C+zlogR$), power ($S = CR^z$) and quadratic ($S = C +zR +yP^2$) functions to non transformed data. The best model was chosen on the basis of analysis of the distribution of the residuals and the highest $r^2$.

Patterns in community composition were examined using non-metric multidimensional scaling (NMS) with the PC-ORD statistical package (McCune and Mefford 1995). The Sorensen distance measure was used to determine similarity between samples. Initial examination of stress patterns in the data suggested three dimensions were appropriate for the final ordination, which was established with 500 iterations of the data. Relationships between the ordination axes and the measured variables were examined using simple correlation (SAS Institute Inc. 1988).

To determine the significance of differences in invertebrate community composition between high and low productivity treatments and between weeks we performed an analysis of similarities (ANOSIM) using the PRIMER statistical package

(Clarke and Warwick 1994). ANOSIM is a non-parametric procedure that evaluates whether the average similarities between samples within groups are closer than the average similarities of all pairs of replicates between groups (Clarke and Warwick 1994). The mean density of taxa that contributed most ($\geq 90\%$) to the dissimilarity between high and low productivity treatments was evaluated using the SIMPER procedure in the PRIMER statistical package.

## Results

### Effects of Productivity

Periphyton and organic matter

All riffle sections had similar levels of algal and organic matter concentration (Table 1). The canopies were successful in reducing algal growth with pigment concentration six times higher outside than inside canopies. After one week there was no change in pigment concentration with increasing time (Table 1). Organic matter concentration on the stream bed did not change over the length of the experiment and was not affected by the presence or absence of a canopy (Table 1).

**Table 1** Results of split-plot ANOVA testing for differences in Productivity and Week between macroinvertebrate community metrics and resources measured in Taungatara Stream, New Zealand, in the autumn of 2003. H = High productivity and L = Low productivity, 1 = week 1, 2 = week 2, 3 = week 3, 4 = week 4, lines join treatments with no significant differences, * = P 0.05-0.01 and ** = P < 0.01.

| | Section $F_{2,2}$ | Productivity $F_{1,2}$ | Tukey's | Week $F_{3,12}$ | Tukey's | Productivity*Week $F_{3,12}$ |
|---|---|---|---|---|---|---|
| Number of Taxa | 8.79 | 28.96* | H > L | 1.34 | | 0.35 |
| Number of Individuals | 8.58 | 31.18* | H > L | 1.47 | | 1.31 |
| Rarefied Number of Taxa | 0.3 | 0.41 | | 1.38 | | 1.23 |
| Simpson's Diversity Index | 0.02 | 1.28 | | 6.61** | 4 2 3 1 | 2.61 |
| Shannon's Diversity Index | 0.2 | 0.05 | | 6.14** | 4 2 3 1 | 2.24 |
| Chlorophyll *a* | 1.34 | 55.53* | H > L | 6.42** | 3 2 4 1 | 3.33 |
| Phaeophytin | 3.53 | 26.22* | H > L | 3.92* | 1 3 2 4 | 0.47 |
| Total pigment | 1.59 | 49.21* | H > L | 7.09* | 3 2 4 1 | 1.52 |
| CPOM | 0.2 | 0.03 | | 3.04 | | 1.35 |
| FPOM | 0.85 | 0.26 | | 2.38 | | 1.29 |
| Total Organic Matter | 0.72 | 0.04 | | 0.5 | | 1.57 |

Invertebrate abundance and diversity patterns

Forty two invertebrate taxa were collected from the stream benthos during the experiment. Riffle sections did not differ in invertebrate community metrics (Table 1). Number of invertebrate taxa was higher outside the canopies and number of individuals was 4 times greater in the high productivity treatments (Table 1). Rarified species number, Simpson's and Shannon's Indices of diversity were not different between productivity treatments (Table 1). Both number of animals and richness, were highly correlated with algal pigment concentration (Table 2). The best model describing the relationship between invertebrate richness and algal biomass was the power function (P< 0.001) although the quadratic model had similar $r^2$ (Fig. 1). Number of invertebrate taxa and individuals increased with algal biomass but did not decrease at higher levels.

**Table 2** Spearman correlation coefficients between resource measures and number of invertebrate taxa and individuals, evenness, and functional feeding group densities and the two most abundant taxa in each functional feeding group collected in Surber samples in Taungatara Stream, New Zealand, in the autumn of 2003, * = P 0.05-0.01, ** = P < 0.01 (OM= organic matter).

| | CPOM | FPOM | Total OM | Chlorophyll $a$ | Phaeophytin | Total Pigment | NI |
|---|---|---|---|---|---|---|---|
| Number of Taxa | 0.03 | 0.07 | 0.09 | 0.55** | 0.61** | 0.6** | 0.85** |
| Number of Individuals (NI) | -0.01 | 0.17 | 0.11 | 0.67** | 0.68** | 0.66** | |
| Rarified Number of Taxa | 0.08 | -0.04 | 0.08 | -0.06 | -0.25 | 0.02 | -0.29 |
| Simpson Index of Diversity | 0.21 | -0.26 | 0.18 | -0.02 | -0.33 | 0.08 | -0.2 |
| Shannon Index of Diversity | 0.15 | -0.15 | 0.18 | 0.06 | -0.24 | 0.15 | -0.09 |
| **Sessile Browser** | 0.12 | 0.1 | 0.21 | 0.67** | 0.63** | 0.67** | |
| *Iaonella forsythi* | 0.25 | 0.08 | 0.27 | 0.83** | 0.77** | 0.84** | |
| *Iaoridiamesa* spp. | 0.34 | 0.07 | 0.37 | 0.79** | 0.52** | 0.76** | |
| **Mobile Browser** | -0.04 | 0.24 | 0.11 | 0.62** | 0.7** | 0.6** | |
| *Pycnocentrodes* spp. | -0.01 | 0.2 | 0.12 | 0.5* | 0.62** | 0.48** | |
| *Iydora* sp. | -0.2 | 0.21 | -0.1 | 0.16 | 0.43* | 0.07 | |
| **Filterer** | -0.1 | -0.01 | 0.17 | 0.2 | -0.11 | 0.21 | |
| *Coloburiscus humeralis* | -0.17 | 0.12 | 0.12 | 0.16 | 0.06 | 0.18 | |
| *Ioteapsyche* spp. | -0.12 | 0.17 | 0.13 | 0.27 | -0.02 | 0.21 | |
| **Shredder** | 0.09 | 0.12 | 0.36 | 0.04 | 0.25 | 0.08 | |
| *Olinga feredayi* | 0.02 | 0.08 | 0.31 | 0.01 | 0.23 | 0.09 | |
| *Pycnocentria funerea* | 0.45* | -0.02 | 0.34 | 0.15 | 0.05 | 0.2 | |
| **Predator** | 0.02 | -0.13 | -0.13 | 0.43** | 0.4** | 0.5** | 0.5** |
| *Archichauliodes diversus* | 0 | -0.18 | -0.09 | 0.36 | 0.24 | 0.43* | 0.32 |
| *Hydrobiosidae* | 0.11 | -0.12 | -0.03 | 0.48** | 0.42* | 0.55** | 0.7** |
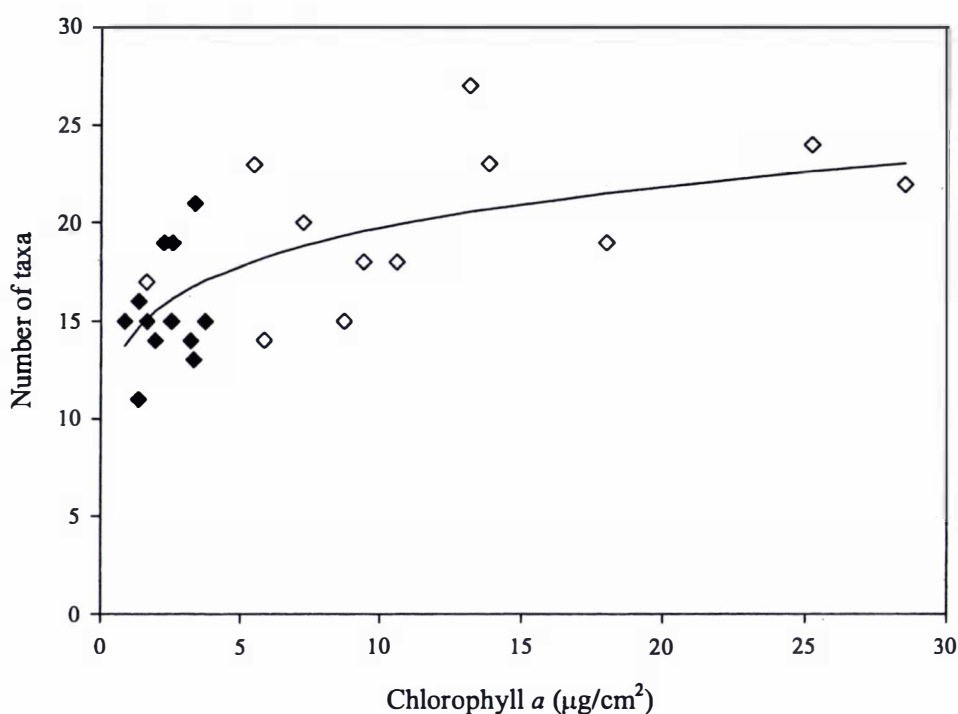
**Figure 1** Productivity-species richness relation for invertebrate communities collected on Surber samples in Low (solid symbols) and High (open symbols) productivity treatments in the Taungatara Stream, New Zealand, in the autumn of 2003, $(y = 13.9(x^{0.15})$; $r^2 = 0.43)$.

Taxonomic composition and community structure

Coleoptera, Ephemeroptera and Trichoptera constituted almost 80% of the animals in the communities under the canopies while Diptera and Trichoptera alone constituted more than 75% of the animals outside the canopies (Table 3). *Hydora* sp. and *Pycnocentrodes* spp. dominated invertebrate communities in both high and low productivity treatments along with *Coloburiscus humeralis* and *Naonella forsythi* in low and high productivity treatments, respectively. Community composition differed between productivity treatments (R= 0.42, P< 0.01) but not over time (R= 0.35, P= 0.11). The reduced productivity changed relative abundances rather than the presence or absence of taxa (Table 3). Six of the most abundant taxa had higher densities outside the canopies, the chironomids *N. forsythi*, *Eukiefferiella* spp. and *Maoridiamesa* spp. and the cased-caddisflies *Beraeoptera roria*, *Confluens hamiltoni* and *Pycnocentrodes* spp (Table 3).

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Numbers of *Austrosimulium* spp. and *Potamopyrgus antipodarum* were twice as high inside as outside the canopies, but these differences were not significant (Table 3).

**Table 3** Densities (ind./m$^2$) of the most abundant taxa in high and low productivity treatments and results of split-plot ANOVA testing for differences in Productivity (P) and Week (W) for these taxa collected in Surber samples in Taungatara Stream, New Zealand, in the autumn of 2003. Taxa are listed in order of decreasing importance in differentiating communities between productivity treatments. H = High productivity and L = Low productivity, 1 = week 1, 2 = week 2, 3 = week 3, 4 = week 4, lines join averages with no significant differences, * = P 0.05-0.01 and ** = P < 0.01.

| | High Productivity | | Low Productivity | | Section | P | | | W | | P*W |
| | Mean | SE | Mean | SE | $F_{2,2}$ | $F_{1,2}$ | Tukey's | $F_{3,12}$ | Tukey's | $F_{3,12}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| *entrodes* spp. | 122.67 | ± 30.17 | 35.75 | ± 6.54 | 63.2* | 128.5** | H > L | 1.81 | | 0.71 |
| *lla forsythi* | 85.42 | ± 32.98 | 1.50 | ± 0.38 | 2.85 | 42.74* | H > L | 11.67** | 3 2 4 1 | 10.58** |
| *1* spp. | 64.58 | ± 15.8 | 38.42 | ± 5.85 | 2.27 | 0.81 | | 1.41 | | 0.72 |
| *liamesa* spp. | 38.75 | ± 11.3 | 1.33 | ± 0.64 | 0.75 | 26.41* | H > L | 7.75** | 3 4 2 1 | 2.57 |
| *eriella* spp. | 31.92 | ± 9.6 | 1.08 | ± 0.38 | 1.03 | 7.1 | | 8.48** | 3 2 4 1 | 4.14* |
| *ptera roria* | 26.42 | ± 6.2 | 4.92 | ± 1.56 | 1.68 | 25.85* | H > L | 3.17 | | 0.7 |
| *pyrgus antipodarum* | 4.67 | ± 2.3 | 13.83 | ± 6.54 | 3.19 | 8.22 | | 2.1 | | 0.35 |
| *ens hamiltoni* | 10.17 | ± 4.44 | 0.83 | ± 0.34 | 0.68 | 5.56 | | 0.26 | | 1.09 |
| *riscus humeralis* | 14.42 | ± 2.81 | 14.17 | ± 2.2 | 8.74 | 0.04 | | 0.55 | | 2.01 |
| *idium* spp. | 7.08 | ± 2.45 | 2.75 | ± 1.06 | 4.96 | 4.24 | | 14.86** | 4 1 2 3 | 0.13 |
| *simulium* spp. | 3.08 | ± 0.87 | 6.17 | ± 1.5 | 0.38 | 1.78 | | 8.48** | 3 2 4 1 | 2.21 |
| *syche* spp. | 5.83 | ± 1.83 | 4.92 | ± 1.43 | 27.14* | 3.2 | | 1.55 | | 0.07 |

Mobile Browsers (MB) dominated both high and low productivity treatments and were almost three times more numerous outside than inside the canopies ($F_{1,2}$= 39.65, P< 0.05). Densities of sessile browsers (SB) were 9 times greater in the high productivity treatments ($F_{1,2}$= 23.3, P< 0.05), possibly as a result of the high numbers of chironomid larvae (Table 3). Densities of shredders, filterers and predators were not affected by the canopy ($F_{1,2}$<2.2, P> 0.05). Densities of both MB and SB were correlated with algal pigment concentration (Table 2). Filterer and shredder densities were not correlated with resource levels although densities of the leaf eater *Pycnocentria funerea* were positively correlated with the quantity of CPOM (Table 2). Predator densities were positively correlated with number of individuals and pigment concentration (Table 2).
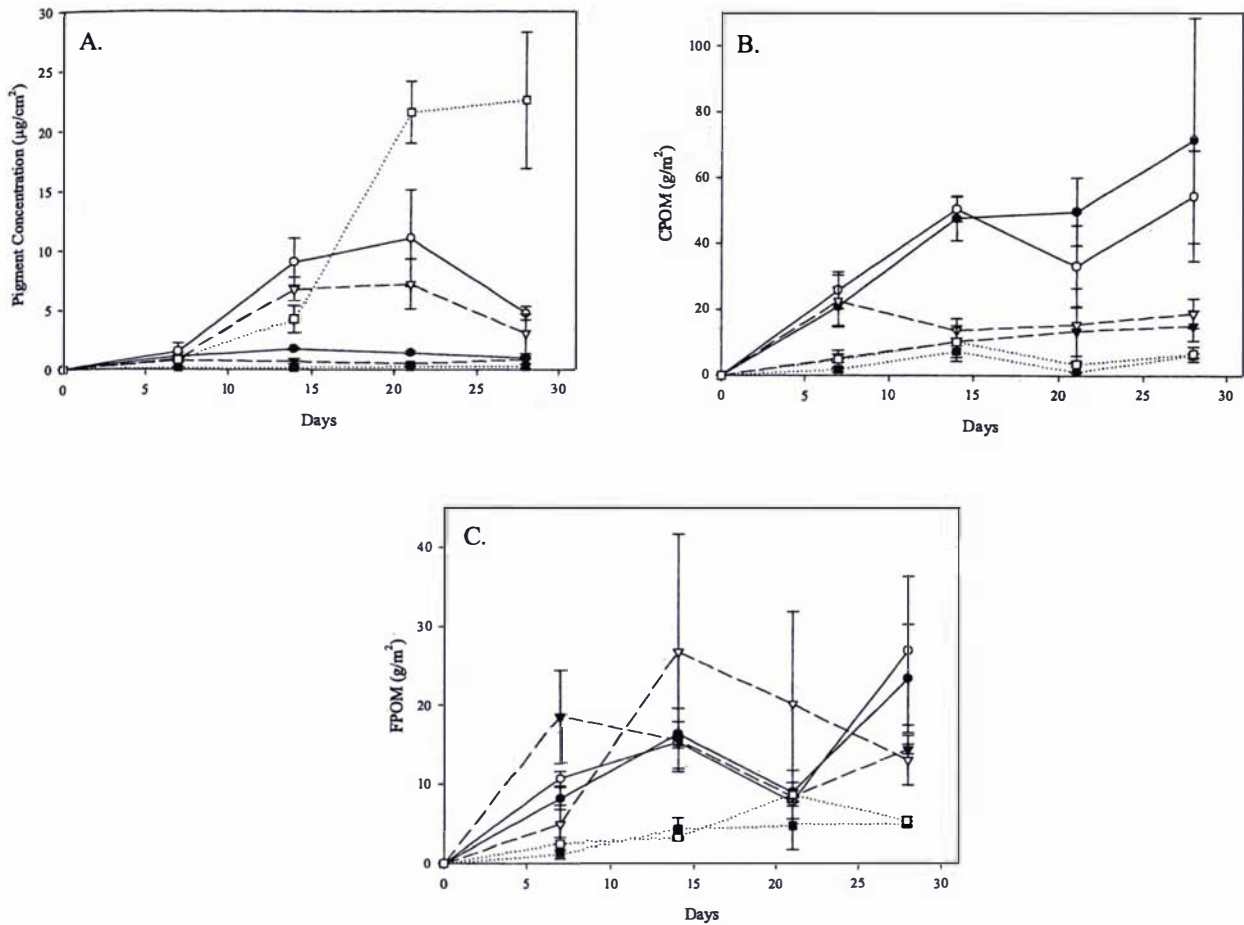
**Figure 2** Mean (± 1 SE) A. Alga pigment concentration (chlorophyll *a* plus phaeophytin) B. Coarse particulate organic matter and C. Fine particulate organic matter collected in artificial substrata after 7, 14, 21 and 28 days of colonization in the Taungatara Stream, New Zealand, in autumn 2003 (□⋯□, Brick-High Productivity; ■⋯■, Brick-Low Productivity; ▽⋯▽, Grass-High; ▼⋯▼, Grass-Low; O—O, Twine-High; ●—●, Twine-Low).

**Interactions of Productivity and Habitat Structure**

Periphyton and organic matter

Pigment concentration was 10 times higher on all substrata placed outside the canopies (Fig. 2 and Table 4). More algae colonized with increasing exposure time, although differences were only significantly between week 1 and the other times (Fig. 2 and Table 4). Surprisingly, Bricks had more than twice the concentration of chlorophyll *a* than the T and G substrata, while T and G substrata had twice as much phaeophytin as Bricks.

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Overall T substrata accumulated significantly more periphyton than G substrata (Fig. 2 and Table 4).

Concentration of organic matter increased with time (Fig. 2, Table 4). T substrata had twice as much organic matter as G substrata, and 6 times more organic matter than Bricks (Fig. 2 and Table 4). FPOM concentration was not different between T and G substrata but was almost 4 times greater on these when compared to Bricks. The presence of a canopy had no effect on the amount of organic matter collected (Fig. 2 and Table 4).

Invertebrate abundance and diversity patterns

Invertebrates colonizing artificial substrates increased in richness, evenness, rarified number of species and density from week 1 to week 4 (Fig. 3 and Table 4). Absence of canopies increased both number of invertebrate taxa and individuals, although it decreased rarified number of taxa, Simpson's and Shannon's indices of diversity and Hill's modified ratio (Fig. 3 and Table 4). Thus, the effect of increased productivity was to increase dominance without the elimination of invertebrate taxa.

Habitat complexity increased number of invertebrate individuals and taxa (Table 4). T substrates had slightly more taxa than G substrata and twice as many taxa as Bricks. Number of individuals was 4 times higher on T substrata and 3 times higher on G substrata than on Bricks (Fig. 3 and Table 4). All evenness measures increased with higher habitat complexity, although only Shannon's index of diversity showed significant differences (Table 4). Rarified number of species was higher on T and G substrata than on Bricks (Fig. 3 Table 4).

Invertebrate densities were not statistically different when accounting for total surface area ($F_{2,48}= 0.82$; $P= 0.49$). Under the assumptions of the SPH we expected to find more species on T, than on G substrata and more on T and G substrata than on Bricks because a larger area has been sampled. However, the rarified number of taxa indicates that the ratio of number of taxa/number of individuals was higher for T and G substrata than for Bricks, thus the increase in number of invertebrate taxa with increasing habitat complexity cannot be simply explained by a larger sampled area. Hill's modified ratio on the other hand, was higher on bricks than on T and G substrata (Table 4).

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Table 4 Three way ANOVA results testing for differences in Habitat Complexity (HC), Productivity (P) and Week (W) for macroinvertebrate community metrics and resources measured after 7, 14, 21 and 28 days of colonization of artificial substrata in Taungatara Stream, New Zealand, in the autumn of 2003. T = Twine, G = Grass, B = Brick, H = High productivity and L = Low productivity, 1 = week 1, 2 = week 2, 3 = week 3, 4 = week 4, lines join treatments with no significant differences, * = P 0.05-0.01 and ** = P < 0.01.

| | Section | HC | Tukey's | P | Tukey's | W | Tukey's | HC*P | HC*W | P*W | HC*P*W | Axis 1 | Axis 2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $F_{2,46}$ | $F_{2,46}$ | | $F_{1,46}$ | | $F_{3,6}$ | | $F_{2,46}$ | $F_{6,46}$ | $F_{3,46}$ | $F_{6,46}$ | | |
| Chlorophyll *a* | 1.4 | 278.48** | B T G | 430.59** | H > L | 1.38 | | 319.65** | 39.3** | 41.52** | 35.79** | -0.26 | -0.45 |
| Phaeophytin | 1.45 | 20.7** | T G B | 188.51** | H > L | 5.09* | 3 2 4 1 | 0.24 | 4.07** | 15.77** | 3.42** | -0.48 | -0.61 |
| Total pigment | 0.92 | 7.08** | T B G | 318.83** | H > L | 6.11* | 3 2 4 1 | 21.14** | 5.98** | 26.15** | 4.72** | -0.41 | -0.59 |
| CPOM | 3.19 | 82.37** | T G B | 3.37 | | 8.61** | 4 2 3 1 | 1.34 | 1.07 | 1.37 | 0.73 | -0.62 | -0.30 |
| FPOM | 2.24 | 34.65** | T G B | 0.42 | | 3.44 | | 1.12 | 1.64 | 0.53 | 1.64 | -0.45 | -0.30 |
| Total Organic Matter | 2.08 | 86.27** | T G B | 2.38 | | 11.22** | 4 2 3 1 | 1.08 | 1 | 0.4 | 0.65 | -0.62 | -0.35 |
| Number of Taxa | 11.71** | 127.47** | T G B | 28.26** | H > L | 25.57** | 4 3 2 1 | 0.2 | 0.9 | 0.45 | 0.88 | -0.70 | -0.46 |
| Number of Individuals | 13.97** | 107.29** | T G B | 102.47** | H > L | 19.83** | 4 3 2 1 | 0.48 | 2.16 | 6.31** | 2.2 | -0.80 | -0.65 |
| Rarefied Number of Taxa | 0.1 | 7.3** | T G B | 22.95** | L > H | 29.3** | 4 3 2 1 | 9.14** | 1.27 | 8.87** | 3.18** | | |
| Simpson's Diversity Index | 0.96 | 1.57 | | 15.56** | L > H | 0.57 | | 7.58** | 1.08 | 3.4 | 2.16 | | |
| Shannon's Diversity Index | 2.04 | 17.69** | T G B | 7.96** | L > H | 0.58 | | 10.25** | 0.44 | 4.71** | 1.96 | | |
| Hill's Modified Ratio (E5) | 0.19 | 12.08** | B G T | 24.36** | L > H | 3.71 | | 4.27** | 2.17 | 0.67 | 1.62 | | |
| Habitat Complexity | | | | | | | | | | | | -0.61 | -0.27 |
| Days after colonization | | | | | | | | | | | | -0.40 | -0.25 |
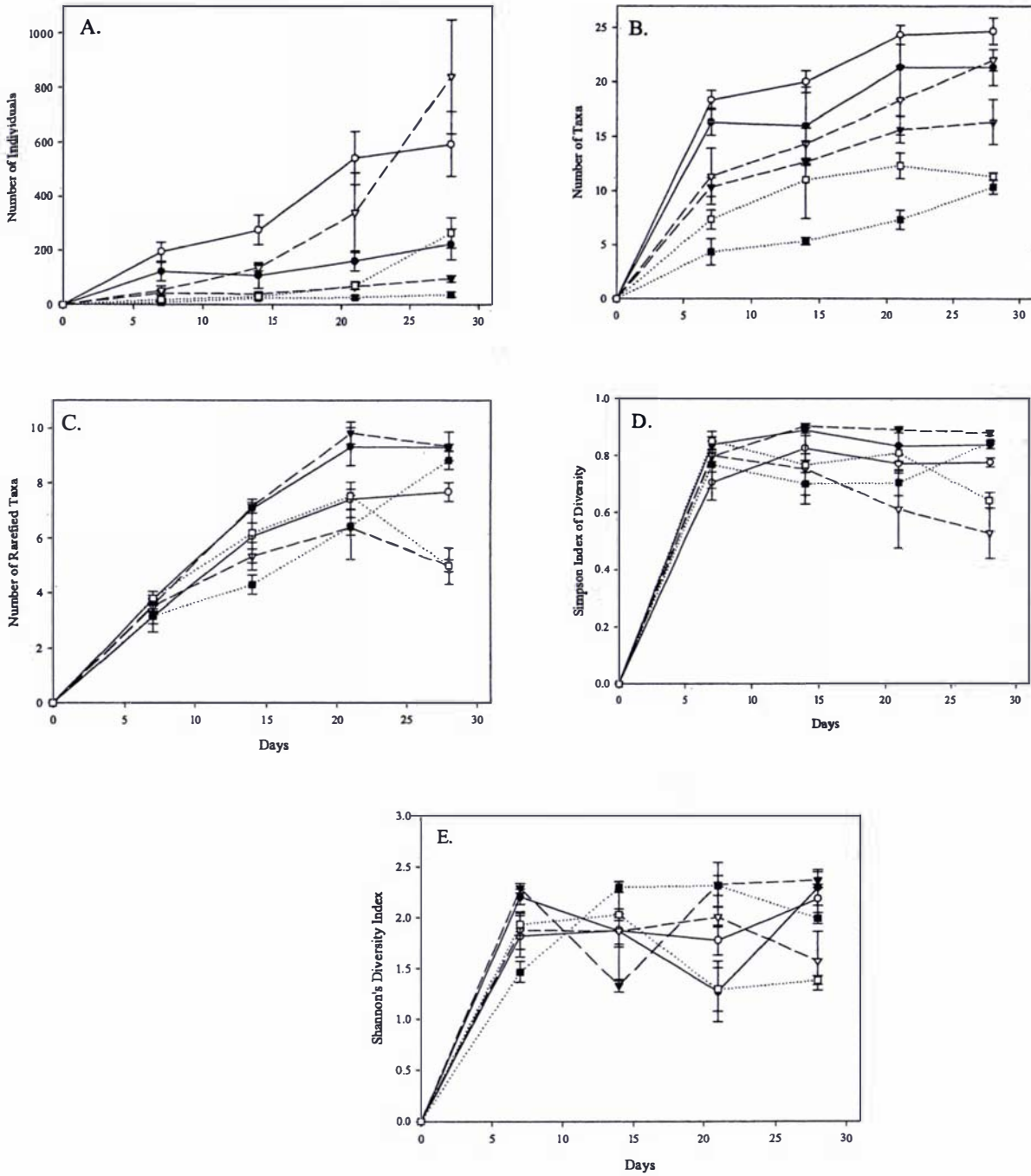
**Figure 3** Mean (± 1 SE) A. Number of individuals, B. Number of taxa, C. Rarified number of taxa D. Simpson diversity index and E. Shannon diversity index for invertebrate communities after 7, 14, 21 and 28 days of colonization of artificial substrata in the Taungatara Stream, New Zealand, in the autumn of 2003 (□····□, Brick-High Productivity; ■····■, Brick-Low Productivity; ▽⁻⁻▽, Grass-High; ▼⁻⁻▼, Grass-Low; O——O, Twine-High; ●——●, Twine-Low).

Number of invertebrate taxa and individuals, were both positively correlated with organic matter and algal pigment concentration (Table 5). A power function best described the relationship between number of taxa with productivity and organic matter (Fig. 4).

**Table 5** Spearman correlation coefficients between resources and numbers of invertebrate taxa and individuals, functional feeding group densities and the two most important taxa in each functional feeding group collected after 7, 14, 21 and 28 days of colonization on artificial substrata in Taungatara Stream, New Zealand, in the autumn of 2003. * = P 0.05-0.01, ** = P < 0.01.

| | CPOM | FPOM | Total OM | Chlorophyll *a* | Phaeophytin | Total Pigment | NI |
|---|---|---|---|---|---|---|---|
| Iumber of Taxa | 0.75** | 0.57** | 0.78** | 0.33** | 0.58** | 0.48** | 0.87** |
| Iumber of Individuals (NI) | 0.64** | 0.5** | 0.68** | 0.4** | 0.68** | 0.6** | |
| :arefied Number of Taxa | 0.23 | 0.27* | 0.25* | 0.11 | 0.09 | 0.1 | 0.17 |
| impson Index of Diversity | 0.16 | 0.22 | 0.14 | -0.11 | -0.18 | -0.17 | -0.27* |
| hannon Index of Diversity | 0.46** | 0.46** | 0.48** | 0.66* | 0.51* | 0.66* | 0.14 |
| **essile Browser** | 0.42** | 0.42** | 0.47** | 0.41** | 0.67** | 0.61** | |
| *I. forsythi* | 0.36** | 0.37** | 0.4** | 0.41** | 0.7** | 0.64** | |
| *Iaoridiamesa* spp. | 0.23** | 0.25* | 0.29* | 0.46** | 0.69** | 0.65** | |
| **Iobile Browser** | 0.71** | 0.56** | 0.76** | 0.26* | 0.59** | 0.47** | |
| *ycnocentrodes* spp. | 0.62** | 0.51** | 0.69** | 0.27* | 0.63** | 0.53** | |
| *Iydora* sp. | 0.62** | 0.49** | 0.64** | 0.11 | 0.37** | 0.25** | |
| **ilterer** | 0.65** | 0.47** | 0.68** | 0.09 | 0.29* | 0.18 | |
| *I. humeralis* | 0.68** | 0.43** | 0.7** | 0.14 | 0.32** | 0.21 | |
| *iustrosimulium* spp. | 0.43** | 0.29* | 0.45** | 0.09 | 0.24* | 0.17 | |
| **hredder** | 0.56** | 0.29* | 0.51** | 0.27* | 0.19 | 0.16 | |
| *I. feredayi* | 0.53** | 0.23 | 0.46** | 0.17 | 0.08 | 0.06 | |
| *I. funerea* | 0.41** | 0.21 | 0.36** | 0.11 | 0.17 | 0.13 | |
| **redator** | 0.56** | 0.52** | 0.63** | 0.23 | 0.46** | 0.36** | 0.75** |
| Iydrobiosidae | 0.62** | 0.44** | 0.61** | 0.26* | 0.48** | 0.4** | 0.69** |
| *I. diversus* | 0.25* | 0.16 | 0.23* | 0.01 | -0.01 | -0.04 | 0.31** |

Taxonomic composition and community structure

Diptera and Trichoptera numerically dominated macroinvertebrate communities accounting for 70% of total abundance in week 1 and more than 80% in week 4. They also dominated all substrata, constituting 75%, 87%, and 80% of the invertebrate communities in T, G and B treatments, respectively. This dominance was a result of the densities of the chironomids *N. forsythi*, *Maoridiamesa* spp. and *Eukiefferiella* spp., the black fly *Austrosimulium* spp. and the cased-caddisfly *Pycnocentrodes* spp. (Table 6).

The ephemeroptera was also numerically important inside the canopies, because of the densities of *C. humeralis* and *Austroclima jollyae*.
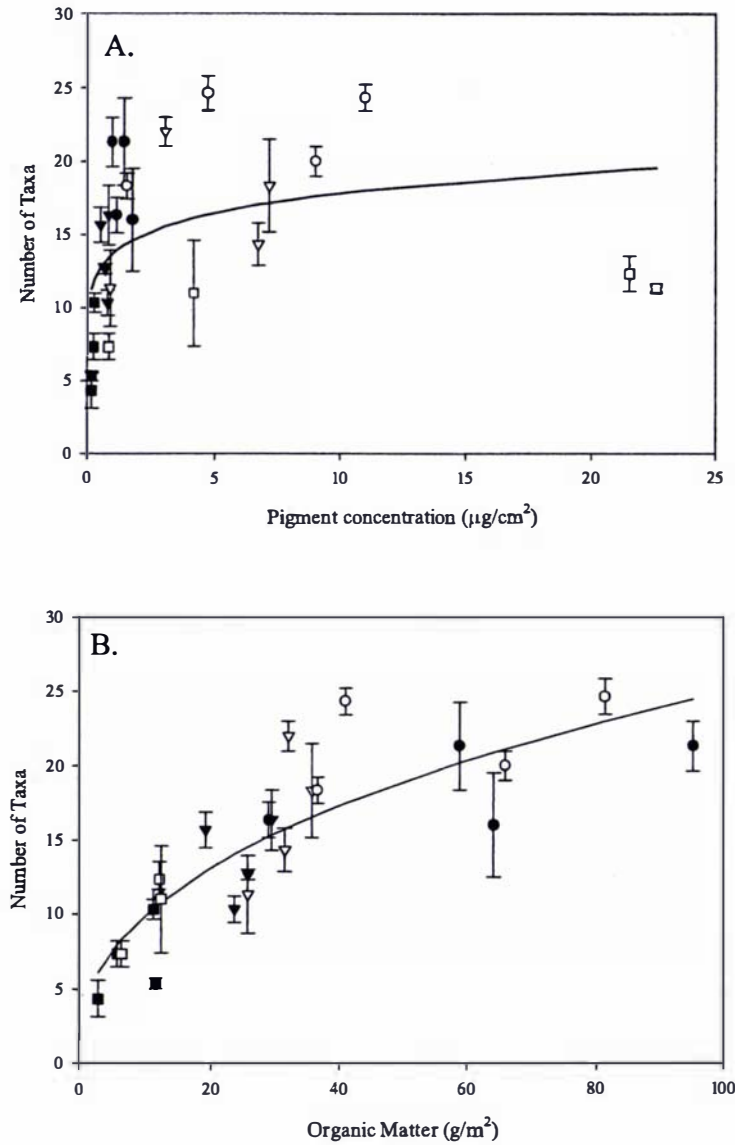


**Figure 4** Relationships between A. algal biomass and B. organic matter with number of invertebrate taxa collected after 7, 14, 21 and 28 days of colonization of artificial substrata in the Taungatara Stream, New Zealand, in the autumn of 2003 (algae biomass: $y = 12.2(x^{0.18})$; $r^2 = 0.32$; organic matter: $y = 3.1(x^{0.47})$; $r^2 = 0.79$) (□, Brick-High Productivity; ■, Brick-Low Productivity; ▽, Grass-High; ▼, Grass-Low; ○, Twine-High; ●, Twine-Low).

Invertebrate communities on T, G and B substrata and in high and low productivity treatments were significantly different (R> 0.387 in all cases, P< 0.001). Densities of the most abundant taxa were higher on T and G substrata than on Bricks and they increased with time, except for *Austrosimulium* spp. which decreased in all substrata after week 3. The densities of cased-caddisflies *Pycnocentrodes* spp. and *O. feredayi* did not change over time (Fig. 5 and Table 6). *Hydora* sp., *C. humeralis*, *Austrosimulium* spp., *O. feredayi* and *P. funerea* did not show differences between high or low productivity treatments, but the remaining taxa showed higher densities outside the canopies, except for *P. antipodarum* which was more abundant under the canopies (Fig. 5 and Table 6).

Final stress for the NMDS analysis was 8.9, indicating a reliable ordination (McCune and Mefford 1995). Axis 1 and axis 2 explained 53% and 36% of the total variance, respectively. Twine communities occurred to the left of axis one while more simple substrata graded to the right (Fig. 6). High productivity treatments occurred towards the bottom of axis two while low productivity communities were towards the upper part of axis two. The densities of the most important taxa increase to the left bottom corner of the ordination (Table 6). Amount of resources, habitat complexity and days of colonization were all negatively correlated with axes one and two of the NMDS (Table 4).

All functional feeding groups had higher densities and diversity on more complex substrata ($F_{2,46}$ > 10.4, P< 0.001). MB and SB had higher densities and diversity outside the canopies ($F_{1,46}$ > 17.1, P< 0.05), whereas filterer, predator and shredder density and diversity were not different between high and low productivity treatments ($F_{1,46}$ < 3.44, P> 0.05). MB and SB were positively correlated with organic matter and algal pigment concentration (Table 5). Filterers and shredders were positively correlated with organic matter. Total organic matter was most strongly correlated with *C. humeralis* and *Austrosimulium* spp. density, while CPOM was most strongly correlated with *O. feredayi* and *P. funerea* density (Table 5). Predator densities were positively correlated with total number of invertebrate individuals (Table 5). In general, densities of functional feeding groups correlated well with food resources.
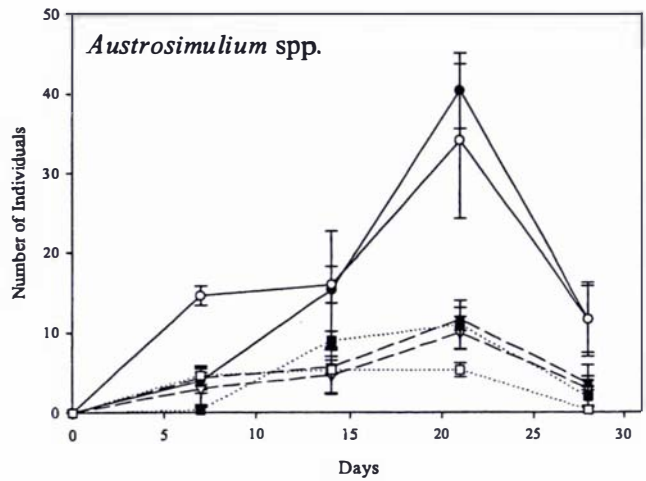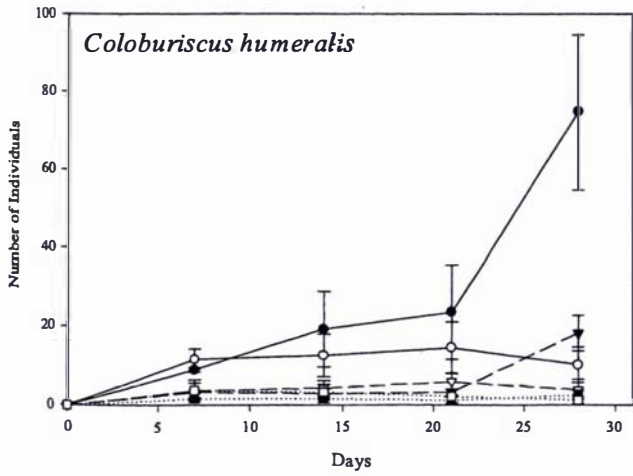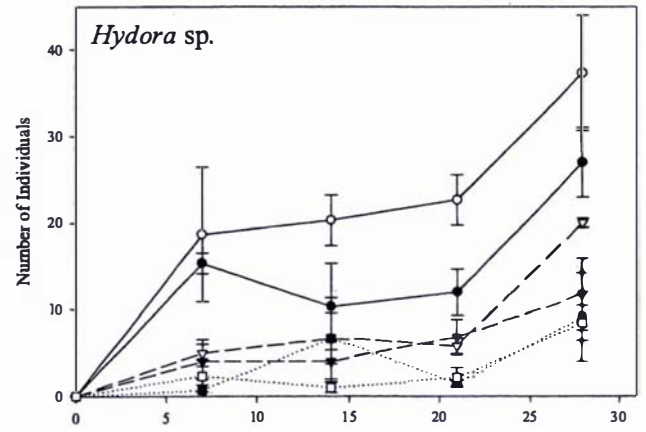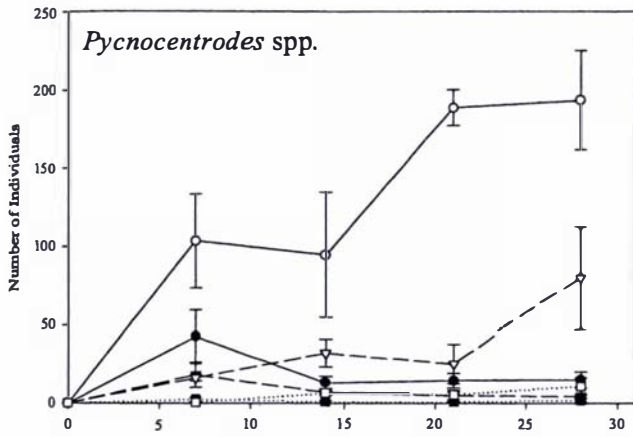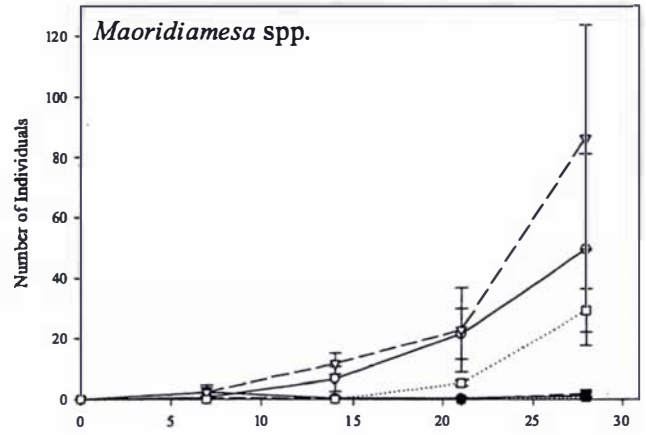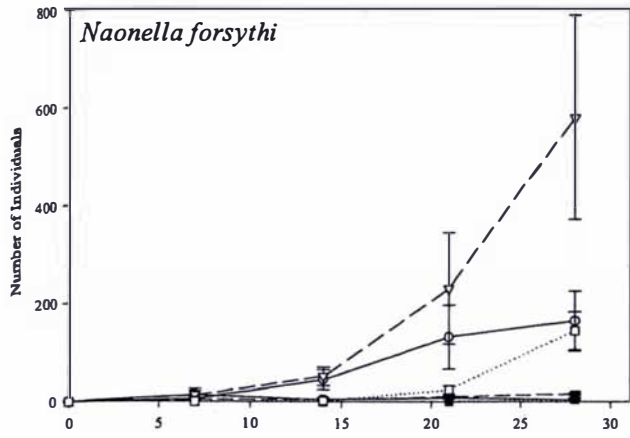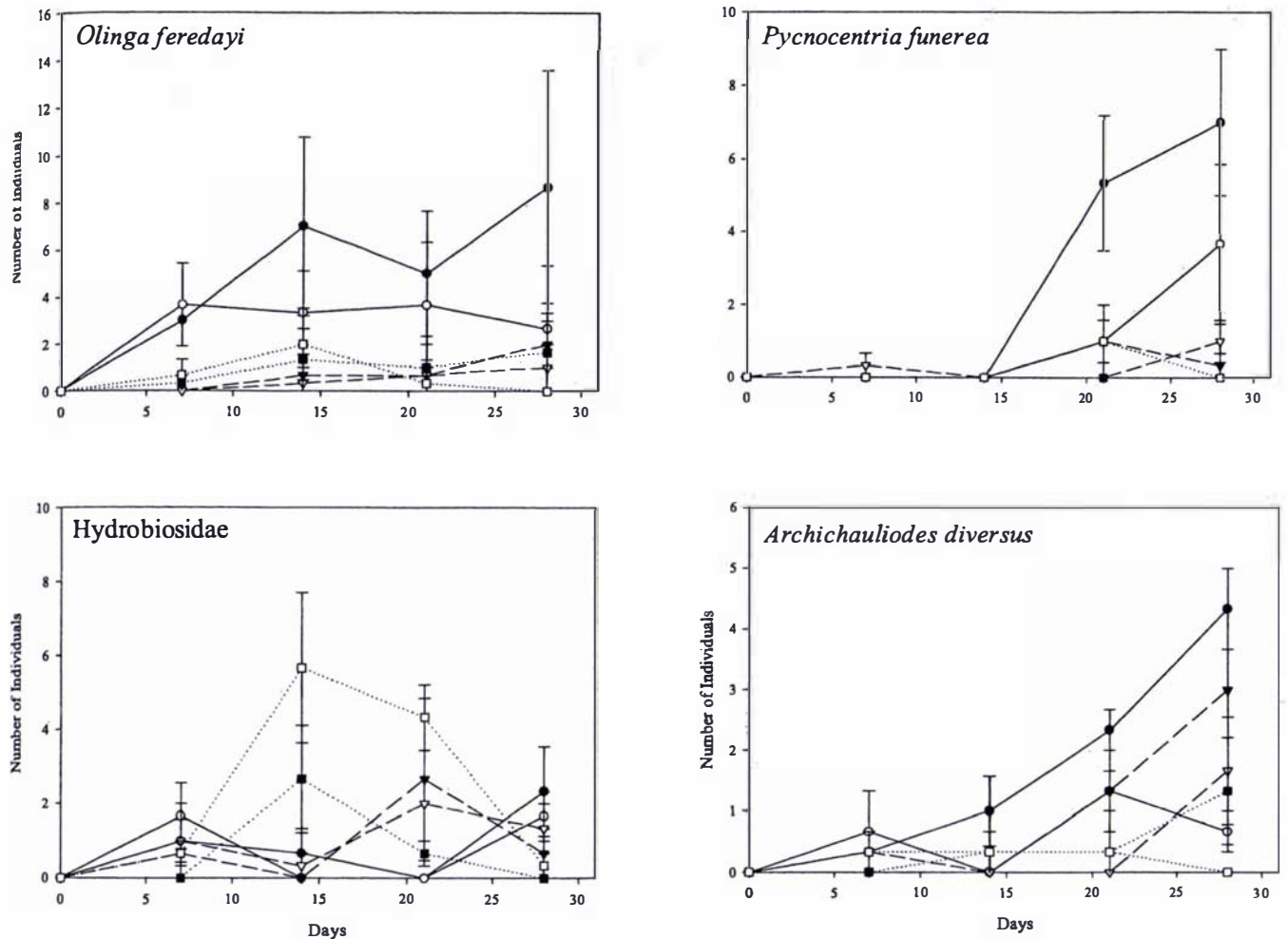
**Figure 5** Mean number of individuals (± 1 SE) of the two most abundant taxa in each functional feeding group after 7, 14, 21 and 28 days of colonization of artificial substrata in the Taungatara Stream, New Zealand, in autumn 2003 (□⋯□, Brick-High Productivity; ■⋯■, Brick-Low Productivity; ▽⋯▽, Grass-High; ▼⋯▼, Grass-Low; O—O, Twine-High; ●—●, Twine-Low).

## Discussion

Increased algal biomass and habitat complexity both led to higher number of invertebrate taxa and individuals. Invertebrate diversity was lower under the canopies because there were fewer individuals and reduced amounts of food. Habitat complexity increased diversity because more food and space were available.

**Table 6** Results of three way ANOVA testing for differences in Habitat Complexity (HC), Productivity (P) and Week (W) for the most abundant taxa overall and the two most abundant taxa in each functional group collected after 7, 14, 21 and 28 days of colonization of artificial substrata in Taungatara Stream, New Zealand, in the autumn of 2003. Kendall rank correlation coefficients of these taxa with axis one and two of NMDS are also given. Taxa are listed in order of decreasing importance in differentiating communities. H = Habitat complexity, P = Productivity, W = Week, T = Twine, G = Grass, B = Brick, H = High productivity and L = Low productivity, 1 = week 1, 2 = week 2, 3 = week 3, 4 = week 4, lines join treatments with no significant differences, * = P 0.05-0.01 and ** = P < 0.01.

| | Section | HC | Tukey's | P | Tukey's | W | Tukey's | HC*P | HC*W | P*W | HC*P*W | Axis 1 | Axis 2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $F_{2,46}$ | $F_{2,46}$ | | $F_{1,46}$ | | $F_{3,6}$ | | $F_{2,46}$ | $F_{6,46}$ | $F_{3,46}$ | $F_{6,46}$ | | |
| *N. forsythi* (SB) | 10.11** | 31.45** | G T B | 106.32** | H > L | 30.35** | 4 3 2 1 | 0.74 | 1.8 | 14.07** | 0.98 | -0.56 | -0.81 |
| *Pycnocentrodes* spp. (MB) | 3.64* | 111.46** | T G B | 82.12** | H > L | 2.3 | | 5.2** | 1.52 | 8.9** | 0.6 | -0.58 | -0.57 |
| *Hydora* spp. (MB) | 1.21 | 39.07** | T G B | 2.69 | | 8.9* | 4 3 2 1 | 1.1 | 0.59 | 0.07 | 1.17 | -0.73 | -0.34 |
| *Maoridiamesa* spp. (SB) | 7.64** | 9.13** | G T B | 126.59** | H > L | 31.52** | 4 3 2 1 | 4.07* | 1.01 | 18** | 0.88 | -0.55 | -0.81 |
| *C. humeralis* (F) | 4.8* | 42.57** | T G B | 2.97 | | 4.27* | 4 3 2 1 | 1.51 | 0.84 | 4.92* | 0.51 | -0.46 | -0.17 |
| *Austrosimulium* spp. (F) | 0.14 | 22.79** | T G B | 0.21 | | 12.65** | 3 2 1 4 | 2.65 | 0.84 | 2.92 | 1.1 | -0.31 | 0.01 |
| *Eukiefferiella* spp. (SB) | 4.66* | 4.83* | T G B | 67.41** | H > L | 5.72* | 4 3 2 1 | 2.87 | 4.55** | 9.93** | 4.13** | -0.53 | -0.60 |
| *P. antipodarum* (SB) | 2.6 | 7.99** | T G B | 4.13* | L > H | 6.36* | 4 2 3 1 | 0.4 | 0.43 | 3.65* | 0.76 | -0.39 | 0.13 |
| *O. feredayi* (S) | 9.33* | 15.78** | T B G | 2.11 | | 3.18 | | 0.11 | 0.55 | 0.92 | 0.13 | -0.40 | 0.09 |
| Hydrobiosidae (P) | 8.94* | 23.13* | T G B | 5.81* | H > L | 5.45* | 4 3 2 1 | 0.03 | 0.88 | 2.42 | 0.84 | -0.57 | -0.46 |
| *P. funerea* (S) | 1.61 | 19.64** | T G B | 2.1 | | 6.72** | 4 3 2 1 | 4.63* | 8.16** | 2.03 | 2.46** | -0.35 | -0.24 |
| *A. diversus* (P) | 3.38* | 7.51* | T G B | 11.22** | H > L | 9.46* | 4 3 2 1 | 1.44 | 2.09 | 3.07* | 1.1 | -0.29 | 0.08 |
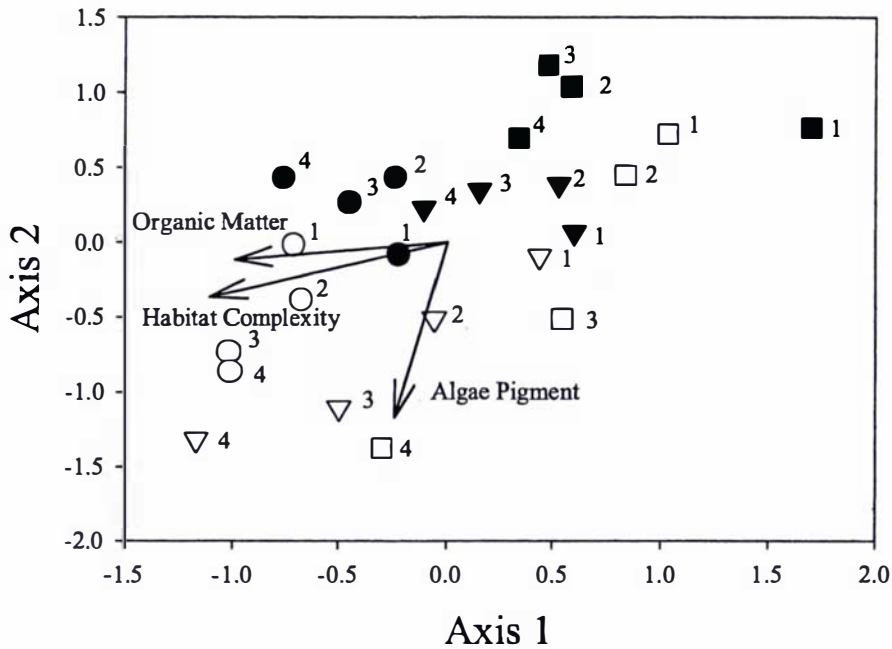
**Figure 6** Non-metric multidimensional scaling (NMDS) plot of axis 1 against axis 2 for invertebrate communities after 7, 14, 21 and 28 days of colonization of artificial substrata in the Taungatara Stream, New Zealand, in autumn 2003 (□, Brick-High Productivity; ■, Brick-Low Productivity; ▽, Grass-High; ▼, Grass-Low; ○, Twine-High; ●, Twine-Low). Arrows show relationships between environmental variables and axis one and two of the ordination (cutoff value =0.20).

The best model predicting invertebrate taxa richness from food resource levels for both Surber samples and artificial substrata was the power function. This indicates that the rate of increase in invertebrate richness diminishes with increasing level of resources. For a variety of ecosystems, it has been shown that larger amounts of resources enhance species richness until competitive exclusion takes place and diversity is reduced (Rosenzweig and Abramsky 1993, Huston 1994). Species richness has been shown to be low in highly enriched aquatic systems (Boothroyd and Stark 2000), but it is usually as a consequence of oxygen depletion (Abrams 1995), not competitive exclusion. Pristine, highly enriched sections of streams are usually found in the lower parts of the catchments, and they are also hypothesized to have lower species richness because of a reduction in habitat heterogeneity (Vannote et al. 1980). In this study, we did not observe

a decrease in the number of invertebrate taxa with greater amounts of resources. It may be argued that our resource range only covers the lower part of a bell-shaped curve relationship (Abrams 1995, Guo and Berry 1998). However, when we compare our results with other studies that have examined the relationship between invertebrate richness and resource levels in pristine streams, our values cover a large range (Death 2002, Zimmermann and Death 2002, Barquín and Death 2004, Chapter one). We hypothesize that the slower rate of increase of species richness with increasing productivity is due to the inability of some colonizers to actually reach individual patches in the stream.

The mechanisms by which greater habitat complexity increased invertebrate richness are more difficult to clarify than the direct link between invertebrate numbers and quantity of food resources. The Sampling Phenomenon Hypothesis (SPH) and the Resource Availability Hypothesis (RAH) are the most commonly preferred hypotheses to explain the observed increase in species richness with habitat complexity. Under the assumptions of the SPH it is generally argued that habitat complexity may enhance species richness by three mechanisms: providing more refuge for predators, increasing food levels or increasing the amount of living space. These processes will in turn increase the number of individuals and as a consequence the number of species found per unit area (Dean and Connell 1987a, b). On the other hand, under the RAH an increase in species richness with greater habitat complexity is predicted to occur because more niches are available and therefore more species inhabit a given area (Dean and Connell 1987a, b). Our results are at odds with the SPH. First, predators were more numerous on complex substrata, although their effect on prey may not have been greater. Secondly, although habitat complexity increased the amount of food and living space, the observed increase in species richness was higher than that expected if we were simply sampling larger surface areas.

The SPH assumes that given increased surface area but similar resources species diversity will occur in the same relative proportions in both simple and complex habitats (O'Connor 1991). In our study, evenness and rarified number of species were both greater on more complex substrata, despite having larger invertebrate densities, whereas Hill's modified ratio (E5) was lower. At a first glance, these results seem to contradict each

other, however, rarified number of species and Shannon's index of diversity are both more sensitive to rare taxa than Simpson's index of diversity or E5 (Ludwig and Reynolds 1988). Secondly, E5 can decrease both because of higher numbers of very abundant taxa or because of lower numbers of abundant taxa (Ludwig and Reynolds 1988). Of the total taxa found on Brick (B) substrata, 25% could be considered abundant taxa (i.e., comprising >5% of total densities) compared with only 10% on Twine (T) and Grass (G) substrata. Thus, E5 was larger on B than on T and G substrata because of higher numbers of abundant taxa, while Shannon's index of diversity and rarified number of species were both higher on T and G than in B substrata because of greater numbers of rare taxa. Consequently, greater habitat complexity increased taxa richness and evenness by enhancing the number of rare species in a ratio different to that which would have been expected under the SPH. The increased number of invertebrate taxa on more complex substrata is thus not only caused by an area effect but also by an increase in the number of niches, as hypothesized by the RAH.

In general, the amount and diversity of food resources increased with time and with the complexity of the substrata. Under the predictions of the RAH, we would expect to find higher species richness on those substrata that provide larger quantities and diversity of food resources, and this did occur on T and G substrata in high productivity treatments. Lower algal biomass resulted in decreased numbers of invertebrate individuals on all types of substrata, although it only reduced the number of taxa on Brick substrata (Table 7). This is most likely due to the reduction of algal biomass on Bricks, whereas on T and G substrata other available resources (i.e. FPOM, CPOM) maintained numbers of invertebrate taxa and individuals. Secondly, on T and G substrata rarified number of species was higher in low than in high productivity treatments. This was the result of a reduction in number of individuals in low productivity treatments, and not the loss of invertebrate taxa in higher productivity treatments (Table 7). These results support the idea that habitat complexity enhanced the diversity and amount of resources increasing the ratio of number of individuals to taxa, providing further support for the idea that more niches were available on T and G substrata (i.e. supporting the RAH).

**Table 7** Results of Tukey's post hoc analysis for the interaction between the ANOVA factors productivity and habitat structure, = joins means with no significant differences, HT= High Twine, LT= Low Twine, HG= High Grass, LG= Low Grass, HB= High Brick and LB= Low Brick.

|  | **Productivity** | **Habitat** |
|---|---|---|
| Number of Taxa | HT > LT | HT > HG > HB |
|  | HG = LG | LT > LG > LB |
|  | HB > LB |  |
| Number of Individuals | HT > LT | HT > HG > HB |
|  | HG > LG | LT > LG > LB |
|  | HB > LB |  |
| Rarefied Number of Taxa | HT < LT | HT = HB = HG |
|  | HG < LG | LG = LT > LB |
|  | HB = LB |  |
| Simpson's Diversity Index | HT = LT | HB = HT = HG |
|  | HG < LG | LG = LT = LB |
|  | HB = LB |  |
| Shannon's Diversity Index | HT = LT | HT = HB = HG |
|  | HG < LG | LT = LG > LB |
|  | HB = LB |  |
| Hill's Modified Ratio (E5) | HT = LT | HB > HT = HG |
|  | HG < LG | LB = LG =LT |
|  | HB = LB |  |

T and G substrata created more niches by either enhancing food or space resources. Many studies have demonstrated the importance of food resources (i.e., amount of detritus, algae and epilithic layers) in determining the number of invertebrate taxa and individuals (Egglishaw 1969, Rounick and Winterbourn 1983, Behmer and Hawkins 1986, Death 2002). The effect of food resource availability on invertebrate communities is also demonstrated in most studies dealing with invertebrate colonization of artificial substrata, where colonization of substrates by fungi, bacteria and algae, as well as the accumulation of detritus is a step ahead of invertebrate colonization (Khalaf and Tachet 1980, Shaw and Minshall 1980, Lamberti and Resh 1985, Biggs 1988, Casey and Kendall 1996). In our study, the colonization process was also affected by the amount and diversity of food present on the substrates. There was no apparent succession of taxa colonizing substrates, and the relative importance of the most abundant taxa colonizing substrates was similar to that observed in the benthos (Table 3 and 6). In addition to increasing food resources, it may also be argued that our more complex

substrates provided a structure that partitioned space vertically and horizontally, thereby allowing more species to coexist through tighter species packing.

A number of other studies have rejected the SPH and accepted the RAH when testing for increases in invertebrate richness on more complex rocks (Douglas and Lake 1994, Downes et al. 1998) and woody debris (O'Connor 1991), but see Clements (1987) and Dean and Connell (1987b). In order to accept the RAH as the mechanism that generates the observed patterns in diversity it is necessary that the stream invertebrate fauna has a certain degree of specialization (Schoener 1974). More research needs to be done on the food and space requirements and niche overlap of stream invertebrates in order to test this hypothesis further.

Functional feeding group densities correlated well with the abundance of their respective food resources, and increased towards the end of the 4 week period. Decreased productivity only affected the densities of those taxa, and therefore functional feeding groups, which directly feed on algae or algal detritus. The densities of filterers and shredders were not altered by changes in algal biomass. Predators were also correlated with algal biomass, but we believe this relationship is an indirect result of the link between prey densities and algal concentration. The increase of invertebrate densities on all substrates towards the end of the experiment indicates a clear response of the fauna to the amount of food present on those substrates. Some taxa also seemed to be responding to factors other than food abundance. For example, *Austrosimulium* spp. and *P. antipodarum* showed a preference for bare substrates that maximize attachment and feeding requirements, respectively. Similar responses have been reported in other studies of Simuliidae (Gersabeck and Merritt 1979, Quinn et al. 1997) and *Potamopyrgus sp.* (Towns 1981, Quinn et al. 1997).

Finally, larger quantities of chlorophyll *a* on Bricks and larger concentrations of phaeophytin (the product of degradation of chlorophyll *a*) on T and G substrata could indicate that Bricks were a better substrate for algal colonization than the T and G substrata. It is possible that T and G substrata were simply collecting senescent drifting algae, rather than being actively colonized. However, if this were the case phaeophytin concentration would be similar on T and G substrata both outside and inside the canopies. This was not so as phaeophytin concentrations were significantly higher on T and G

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substrata in more productive areas. A plausible explanation for the larger accumulation of phaeophytin on T and G substrata placed outside canopies is that these substrates also accumulated more silt and organic matter (Pers. Obs.), which could shade algae that had already colonized those substrates.

In conclusion, both higher productivity and habitat complexity increased the number of invertebrate taxa present in a given area, although through different mechanisms. Productivity increased the number of individuals per unit area and as a consequence the number of invertebrate taxa. Habitat complexity increased the habitable area and the amount and type of resources, which increased the presence of rare taxa and thus total species richness and evenness. Number of invertebrate taxa was never reduced as a consequence of larger invertebrate densities, and thus, competitive exclusion was not an important mechanism regulating invertebrate communities during the four weeks experiment. This study reinforces the importance of the physical environment, habitat structure and amount and type of resources, as a determinant of local invertebrate diversity.

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**4**

**The effect of natural versus experimental disturbance on invertebrate communities inhabiting high and low productivity stream patches**

## Abstract

The effect of primary productivity and physical disturbance on stream invertebrates was investigated using artificial canopies to reduce algal growth and by kicking and raking patches of the stream bed (10 m$^2$). The fortuitous occurrence of a spate with a recurrence interval of 3 months during the experiment provided the opportunity to compare the effects of natural versus experimental disturbance on the benthic invertebrate fauna. Invertebrate fauna in high productivity patches recovered more quickly than fauna in low productivity patches after both experimental and natural disturbance. Numbers of invertebrate individuals in low productivity patches showed differences with respect to high productivity patches even 25 days after the canopies were removed. This may have been a result of change in the nature of the algal communities on the substrates to *Stigeoclonium*, which is characterized by grazer-resistant basal cells. The experimental disturbance reduced numbers of invertebrate taxa and individuals more dramatically than the spate. However, increases in numbers of invertebrate taxa and individuals were similar after the experimental and natural disturbance, although numbers of individuals did not recover completely after 25 days of the experimental disturbance. Our experiment demonstrates that primary productivity limits the recovery of the invertebrate fauna after a physical disturbance, and that the intensity and frequency of physical disturbances play an important role in rearranging and redistributing lotic invertebrate communities.

**Key words:** Diversity, experimental disturbance, invertebrate communities, patch dynamics, primary productivity, spate

## Introduction

Physical disturbance has been shown to cause fluctuations in many biological communities, by reducing the number of individuals, the level of resources and by changing the physical habitat (Connell 1978, Sousa 1979, Pickett and White 1985, Hubbell 2001). In streams, one of the most common types of physical disturbance is increase in flow, which plays an important role in determining invertebrate community structure and dynamics (Resh et al. 1988, Yount and Niemi 1990, Lake 2000). The influence of floods on stream invertebrate communities has been extensively documented, by studying isolated flood events (Scrimgeour and Winterbourn 1989, Giller et al. 1991, Flecker and Feifarek 1994), by comparative studies in streams with different hydrological regimes (Robinson et al. 1993, Death and Winterbourn 1995, Barquín and Death 2004) and by experimental manipulations (Death 1996, Matthaei et al. 1996, McCabe and Gotelli 2000). In general, flood induced disturbances have been shown to reduce numbers of invertebrate individuals and taxa, the amount of algae and organic matter present on the stream bed and to rearrange the physical habitat (Resh et al. 1988, Reice et al. 1990, Vinson and Hawkins 1998, Lake 2000).

Most of the experimental work related to disturbance in streams has been based on the experimental manipulation of small artificial substrates such as bricks (Robinson and Minshall 1986, Bond and Downes 2000), baskets (Reice 1985, Death 1996) or small patches of the stream bed (Clifford 1982, Marchant et al. 1991). The experimental approach is usually preferred because it allows replication and better control of the factors under study, but the smaller scale of such experiments has been criticized as not being suitable to study the impacts of floods on a whole stream (Minshall 1988). However, we believe these small scale studies can be useful to study the recovery of invertebrate stream communities after small spates (Mackay 1992), and provide valuable information on the recovery dynamics of individual rocks and substratum patches (Minshall 1988). To our knowledge only two studies have contrasted the effects of natural versus experimental disturbances in streams (Brooks and Boulton 1991, Matthaei et al. 1997), because of the difficulty in predicting the occurrence of a natural spate. In the present study, the fortuitous occurrence of a small spate with a recurrence time of 3

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months enabled us to compare the recovery of naturally versus experimentally disturbed invertebrate communities.

Recent studies have identified the importance of food resource levels on the recovery of invertebrate faunas following disturbance, suggesting that invertebrate recovery only occurs following recovery of periphytic communities (Death 2002, Minchin and Death 2002, Death 2003). There are few studies that have examined experimentally the combined effects of disturbance and productivity on the invertebrate fauna (e.g., Zimmermann 2001). In the present study, we investigated the recovery of stream invertebrate fauna following a natural and experimental disturbance in ambient and reduced productivity treatments. The objective was to compare the rate of recovery of the invertebrate fauna in high and low productivity patches after natural and experimental disturbance. We were also interested in whether the reduction of productivity caused by the presence of a canopy had similar effects on invertebrate communities to the reduction of productivity caused by the disturbances. We predicted that more time would be needed to recover to pre-flood levels after the natural disturbance than after the experimental disturbance, as the natural disturbance may affect larger sections of the stream. We also predicted that the high productivity treatments should recover more quickly than the low productivity treatments.

## Materials and methods

### Study Site

The experiment was conducted in Taungatara Stream, a spring-fed stream draining Mt Taranaki an andesitic volcano in the North Island of New Zealand. We selected a 200 m stretch in open pasture, although the stream runs for 2.5 km through native broadleaf-Podocarp forest prior to this. Channel width averaged 4.4 m and the streambed was dominated by cobbles and pebbles, with no macrophytes or bryophytes present in the channel. Base flow measured every week averaged 0.4 $m^3$/s, with water depths from 15 to 36 cm and velocities from 0.3 to 0.7 $m^2$/s. Water temperature oscillated during the experiment between 10 and 14 °C, pH between 8.1 and 8.5 and conductivity between 107 and 133 µs/cm. Nitrate and phosphate concentrations were low, 0.3 mg/ml and 0.5

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mg/ml, respectively. Further information on this study site and their invertebrate communities are given in Chapter one and three.

## Experimental design

In March 2003 three riffle sections were conditioned for the experiment by removal of any large boulders. These uniform riffle sections (approximately 60 $m^2$) were divided randomly into high (H, no canopy) and low (L, canopy) productivity treatment. Canopies were approximately 5 m long by 7 m wide and were constructed from black polythene sandwiched between two layers of 5 $cm^2$ wire mesh, and supported by wooden beams secured on each bank. Each canopy covered the whole width of the stream with both upstream and downstream ends being covered by black polythene skirts. The canopies rested 0.75 to 2 m above the water level. Between 19 May and 21 May 2003 a high rain fall event occurred (>180 mm, Fig. 1), providing a natural disturbance treatment to both high and low productivity treatments. In two of the three riffle sections, low and high productivity treatments were randomly divided into an undisturbed area (control) and a disturbed area (approx 10 $m^2$ each). Experimental disturbance was applied on 25 May by turning every single stone in the patch and by sweeping the substrate with a stiff wire broom. On the same date all three canopies were removed.

## Sampling procedure

In each of the reaches, one Surber sample (area= 0.1 $m^2$; mesh = 250 $\mu m$) was randomly collected from control areas in each of the high and low productivity treatments. This was done 10 and 16 days before canopy removal (B1 and B2, respectively, Fig.1) and one (A1), four (A4), 11 (A11), and 25 (A25) days after the canopies were removed and the experimental disturbance was applied (Fig. 1). Two Surber samples were also taken from the experimentally disturbed areas on days A0, A1, A4, A11, and A25. The study was originally designed to apply disturbance at two contrasting intensities, but subsequent analysis of the fauna revealed no differences in invertebrate community metrics between these two intensity treatments. Thus, community metrics from these two Surber samples were averaged for further analysis. All samples were preserved in 10% formalin and returned to the laboratory for identification to the lowest possible taxonomic level using

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available keys (Winterboum et al. 2000). Coarse particulate organic matter (CPOM, >1 mm) and fine particulate organic matter (FPOM, 1-0.45 mm) remaining after invertebrates were removed were dried to constant weight at 95 °C, weighed and ashed at 550 °C for 2 h to yield ash free dry weight.
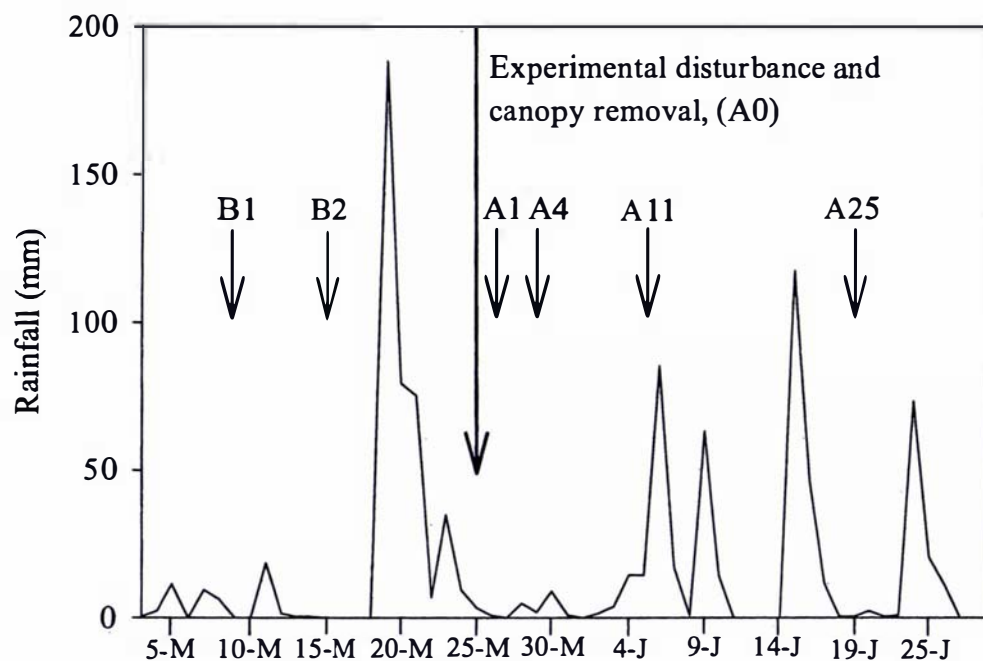


**Figure 1** Rainfall and sample dates during the disturbance experiment carried out in Taungatara stream, New Zealand, in the autumn of 2003.

Two and four stones (maximum length: 38-75 mm) were collected from control and experimentally disturbed areas, respectively, for measuring periphyton biomass. Stones were kept frozen until pigments were extracted in 90% acetone at 5 °C for 24 h in the dark. Absorbancies were read on a Varian-CARY 50 Conc. UV/visible spectrophotometer and converted to pigment concentration (chlorophyll *a* and phaeophytins) following Steinman and Lamberti (1996). Total stone surface area was calculated using the equation of Graham et al. (1988). As only a part of the stone is exposed to light (we assumed half the total surface area), estimates of algae pigment

concentration were corrected for stone surface area by dividing in half the total stone surface area.

## Statistical analysis

Shannon and Simpson indices of diversity, and rarified number of species were calculated for each treatment and day using the PRIMER statistical package (Clarke and Warwick 1994). Rarified number of species was corrected for the lowest number of individuals found in each day (42). A single value of chlorophyll *a* and phaeophytin per productivity treatment and day was obtained by averaging the values obtained from the two and four stones collected in each control and disturbed treatment, respectively.

Split-plot analysis of variance (ANOVA) was used to test for effects of productivity and natural disturbance on fauna and resource variables. Each stream section was regarded as a block and productivity as the treatment on the main plot, whereas time before and after disturbance constituted the treatment on the split-plot. Block and productivity effects were tested with the error term Section*Productivity, while the effects of time and the interaction of productivity and time were tested with the error term Section*Day(Productivity).

Split-split-plot ANOVA was used to test for the effects of productivity, experimental disturbance, and time after disturbance on fauna and resource levels variables. Again, each stream section was regarded as a block and productivity as the main treatment on the main plot, whereas disturbance constituted the treatment on the split-plot. Finally, days after disturbance were regarded as the main effect on the split-split-plot. Block and productivity effects were tested with the error term Section*Productivity, while the effects of disturbance and the interaction of productivity and disturbance were tested with the error term Section*Disturbance(Productivity). The effects of time and all the interaction terms were tested with the error term Canopy*Day(Productivity*Disturbance). ANOVAs were performed in SAS (1988) with type III sums of squares and Tukey's post hoc means test when significant differences were found. Variables were logarithmically transformed to remove heteroscedasticity when necessary.

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Absolute recolonization rates were calculated as the difference between the mean number of taxa or mean number of individuals on each high and low productivity treatments on consecutive sampling days divided by the sampling interval in days. The resistance of the invertebrate fauna to the natural and experimental disturbance was assessed as the percentage of taxa and number of individuals remaining after disturbance. For the natural disturbance we divided values on A1 by values on B2, and for the experimental disturbance values on A0 by control values on A1.

Patterns in community composition were examined using non-metric multidimensional scaling (NMS) with the PC-ORD statistical package (McCune and Mefford 1995). The Sorensen distance measure was used to determine similarity between samples. Initial examination of stress patterns in the data suggested three dimensions were appropriate for the final ordination, which was established with 500 iterations of the data. Relationships between the ordination axes and the measured variables were examined using simple correlation (SAS Institute Inc. 1988).

To determine the significance of differences in invertebrate community composition between productivity, disturbance and time, we performed an analysis of similarities (ANOSIM) using the PRIMER statistical package (Clarke and Warwick 1994). ANOSIM is a non-parametric procedure that evaluates whether the average similarities between samples within groups are closer than the average similarities of all pairs of replicates between groups (Clarke and Warwick 1994). The mean density of taxa that contributed most ($\geq 90\%$) to the dissimilarity between different dates was evaluated using the SIMPER procedure in the PRIMER statistical package.

## Results

### Effects of natural disturbance

Periphyton and organic matter

Organic matter concentration was reduced by the natural disturbance in low productivity treatments but not in high productivity treatments and it was not affected by the presence of a canopy (Fig. 2). After the natural disturbance, concentration of organic matter reached a maximum on days 4 and 11 in high productivity and low productivity treatments, respectively, although differences between days were not significant (Table

1). The minor flow peaks before sampling on day 25 also reduced the amount of organic matter present on the stream bed. Algal pigment concentration was more than two times higher outside than inside the canopies before the spate and was reduced in both productivity treatments following the disturbance (Fig. 2). Algal pigment levels reached a maximum after disturbance on day 11 in both high and low productivity treatments, but decreased again on day 25 (Fig. 2, Table 1).
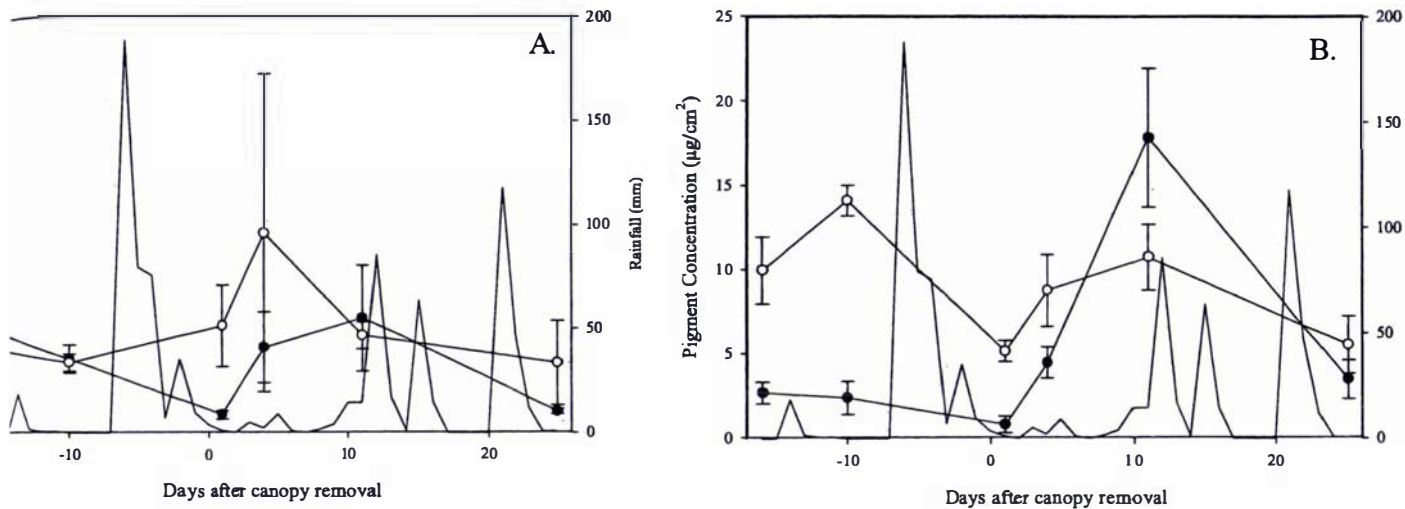


**Figure 2** Mean (± 1 SE) A. Organic matter and B. Algae pigment concentration collected in high (open circles) and low (solid circles) productivity treatments before and after a natural disturbance in Taungatara stream, New Zealand, in the autumn of 2003.

Diversity patterns and invertebrate abundance

A total of 50 taxa were collected from the controls during the length of the experiment, 42 and 43 taxa were collected from high and low productivity treatments, respectively. The natural disturbance reduced the number of invertebrate taxa in both high and low productivity treatments (Fig. 3). The percentage of taxa remaining after the spate, i.e. the resistance of the fauna (Table 2), was slightly higher in high productivity treatments than in low productivity treatments. After the disturbance, numbers of invertebrate taxa reached a maximum on day 11 in both high and low productivity treatments, and decreased on day 25 (Fig. 3, Table 1). Recovery rates for numbers of taxa were faster in high than in low productivity treatments between days A1-A4, but slower

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between A4-A11 (Table 2). Recovery was not apparent in low productivity treatments until day 11 (Table 2). Number of invertebrate taxa was always higher in high than in low productivity treatments, even 25 days after canopy removal, although differences were not significant (Fig. 3, Table 1).

**Table 1** Split-plot ANOVA results testing for differences in productivity and days after disturbance factors for macroinvertebrate parameters and resources measured in Taungatara Stream, New Zealand, in the autumn of 2003. Kendall rank correlation coefficients of these variables with axis one and two of NMDS are also given. H = High productivity and L = Low productivity, B1= 16 days before canopy removal, B2= 10 days before canopy removal, A1= 1 day after canopy removal, A4= 4 days after canopy removal, A11= 11 days after canopy removal and A25= 25 days after canopy removal, * = p 0.05-0.01, ** = p < 0.01, and lines join means with no significant differences.

| | Block $F_{2,2}$ | Productivity $F_{1,2}$ | Tukey's | Day $F_{5,20}$ | Tukey's | P*Day $F_{5,20}$ | Axis 1 | Axis 2 |
|---|---|---|---|---|---|---|---|---|
| ıber of Taxa | | 18.52* | H>L | 3.3* | B2 A11 A4 B1 A1 A25 | 0.88 | 0.49 | 0.17 |
| ıber of Individuals | 6.58 | 25.33* | H>L | 1.98 | | 0.68 | 0.9 | 0.03 |
| fied Number of Taxa | 0.4 | 0.78 | | 19.92** | B2 A11 B1 A25 A1 A4 | 0.77 | | |
| non Diversity Index | 0.33 | 5.68 | | 2.36 | | 0.43 | | |
| pson Diversity Index | 0.92 | 2.97 | | 1.88 | | 0.45 | | |
| ɪrophyll a | 16.14 | 1077.5** | H>L | 8.92** | A11 A4 B2 B1 A25 A1 | 5.16** | 0.73 | -0.03 |
| ɔphytin | 0.34 | 130** | H>L | 8.71** | A11 B2 B1 A4 A25 A1 | 5.03** | 0.58 | 0.12 |
| ɪ Pigment | 2.27 | 106.1** | H>L | 7.81** | A11 A4 B2 B1 A25 A1 | 4.64** | 0.7 | 0 |
| ɔM | 1.32 | 2.62 | | 1.61 | | 1.21 | 0.2 | -0.05 |
| M | 0.49 | 2.16 | | 6.51** | B1 A4 A11 B2 A25 A1 | 0.34 | 0.3 | 0.39 |
| ɪ Organic Matter | 1.5 | 2.99 | | 2.09 | | 1.23 | 0.21 | 0 |

Rarified number of taxa followed similar patterns to number of invertebrate taxa and was higher before the disturbance took place and on day 11 (Fig 3, and Table 1). Evenness was not affected by productivity treatment or time after the disturbance (Fig. 3, Table 1). Number of invertebrate individuals was always larger in high than in low productivity treatments, even 25 days after the canopy was removed (Fig. 4, Table 1). The natural disturbance reduced the number of invertebrate individuals by almost half in both high and low productivity treatments, and by day 4 densities were similar to levels on preflood dates, however, changes in number of invertebrate individuals were not

significantly different between sampling days (Fig. 4, Table 1). Faunal resistance, i.e. percentage of individuals remaining after the spate, was higher in low than in high productivity treatments (Table 2). Rates of recolonization in terms of number of individuals were faster for high than for low productivity patches between days A1-A4, although slower between A4-A11 (Table 2).
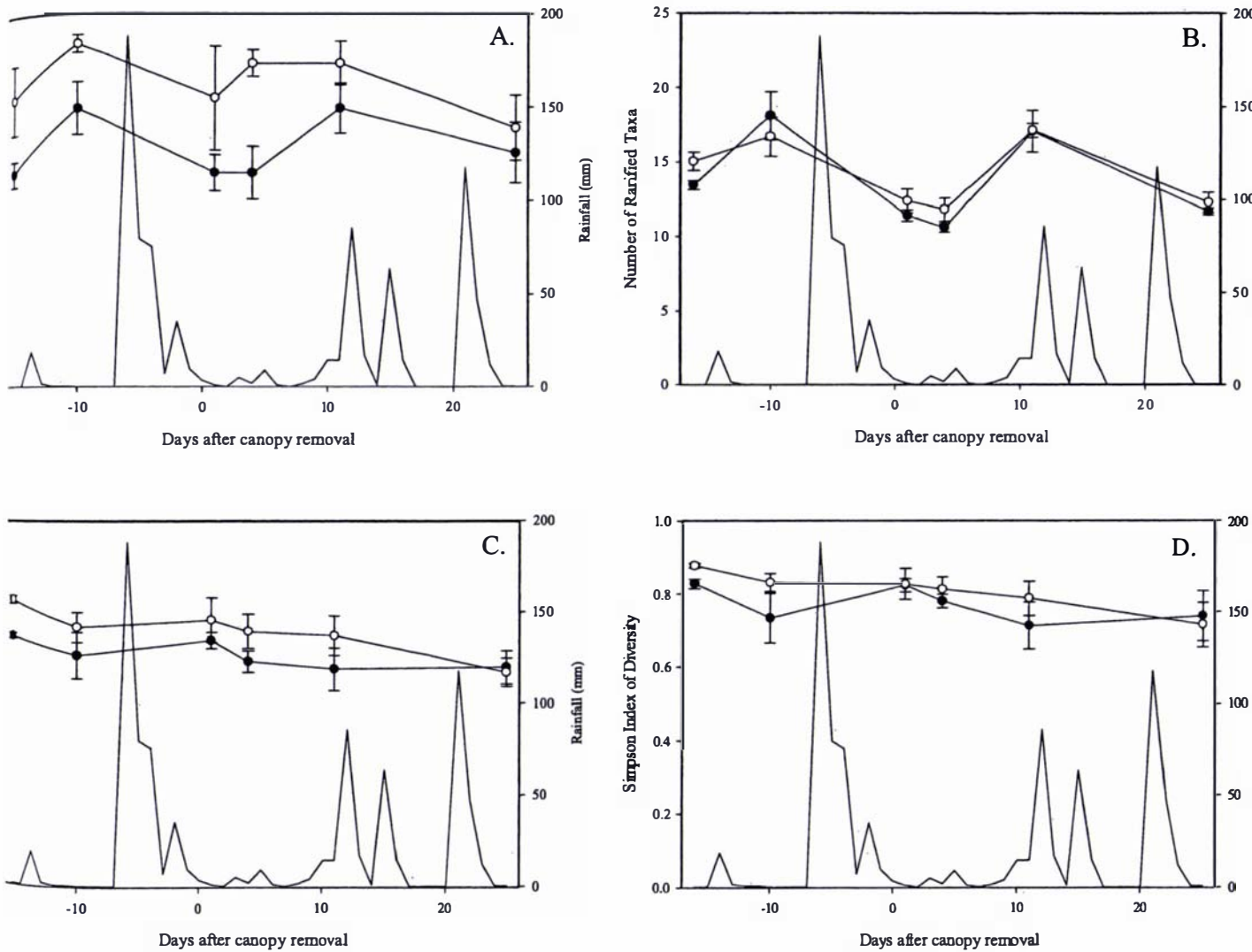


**Figure 3** Mean (± 1 SE) A. number of individuals, B number of taxa, C rarified number of taxa, D Shannon diversity index and E Simpson diversity index for invertebrate communities in high (open circles) and low (solid circles) productivity treatments before and after a natural disturbance in Taungatara stream, New Zealand, in the autumn of 2003.

**Table 2** Resistance and colonization rates of invertebrates recolonizing high and low productivity treatments in Taungatara Stream, New Zealand, in autumn 2003. A1= 1 day after canopy removal, A4= 4 days after canopy removal, A11= 11 days after canopy removal and A25= 25 days after canopy removal.

|  | High Productivity | Low Productivity |
|---|---|---|
| Number of Taxa (T) |  |  |
| Mean Number of Taxa | 20.4 | 16 |
| Resistance | 84% | 77% |
| Rate of recolonization |  |  |
| $(T\ m^{-2}\ d^{-1})$ |  |  |
| A1-A4 | 0.78 | 0.01 |
| A4-A11 | 0.01 | 0.62 |
| A11-A25 | -0.31 | -0.21 |
| Number of Individuals (I) |  |  |
| Mean Number of Individuals | 332.7 | 152.7 |
| Resistance | 47.30% | 58.50% |
| Rate of recolonization |  |  |
| $(I\ m^{-2}\ d^{-1})$ |  |  |
| A1-A4 | 61.56 | 25.67 |
| A4-A11 | -1.57 | 4.95 |
| A11-A25 | -4.81 | -1.26 |

Taxonomic composition and community structure

Nine taxa contributed almost 80 % to the densities of the communities in both high and low productivity treatments (Fig. 4). Community composition was similar between high and low productivity treatments (ANOSIM, R= 0.19, P= 0.07), differing only in the reduced number of individuals in low productivity treatments, and not in the presence or absence of any taxa. Invertebrate communities in low productivity treatments had lower densities of chironomids (Fig. 4), and more *Olinga feredayi* and *Austrosimulium* spp.. The natural disturbance reduced the densities of all key taxa except *Coloburiscus humeralis* and *Deleatidium* spp., whose densities increased after the disturbance, and *Austroclima jollyae*, which remained constant (Fig. 4). Community composition was only different between days B2 and A1, B2 and A25 (ANOSIM, R=0.37 and R= 0.39, P< 0.05, respectively), and between days A1 and A11 (ANOSIM, R= 0.37, P< 0.05).

Final stress for the NMDS analysis was 9.1, indicating a reliable ordination (McCune and Mefford 1995). Axis 1 and axis 2 explained 69% and 23% of the total variance, respectively. High productivity treatment communities occurred to the right of axis one while low productivity graded to the left (Fig. 5). Communities sampled after the

natural disturbance occurred to the bottom of axis two, whereas pre-disturbance communities were to the upper part of axis two. Total number of invertebrate taxa and individuals, and amount of resources, were all positively correlated with axis one, whereas days after disturbance was negatively correlated with axis two of the NMDS (Table 1).
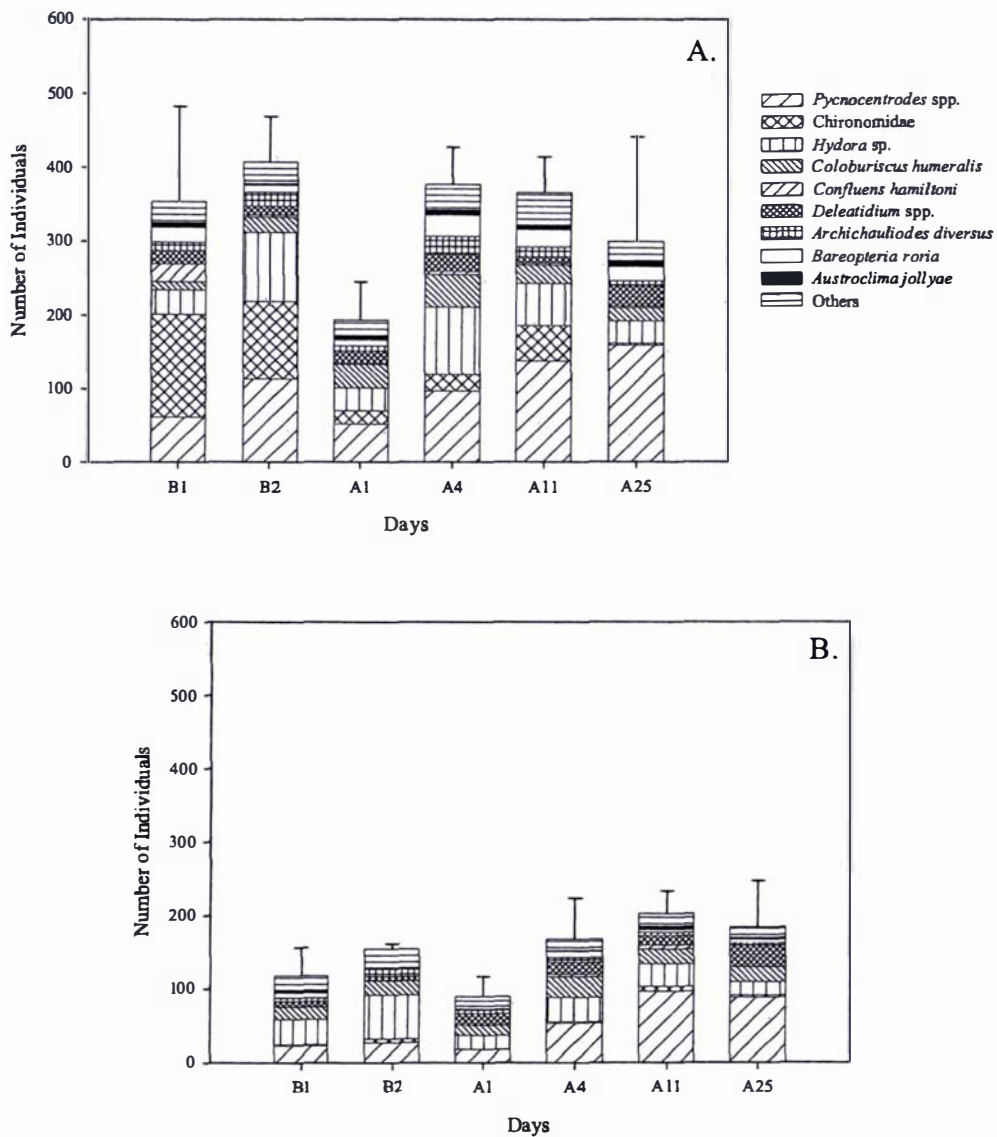


**Figure 4** Mean (± 1 SE) number of individuals that comprise the most abundant taxa for high (A) and low (B) productivity treatments collected in Taungatara stream, New Zealand, in the autumn of 2003.
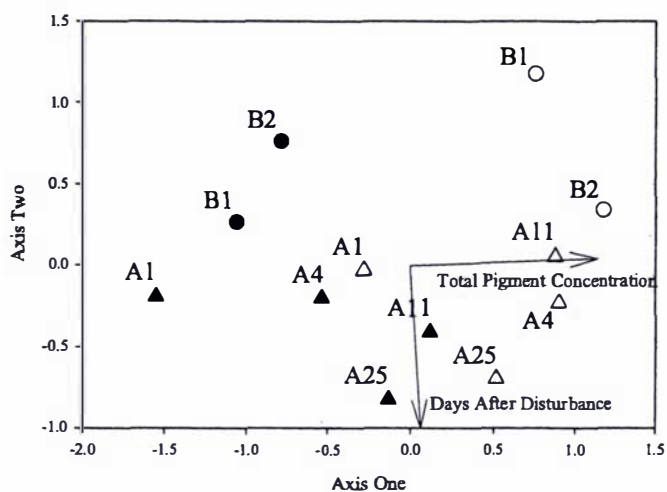
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**Figure 5** Non metric multidimensional scaling (NMDS) plot of axis 1 against axis 2 for mean invertebrate communities collected in Surber samples in high (open symbols) and low (solid symbols) productivity treatments in Taungatara stream, New Zealand, in the autumn of 2003. Samples collected before and after the natural disturbance are represented by circles and triangles, respectively.

## Effects of experimental disturbance

Periphyton and organic matter

Organic matter concentration was reduced by the experimental disturbance, although it recovered quickly by day 1, and remained constant (Fig. 6, Table 3). The experimental disturbance reduced algal pigment concentration. Algal pigment concentration increased in all treatments until it reached a maximum on day 11, but had decreased in all treatments by day 25 (Fig. 6, Table 3).

Diversity patterns and invertebrate abundance

A total of 46 invertebrate taxa were collected from disturbed and control treatments during the experiment. The experimental disturbance reduced the number of invertebrate taxa by almost half in both high and low productivity treatments (Table 4). Number of invertebrate taxa was significantly lower on day 0 and day 1 in all treatments and recovered progressively until it reached a maximum on day 11. Species richness reached control levels in disturbed treatments by day 4 and day 11 in low and high productivity treatments, respectively (Fig. 7, Table 3). Recovery rates were slightly greater for low

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than for high productivity treatments. The most important factor influencing number of invertebrate taxa was days after the disturbance (Table 3).
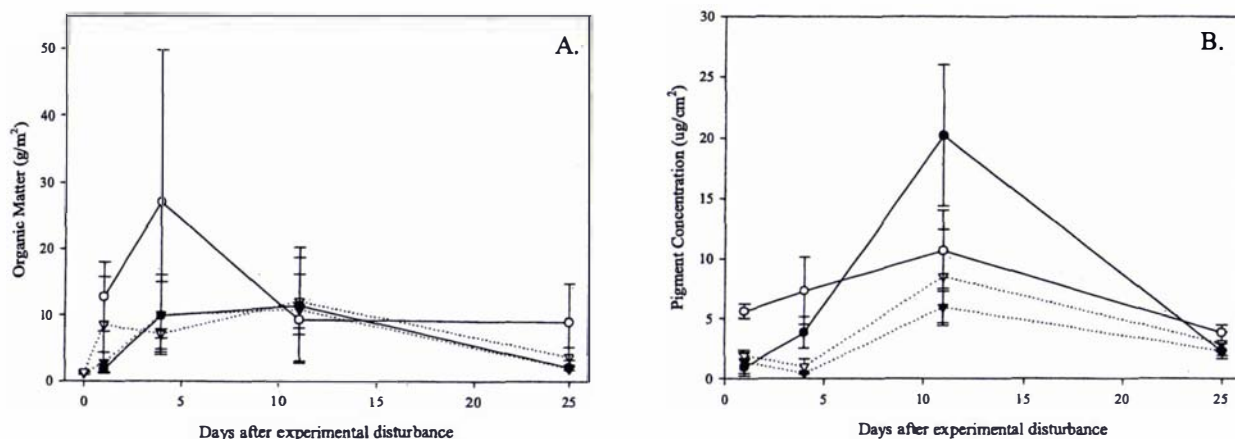


**Figure 6** Mean (± 1 SE) A. Organic matter and B. Algae pigment concentration collected in control (circles) and disturbed patches (triangles) in high (open symbols) and low (solid symbols) productivity treatments in Taungatara stream, New Zealand, in the autumn of 2003.

Rarified number of species followed a similar pattern to the number of invertebrate taxa, reaching a maximum in all treatments on day 11 (Fig. 7, Table 3). Evenness decreased towards day 25 and there were no differences between high and low productivity or disturbed and control treatments (Fig. 7, Table 3). Number of individuals was almost two times higher in control than in disturbed treatments, and increased in all patches towards day 25, when it reached its maximum (Fig. 8, Table 3). The experimental disturbance caused an 85% reduction in the number of invertebrates in both high and low productivity treatments (Table 4). Recovery rates expressed as numbers of individuals were generally faster in high than in low productivity treatments (Table 4). Productivity did not have a significant effect on the number of individuals, but comparing each patch separately control and disturbed patches in high productivity treatments had higher number of individuals than in low productivity treatments (Table 3). Twenty five days after canopy removal there were still marked differences in the numbers of invertebrate individuals between high and low productivity treatments (Fig. 8).

**Table 3** Split-split-plot ANOVA results testing for differences in productivity, disturbance and days after disturbance factors for macroinvertebrate parameters and resources measured in Taungatara Stream, New Zealand, in autumn 2003. Kendall rank correlation coefficients of these variables with axis one and two of NMDS are also given. H = High productivity and L = Low productivity, C= Control, D=Disturbed, A0 = immediately after experimental disturbance, A1 = one day after experimental disturbance, A4= 4 days after experimental disturbance, A11= 11 days after experimental disturbance and A25= 25 days after experimental disturbance, * = p 0.05-0.01, ** = p < 0.01, and lines join means with no significant differences.

| | Block $F_{1,1}$ | Productivity $F_{1,1}$ | Disturbance $F_{1,2}$ | Tukey's | Day $F_{3,12}$ | Tukey's | P*Dist $F_{3,12}$ | P*Day $F_{3,12}$ | Dist*Day $F_{3,12}$ | P*Dist*Day $F_{3,12}$ | Axis 1 | Axis 2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of Taxa | 2.04 | 29.47 | 9.48 | | 15.19** | A11 A25 A4 A1 A0 | 6.43 | 1.57 | 9.91** | 0.69 | 0.616 | -0.482 |
| Number of Individuals | 1.03 | 63.94 | 464.71** | C > D | 7.41* | A25 A11 A4 A1 A0 | 65.15* | 0.39 | 0.68 | 0.28 | 0.699 | -0.791 |
| Rarified Number of Taxa | 0.53 | 19.84 | 5.66 | | 67.09* | A11 A25 A4 A1 A0 | 0.65 | 2.88 | 18.27** | 0.68 | | |
| Shannon Diversity Index | 0.58 | 7.67 | 0.54 | | 4.85* | A4 A1 A0 A11 A25 | 0.21 | 2.02 | 4.92** | 0.5 | | |
| Simpson Diversity Index | 0.45 | 2.47 | 0.45 | | 4.6* | A1 A4 A0 A11 A25 | 0.17 | 1.05 | 1.74 | 0.61 | | |
| Chlorophyll *a* | 0.17 | 3.4 | 31.27* | C > D | 22.71** | A11 A25 A4 A1 | 1.02 | 1.42 | 4* | 2.29 | 0.669 | -0.38 |
| Phaeophytin | 0.18 | 0.55 | 14.37* | C > D | 15.05** | A11 A25 A1 A4 | 0.07 | 3.32* | 1.91 | 2.19 | 0.603 | -0.341 |
| Total Pigment | 0.01 | 1.9 | 29.3* | C > D | 13.25** | A11 A25 A4 A1 | 0.68 | 2.09 | 3.95* | 1.29 | 0.643 | -0.354 |
| CPOM | 0.88 | 42.07 | 1.41 | | 3.37* | A4 A11 A1 A25 A0 | 1.29 | 0.48 | 0.6 | 0.32 | 0.485 | -0.21 |
| FPOM | 12 | 9.77 | 0.75 | | 2.68 | | 1.05 | 0.31 | 0.93 | 0.79 | 0.386 | -0.294 |
| Total Organic Matter | 0.5 | 40.26 | 0.37 | | 3.33* | A4 A11 A1 A25 A0 | 0.39 | 0.49 | 0.53 | 0.33 | 0.529 | -0.229 |
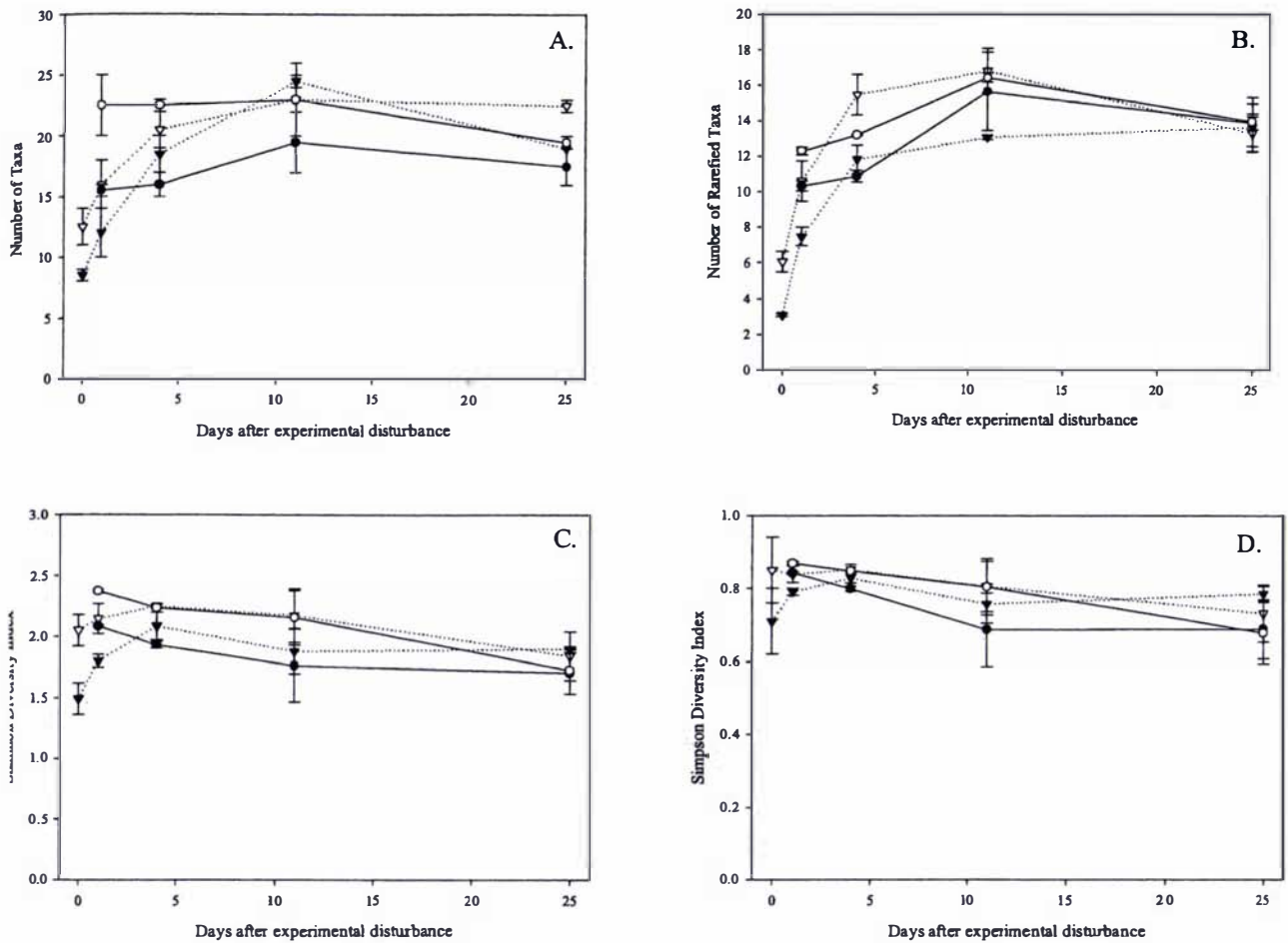
**Figure 7** Mean (± 1 SE) A. number of taxa, B rarified number of taxa, C Shannon diversity index and D Simpson diversity index for invertebrate communities in control (circles) and disturbed patches (triangles) and high (open symbols) and low (solid symbols) productivity treatments in Taungatara stream, New Zealand, in the autumn of 2003.

Taxonomic composition and community structure

The densities of 10 taxa contributed more than 80 % to the differences between the high and low productivity treatments (Fig. 8). Community composition differed between high and low productivity treatments when averaged across disturbance treatments (ANOSIM, R= 0.112, P< 0.05), mostly because of reduced densities in the low productivity treatments. Densities of chironomids and other dipterans, such as *Aphrophila* sp. were lower, and the densities of *Potamopyrgus antipodarum* higher in low productivity treatments (Fig. 8).

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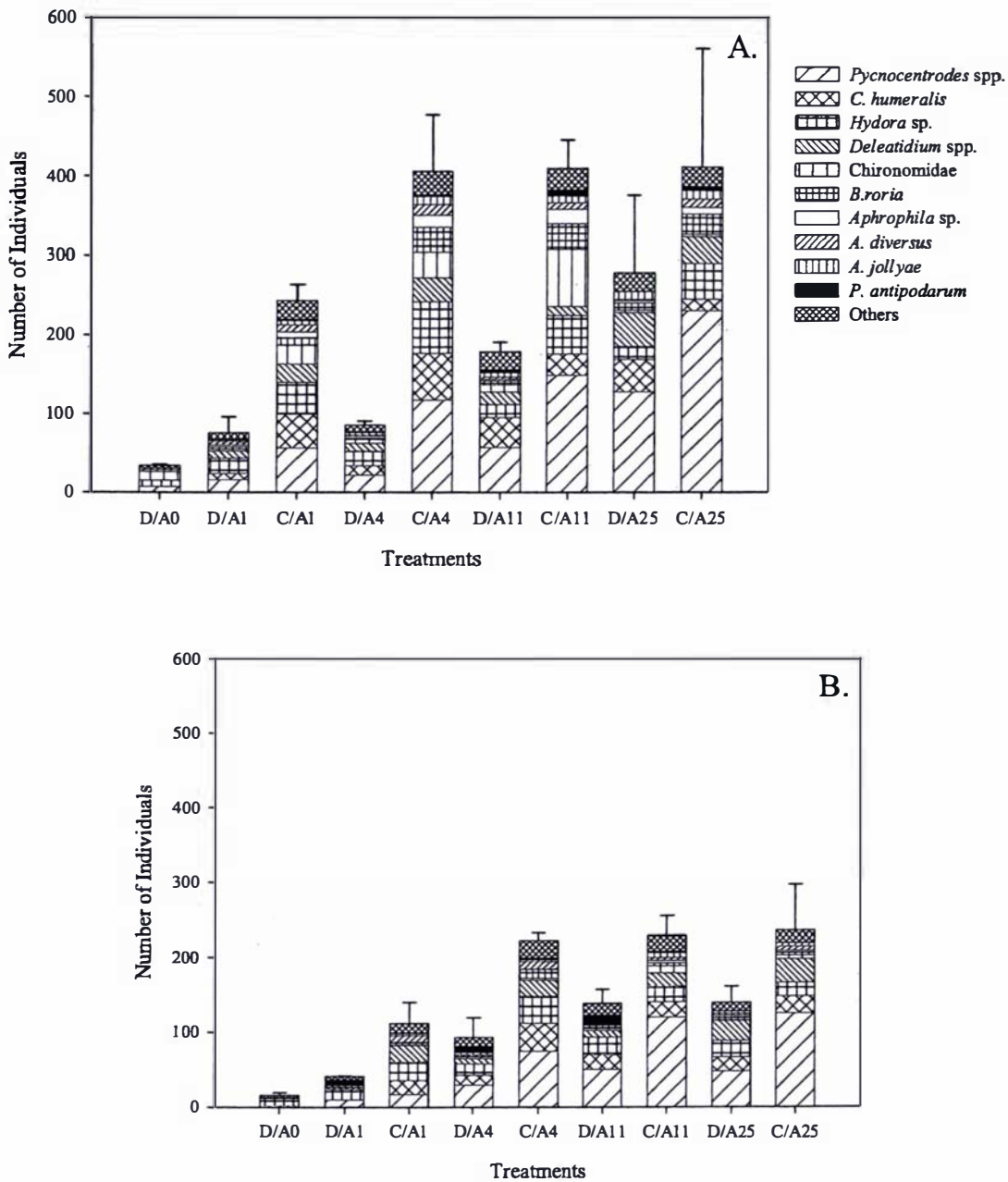
**Figure 8** Mean (± 1 SE) number of individuals that comprise the most abundant taxa for high (A) and low (B) productivity treatments collected in controls (C) and disturbance (D) treatments in Taungatara stream, New Zealand, in the autumn of 2003.

Invertebrate communities from control and disturbed treatments were also different (ANOSIM, R= 0.648, P< 0.001), as densities of all taxa were reduced by the

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experimental disturbance, except for *Austrosimulium* spp., *Costachorema* sp., Eriopterini sp. and *P. antipodarum*. The densities of all the most abundant taxa increased until day 4. After day 4 *A. diversus*, *B. roria*, *C. humeralis*, *Deleatidium* spp. and *Hydora* sp. stabilized, while the rest of the key taxa kept increasing until day 25. From day 11 to day 25 some taxa e.g. *Aphrophila* sp., Chironomidae, *C. hamiltoni*, *O. feredayi* and *P. antipodarum* experienced a marked decrease. Differences in community structure were greater between A0 and A1 with A4, A11 and A25 (ANOSIM pair-wise comparisons R ranged between 0.24 and 0.703, P<0.001). Community composition was not different between A1 and A0 or between A11 and A25 (ANOSIM, R=0.141 and R=-0.076, respectively, P> 0.05).

**Table 4** Resistance and colonization rates for invertebrates recolonizing control and disturbed patches in high and low productivity treatments in Taungatara Stream, New Zealand, in the autumn of 2003. A0 = immediately after experimental disturbance, A1 = one day after experimental disturbance, A4= 4 days after experimental disturbance, A11= 11 days after experimental disturbance and A25= 25 days after experimental disturbance.

| | High-Control | High-Disturbed | Low-Control | Low-Disturbed |
|---|---|---|---|---|
| Number of taxa (T) | | | | |
| Mean number of taxa | 21.90 | 18.90 | 17.13 | 16.50 |
| Resistance | | 55.56% | | 54.80% |
| Rate of recolonization | | | | |
| (T 0.1 m$^{-2}$ d$^{-1}$) | | | | |
| A0-A1 | | 3.50 | | 3.50 |
| A1-A4 | 0.00 | 1.50 | 0.17 | 2.17 |
| A4-A11 | 0.07 | 0.36 | 0.50 | 0.86 |
| A11-A25 | -0.25 | -0.04 | -0.14 | -0.39 |
| Number of individuals (I) | | | | |
| Mean number of individuals | 367.60 | 130.50 | 199.80 | 85.60 |
| Resistance | | 14.00% | | 14.30% |
| Rate of recolonization | | | | |
| (I 0.1 m$^{-2}$ d$^{-1}$) | | | | |
| A0-A1 | | 41.50 | | 25.00 |
| A1-A4 | 54.17 | 3.33 | 36.83 | 17.33 |
| A4-A11 | 0.50 | 13.32 | 0.93 | 6.50 |
| A11-A25 | 0.14 | 7.13 | 0.46 | 0.05 |

Final stress for the NMDS analysis was 8.9, indicating a reliable ordination (McCune and Mefford 1995). Axis 1 and axis 2 explained 67% and 29% of the total

variance, respectively. High productivity treatment communities occurred to the right of axis one while low productivity communities graded to the left (Fig. 9). Communities from control treatments were more similar between high productivity treatments than between low productivity treatments. Community composition tended to be more similar between disturbed and control treatments towards day 25 (Fig. 9). Total number of invertebrate taxa and individuals, amount of resources and days after disturbance were all positively correlated with axis one and negatively correlated with axis two of the NMDS (Table 1).
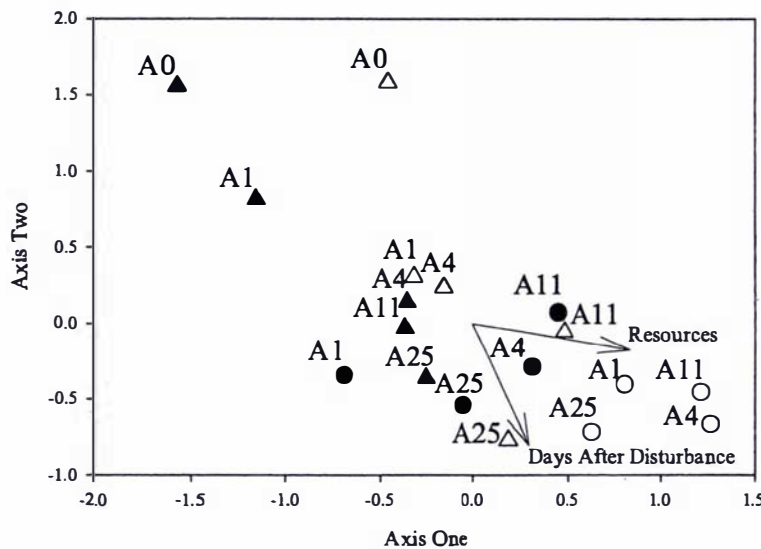


**Figure 9** Non metric multidimensional scaling (NMDS) plot of axis 1 against axis 2 for mean invertebrate communities collected in Surber samples in high (open symbols) and low (solid symbols) productivity treatments in Taungatara stream, New Zealand, in the autumn of 2003. Controls and disturbed patches are represented by circles and triangles, respectively.

## Discussion

Both natural and experimental disturbances reduced the amount of resources and number of invertebrate individuals and taxa. Similar results have been found by many researchers (Scrimgeour and Winterbourn 1989, Death 1995, McCabe and Gotelli 2000). The canopies reduced the abundance of algae and as a result the number of invertebrates. The increase in number of invertebrates led to a passive increase in the number of taxa.

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Taxa that rely on periphytic algae, e.g. chironomid larvae, are more influenced by the presence of a canopy than taxa that depend on other food sources, e.g. *Austrosimulium* spp., *C. humeralis* and *O. feredayi*. Several others have found similar effects in reducing productivity on stream invertebrates by means of an artificial canopy (Towns 1981, Quinn et al. 1997, Zimmermann and Death 2002, Chapter three). Only one of these has investigated the combined effects of productivity and physical disturbance on stream invertebrate communities (Zimmermann and Death 2002), although the scale of the experiment was much smaller.

Food resource levels after canopy removal were greater in high than in low productivity treatments. The larger amount of algal biomass in high than in low productivity treatments was paralleled by a quicker recovery in terms of both number of invertebrate taxa and individuals after the natural disturbance. Number of individuals also increased faster in the first days after the experimental disturbance in high than in low productivity treatments. This suggests periphyton levels may control recolonization of the invertebrate fauna (Death 2002, Minchin and Death 2002, Death 2003).

Community composition was most different between high and low productivity treatments immediately after canopy removal and tended to be more similar towards the end of the experiment (see NMS graphs). However, even 25 days after removal of the canopies there were still differences in invertebrate communities between high and low productivity treatments. Algal concentration recovered to preflood levels by day 11, so differences in invertebrate densities between high and low productivity treatments can not be attributed to periphyton biomass alone. It may be that periphyton quality rather than quantity is responsible for the observed differences in invertebrate densities. Steinman et al. (1990) found that basal cells of the filamentous green alga *Stigeoclonium* can survive more than 92 days of darkness with only moderate losses of chlorophyll *a* and begin photosynthesizing almost immediately upon re-exposure to light. *Stigeoclonium* is a heterotrichous alga, which has the potential to expand from an assemblage of basal cells, under heavy grazing or intense disturbance, to a filamentous form, in the absence of grazing and disturbance (Petersen 1996). *Stigeoclonium* is a widespread alga that can dominate periphytic communities in moderate to fast flowing New Zealand streams with conductivities ranging from 50 to 120 μs (Biggs and Price

1987). The patches in low productivity treatments may have been colonized mainly by the expansion of basal cells of *Stigeoclonium*, which is resistant to grazing. Thus, although chlorophyll *a* levels were similar in high and low productivity treatments after canopy removal the amount of available resources may have been different.

The experimental disturbance reduced invertebrate abundances by 85% whereas invertebrate richness was reduced by 45% in both high and low productivity treatments. The natural disturbance reduced invertebrate abundances by only 40 - 50% and invertebrate richness by 16% to 23%. Recovery of invertebrate richness to pre-disturbance levels was achieved after 4 and 11 days for high and low productivity treatments respectively, and recovery of abundances was attained in 4 days. Invertebrate communities seemed to recover in between 8 to 15 days after the natural disturbance. These results agree with the recovery times reported by others for small-scale colonization studies, which range between 10-25 days for invertebrate richness and 10-30 days for invertebrate abundances (Mackay 1992), or more than two months (Matthaei and Townsend 2000).

There appear to only be two studies that have compared the effects of natural and experimental disturbances (Brooks and Boulton 1991, Matthaei et al. 1997). Our experimental disturbance had similar effects on the invertebrate fauna to that created by Matthaei et al. (1997). The latter authors reduced invertebrate abundances and invertebrate richness by 92% and 42%, respectively, whereas the experimental disturbance of Brooks and Boulton (1991), decreased invertebrate richness by 83%. The natural disturbance in our study, however, had a lower impact than the ones studied by Brooks and Boulton (1991) and Matthaei et al. (1997), that reduced invertebrate abundances and richness by 70% and 45%, and 90 and 19%, respectively. The effects of both the natural and experimental disturbance on the invertebrate fauna were similar in our study. The recovery of the experimentally disturbed patches was similar to the recolonization of patches after the spate, being more a redistribution of the benthos rather than a recovery after a major catastrophic flood (Townsend and Hildrew 1976).

The higher reduction of invertebrates after the experimental disturbance than after the spate may be because of the more patchy effect of the natural disturbance than the experimental disturbance. Several studies have shown that spates (Matthaei et al. 1999,

Matthaei and Townsend 2000) or even base flow (Miyake and Nakano 2002) can generate a mosaic of scour and fill patches. Thus, it is likely that the natural disturbance did not affect all patches equally, whereas we took care in applying the same level of experimental disturbance to all patches. However, we concur with these authors that manipulative experiments conducted at these medium sized scales (10 m$^2$ patches) provide considerable insight into the recovery dynamics of benthos on individual stones or patches as in Minshall (1988).

Overall it seems that time after disturbance was the most important factor in determining the recovery of the invertebrate fauna in this study. Faunal communities recovered after 11 days of the major peak flow. After day 11 a sequence of minor rainfall peaks (< 100 mm) lowered resource levels again and consequently decreased the number of invertebrate individuals and taxa. These minor peaks only affected the most sensitive taxa to spates e.g. *Aphrophila* sp., Chironomidae, *C. hamiltoni*, *O. feredayi* and *P. antipodarum*, while most of the other taxa experienced no effect or even an increase in their densities towards day 25. Time after disturbance has also been identified in numerous studies as having an effect on number of invertebrate individuals and taxa (Flecker and Feifarek 1994, Death 1996, Matthaei and Townsend 2000, McCabe and Gotelli 2000), as time between disturbances increases. Our results show the importance of major and minor peak flows in regulating resource levels and the number of invertebrate taxa and individuals. Flow related disturbance is clearly an important agent in generating spatial variation observed in stream benthic communities.

In conclusion, the biomass and composition of the periphytic community controls the recovery of the invertebrate fauna after minor natural disturbances and experimental disturbances of medium size patches (10 m$^2$). Resource levels set an upper limit to the number of individuals, and thus number of taxa, that may recolonise a disturbed patch. The intensity of the disturbance influences benthic invertebrate communities by affecting the resistance of the community to the disturbance, while frequency of the disturbance affects the recolonizing mechanisms by affecting the resilience of the community to the disturbance. Physical disturbances are therefore an important factor in lotic freshwater systems affecting the temporal and spatial dynamics of resources and invertebrate communities.

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## Acknowledgements

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# 5

**Downstream changes in springbrook invertebrate communities; the effect of increased temperature range**

# Abstract

Temperature patterns were investigated in five runoff and seven spring-fed streams between April and November 2001/2002 in the North and South Islands of New Zealand. Invertebrate fauna were sampled at 4 distances (0, 100, 500 m and 1 km) from seven spring sources. We recorded temperature at the source of 4 spring-fed streams and at 1 km downstream. Food resources and physico-chemical parameters did not change substantially over the 1 km length studied, with the exceptions of water velocity and organic matter biomass which increased and decreased, respectively. Temperature variability was greater for runoff-fed streams than for springs, and it increased with greater distance from the source. Flow, altitude, and the number and type of (i.e., spring or runoff-fed) tributaries joining the springbrook channel determined the degree of temperature variability downstream of the spring sources. Moving downstream, invertebrate communities progressively incorporated taxa with higher mobility and those more common to runoff-fed streams. Chironomids and non-insect taxa had higher densities at the spring sources. Chironomid larvae also dominated communities numerically at 100 and 500 m downstream from the sources along with *Pycnocentria* spp. and *Zelolessica* spp. Changes in substrate composition, stability and invertebrate drift are more likely explanations of the observed longitudinal patterns in the invertebrate communities than changes in temperature regimes. The New Zealand invertebrate fauna does not seem as dependent on thermal habitat characteristics as their Northern Hemisphere counterparts.

**Key words:** Diversity, invertebrate communities, longitudinal patterns, thermal constancy

## Introduction

One of the main characteristics of running waters is their unidirectional transport of materials and organisms along the longitudinal stream gradient (Hynes 1970). The composition and structure of stream biotic communities have been shown to change in response to longitudinal changes in habitat characteristics, such as temperature, current velocity, depth, width, discharge, substratum, turbidity and food availability (Hynes 1970, Fisher 1982, Allan 1996). Early observations of spatial succession in stream communities from headwaters to large rivers provided for the subdivision of running waters into Kryon, Krenon, Rhithron and Potamon biotopes (Hynes 1970, Hawkes 1975, Ward 1994). Kryal and krenal zones are the uppermost reaches of glacier and spring-fed streams, respectively, while the rhithral zone is concerned with the upper parts of snow and runoff-fed streams (Ward 1994). The idea of a longitudinal change along the stream gradient, culminated in the formulation of the river continuum concept (Vannote et al. 1980); that has been the focus of much discussion elsewhere (Hawkins and Sedell 1981, Winterbourn et al. 1981, Statzner and Higler 1985, Perry and Schaeffer 1987).

Kryal biotopes are characterized by a distinct and predictable change in invertebrate faunal assemblage, with chironomids from the genus *Diamesa* dominating where maximum temperatures are $\leq 2$ °C and diversity increasing downstream with simuliids, plecopterans, trichopterans, ephemeropterans and other chironomids starting to occur as thermal amplitude and physical stability increase (Milner and Petts 1994, Ward 1994, Milner et al. 2001), but see (Maiolini and Lencioni 2001). However, downstream invertebrate community patterns are not so distinctive in Krenal biotopes. The difficulty of establishing a general pattern for changes in invertebrate communities in Krenal biotopes may be related to the more diverse nature of their groundwater supply compared with glaciers; Also, Krenal biotopes may be found at different altitudes for a given latitude, while Kryal biotopes are not (Ward 1994, Barquín and Death 2004, Chapter one). The thermal characteristics of spring sources, which include diurnal and seasonal constancy, summer cold and winter warm conditions and delayed thermal maxima, can have deleterious effects on the stream invertebrate fauna (Sweeney and Vannote 1978, Vannote and Sweeney 1980, Ward and Stanford 1982), as seen in stream sections below dams and reservoirs (Lehmkuhl 1972, Ward and Stanford 1979, Vinson 2001). In

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general, the thermal and flow constancy of spring sources have been shown to decrease invertebrate diversity compared with downstream reaches and nearby runoff-fed streams (Davidson and Wilding 1943, Ward and Dufford 1979, Meffe and Marsh 1983, Erman and Erman 1992, Barquín and Death 2004).

In a recent study of 36 rheocrene springs and runoff-fed streams in New Zealand, invertebrate spring communities were shown to be more diverse than those in nearby runoff-fed streams (Chapter one). These results seem to contradict the generally observed pattern of a reduced invertebrate fauna in springs. Thus, in the present study we were interested in assessing the thermal variability of some of the runoff and spring-fed streams studied by (Chapter one). We also investigated longitudinal changes in the invertebrate fauna in some of their spring-fed streams. We expected to find higher thermal variability in runoff-fed than spring-fed streams, and an increase in thermal amplitude as we moved downstream from the spring sources. We also expected changes in temperature range to occur faster for the smaller than for the bigger springbrooks. Changes in temperature range were also anticipated to be faster or slower if there was a runoff-fed or a spring-fed stream entering the main channel, respectively. Higher temperature variability may be associated with higher flow variability, which has been shown to reduce invertebrate diversity (Death 1996, Vinson and Hawkins 1998, Chapter four).Thus, invertebrate diversity is hypothesized to be higher at sites with larger thermal ranges but without increased flow variability (i.e., springbrooks without any major runoff-fed streams entering the main channel).

## Materials and methods

### Study Sites

Study sites were spring and runoff-fed streams in Waimakariri basin and Kahurangi (Nelson) National Parks in the South Island and Tongariro (Ruapehu) and Mt Taranaki National Parks in the North Island of New Zealand (Table 1). All springbrooks were fed by rheocrene springs, where emerging water immediately forms a stream (Danks and Williams 1991). Streams ran through colluvium deposits (Waimakariri basin), karst regions (Kahurangi-Nelson), and volcanic areas (Ruapehu and Taranaki). The spring sources had a wide range of substrate composition, ranging from bedrock and large

boulders (Riwaka and Pearse River Resurgences) to coble substrate (Slip Spring) with sand, silt and mud (Hawdon Valley, Ohinepango, Waitaiki Stream and Taungatara Stream Springs). Although substratum at spring sources was largely covered by moss, downstream stony bottoms with no macrophyte growth dominated. The vegetation in the lower part of these regions is typical southern beech forest, except in Taranaki where it is Podocarp broad leaf forest. Stream altitude varied from 120 to 1100 m a.s.l with sites at higher altitudes located in subalpine scrub.

**Physicochemical measures**

A number of physicochemical variables were measured between November and December 2001, concurrently with invertebrate sampling (see below). Conductivity and temperature were measured with an Orion 122 meter and pH with a pHTestr 2 meter. In order to estimate flow, a stream transect was randomly selected and five measures taken of current velocity with a Flo-mate Marsh-McBirney 2000 at equidistant intervals. Width and depth were measured at five to seven points across these transects. A water sample was taken and analyzed in the laboratory for free inorganic nitrate and orthophosphate using ion chromatography in a Hach DR2000 UV/visible spectrophotometer.

To assess differences in the variability of water temperature regimes between spring and runoff-fed streams 12 temperature loggers (Onset, HOBO-H8) were placed in streams from May to November 2001. These were put within the first 50 m of 6 spring sources (Cass and Slip springs in Waimakariri; Riwaka Resurgence in Nelson; Ohinepango and Waitaiki springs in Ruapehu; Taungatara spring in Taranaki) and along 6 nearby runoff fed streams (Cave Stream and Whitewater River in Waimakariri; Riwaka South Branch Stream in Nelson; Omarae Stream and Waihohonu River in Ruapehu; Punehu Stream in Taranaki). Temperature loggers were also used to assess longitudinal variations in temperature downstream from spring sources between April and November 2002. Loggers were placed within the first 50 m and at 1 km from the source of 2 springs (Ohinepango and Waihohonu springs in Ruapehu), and within the first 50 m and at 1 and 2 km from the source in two other springs (Waitaiki spring in Ruapehu; Taungatara spring in Taranaki). Loggers were set to record temperature hourly.

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**Biological collections**

Seven springs (Slip and Hawdon Springs in Waimakariri, W1-W2; Pearse and Riwaka Resurgences in Nelson, N1-N2; Ohinepango and Waitaiki Springs in Ruapehu, R1-R2; Taungatara Spring in Taranaki, T1) were selected to study changes in macroinvertebrate fauna downstream from the spring source. Three 0.1 m$^2$ Surber samples (mesh = 250 μm) were collected at random from each spring source and from 15-30 m riffles at approximately 100 m, 500 m and 1 km downstream during December 2001. Samples were preserved in 10% formalin and returned to the laboratory for identification to the lowest possible taxonomic level using available keys (Winterbourn et al. 2000). The fauna was grouped into functional feeding groups (FFG) following Cowie (1990), Death (1995) and Winterbourn (2000a).

Coarse particulate organic matter (CPOM, >1 mm) and fine particulate organic matter (FPOM, 0.25-1 mm) remaining after invertebrates were removed were also dried to constant weight at 95 °C, weighed and ashed at 550 °C for 2 h to yield ash free dry weight. Three stones (maximum planar dimensions: 30-80 mm) were collected from each sampling location for measuring periphyton biomass. Stones were kept frozen until pigments were extracted in 90% acetone at 5 °C for 24 h in darkness. Absorbancies were read on a Varian-CARY 50 Conc. UV/visible spectrophotometer and converted to pigment concentration (chlorophyll *a* and phaeophytins) following Steinman and Lamberti (1996). Total stone surface area was calculated using the equation of Graham et al. (1988). As only a part of the stone is exposed to light (we assumed half the total surface area), estimates of algae pigment concentration were corrected by dividing the total stone surface area in half.

**Statistical analysis**

We calculated Shannon's, Simpson's and rarified diversity values for each of our Surber samples using the PRIMER statistical package (Clarke and Warwick 1994). The minimum number of individuals in our Surber samples was 41, so species richness was corrected to this number of animals. The springs investigated in this study differed in altitude, flow and in the number of tributaries joining the springbrook channel, all characteristics which may affect longitudinal variation in temperature (Smith and Lavis

1975, Crisp and Howson 1982, Ward 1985). Thus, sites were not treated as replicates and differences in faunal parameters and resource levels were tested with two-way analysis of variance (ANOVA) with site and distance from the source as treatment levels. Both factors of the ANOVA were treated as fixed factors (SAS Institute Inc. 1988). In order to examine the longitudinal variation of fauna and resource variables in each spring special attention was paid to the interaction between both main factors. One-way ANOVA was used to test for differences in thermal amplitude with distance from the source as the main factor. Variables were logarithmically transformed to remove heteroscedasticity if necessary. Tukey's post hoc means test was used to determine where significant differences occurred if the ANOVA revealed they were present (SAS Institute Inc. 1988).

Patterns in community composition were examined using non-metric multidimensional scaling (NMS) with the PC-ORD statistical package (McCune and Mefford 1995). The Sorensen distance measure was used to determine similarity between samples. Initial examination of stress patterns in the data suggested three dimensions were appropriate for the final ordination, which was established with 500 iterations of the data. Relationships between the ordination axes and the measured local and regional environmental variables were examined using Kendall rank correlation (SAS Institute Inc. 1988).

To determine the significance of invertebrate community differences we performed an analysis of similarities (ANOSIM) on invertebrate communities collected at the four different distances from the source using the PRIMER statistical package (Clarke and Warwick 1994). The mean density of taxa that contributed most ($\geq$ 80%) to the dissimilarity between different locations from the source was evaluated using the SIMPER procedure in the PRIMER statistical package. Bray –Curtis similarity distances were also calculated with the SIMPER procedure to compare springbrook and stream communities within and between regions.

**Table 1** One way ANOVA results testing for differences in physicochemical variables measured at 0 m, 100 m, 500 m and 1 km from the source of seven New Zealand spring-fed streams, in the austral summer of 2001. Kendall rank correlation coefficients with axis two and three of NMDS are also given. *= p 0.05-0.01, **= p < 0.01.

| Sites | Distance from source (m) | Altitude (m) | pH | Temperature (°C) | Conductivity (µS/cm) | Flow (m3/s) | Depth (m) | Velocity (m/s) | Width (m) | Oxygen (mg/ml) | Nitrates (mg/ml) | Phosphates (mg/ml) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pearse | 0 | 380 | 8.5 | 7.1 | 180 | 2.22 | 36 | 0.68 | 12.0 | 10.7 | 0.12 | 0.07 |
| Resurgence | 100 | | 8.4 | 7.2 | 177 | 1.6 | 36.8 | 0.59 | 11.1 | 11.0 | 0.1 | 0.09 |
| (N1) | 500 | | 8.5 | 7.4 | 180 | 3.64 | 31.6 | 0.89 | 18.0 | 11.0 | 0.1 | 0.06 |
| | 1000 | | 8.5 | 7.8 | 179 | 2.35 | 43 | 0.59 | 12.0 | 11.0 | | 0.07 |
| Riwaka | 0 | 120 | 8.4 | 10.2 | 243 | 1.84 | 44.8 | 0.77 | 7.3 | 10.4 | 0.21 | 0.13 |
| Resurgence (N5) | 100 | | 8.5 | 10.4 | 177 | 1.46 | 18.4 | 0.8 | 10.1 | 10.5 | 0.22 | 0.07 |
| | 500 | | 8.4 | 10.3 | 243 | 1.47 | 24.2 | 0.68 | 11.6 | 10.7 | 0.22 | 0.05 |
| | 1000 | | 8.6 | 12.6 | 170 | 1.17 | 20.4 | 0.82 | 9.0 | 11.3 | 0.2 | 0.07 |
| Slip | 0 | 800 | 7.5 | 8.1 | 45.1 | 0.17 | 13.2 | 0.54 | 3.2 | 8.3 | 0.1 | 0.12 |
| Spring (W1) | 100 | | 7.8 | 8.5 | 62.6 | 0.18 | 12 | 0.59 | 2.5 | 9.1 | 0.08 | 0.09 |
| | 500 | | 7.9 | 8.4 | 43 | 0.36 | 20 | 0.62 | 3.7 | 10.2 | 0.08 | 0.12 |
| | 1000 | | 7.9 | 9.4 | 40.9 | 0.53 | 20.2 | 0.89 | 3.9 | 9.8 | 0.04 | 0.04 |
| Hawdon Valley | 0 | 800 | 7.6 | 7.3 | 51.6 | 0.03 | 6.6 | 0.27 | 2.0 | 9.6 | 0.06 | 0.11 |
| Spring (W2) | 100 | | 7.8 | 7.0 | 54.3 | 0.47 | 22 | 0.28 | 5.6 | 10.3 | 0.06 | 0.11 |
| | 500 | | 7.8 | 7.3 | 40.8 | 1.02 | 20.4 | 0.64 | 10.3 | 11.0 | 0.06 | 0.08 |
| | 1000 | | 7.7 | 8.9 | 58 | 1.5 | 21.8 | 1.09 | 8.2 | 10.7 | 0.05 | 0.09 |
| Ohinepango | 0 | 1110 | 6.9 | 5.7 | 37 | 0.07 | 13.4 | 0.33 | 1.8 | 10.5 | 0.07 | 0.16 |
| Spring (R1) | 100 | | 7.1 | 6.1 | 65 | 1.62 | 31.2 | 0.53 | 9.7 | 10.7 | 0.1 | 0.31 |
| | 500 | | 7.4 | 6.1 | 49 | 1.5 | 42.4 | 0.79 | 5.6 | 11.5 | 0.04 | 0.18 |
| | 1000 | | 7.5 | 5.1 | 65 | 2.65 | 59.25 | 0.83 | 9.0 | 11.2 | 0.11 | 0.17 |

**Table 1** (Continuation)

| Sites | Distance from source (m) | Altitude (m) | pH | Temperature (°C) | Conductivity (µS/cm) | Flow (m3/s) | Depth (m) | Velocity (m/s) | Width (m) | Oxygen (mg/ml) | Nitrates (mg/ml) | Phosphates (mg/ml) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Waitaiki | 0 | 690 | 7.7 | 6.8 | 76 | 0.31 | 23.1 | 0.1 | 18.0 | 10.9 | 0.07 | 0.29 |
| Spring (R2) | 100 | | 8.2 | 6.6 | 104 | 0.4 | 19.8 | 0.48 | 5.5 | 11.7 | 0.13 | 0.45 |
| | 500 | | 8.0 | 7 | 105 | 0.25 | 12.18 | 0.9 | 3.1 | 11.8 | 0.07 | 0.31 |
| | 1000 | | 7.7 | 7 | 78 | 0.52 | 27.66 | 0.3 | 7.8 | 11.6 | 0.07 | 0.3 |
| Taungatara | 0 | 560 | 7.8 | 7.7 | 112 | 0.43 | 25.2 | 0.22 | 9.0 | 10.2 | 0.16 | 0.55 |
| Spring (T1) | 100 | | 7.8 | 7.8 | 109 | 0.16 | 14.2 | 0.43 | 3.2 | 10.5 | 0.12 | 0.57 |
| | 500 | | 7.8 | 8.4 | 109 | 0.14 | 17.4 | 0.34 | 2.6 | 10.4 | 0.1 | 0.58 |
| | 1000 | | 7.8 | 9.2 | 81 | 0.37 | 19.2 | 0.52 | 5.2 | 10.2 | 0.09 | 0.61 |
| Axis two | | | -0.42 | -0.38 | -0.52 | -0.28 | -0.2 | -0.19 | -0.2 | 0.03 | -0.3 | 0.09 |
| Axis three | | | -0.04 | 0.01 | -0.14 | 0.16 | 0.05 | 0.08 | 0.11 | -0.17 | 0.01 | -0.34 |
| $F_{3,24}$ | | | 0.3 | 0.5 | 0.1 | 1.4 | 0.7 | 2.9* | 0.1 | 1.9 | 0.5 | 0.2 |

# Results

## Physicochemical characteristics

Temperature, which ranged from 5.1 to 12.6 °C, consistently increased downstream in the seven studied springs. Depth (range: 7-60 m), width (range: 2-18 m) and flow (range: 0.1-3.6 m³/s) tended to increase with distance from the source, while conductivity (range: 40-243 μS/cm), nitrate (range: 0.04-0.2 mg/ml) and phosphate concentration (range: 0.04-0.6mg/ml) tended to decrease (Table 1). In contrast, pH, which ranged from 6.9 to 8.5 and oxygen concentration, which ranged from 8.3 to 11.8 mg/ml, did not exhibit clear downstream changes (Table 1). Conductivity was higher in springs of the Nelson region, while phosphate concentration was higher in Ruapehu and Taranaki springs (Table 1). Ohinepango Spring and Pearse and Riwaka Resurgence were the springs with largest flows, followed by Hawdon Valley Spring, with Slip, Waitaiki and Taungatara springs the smallest (Table 1).

Temperature patterns of runoff and spring-fed streams

Thermal range from May to November 2001 was higher in the runoff-fed streams Cave Stream (12 °C), Whitewater River (11 °C) and Waihohonu River (8 °C). The highest daily maximum and lowest daily minimum temperatures were also recorded from Cave Stream (13 and 1 °C, respectively). Springs had a much more constant temperature than runoff-fed streams, Riwaka resurgence had the highest mean temperature (10 °C), followed by Cass (8.2 °C), Slip (8 °C), Taungatara (7.7 °C), Waitaiki (6.6 °C) and Ohinepango springs (5.8 °C). The highest and lowest temperature ranges during the seven month period were recorded at Cass and Ohinepango springs (2.5 and 0.1 °C, respectively). Mean monthly thermal amplitude was more than 10 times larger in runoff-fed than spring-fed streams ($F_{1,10}$ = 76.32, P<0.0001). The number of degree-days accumulated per month was more constant in spring-fed than runoff-fed streams, and in general springs accumulated more or similar heat than nearby runoff-fed streams during the seven month period (Fig. 1). The total number of degree-days, or heat accumulated during the seven month period was negatively correlated with stream altitude ($r_s$: -0.72).
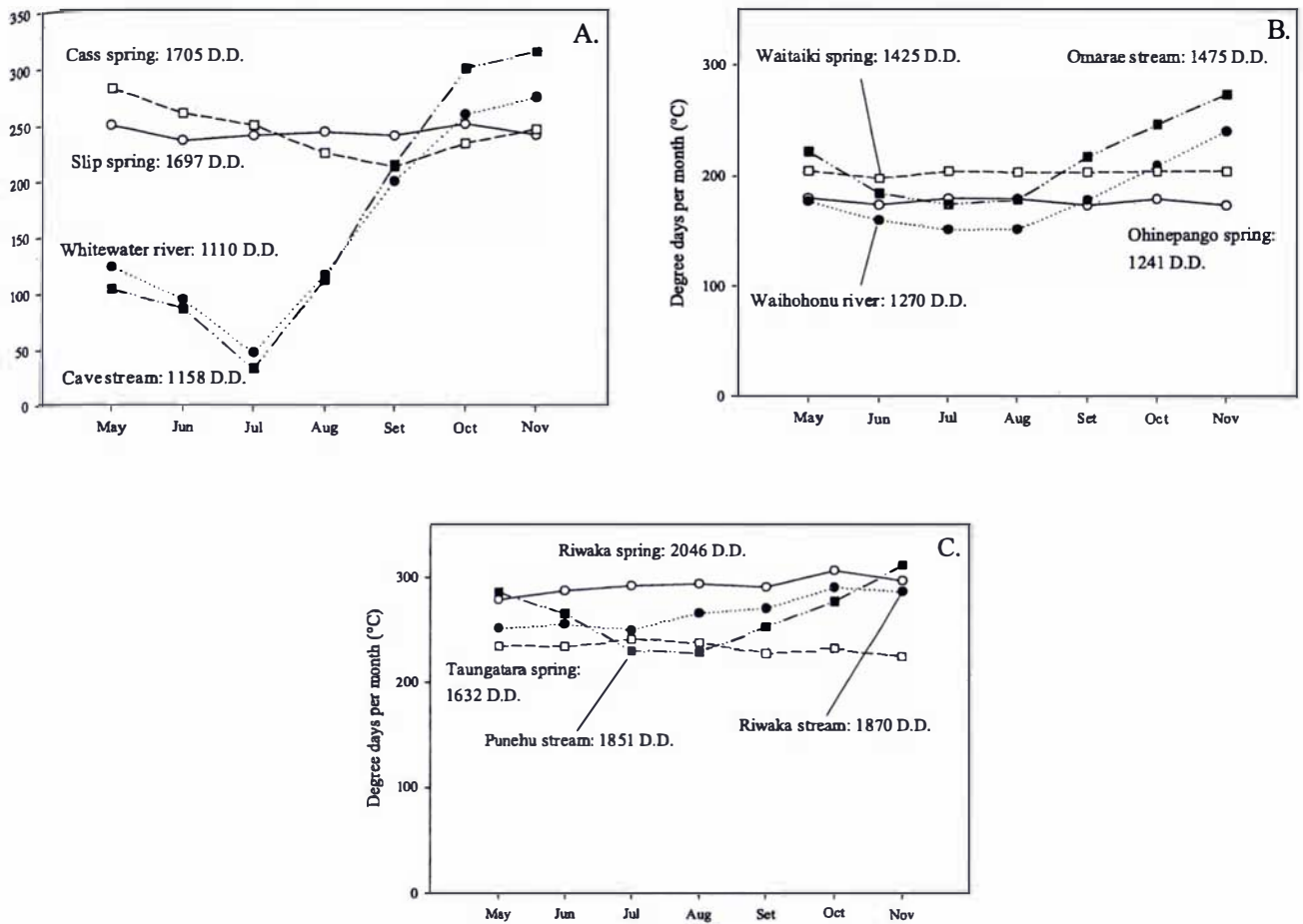
**Figure 1** Distribution of monthly degree-day accumulations for two spring-fed (open symbols) and two runoff-fed (solid symbols) streams in A. Waimakariri basin, B. Ruapehu and C. Nelson and Taranaki, New Zealand, from May to November 2001. Total degree-days (D.D.) accumulated during the seven month period are also given.

Spring-fed stream longitudinal temperature patterns

Temperature range increased with distance from the spring source, with the largest daily thermal amplitudes from April to November 2002 recorded 2 km from Taungatara Spring (6.6 °C) and 1 km from Taungatara and Waihohonu Spring sources (3.2 and 3.1°C, respectively). Correspondingly, the highest daily maximum temperature in the 8 month period was recorded 2 km downstream from the Taungatara Spring source (11.2 °C) and 1 km downstream from Taungatara and Waihohonu Spring sources (9.4 and 8.2 °C, respectively). Mean monthly temperature range was on average 5 times lower at the

source of the spring than downstream 1 km, and 8 times lower at the source than 2 km downstream (Fig. 2; $F_{2,68}$ = 144.81, P< 0.001). From April to November 2002 mean monthly temperature range at Ohinepango Spring source was similar to that recorded 1 km from the source (Fig. 2), although the number of degree-days accumulated was higher (0 m: 1226; 1 km: 1477). The number of degree-days accumulated during the 8 month period increased downstream from Taungatara and Waitaiki Spring sources (Taungatara Source: 1856, 1 km: 1863, 2 km: 1941; Waitaiki Source: 1625, 1km: 1661, 2km: 1674), but not for Waihohonu spring (Source: 1728, 1 km: 1639).
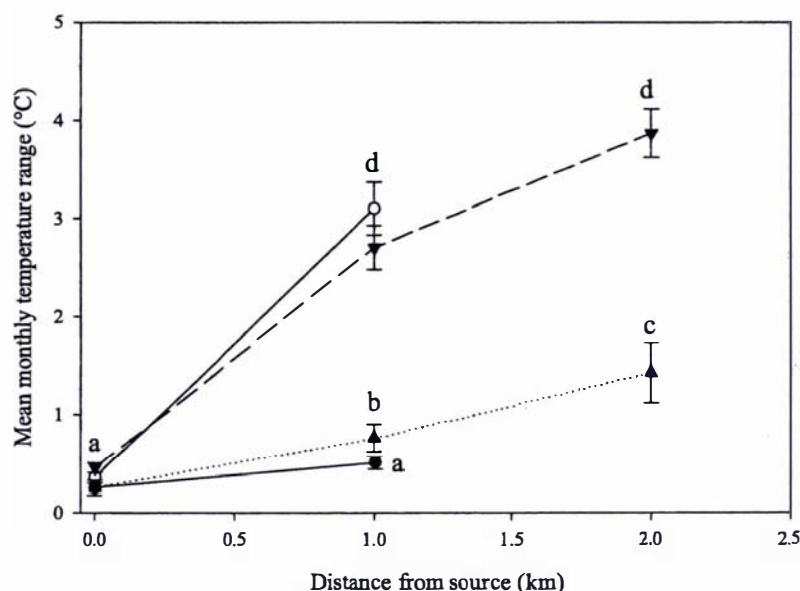


**Figure 2** Variations in the mean (± 1 SE) monthly temperature range with distance from source in three spring-fed streams from Ruapehu (●——●, Ohinepango spring; ▲····▲, Waitaiki stream; ○——○, Waihohonu spring) and one from Taranaki (▼····▼, Taungatara stream), New Zealand, measured from April to November 2001. Different letters indicate statistical differences between mean temperature ranges.

**Periphyton, organic matter**

Overall periphyton biomass did not change substantially downstream from the spring sources (Table 2), however, pigment concentration was lower 1 km from the spring source than at any of the other sampling sites in 5 of the sampled springs (Hawdon,

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Ohinepango, Slip, Taungatara and Waitaiki Springs) (Fig. 3). Periphyton biomass was lower in Ohinepango Spring and higher in Riwaka Resurgence (Table 2). On average concentrations of coarse and fine organic matter were more than 4 times higher at spring sources than 1 km from the source (Table 2, Fig. 3). Pearse Resurgence had the lowest concentration of CPOM of all the springs surveyed (Table 2).

**Table 2** Results of two way ANOVA testing for differences in site and distance from the source for invertebrate community parameters and resource levels measured at 0 m (1), 100 m (2), 500 m (3) and 1 km (4) from the source of seven New Zealand spring-fed streams, in the austral summer of 2001. Kendall rank correlation coefficients of level of resources with axis two and three of NMDS are also given. *= p 0.05-0.01, **= p < 0.01.

| | Site | | Distance | | Interaction | | |
|---|---|---|---|---|---|---|---|
| | $F_{6,55}$ | Tukey's | $F_{3,55}$ | Tukey's | $F_{18,55}$ | Axis 2 | Axis 3 |
| CPOM | 8.6** | W2 N2 R2 T1 W1 R1 N1 | 19.61** | 1 3 2 4 | 5.71** | 0.09 | -0.03 |
| FPOM | 1.86 | | 18.76** | 1 2 3 4 | 1.45 | 0.22 | 0.06 |
| Chlorophyll *a* | 6.08** | N2 R2 W1 N1 T1 W2 R1 | 2.06 | | 1.24 | -0.12 | 0.02 |
| Number of Taxa | 12.83** | N2 W1 W2 T1 N1 R2 R1 | 10.5** | 4 3 2 1 | 3.06** | | |
| Number of Individuals | 14.31** | W1 W2 N2 N1 R1 R2 T1 | 1.32 | | 4.68** | | |
| Rarified Number of Taxa | 28.17** | T1 N2 R2 W2 N1 W1 R1 | 22.12** | 4 3 2 1 | 1.8* | | |
| Shannon Diversity Index | 22.66** | T1 N2 R2 W2 N1 W1 R1 | 19.02** | 3 4 2 1 | 2.1* | | |
| Simpson Diversity Index | 1.74 | | 2.44 | | 0.88 | | |

**Invertebrate abundance and diversity patterns**

A total of 79 insect and 10 non-insect taxa were collected from the springs and their associated springbrooks. The highest number of taxa was recorded at Slip spring (52), followed by Riwaka Resurgence (51), Hawdon Valley Spring (50), Waitaiki Spring (46), Taungatara Spring (45) and Pearse Resurgence (44). In contrast, only 31 taxa were collected from Ohinepango Spring and its springbrook. Overall, total number of taxa and mean number of taxa per Surber sample both increased with distance from the source (Fig. 4, Table 2). Total number of taxa was higher 500 m downstream of Ohinepango, Waitaiki and Hawdon Valley springs (21, 32 and 33 taxa, respectively) and 1 km from the source of Pearse, Riwaka and Taungatara springs (29, 39 and 33 taxa, respectively).
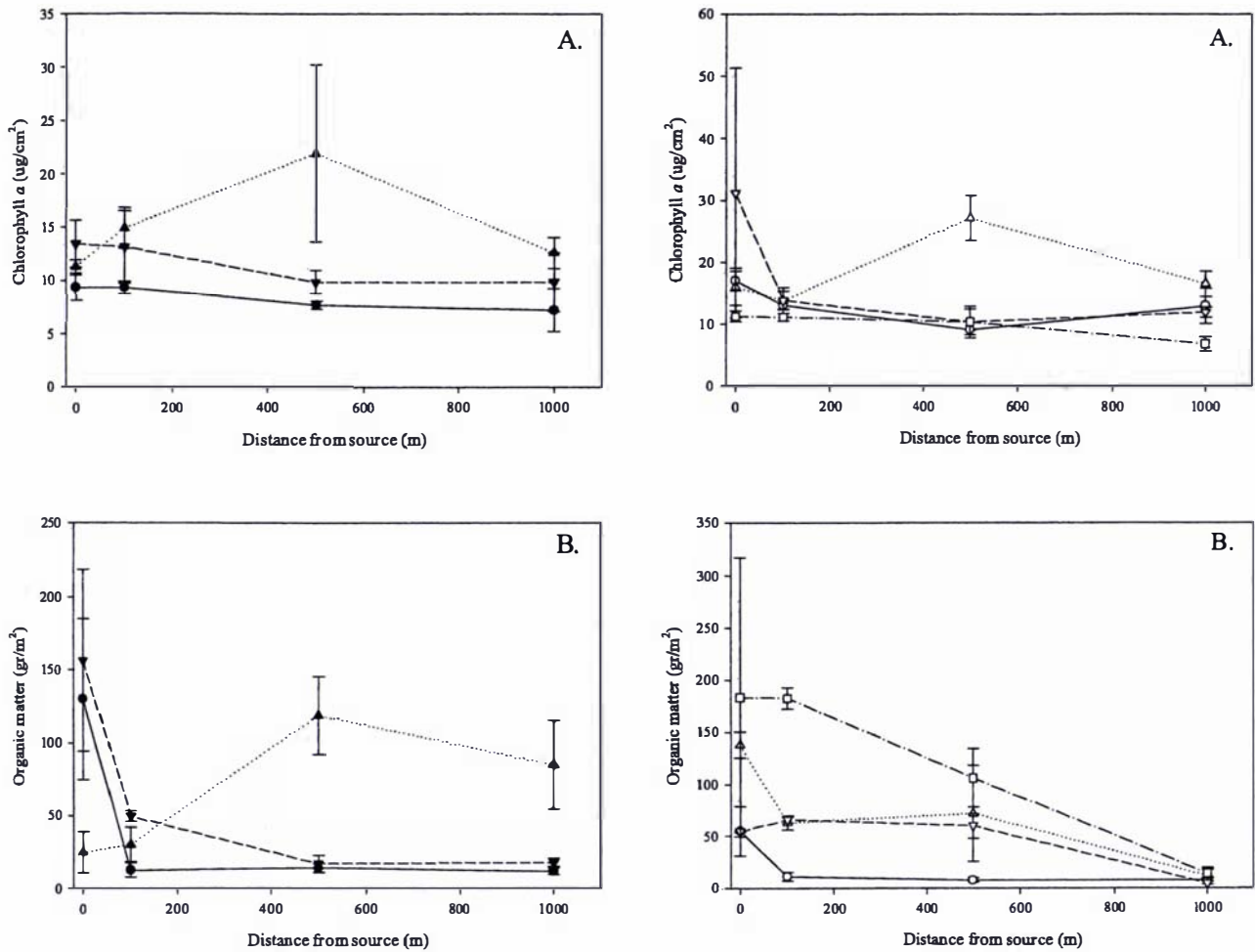
**Figure 3** Mean (± 1 SE) A. algae pigment concentration (chlorophyll *a*) and B. organic matter collected in seven spring-fed streams in New Zealand at different distance from the source, in the austral summer of 2002 (□-·—·-□, Hawdon spring; O——O, Pearse river; ∇···∇, Slip spring; △····△, Riwaka spring; ●——●, Ohinepango spring; ▲···▲, Waitaiki stream; ▼···▼, Taungatara stream).

When we look at changes in the mean number of invertebrate taxa at each site separately, we can see that downstream increases occurred only in Riwaka Resurgence and Taungatara Spring (Table 3). Most springs showed a downstream decrease in the number of individuals although it was only significant for Slip and Waitaiki Springs (Fig. 4, Table 3). Number of invertebrate individuals was almost 3 times lower in Taungatara Spring than in the rest (Table 2). Rarified number of species and evenness increased with

distance from the source in all surveyed springs (Fig. 4, Table 2), although differences were only marked between 500 m and 1 km from the spring source in Hawdon Valley and Waitaiki Springs (Table 3). Both rarified number of species and Shannon index of diversity were significantly higher in Riwaka Resurgence and Taungatara and Waitaiki Springs (Table 2). In Ohinepango, Taungatara and Waitaiki Springs the downstream increase in total number of taxa was positively correlated with the number of degree-days and the monthly temperature range ($r_s$: 0.8 in both cases, P< 0.001).

**Table 3** Tukey's post-hoc tests for the interaction between site and distance from the source given by the two way ANOVA for invertebrate community parameters measured at 0 m (1), 100 m (2), 500 m (3) and 1 km (4) from the source of seven New Zealand spring-fed streams, in the austral summer of 2001, n.s. = P> 0.05, lines join distances with no statistical differences, Bold characters are spring-fed streams with significant differences in some community metrics.

| Number of Taxa | | Rarified Number of Taxa | |
|---|---|---|---|
| Site | Distance | Site | Distance |
| Slip spring | n.s. | Slip spring | n.s. |
| Hawdon spring | n.s. | **Hawdon spring** | 3 4 2 1 |
| Pearse river | n.s. | Pearse river | n.s. |
| **Riwaka spring** | 4 2 3 1 | Riwaka spring | n.s. |
| Ohinepango spring | n.s. | Ohinepango spring | n.s. |
| Waitaiki spring | n.s. | **Waitaiki spring** | 4 2 3 1 |
| **Taungatara spring** | 4 3 2 1 | Taungatara spring | n.s. |
| Number of Individuals | | Shannon Diversity Index | |
| Site | Distance | Site | Distance |
| **Slip spring** | 1 3 2 4 | Slip spring | n.s. |
| Hawdon spring | n.s. | **Hawdon spring** | 3 4 2 1 |
| Pearse river | n.s. | Pearse river | n.s. |
| Riwaka spring | n.s. | Riwaka spring | n.s. |
| Ohinepango spring | n.s. | Ohinepango spring | n.s. |
| **Waitaiki spring** | 1 3 4 2 | **Waitaiki spring** | 4 2 3 1 |
| Taungatara spring | n.s. | Taungatara spring | n.s. |
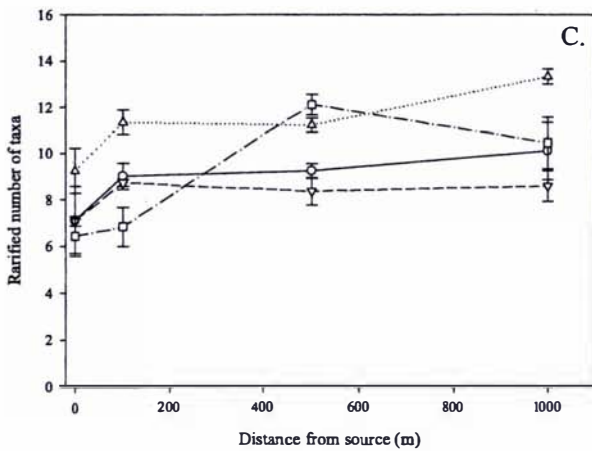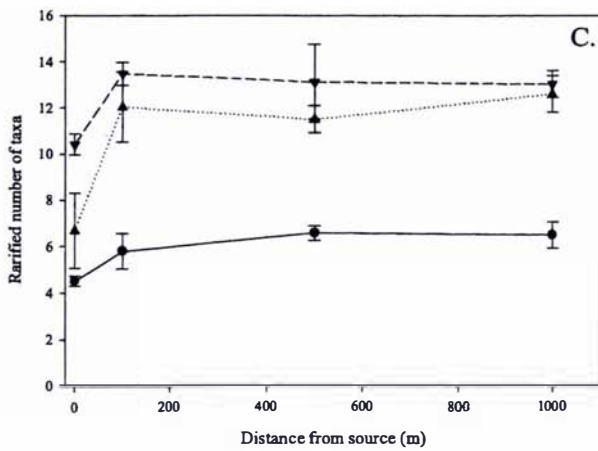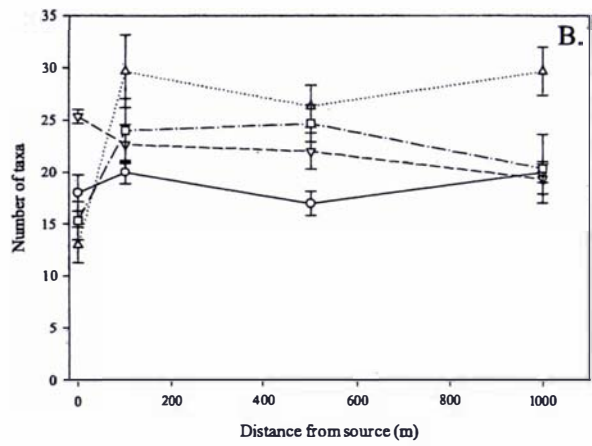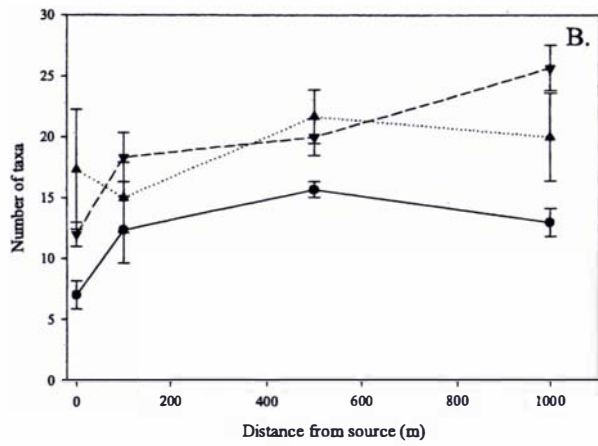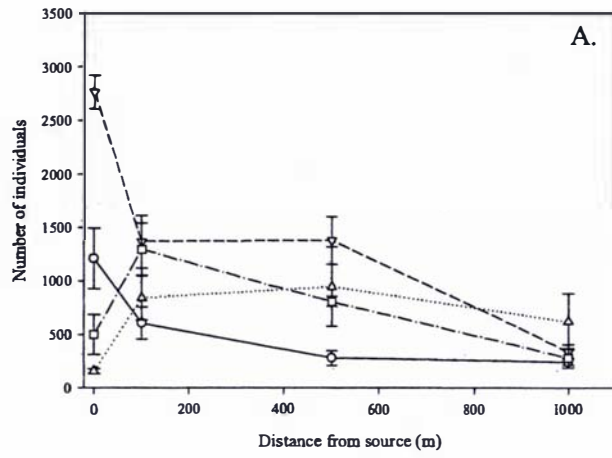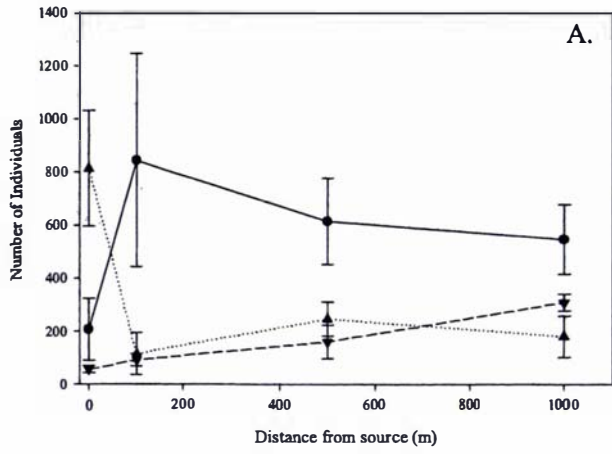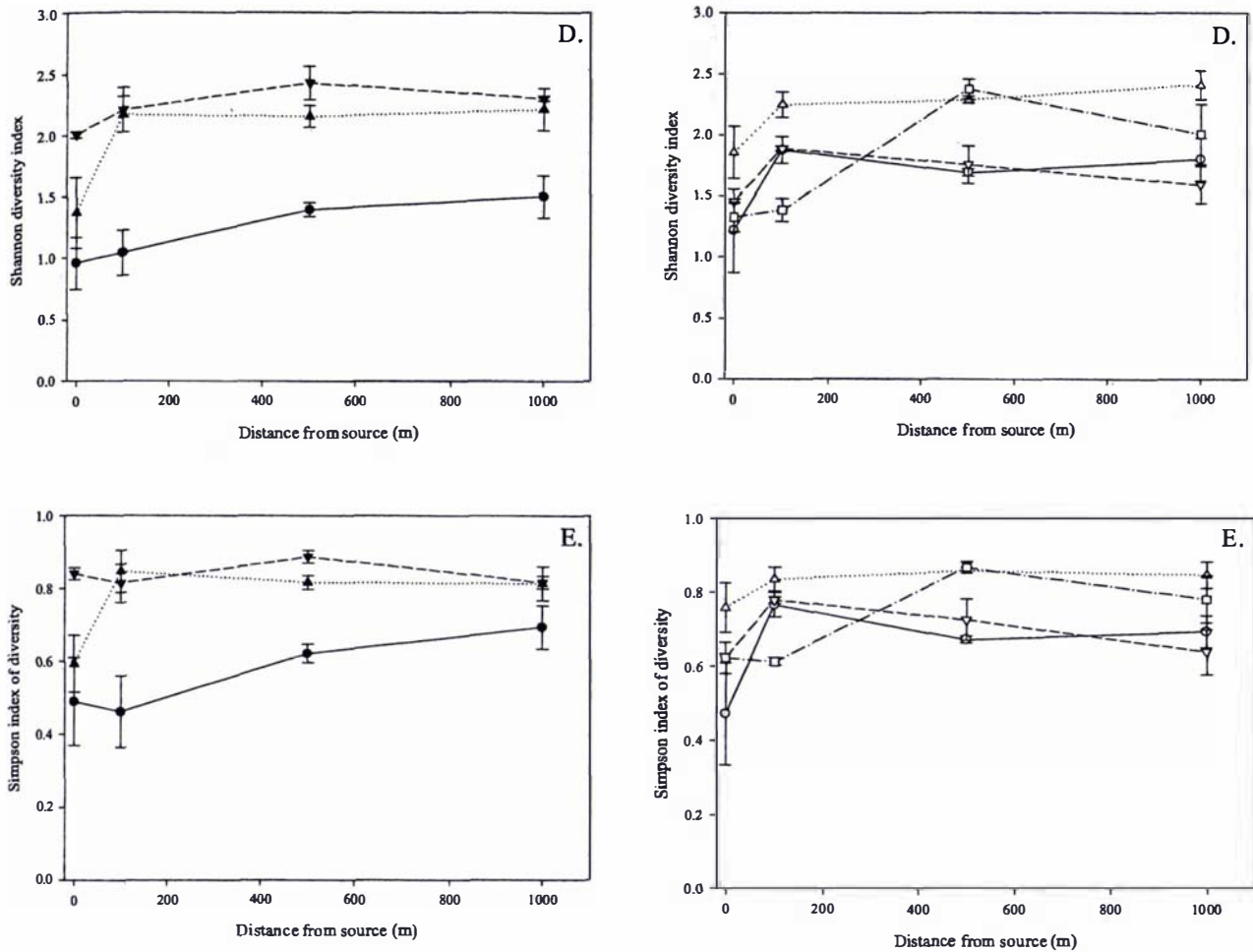
**Figure 4** Mean (± 1 SE) A. Number of Individuals, B. Number of Taxa, C. Number of rarified taxa D. Shannon diversity index and E. Simpson diversity index for invertebrate communities collected in seven spring-fed streams in New Zealand, in the austral summer of 2002 (□-·-·-□, Hawdon spring; O—O, Pearse river; ▽⁻⁻⁻▽, Slip spring; △·····△, Riwaka spring; ●—●, Ohinepango spring; ▲·····▲, Waitaiki stream; ▼·····▼, Taungatara stream).

## Community structure

### Taxonomic composition

Insect taxa dominated at all spring sources, comprising from 60 to 98% of the total number of animals in the community, except at Waitaiki and Hawdon valley spring sources, where Oligochaeta and *Potamopyrgus antipodarum*, and Oligochaeta, *Paraleptamphopus subterraneus* and Nematoda comprised 74 and 53% of the

invertebrate communities, respectively. The density of non-insect taxa was 15 times higher at the two upstream locations compared with the two further downstream ($F_{3,55}$ = 39, P< 0.0001); Nematoda, *P. antipodarum*, Oligochaeta, *P. subterraneus* and *Paracalliope fluviatilis* constituted 30% of the animals in the spring source community (Table 4). Coleoptera and Ephemeroptera densities were more than 5 times higher at 1 km than at the spring source ($F_{3,55}$ = 14.5 and 81.6, respectively, P< 0.0001). *Hydora* sp. and Hydraenidae beetles increased in density downstream (in W2, N1, N2, R1 and T1), to constitute more than 5% of the invertebrate community 1 km from the source. The mayfly *Deleatidium* spp. increased in numbers downstream in all springs, accounting for less than 2% at the spring sources to more than 27% of the total invertebrate community 1 km from the spring source (Table 4). *Austroclima* spp. (in N2, R2 and T1) and *Coloburiscus humeralis* (in W2 and T1) also contributed to the downstream increase in mayfly densities (Table 4).

Trichoptera were 5 times less abundant at the spring sources than at any other distance from the spring sources ($F_{3,55}$ = 3.6 and 16.4, respectively, P< 0.0001; Table 4). The cased caddisflies *Pycnocentria* spp. (in W1, W2, N2, R2 and T1) and *Zelolessica* spp. (in W2, N1, N2, R1, R2 and T1) reached their highest densities 100 and 500 m from the sources, whereas *Beraeoptera roria*, *Olinga feredayi* and *Pycnocentrodes* spp., were in greater abundance 1 km from the spring sources (in W1, W2, N2 and T1), where they constituted more than 13% of the overall invertebrate community (Table 4). Densities of Diptera were 3 times higher at the two upstream locations compared with the two further downstream ($F_{3,55}$ = 3.6, P< 0.001). Chironomids reached maximum densities at 0 (in W1, W2, N1, R2 and T1) and 100 m (in N2 and R2). Overall, they decreased in relative abundance from 58% at the spring sources to 27% at 1 km.

Richness of Coleoptera, Ephemeroptera and Trichoptera increased with distance from the source ($F_{3,55}$ = 19.6, 38.9 and 11.7 respectively, P<0.001), while non-insect taxa had more number of taxa at the spring sources ($F_{3,55}$ = 13.1, P<0.001). Diptera and Plecoptera did not show any differences in diversity with distance downstream ($F_{3,55}$ = 1.9 and 2.3 respectively, P>0.05).

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Table 4 Results of two way ANOVA testing for differences in site and distance from the source for the three most abundant taxa in each functional feeding group collected at 0 m (1), 100 m (2), 500 m (3) and 1 km (4) from the source of seven New Zealand spring-fed streams, in the austral summer of 2001. Kendall rank correlation coefficients of these taxa with axe two and three of NMDS are also given. Overall they explain almost 80% of the differences between invertebrate communities at different distances from the source.

| Distance from source | 0 | | 100 | | 500 | | 1000 | | $F_{6,55}$ | Site Tukey's | $F_{3,55}$ | Distance Tukey's | Interaction $F_{18,55}$ | Axis 2 | Axis 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Sessile Browser** | 667.3 | ±183.2 | 435.8 | ±86.2 | 255.4 | ±49.6 | 111.3 | ±35.6 | 11.7** | W1 W2 R1 N1 N2 R2 T1 | 8.1** | 1 2 3 4 | 4.56** | | |
| Chironomidae | 471.3 | ±153.2 | 267.4 | ±69.9 | 216.9 | ±48.3 | 100.1 | ±36.5 | 8.6** | R1 W1 N1 N2 W2 R2 T1 | 6.2** | 1 2 3 4 | 3.93** | 0.2 | 0.5 |
| *Potamopyrgus antipodarum* | 107.2 | ±44.6 | 161.4 | ±62.9 | 23.6 | ±10.7 | 4.4 | ±2.7 | 80.4** | W1 W2 R2 T1 R1 N1 N2 | 14** | 2 1 3 4 | 14.31** | 0.5 | 0.0 |
| Oligochaeta | 90.2 | ±32.2 | 7.5 | ±4.7 | 15.0 | ±5.3 | 4.0 | ±1.5 | 29.9** | W1 W2 R2 N1 T1 R1 N2 | 22.1** | 1 3 2 4 | 5.98** | 0.3 | 0.2 |
| **Mobile Browser** | 103.6 | ±23.1 | 259.2 | ±53.1 | 312.4 | ±66.1 | 196.8 | ±25.7 | 18.6** | W1 N2 N1 W2 R2 T1 R1 | 18.2** | 3 4 2 1 | 3.62** | | |
| *Deleatidium* spp. | 13.6 | ±4.3 | 64.5 | ±21.7 | 132.9 | ±50.8 | 99.6 | ±13.6 | 38.7** | W1 N1 N2 W2 T1 R2 R1 | 42.4** | 4 3 2 1 | 3.61** | -0.1 | 0.2 |
| *Pycnocentria* spp. | 2.4 | ±0.8 | 107.7 | ±39.2 | 66.3 | ±22.2 | 3.9 | ±1.3 | 38** | W2 N2 R2 T1 W1 R1 N1 | 46.7** | 2 3 4 1 | 9.22** | 0.3 | 0.2 |
| *Zelolessica* spp. | 5.9 | ±2.6 | 21.0 | ±9.1 | 49.8 | ±25.4 | 7.9 | ±4.7 | 18.2** | R1 N2 T1 N1 R2 W1 W2 | 5.3** | 3 2 1 4 | 4.28** | -0.1 | -0.1 |
| **Filterer** | 2.9 | ±1.5 | 15.8 | ±7 | 11.0 | ±5.1 | 18.6 | ±6.2 | 13.1** | W1 T1 W2 N2 R1 N1 R2 | 10.8** | 4 3 2 1 | 3.13** | | |
| *Austrosimulium* spp. | 0.0 | ±0 | 9.2 | ±6.8 | 3.1 | ±1.5 | 7.7 | ±4.7 | 33.9** | W1 W2 R1 N1 T1 R2 N2 | 15.2** | 4 3 2 1 | 8.18** | 0.2 | 0.2 |
| *Coloburiscus humeralis* | 0.1 | ±0.1 | 1.4 | ±1.1 | 4.9 | ±3.4 | 6.6 | ±3.6 | 3.9** | W2 T1 N2 R2 W1 N1 R1 | 2.9** | 4 3 2 1 | 1.23 | -0.2 | -0.3 |
| Hydropsychidae | 0.0 | ±0 | 5.0 | ±2.6 | 2.7 | ±1.8 | 4.0 | ±1.8 | 30.7** | T1 N2 R2 W1 W2 N1 R1 | 10.1** | 4 2 3 1 | 4.87** | -0.2 | -0.5 |

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**Table 4** (Continuation)

| Distance from source | 0 | | 100 | | 500 | | 1000 | | $F_{6,55}$ | Site Tukey's | $F_{3,55}$ | Distance Tukey's | Interaction $F_{18,55}$ | Axis 2 | Axis 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Predator** | 27.4 | ± 6.4 | 12.9 | ± 2.7 | 13.1 | ± 2.6 | 9.2 | ± 2.1 | 4.9** | W2 R1 W1 N2 N1 T1 R2 | 3.6** | 1 3 2 4 | 2.98** | | |
| Flatworms | 4.8 | ± 3.2 | 4.6 | ± 2.6 | 7.8 | ± 3.2 | 2.2 | ± 0.9 | 119.9** | W1 W2 R2 R1 T1 N2 N1 | 6.1** | 3 4 1 2 | 7.59** | 0.4 | 0.1 |
| Nematoda | 12.1 | ± 5.4 | 0.1 | ± 0.1 | 0.0 | ± 0 | 0.0 | ± 0 | 7.8** | R1 W2 R2 T1 W1 N2 N1 | 33.2** | 1 2 3 4 | 7.1** | 0.2 | 0.0 |
| Muscidae | 5.1 | ± 2.2 | 1.7 | ± 0.7 | 2.1 | ± 0.8 | 0.2 | ± 0.1 | 9.1** | W1 W2 N1 R1 R2 N2 T1 | 6.3** | 1 3 2 4 | 2.35** | 0.3 | 0.5 |
| **Shredder** | 10.2 | ± 3.8 | 10.5 | ± 1.5 | 36.0 | ± 11 | 25.1 | ± 10.5 | 6.8** | T1 W1 R2 N1 N2 W2 R1 | 6.1** | 3 4 2 1 | 5.0** | | |
| *Olinga feredayi* | 0.2 | ± 0.2 | 2.9 | ± 1.2 | 20.3 | ± 10.1 | 18.7 | ± 10.8 | 44.9** | W1 N2 N1 W2 T1 R1 R2 | 21.1** | 3 4 2 1 | 15.64** | 0.1 | 0.2 |
| *Austroperla cyrene* | 5.7 | ± 3.6 | 3.2 | ± 1 | 2.0 | ± 0.6 | 1.7 | ± 0.8 | 7** | N1 R2 N2 R1 T1 W2 W1 | 0.9 | | 1.49 | -0.1 | -0.1 |
| *Zelandoperla decorata* | 0.1 | ± 0.1 | 0.5 | ± 0.2 | 1.7 | ± 0.8 | 1.2 | ± 0.5 | 8.3** | R2 N1 T1 R1 N2 W1 W2 | 5.9** | 3 4 2 1 | 3.6** | -0.2 | -0.5 |

ANOSIM indicated that invertebrate communities were different between spring sources and 1 km downstream (R= 0.337, P < 0.01) and between 100 m and 1 km downstream of the source (R= 0.195, P < 0.05). Invertebrate communities of the studied springbrooks were more similar to each other at 1 km from the source (Bray-Curtis average similarity = 31.7) and most dissimilar at the spring sources (Bray-Curtis average similarity = 15).
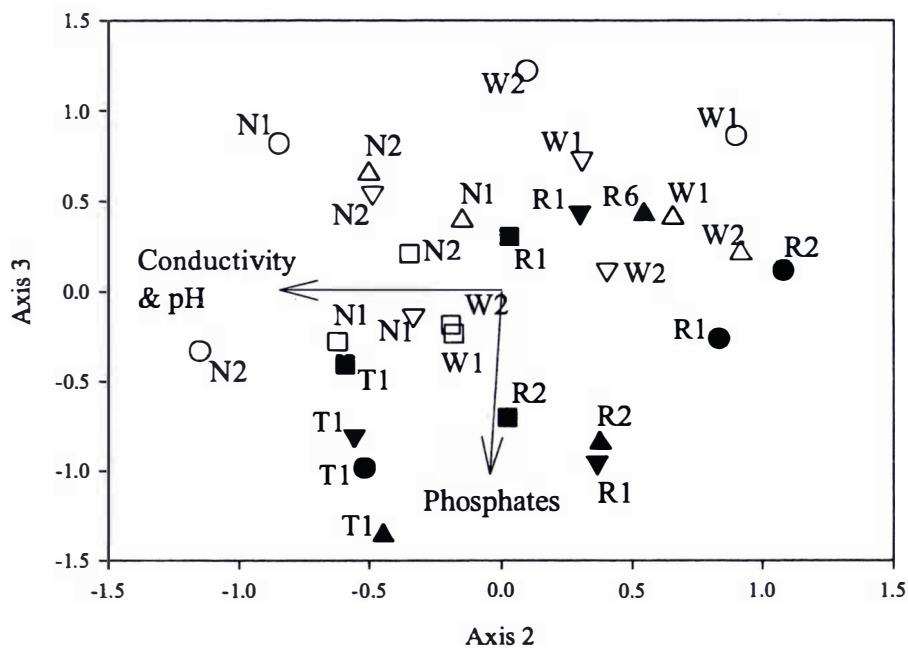


**Figure 5** Non-metric multidimensional scaling (NMDS) plot of axis 2 against axis 3 for invertebrate communities collected in seven spring-fed streams in New Zealand, in the austral summer of 2002 (O, Source; △, 100 m; ▽, 500 m; □, 1 km; closed symbols are spring-fed streams from the North Island and open symbols represent spring-fed streams from the South Island). Arrows show relationships between environmental variables and axes two and three of the ordination (cutoff value =0.3). W1= Slip Spring, W2= Hawdon Valley Spring, N1= Pearse Resurgence, N2= Riwaka Resurgence, R1= Ohinepango Spring, R2= Waitaiki Spring and T1= Taungatara Spring.

NMDS graded North Island springs to the bottom of axis three and South Island springs to the upper part (Fig. 5). Axis two and axis three explained 22% and 39% of the

total variance, respectively. Final stress for the NMDS analysis was 12.93, indicating a reliable ordination (McCune and Mefford 1995). The NMDS corroborates that the greatest similarity between invertebrate communities was 1 km from the spring source, (grouped in the middle of the ordination) whereas the spring source invertebrate communities were most dissimilar and were at the periphery of the ordination (Fig. 5). Conductivity and pH were negatively correlated with axis two, while phosphate concentration was negatively correlated with axis three (Table 1).

Functional feeding group composition

Sessile browsers (SB) decreased progressively in relative abundance from the spring sources, whereas mobile browsers (MB) increased (Fig. 6, Table 4). Filterers also increased in relative abundance downstream from the spring sources, principally as a result of the increased densities of *Austrosimulium* spp., *C. humeralis* and caddisflies from the Hydropsychidae family (Table 4). Predator densities were similar at all distances from the spring sources, but Shredders had less relative abundance at the spring sources in comparison with downstream locations (Fig. 6, Table 4).
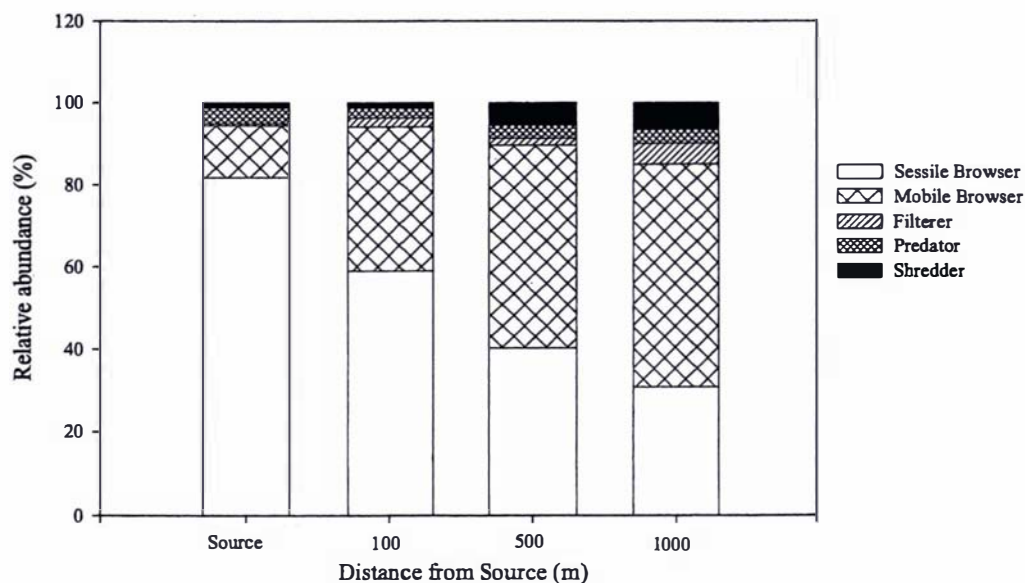


**Figure 6** Longitudinal variation in the relative abundance of functional feeding groups collected in seven spring-fed streams in New Zealand in the austral summer of 2001.

## Discussion

Temperature variation was much larger in runoff-fed compared with spring-fed streams. As in other New Zealand streams (Johnson 1971, Fowles 1975, Grant 1977), minimum temperatures were reached in June-July. Mean monthly temperature patterns recorded from Cave Stream more than 30 years ago closely resemble the temperature data we collected for that stream, with a minimum in June (1 °C) and a maximum in January (10 °C) (Johnson 1971). Other studies on New Zealand (Michaelis 1976, Cowie and Winterbourn 1979) and overseas (Ferrington 1995, Botosaneanu 1998) springs have shown that temperatures of the springs closely reflect the mean annual air temperature of the surrounding regions. In this study, mean temperatures over the study period for Slip and Cass springs (8 and 8.2 °C) and Riwaka Resurgence (10 °C) fall close to the mean annual temperatures for Waimakariri (8.6 °C) and Nelson (11.8 °C), respectively. The correlation between altitude and heat accumulated through the seven month period is also related to the interaction between air and water temperatures (Smith and Lavis 1975, Crisp and Howson 1982, Stefan and Preud'homme 1993).

Food resources (i.e., periphyton biomass) and physicochemical parameters did not vary much along the length of the springbrooks, except for the increase in temperature and water velocity and the decrease in organic matter away from the spring source. This is consistent with the findings of other studies, which reported increased water velocities (Minshall 1968), slight increases in pH and dissolved oxygen (Davidson and Wilding 1943, Sloan 1956) and a reduction in nitrates (Ward and Dufford 1979) as distance from the spring source increased. The increase in water velocity downstream may explain the decrease in organic matter, as the transport capacity of the current is enhanced with higher velocities. Also, some runoff-fed tributaries joined the springbrook channel in the first few kilometers from Slip and Hawdon Valley springs, increasing the instability of the stream bed and thus reducing the amount of organic matter (Chapter one). However, the periphyton communities do not seem to reflect this decrease in stability.

Thermal amplitude consistently increased with distance from the source, although the rate of increase varied between springs (Fig. 2). Other studies have also reported increases in thermal amplitude of 3 °C (Sloan 1956), 10 °C (Minshall 1968, Ward and Dufford 1979) and up to 20 °C (Meffe and Marsh 1983) approximately 1 km downstream

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from spring sources. We believe that the interaction between the size of spring discharge, the difference between water and air temperatures of the surroundings (altitude) and the type (spring, runoff, snow or glacier-fed streams) and number of tributaries that enter the springbrook channel determine the degree of temperature variation as one moves downstream from spring sources (Ward 1985). In this study, Taungatara and Ohinepango springbrooks had no tributaries entering along the studied length, however, Ohinepango Spring had a much higher flow (1.6 $m^3$/s at 100 m) than Taungatara Spring (0.2 $m^3$/s at 100 m). Consequently, mean monthly thermal amplitude was still nil 1 km from the source of Ohinepango Spring, but had increased by more than 2 °C in Taungatara Spring. Waitaiki Spring had a comparable flow (0.4 $m^3$/s at 100 m) to Taungatara Spring, however, there was one large spring joining before the 1 km sampling site and another before the 2 km location. It is possible that these additions may have reduced the rate of increase in temperature range in the Waitaiki springbrook.

Changes in periphyton biomass, organic matter and physicochemical parameters did not seem to parallel the downstream changes observed in the invertebrate fauna. Invertebrate richness, rarified number of taxa and evenness all increased downstream from the sources, and were all positively correlated with an increase in temperature amplitude downstream. However, correlation does not equate with causation, and the increase in the number of taxa in almost every spring was greater from the source to 100 m compared with that from 100 m to 1 km (Fig. 4, Tables 2 and 3). This indicates that patterns in invertebrate richness cannot be exclusively explained by an increase in temperature amplitude, as changes in thermal amplitude from the spring source to 100 m are much smaller than those from 100 m to 1 km from the source.

Minshall (1968) attributed the spatial patterns of the invertebrate fauna of a woodland springbrook in Kentucky to changes in thermal amplitude, flow and substrate composition. We believe that in our study, substrate may also be playing an important role in determining the differences between invertebrate communities located at the spring source and immediately downstream. Pearse and Riwaka resurgences have exposed bedrock and much larger substrate at the mouth of the spring than in downstream reaches, whereas Hawdon Valley, Ohinepango, Waitaiki and Taungatara springs had more sand, silt and mud at their spring origins than at downstream locations, and this has

been shown to limit the distribution of invertebrate fauna (Hynes 1970, Minshall 1984, Allan 1996). The higher amount of non-insect taxa, especially Oligochaeta and Nematoda, found at Hawdon Valley, Ohinepango and Waitaiki spring sources can be attributed to the preference of these taxa for soft substrates (Hynes 1970, Allan 1996). Moreover, another factor that may be increasing the differences in invertebrate communities between spring sources and 100 m from the source is the lack of animals and organic matter drifting in the first few meters of the spring (Barquín and Death 2004, Chapter one). Lack of organic matter in the water column may also explain the relative paucity of filter feeders in the spring sources.

Invertebrate communities at spring sources were more different to each other than invertebrate communities 1 km from the source. The observed change in community composition, for example the change in relative abundance between sessile browsers and mobile browsers, may be related to the higher variability of the flow moving downstream. Chironomids and non-insect taxa were abundant at the sources, whereas chironomids, *Pycnocentria* spp. and *Zelolessica* spp. were abundant at middle distances from the sources. These are all taxa that are known to be negatively affected by flow disturbance (Chapter one and four). Finally, invertebrate communities at 1 km from the spring source accumulated more taxa that are common to runoff-fed streams, for example Hydropsychidae, *Pycnocentrodes* spp., *B. roria*, *O. feredayi*, elmid beetles, and the mayflies *Deleatidium* spp. and *C. humeralis* (Chapter one). The greater similarities between invertebrate communities inhabiting runoff-fed streams may thus be a direct consequence of a higher frequency of floods, limiting which invertebrate fauna can survive. In chapter one we also found invertebrate communities from runoff-fed streams to be more similar to each other than invertebrate communities from spring-fed streams. Springs, which lack invertebrate drift, and thus, can only be colonized by upstream movements, hyporheic or aerial sources, may also be considered a more isolated habitat than runoff-fed streams. This higher degree of isolation may confer greater local variability to the invertebrate communities in spring-fed streams. Moreover, drift may also be responsible for accumulating taxa as one moves downstream. The longer the length of stream between the spring source and any point, the higher the likelihood that any given taxon may be found at that point.

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In overseas studies, thermal constancy has been proposed as the main factor reducing invertebrate diversity below hypolimnetical reservoirs (Lehmkuhl 1972, Ward and Stanford 1979, Vinson 2001) and at spring sources (Davidson and Wilding 1943, Ward and Dufford 1979, Meffe and Marsh 1983). We have not found any published studies showing similar effects in the New Zealand invertebrate fauna. However, in this study a positive relationship between number of invertebrate taxa and temperature was found, although this longitudinal variation was more likely a result of changes in substrate stability and composition. Why then is the New Zealand invertebrate fauna not as adversely affected by thermal constancy as its Northern Hemisphere counterpart? Canopy cover has been shown to exert an important control on stream water temperatures (Edington 1965, Ward 1985), producing winter warm and summer cold conditions that diminish heat transfer to air. New Zealand forests are predominantly evergreen forests, which provide an effective cover that would minimize daily temperature variations all year round. Moreover, the lack of synchronized life cycles in many New Zealand stream insects has been reported elsewhere (Winterbourn 1997, Scarsbrook 2000, Winterbourn 2000b). These characteristics may also free New Zealand stream insect fauna from temperature cues. Therefore, it may be that the New Zealand invertebrate fauna has certain advantages over its Northern Hemisphere counterparts in colonizing springs and springbrooks.

In conclusion, temperature amplitude was lower in the studied springs than in the runoff-fed streams. Thermal amplitude increased downstream from the spring sources, with flow, altitude and number and type of tributaries determining the rate of increase. Number of invertebrate taxa and evenness were positively correlated with an increase in temperature amplitude. Changes in substrate composition and stability along with the contribution of invertebrate drift to communities in downstream reaches may be enough to explain the observed longitudinal patterns in invertebrate communities. It seems likely that more members of the New Zealand invertebrate fauna have the ability to cope with thermal constancy in spring-fed streams than its Northern Hemisphere counterpart.

## Acknowledgements

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# Synthesis

This study has demonstrated that spatial patterns of stream invertebrate communities are affected by a number of factors that interact at different scales (Fisher 1992, Raffaelli et al. 1992). At the patch scale both productivity (i.e. algal biomass) and habitat structure (presence/absence of moss) increased the number of invertebrate taxa present in a given area, although through different mechanisms. Productivity increased the number of individuals per unit area and as a consequence the number of invertebrate taxa. Habitat complexity increased the habitable area and the amount and type of resources, which increased the presence of rare taxa and thus total species richness and evenness. The Resource Availability Hypothesis (Dean and Connell 1987, O'Connor 1991, Douglas and Lake 1994) was accepted as the most valid explanation of the mechanisms that produce the relationship between habitat complexity and number of invertebrate taxa.

The recovery of the invertebrate fauna after a natural or experimental disturbance of a streambed patch was highly dependant on the algal abundance and composition of the periphytic community. Resource levels may set an upper limit to the number of individuals, and thus number of taxa, that may recolonise a disturbed patch. The intensity of the disturbance influences benthic invertebrate communities by affecting the resistance of the community to the disturbance, while frequency of the disturbance affects the recolonizing mechanisms by affecting the resilience of the community to the disturbance.

At the scale of the stream reach, stability enhanced levels of food resources, habitat complexity and heterogeneity and this resulted in higher numbers of invertebrate taxa and individuals. Number of invertebrate taxa increased linearly with stability, and there was no evidence of a reduction on the number of invertebrate taxa with increasing stability (or productivity). There was clearly no support for the Intermediate Disturbance Hypothesis (Connell 1978) or the Dynamic Equilibrium Hypothesis (Huston 1994) to stream invertebrate communities.

The stability and composition of the substrata also played an important role in determining invertebrate assemblage composition. Higher rates of disturbance in runoff-fed streams or at 1 km from the source of the springs resulted in higher abundances of some taxa, e.g.: *Deleatidium* spp., *C. humeralis*, *Aoteapsyche* spp., *B. roria*, *Pycnocentrodes* spp. and the beetle *Hydora* sp., while substrate stability and presence of

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softer substrates in some of the spring sources favored higher densities of Chironomids, *Pycnocentria* spp., *Zelolessica* spp., *Potamopyrgus antipodarum*, Oligochaeta, *Paraleptamphopus subterraneus* and Nematoda.

At the reach scale predation pressure may also play an important role in controlling invertebrate diversity. The lowest number of invertebrate taxa in the more stable springs of Northern Spain than in the runoff-fed streams may be a result of the higher predation pressure from *Echinogammarus* sp., which dominates the invertebrate predator community. On the other hand, the higher diversity of the invertebrate predator community in New Zealand springbrooks seems to enhance total invertebrate richness. These results are consistent with the predictions of the Harsh-benign Hypothesis (Menge 1976), which predicts that predator pressure should be higher at lower disturbance rates.

Number of invertebrate taxa and evenness were positively correlated with an increase in temperature amplitude moving downstream from the spring sources. However, changes in substrate composition and stability along with the effects of invertebrate drift on downstream reaches seem more likely to explain the observed longitudinal patterns in invertebrate communities.

At the regional scale we found that altitude appears to set the upper limit to invertebrate richness and habitat stability determines the number of invertebrate taxa for a given elevation. Thus, altitude may restrict the dispersal of invertebrate taxa and limit the number of taxa that can reach a given stream. Non-insect taxa need stable flows to be able to colonize upper reaches, whereas flying insects will be highly dependant on temperature Therefore, a dispersal-stability framework is proposed to explain the observed spatial patterns of invertebrate communities. A similar framework has been proposed to explain diversity patterns of invertebrates in marine benthic communities (Palmer et al. 1996) and trees in tropical rainforests (Hubbell 2001).

The examination of spatial patterns of stream invertebrate communities over wide geographical areas has the power to reveal the effects of longer-term disturbances on stream invertebrate communities. For example, there seems to be a well established pattern across different continents of non-insect and insect dominance in lowland and upland springs, respectively, that may be the result of the last glaciation and the differing dispersal ability of insect and non-insect taxa.

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**Appendix 1** Number of invertebrate individuals collected in five Surber samples (area= 0.1 m$^2$) in spring and runoff-fed streams of New Zealand in the autumn of 2001. Site codes are included in appendix 1.1 in Chapter 1.

| es<br>xon | A1 | A2 | A3 | A4 | A5 | A6 | A7 | A8 | A9 | A10 | N1 | N2 | N3 | N4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ari | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| matoda | 21 | 2 | 3 | 1 | 24 | 0 | 6 | 2 | 0 | 0 | 1 | 1 | 1 | 2 |
| tracoda | 19 | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| gochaeta | 342 | 5 | 362 | 54 | 162 | 893 | 61 | 37 | 132 | 9 | 24 | 132 | 81 | 165 |
| rbellaria | | | | | | | | | | | | | | |
| ladia | 319 | 0 | 23 | 20 | 19 | 3 | 4 | 7 | 1 | 0 | 3 | 1 | 1 | 11 |
| valva | | | | | | | | | | | | | | |
| aeriidae | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| ustacea | | | | | | | | | | | | | | |
| phipoda | | | | | | | | | | | | | | |
| acalliope fluviatilis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 1 |
| aleptamphopus subterraneus | 151 | 0 | 13 | 0 | 3 | 0 | 29 | 85 | 0 | 77 | 0 | 0 | 0 | 0 |
| itridae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| steropoda | | | | | | | | | | | | | | |
| aulus sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| naea sp. | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| amopyrgus antipodarum | 2646 | 0 | 82 | 8 | 339 | 0 | 914 | 2314 | 4 | 6 | 0 | 0 | 0 | 1 |
| ecta | | | | | | | | | | | | | | |
| leoptera | | | | | | | | | | | | | | |
| lora sp 1 | 0 | 26 | 0 | 118 | 2 | 5 | 0 | 0 | 32 | 13 | 247 | 652 | 24 | 155 |
| lora sp 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| draenidae | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 5 |
| drophilidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| odactylidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 |
| rtidae | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| tera | | | | | | | | | | | | | | |
| irophila spp. | 36 | 5 | 584 | 4 | 4 | 25 | 0 | 2 | 13 | 15 | 21 | 4 | 22 | 248 |
| ectrotanypus spp. | 2 | 0 | 0 | 3 | 3 | 3 | 23 | 2 | 0 | 1 | 0 | 0 | 0 | 0 |
| trosimulium spp. | 20 | 23 | 84 | 22 | 1 | 73 | 0 | 0 | 6 | 6 | 0 | 3 | 1 | 0 |
| atopogonidae | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 8 | 0 | 0 | 6 | 91 | 2 |
| idae | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| pididae group A | 10 | 0 | 20 | 5 | 7 | 3 | 0 | 0 | 1 | 1 | 3 | 3 | 0 | 25 |
| pididae group B | 4 | 0 | 0 | 0 | 0 | 0 | 65 | 153 | 0 | 0 | 0 | 0 | 0 | 26 |
| opterini | 0 | 47 | 0 | 1 | 3 | 0 | 0 | 0 | 15 | 14 | 2 | 10 | 10 | 1 |
| iefferella spp. | 57 | 48 | 75 | 1 | 59 | 10 | 0 | 0 | 12 | 9 | 7 | 9 | 724 | 71 |
| rrisius pallidus | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| katomini | 1 | 0 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| niwhaniwhanus I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| onia sp. | 1 | 0 | 5 | 0 | 1 | 0 | 11 | 4 | 0 | 0 | 0 | 0 | 0 | 26 |
| oridiamesa spp. | 2264 | 27 | 3663 | 56 | 458 | 17 | 0 | 4 | 11 | 27 | 11 | 11 | 632 | 76 |
| choderus spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| :idae | 70 | 0 | 58 | 0 | 29 | 1 | 1 | 14 | 0 | 0 | 1 | 0 | 2 | 18 |
| *ella forsythi* | 404 | 35 | 257 | 40 | 0 | 154 | 2 | 4 | 68 | 2 | 9 | 21 | 825 | 22 |
| *urupira hudsoni*-group | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 0 | 0 |
| ocladiinae sp A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *trichocladius pluriserialis* | 0 | 0 | 0 | 41 | 2241 | 0 | 1 | 1 | 0 | 78 | 0 | 0 | 0 | 0 |
| *ispinegra approximata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *minae* | 0 | 1 | 1 | 39 | 0 | 22 | 0 | 0 | 17 | 81 | 10 | 5 | 2 | 26 |
| *oedilum* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| hodidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| iomyidae | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| nidae | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *tarsus vespertinus* | 53 | 0 | 0 | 23 | 1 | 0 | 12 | 2 | 1 | 0 | 0 | 0 | 24 | 11 |
| *idotipula* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **emeroptera** | | | | | | | | | | | | | | |
| *tophlebia cruentata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *leptosis perscitus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 |
| *roclima jollyae* | 0 | 0 | 0 | 0 | 0 | 0 | 499 | 75 | 0 | 2 | 0 | 0 | 0 | 13 |
| *roclima sepia* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 | 0 | 0 | 0 | 0 | 0 | 0 |
| *buriscus humeralis* | 0 | 0 | 0 | 34 | 1 | 16 | 13 | 14 | 0 | 0 | 0 | 10 | 1 | 1 |
| *atidium* spp. | 2064 | 994 | 2136 | 961 | 251 | 262 | 96 | 25 | 1314 | 823 | 784 | 986 | 568 | 296 |
| *ybotus* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *ephlebia scita* | 0 | 0 | 0 | 0 | 0 | 0 | 146 | 106 | 0 | 0 | 0 | 0 | 0 | 2 |
| *meletus* spp. | 0 | 0 | 0 | 39 | 117 | 0 | 0 | 0 | 106 | 76 | 4 | 24 | 12 | 26 |
| *cigaster distans* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *lebia* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **iptera** | | | | | | | | | | | | | | |
| ra | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **aloptera** | | | | | | | | | | | | | | |
| *ichauloides diversus* | 5 | 3 | 0 | 47 | 0 | 5 | 0 | 0 | 2 | 10 | 0 | 25 | 51 | 44 |
| **optera** | | | | | | | | | | | | | | |
| *roperla cyrene* | 0 | 0 | 0 | 0 | 0 | 0 | 54 | 20 | 0 | 1 | 0 | 22 | 11 | 138 |
| *aperla* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *aleptoperla* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 1 |
| *iocerca zelandica* | 0 | 0 | 0 | 0 | 0 | 2 | 37 | 62 | 1 | 0 | 0 | 0 | 0 | 0 |
| *iocercodes* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *operla prasina* | 4 | 0 | 22 | 0 | 0 | 0 | 36 | 5 | 3 | 1 | 32 | 74 | 45 | 16 |
| *perla howesi* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 122 |
| *ndobius confusus* | 5 | 0 | 3 | 0 | 0 | 0 | 2 | 2 | 0 | 5 | 5 | 302 | 0 | 38 |
| *ndobius furcillatus* | 40 | 10 | 27 | 9 | 27 | 90 | 1 | 0 | 13 | 12 | 0 | 0 | 0 | 3 |
| *ndoperla decorata* | 0 | 13 | 11 | 17 | 0 | 0 | 0 | 0 | 7 | 2 | 1 | 42 | 1 | 12 |
| *ndoperla fenestrata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 |
| **hoptera** | | | | | | | | | | | | | | |
| *ecentrella magnicornis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *apsyche* spp. | 0 | 505 | 0 | 441 | 0 | 52 | 0 | 0 | 24 | 110 | 1 | 40 | 151 | 1 |
| *opteria roria* | 3 | 14 | 19 | 459 | 130 | 36 | 0 | 1 | 6 | 26 | 0 | 96 | 0 | 5 |
| *fluens hamiltoni* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 23 | 7 | 1090 | 193 | 5 | 89 |
| *achorema* spp. | 60 | 3 | 4 | 20 | 3 | 2 | 0 | 0 | 10 | 9 | 4 | 5 | 4 | 3 |
| *tobiosella* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *mina zealandica* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *ercivalia* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |

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| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *licopsyche* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 33 | 1 | 0 |
| *dsonema alienum* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *dsonema amabile* | 4 | 0 | 1 | 0 | 12 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *drobiosella mixta* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 |
| drobiosidae (Early instars) | 126 | 43 | 472 | 85 | 357 | 102 | 1 | 2 | 15 | 67 | 0 | 11 | 51 | 45 |
| *drobiosis* spp. | 57 | 4 | 115 | 12 | 17 | 3 | 1 | 0 | 10 | 11 | 1 | 0 | 27 | 22 |
| *drochorema* spp. | 3 | 0 | 0 | 0 | 35 | 0 | 1 | 1 | 0 | 1 | 3 | 0 | 0 | 0 |
| *urochorema confusum* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *urochorema forsteri* | 0 | 0 | 0 | 8 | 1 | 0 | 0 | 0 | 0 | 8 | 1 | 0 | 1 | 0 |
| *conesus* sp. | 7 | 0 | 4 | 0 | 3 | 0 | 33 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| *nga feredayi* | 34 | 57 | 138 | 108 | 0 | 45 | 98 | 27 | 35 | 82 | 6 | 104 | 154 | 33 |
| *thopsyche* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *yethira albiceps* | 214 | 0 | 0 | 2 | 221 | 0 | 9 | 2 | 0 | 0 | 0 | 0 | 0 | 2 |
| *ilorheithrus agilis* | 37 | 0 | 5 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 4 | 16 | 48 |
| *ctronemia maclachlani* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *lyplectropus* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *udoconesus* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *lochorema* spp. | 18 | 19 | 0 | 12 | 169 | 62 | 12 | 2 | 32 | 44 | 0 | 3 | 21 | 2 |
| *cnocentrella* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *cnocentria evecta* | 1 | 0 | 0 | 0 | 350 | 0 | 9 | 39 | 0 | 18 | 1 | 0 | 0 | 0 |
| *cnocentria funerea* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *cnocentria hawdoniana* | 173 | 3 | 51 | 0 | 0 | 0 | 878 | 2264 | 4 | 0 | 0 | 0 | 0 | 0 |
| *cnocentria mordax* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *cnocentria sylvestris* | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 11 | 0 | 0 | 0 | 0 | 0 | 25 |
| *cnocentrodes* spp. | 274 | 105 | 52 | 572 | 967 | 40 | 31 | 9 | 1 | 97 | 0 | 0 | 0 | 0 |
| *plectides* spp. | 0 | 0 | 0 | 1 | 26 | 0 | 18 | 11 | 0 | 0 | 0 | 0 | 0 | 0 |
| *plectidina* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *lolessica cheira* | 3 | 0 | 14 | 0 | 1 | 0 | 3 | 0 | 0 | 0 | 5 | 0 | 0 | 0 |
| *lolessica meizon* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 396 |
| *londopsyche ingens* | 0 | 0 | 1 | 0 | 0 | 0 | 12 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |

| es / xon | N5 | N6 | N7 | N8 | R1 | R2 | R3 | R4 | R5 | R6 | R7 | R8 | R9 | R10 | T1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ari | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 |
| matoda | 1 | 1 | 0 | 1 | 0 | 0 | 5 | 3 | 1 | 0 | 23 | 1 | 2 | 34 | 0 |
| tracoda | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| gochaeta | 19 | 0 | 39 | 16 | 1 | 0 | 38 | 68 | 9 | 17 | 24 | 6 | 49 | 60 | 14 |
| rbellaria | | | | | | | | | | | | | | | |
| :ladia | 25 | 0 | 6 | 0 | 0 | 0 | 10 | 23 | 0 | 47 | 16 | 0 | 0 | 14 | 0 |
| valva | | | | | | | | | | | | | | | |
| aeriidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| ustacea | | | | | | | | | | | | | | | |
| phipoda | | | | | | | | | | | | | | | |
| *acalliope fluviatilis* | 727 | 0 | 89 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *aleptamphopus subterraneus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| itridae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 |
| steropoda | | | | | | | | | | | | | | | |
| *aulus* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *inaea* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *amopyrgus antipodarum* | 0 | 0 | 4 | 8 | 0 | 0 | 0 | 583 | 1 | 1 | 3 | 0 | 0 | 28 | 1 |
| secta | | | | | | | | | | | | | | | |
| leoptera | | | | | | | | | | | | | | | |
| *lora* sp 1 | 389 | 49 | 26 | 44 | 1 | 2 | 34 | 231 | 76 | 37 | 6 | 207 | 266 | 50 | 100 |
| *lora* sp 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| iraenidae | 2 | 1 | 2 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 2 | 5 |
| irophilidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| odactylidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 11 | 11 |
| rtidae | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 |
| itera | | | | | | | | | | | | | | | |
| *irophila* spp. | 56 | 83 | 113 | 21 | 0 | 0 | 0 | 0 | 10 | 0 | 10 | 7 | 8 | 0 | 73 |
| *ectrotanypus* spp. | 59 | 16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 1 | 0 |
| *trosimulium* spp. | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 16 | 0 | 3 | 2 | 3 | 3 | 0 |
| atopogonidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 32 | 0 | 0 |
| :idae | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| pididae group A | 3 | 0 | 1 | 2 | 1 | 0 | 11 | 61 | 3 | 161 | 3 | 6 | 15 | 23 | 1 |
| pididae group B | 78 | 2 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 2 | 6 | 6 | 7 | 0 |
| opterini | 6 | 1 | 0 | 47 | 1 | 3 | 3 | 9 | 50 | 0 | 0 | 45 | 35 | 1 | 38 |
| *kiefferella* spp. | 22 | 206 | 0 | 0 | 126 | 16 | 924 | 0 | 11 | 165 | 0 | 0 | 2 | 63 | 10 |
| *rrisius pallidus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| katomini | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 |
| niwhaniwhanus I | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 |
| *ionia* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 17 | 0 | 0 | 0 | 1 | 0 |
| *oridiamesa* spp. | 8 | 925 | 26 | 1 | 168 | 29 | 5978 | 279 | 11 | 6540 | 1 | 8 | 1 | 6 | 1 |
| *schoderus* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 0 |
| iscidae | 0 | 0 | 0 | 0 | 2 | 0 | 117 | 13 | 0 | 42 | 0 | 0 | 0 | 0 | 0 |
| *onella forsythi* | 142 | 0 | 55 | 10 | 0 | 0 | 0 | 84 | 38 | 5 | 29 | 24 | 2 | 28 | 14 |
| *ocurupira hudsoni*-group | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| hocladiinae sp A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 2 | 0 |
| *ratrichocladius pluriserialis* | 0 | 101 | 0 | 0 | 51 | 12 | 61 | 0 | 0 | 0 | 0 | 103 | 82 | 0 | 0 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *ispinegra approximata* | 0 | 0 | 111 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 23 | 0 | 0 |
| *minae* | 8 | 2 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 | 130 | 3 |
| *edilum* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *hodidae* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *iomyidae* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *nidae* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *tarsus vespertinus* | 39 | 26 | 0 | 61 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 9 | 1 |
| *ndotipula* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **emeroptera** | | | | | | | | | | | | | | | |
| *tophlebia cruentata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *leptosis perscitus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 |
| *roclima jollyae* | 395 | 0 | 270 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 15 | 0 | 7 | 79 | 0 |
| *roclima sepia* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 74 | 0 | 0 | 0 | 0 |
| *buriscus humeralis* | 15 | 0 | 2 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 58 | 4 | 4 | 10 | 40 |
| *atidium* spp. | 137 | 539 | 1285 | 2181 | 0 | 1 | 6 | 139 | 44 | 198 | 88 | 384 | 199 | 92 | 167 |
| *ybotus* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *ephlebia scita* | 14 | 0 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *meletus* spp. | 71 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 100 | 21 | 0 | 2 |
| *cigaster distans* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *lebia* spp. | 34 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **iptera** | | | | | | | | | | | | | | | |
| *ra* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **aloptera** | | | | | | | | | | | | | | | |
| *ichauloides diversus* | 27 | 50 | 4 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 23 | 2 | 1 | 0 |
| **optera** | | | | | | | | | | | | | | | |
| *roperla cyrene* | 8 | 12 | 1 | 3 | 0 | 0 | 0 | 2 | 0 | 1 | 43 | 26 | 11 | 8 | 2 |
| *aperla* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *aleptoperla* spp. | 38 | 10 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 5 | 29 | 45 | 15 |
| *iocerca zelandica* | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *iocercodes* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *operla prasina* | 5 | 11 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 3 | 6 | 12 | 12 | 1 | 12 |
| *perla howesi* | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 4 | 0 | 0 | 6 | 0 |
| *ndobius confusus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 44 | 0 | 22 |
| *ndobius furcillatus* | 27 | 0 | 0 | 0 | 0 | 0 | 1 | 117 | 0 | 35 | 0 | 92 | 34 | 312 | 3 |
| *ndoperla decorata* | 0 | 47 | 0 | 0 | 68 | 57 | 39 | 4 | 33 | 10 | 118 | 12 | 13 | 21 | 9 |
| *ndoperla fenestrata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 |
| **hoptera** | | | | | | | | | | | | | | | |
| *ecentrella magnicornis* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 |
| *apsyche* spp. | 23 | 394 | 142 | 148 | 14 | 5 | 0 | 2 | 14 | 0 | 26 | 0 | 0 | 0 | 0 |
| *opteria roria* | 9 | 0 | 30 | 37 | 0 | 0 | 0 | 3 | 0 | 1 | 1 | 16 | 0 | 96 | 13 |
| *fluens hamiltoni* | 38 | 532 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *achorema* spp. | 3 | 2 | 1 | 20 | 5 | 0 | 0 | 13 | 2 | 0 | 0 | 1 | 0 | 0 | 0 |
| *tobiosella* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 3 |
| *omina zealandica* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| *ercivalia* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 0 |
| *copsyche* sp. | 90 | 2 | 23 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 6 | 0 | 172 | 4 |
| *sonema alienum* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *sonema amabile* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *robiosella mixta* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *robiosidae* (Early instars) | 55 | 34 | 159 | 65 | 28 | 1 | 14 | 25 | 16 | 126 | 6 | 30 | 23 | 29 | 3 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *obiosis* spp. | 5 | 21 | 24 | 5 | 15 | 1 | 32 | 8 | 5 | 90 | 3 | 16 | 3 | 17 | 2 |
| *ochorema* spp. | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 8 | 2 |
| *ochorema confusum* | 16 | 0 | 12 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 2 | 0 | 0 |
| *ochorema forsteri* | 10 | 1 | 6 | 33 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 6 | 0 |
| *nesus* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 8 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| *ʒa feredayi* | 18 | 31 | 7 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *opsyche* sp. | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 217 | 0 | 0 | 47 | 121 |
| *thira albiceps* | 0 | 0 | 25 | 0 | 4 | 0 | 0 | 248 | 0 | 0 | 0 | 19 | 0 | 0 | 0 |
| *rheithrus agilis* | 5 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *ronemia maclachlani* | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 |
| *olectropus* spp. | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *doconesus* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *chorema* spp. | 21 | 4 | 4 | 35 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 25 | 2 | 0 | 0 |
| *ocentrella* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *ocentria evecta* | 86 | 0 | 3458 | 103 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 |
| *ocentria funerea* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 216 | 5 | 2 | 302 | 66 |
| *ocentria hawdoniana* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *ocentria mordax* | 2343 | 0 | 2832 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *ocentria sylvestris* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *ocentrodes* spp. | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 |
| *ectides* spp. | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 |
| *ectidina* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 |
| *lessica cheira* | 31 | 1 | 37 | 0 | 0 | 0 | 30 | 69 | 0 | 1072 | 61 | 1 | 0 | 32 | 1 |
| *lessica meizon* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *ndopsyche ingens* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| Sites / Taxon | T2 | T3 | T4 | T5 | T6 | T8 | T10 |
|---|---|---|---|---|---|---|---|
| **Acari** | 0 | 0 | 0 | 0 | 3 | 0 | 0 |
| **Nematoda** | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| **Ostracoda** | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Oligochaeta** | 8 | 10 | 3 | 70 | 10 | 5 | 13 |
| **Turbellaria** | | | | | | | |
| Tricladia | 0 | 0 | 0 | 0 | 0 | 20 | 0 |
| **Bivalva** | | | | | | | |
| Sphaeriidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Crustacea** | | | | | | | |
| **Amphipoda** | | | | | | | |
| *Paracalliope fluviatilis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Paraleptamphopus subterraneus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Talitridae | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| **Gasteropoda** | | | | | | | |
| *Gyraulus* sp. | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Lymnaea* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Potamopyrgus antipodarum* | 0 | 1 | 0 | 3 | 1 | 0 | 0 |
| **Insecta** | | | | | | | |
| **Coleoptera** | | | | | | | |
| *Hydora* sp 1 | 401 | 298 | 100 | 33 | 80 | 0 | 46 |
| *Hydora* sp 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hydraenidae | 1 | 9 | 0 | 7 | 2 | 0 | 0 |
| Hydrophilidae | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Ptilodactylidae | 0 | 1 | 0 | 13 | 0 | 0 | 0 |
| Scirtidae | 0 | 2 | 0 | 54 | 0 | 0 | 0 |
| **Diptera** | | | | | | | |
| *Aphrophila* spp. | 13 | 89 | 6 | 0 | 114 | 0 | 0 |
| *Apsectrotanypus* spp. | 1 | 3 | 2 | 2 | 8 | 0 | 0 |
| *Austrosimulium* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ceratopogonidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Dixidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Empididae group A | 1 | 3 | 0 | 1 | 3 | 3 | 0 |
| Empididae group B | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| Eriopterini | 30 | 5 | 18 | 5 | 7 | 0 | 1 |
| *Eukiefferella* spp. | 39 | 0 | 0 | 0 | 5 | 0 | 0 |
| *Harrisius pallidus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hexatomini | 0 | 0 | 0 | 0 | 0 | 5 | 0 |
| Kaniwhaniwhanus I | 0 | 0 | 54 | 0 | 0 | 0 | 0 |
| *Limonia* sp. | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Maoridiamesa* spp. | 87 | 2 | 82 | 2 | 7 | 1 | 0 |
| *Mischoderus* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Muscidae | 1 | 0 | 2 | 0 | 0 | 0 | 0 |
| *Naonella forsythi* | 0 | 35 | 0 | 0 | 40 | 11 | 16 |
| *Neocurupira hudsoni*-group | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Orthocladiinae sp A | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Paratrichocladius pluriserialis* | 66 | 0 | 0 | 0 | 0 | 0 | 0 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Paucispinegra approximata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Podominae | 1 | 4 | 0 | 14 | 0 | 0 | 4 |
| *Polypedilum* spp. | 0 | 0 | 0 | 11 | 0 | 0 | 0 |
| Psychodidae | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Stratiomyidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Tabanidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Tanytarsus vespertinus* | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Zelandotipula* spp. | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| **Ephemeroptera** | | | | | | | |
| *Acantophlebia cruentata* | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| *Ameleptosis perscitus* | 0 | 5 | 0 | 7 | 1 | 0 | 6 |
| *Austroclima jollyae* | 5 | 3 | 6 | 2 | 5 | 0 | 0 |
| *Austroclima sepia* | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Coloburiscus humeralis* | 94 | 79 | 64 | 39 | 82 | 0 | 0 |
| *Deleatidium* spp. | 819 | 682 | 568 | 213 | 684 | 4 | 244 |
| *Ichthybotus* sp. | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Neozephlebia scita* | 3 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Nesameletus* spp. | 239 | 104 | 454 | 5 | 56 | 0 | 5 |
| *Oniscigaster distans* | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Zephlebia* spp. | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| **Hemiptera** | | | | | | | |
| Sigara | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Megaloptera** | | | | | | | |
| *Archichauloides diversus* | 17 | 6 | 0 | 0 | 12 | 0 | 0 |
| **Plecoptera** | | | | | | | |
| *Austroperla cyrene* | 0 | 0 | 2 | 1 | 0 | 0 | 3 |
| *Cristaperla* spp. | 0 | 1 | 0 | 1 | 0 | 4 | 1 |
| *Megaleptoperla* spp. | 51 | 53 | 3 | 1 | 2 | 0 | 2 |
| *Spaniocerca zelandica* | 0 | 0 | 0 | 0 | 0 | 4 | 0 |
| *Spaniocercodes* sp. | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Stenoperla prasina* | 6 | 5 | 1 | 12 | 12 | 1 | 10 |
| *Taraperla howesi* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Zelandobius confusus* | 1 | 23 | 0 | 26 | 7 | 24 | 9 |
| *Zelandobius furcillatus* | 0 | 6 | 0 | 0 | 0 | 1 | 7 |
| *Zelandoperla decorata* | 92 | 52 | 101 | 0 | 74 | 2 | 0 |
| *Zelandoperla fenestrata* | 0 | 0 | 0 | 0 | 0 | 8 | 0 |
| **Trichoptera** | | | | | | | |
| *Alloecentrella magnicornis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Aoteapsyche* spp. | 46 | 62 | 147 | 1 | 152 | 0 | 0 |
| *Bareopteria roria* | 840 | 191 | 68 | 0 | 32 | 0 | 0 |
| *Confluens hamiltoni* | 0 | 18 | 0 | 0 | 0 | 0 | 0 |
| *Costachorema* spp. | 18 | 5 | 18 | 7 | 5 | 0 | 0 |
| *Cryptobiosella* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ecnomina zealandica* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Edpercivalia* sp. | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| *Helicopsyche* sp. | 22 | 72 | 0 | 3 | 409 | 0 | 0 |
| *Hudsonema alienum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hudsonema amabile* | 0 | 4 | 1 | 5 | 0 | 0 | 0 |
| *Hydrobiosella mixta* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hydrobiosidae (Early instars) | 37 | 34 | 12 | 8 | 51 | 3 | 0 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Hydrobiosis* spp. | 7 | 9 | 9 | 1 | 25 | 6 | 0 |
| *Hydrochorema* spp. | 0 | 4 | 2 | 3 | 7 | 3 | 2 |
| *Neurochorema confusum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Neurochorema forsteri* | 1 | 4 | 0 | 0 | 2 | 1 | 0 |
| *Oeconesus* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Olinga feredayi* | 6 | 12 | 12 | 0 | 59 | 0 | 0 |
| *Orthopsyche* sp. | 46 | 21 | 1 | 54 | 0 | 0 | 1 |
| *Oxyethira albiceps* | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Philorheithrus agilis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Plectronemia maclachlani* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Polyplectropus* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pseudoconesus* sp. | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Psilochorema* spp. | 20 | 13 | 6 | 2 | 3 | 1 | 3 |
| *Pycnocentrella* sp. | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| *Pycnocentria evecta* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pycnocentria funerea* | 4 | 17 | 0 | 0 | 21 | 1 | 1 |
| *Pycnocentria hawdoniana* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pycnocentria mordax* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pycnocentria sylvestris* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pycnocentrodes* spp. | 144 | 4 | 26 | 7 | 600 | 1 | 1 |
| *Triplectides* spp. | 0 | 1 | 0 | 8 | 0 | 0 | 0 |
| *Triplectidina* spp. | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| *Zelolessica cheira* | 0 | 6 | 2 | 2 | 2 | 0 | 0 |
| *Zelolessica meizon* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Zelondopsyche ingens* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

**Appendix 2** Number of invertebrate individuals collected in five Surber samples (area= 0.1 m$^2$) in spring and runoff-fed streams in Northern Spain in July 2002. Site codes are included in Table 1 in Chapter 2.

| Site<br>Taxon | Sp1 | St1 | Sp2 | St2 | Sp3 | St3 | Sp4 | St4 | Sp5 | St5 | Sp6 | St6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Acari** | 0 | 0 | 0 | 4 | 3 | 0 | 0 | 1 | 11 | 0 | 1 | 0 |
| **Nematoda** | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 6 | 0 | 0 | 0 | 0 |
| **Oligochaeta** | 1 | 41 | 5 | 1 | 5 | 20 | 5 | 24 | 17 | 4 | 5 | 16 |
| **Acheta** | | | | | | | | | | | | |
| *Erpobdella* spp. | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Glossiphoniidae | 0 | 1 | 11 | 2 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 3 |
| **Turbellaria** | | | | | | | | | | | | |
| *Dugesia* spp. | 2 | 12 | 0 | 0 | 0 | 0 | 0 | 10 | 26 | 9 | 14 | 5 |
| *Polycelis* spp. | 0 | 0 | 1 | 7 | 55 | 20 | 18 | 0 | 0 | 0 | 0 | 37 |
| **Gasteropoda** | | | | | | | | | | | | |
| *Bythinella* spp. | 10 | 8 | 10 | 2 | 21 | 0 | 70 | 2 | 1235 | 0 | 1342 | 6 |
| *Theodoxus fluviatilis* | 157 | 48 | 12 | 37 | 0 | 0 | 223 | 0 | 1654 | 0 | 265 | 2 |
| *Potamopyrgus* spp. | 7 | 16 | 0 | 0 | 0 | 0 | 2 | 19 | 95 | 0 | 3 | 3 |
| *Ancylus fluviatilis* | 1 | 0 | 3 | 3 | 1 | 0 | 0 | 1 | 2 | 0 | 9 | 19 |
| *Valvata* sp. | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Stagnicola | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| *Planorbarius* sp. | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| *Anisus* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Aplexa hypnorum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| **Bivalva** | | | | | | | | | | | | |
| *Pisidium* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| **Crustacea** | | | | | | | | | | | | |
| *Echinogammarus* spp. | 1113 | 492 | 1013 | 699 | 1527 | 21 | 1516 | 874 | 5584 | 5 | 3128 | 22 |
| Asellidae | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Insecta** | | | | | | | | | | | | |
| **Coleoptera** | | | | | | | | | | | | |
| *Elmis* spp. | 949 | 271 | 735 | 26 | 1332 | 21 | 634 | 126 | 2131 | 27 | 746 | 105 |
| *Esolus* spp. | 0 | 28 | 17 | 43 | 1 | 61 | 0 | 174 | 10 | 46 | 0 | 16 |
| *Dupophilus brevis* | 0 | 76 | 0 | 3 | 0 | 2 | 0 | 4 | 0 | 1 | 0 | 8 |
| *Limnius* spp. | 0 | 52 | 28 | 54 | 53 | 5 | 16 | 30 | 171 | 0 | 5 | 21 |
| *Oulimnius* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 42 | 0 | 0 | 0 | 0 |
| *Stennelmis* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Hydraena* spp. | 0 | 4 | 0 | 0 | 0 | 3 | 0 | 31 | 0 | 32 | 0 | 7 |
| *Riolus* spp. | 0 | 3 | 0 | 1 | 2 | 0 | 0 | 0 | 12 | 0 | 0 | 0 |
| *Scirtes* sp. | 0 | 100 | 0 | 1 | 0 | 100 | 0 | 251 | 0 | 87 | 0 | 41 |
| *Helophorus* sp. | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Diptera** | | | | | | | | | | | | |
| *Atherix* spp. | 1 | 0 | 0 | 5 | 0 | 5 | 0 | 17 | 0 | 10 | 4 | 28 |
| *Antocha* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 4 |
| *Tipulidae* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Atrichops* sp. | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Clinocerinae | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 4 |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| Hemerodromiinae | 0 | 0 | 5 | 0 | 2 | 0 | 0 | 1 | 0 | 7 | 0 | 0 |
| Ceratopogoninae | 0 | 17 | 0 | 0 | 0 | 34 | 1 | 27 | 8 | 12 | 1 | 16 |
| *Dicranota* sp. | 1 | 21 | 8 | 1 | 2 | 0 | 0 | 0 | 1 | 5 | 0 | 0 |
| *Dixa* sp. | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 |
| *Hexatoma* sp. | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 1 |
| Hexatomiini | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 |
| Dolichopodidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 2 |
| Chironomini | 0 | 102 | 0 | 2 | 0 | 22 | 5 | 9 | 26 | 14 | 2 | 148 |
| Orthocladinae | 24 | 1390 | 779 | 44 | 2438 | 39 | 11 | 149 | 292 | 373 | 310 | 175 |
| Tanypodinae | 18 | 41 | 1 | 2 | 0 | 28 | 0 | 33 | 5 | 55 | 2 | 33 |
| Tanytarsini | 0 | 13 | 57 | 8 | 92 | 7 | 3 | 13 | 10 | 29 | 3 | 54 |
| Psychodidae | 0 | 0 | 8 | 0 | 48 | 0 | 4 | 0 | 0 | 0 | 0 | 0 |
| *Prosimulium* spp. | 1 | 188 | 5 | 1055 | 0 | 118 | 1 | 29 | 0 | 87 | 0 | 40 |
| *Scleroprocta* sp. | 0 | 2 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Liponeura* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| **Ephemeroptera** | | | | | | | | | | | | |
| *Baetis* spp. | 3 | 1117 | 1244 | 604 | 3558 | 1253 | 23 | 76 | 120 | 1042 | 195 | 756 |
| *Ephemerella ignita* | 233 | 45 | 670 | 10 | 19 | 58 | 0 | 3 | 0 | 7 | 166 | 9 |
| *Habrophlebia* spp. | 0 | 28 | 0 | 0 | 0 | 31 | 0 | 141 | 0 | 73 | 0 | 61 |
| *Ecdyonurus* spp. | 0 | 207 | 15 | 169 | 0 | 11 | 0 | 82 | 22 | 63 | 20 | 23 |
| *Epeorus* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 43 |
| *Rhithrogena* spp. | 1 | 2 | 2 | 37 | 11 | 4 | 0 | 0 | 0 | 0 | 0 | 3 |
| *Heptagenia* sp. | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ephoron virgo* | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Caenis* sp. | 0 | 0 | 0 | 9 | 0 | 3 | 0 | 0 | 0 | 8 | 0 | 0 |
| **Odonata** | | | | | | | | | | | | |
| *Onychogomphus* sp. | 0 | 1 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Aeshna* sp. | 0 | 1 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Plecoptera** | | | | | | | | | | | | |
| *Euleuctra geniculata* | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 121 | 0 | 0 | 0 | 5 |
| *Leuctra* spp. | 0 | 0 | 0 | 0 | 0 | 21 | 0 | 70 | 0 | 136 | 0 | 51 |
| *Perla marginata* | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 1 | 0 | 43 | 0 | 13 |
| *Isoperla* sp. | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Chloroperla* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| *Siphonoperla* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 3 |
| *Protonemoura* sp. | 1 | 0 | 216 | 0 | 508 | 0 | 0 | 0 | 0 | 7 | 0 | 3 |
| *Nemoura* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| **Trichoptera** | | | | | | | | | | | | |
| *Beraea* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 |
| *Chimarra marginata* | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ecclisopterix* sp. | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Limnephilinae | 0 | 0 | 0 | 0 | 6 | 5 | 0 | 0 | 0 | 4 | 0 | 0 |
| *Ecnomus* sp. | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Threma* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Agapetus* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 0 | 0 | 0 | 11 | 0 |
| *Glossosoma* spp. | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 16 | 3 |
| *Lepidostoma hirtum* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Hydropsyche* spp. | 0 | 10 | 0 | 3 | 0 | 8 | 0 | 10 | 0 | 13 | 0 | 12 |
| *Rhyacophila* spp. | 2 | 64 | 21 | 7 | 62 | 27 | 0 | 11 | 4 | 14 | 6 | 5 |
| *Plectronemia* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Polycentropus* spp. | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 |
| *Holocentropus* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 4 | 0 | 0 |
| *Philopotamus* spp. | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 15 | 0 | 11 |
| *Tinodes* sp. | 0 | 0 | 7 | 1 | 1 | 0 | 0 | 3 | 2 | 0 | 0 | 0 |
| Psichomyiidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| *Ceraclea* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 |
| Goeridae | 0 | 2 | 0 | 0 | 0 | 5 | 0 | 16 | 0 | 1 | 2 | 3 |
| *Odontocerum* sp. | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Sericostoma* spp. | 0 | 1 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 26 | 0 | 5 |
| *Wormaldia* sp. | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 16 |

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