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The distribution of biota from some geothermally influenced waters in the Taupo Volcanic Zone

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NIWA Client Report: EVW01226
June 2001

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Ian Duggan
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Prepared for

Environment Waikato

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Executive Summary

This report discusses the spatial dynamics of algae and macroinvertebrates in the Taupo Volcanic Zone, a project jointly funded by Environment Waikato and NIWA. The main focus of the study was to examine the responses of macroinvertebrates to environmental gradients in stream habitats. A secondary focus was algal community composition.

This aims of the report are to:

- describe the algal and invertebrate communities in a variety of geothermal habitats with a particular emphasis on running water and spring habitats;
- measure invertebrate community changes along geothermal stress gradients, and;
- examine the significant habitat and environmental factors influencing the diversity and distribution of aquatic geothermal invertebrate communities.

Habitats sampled were from Otamakokore Stream (Waikite Valley), Golden Springs, Waipuwerawera Stream, Hakereteke Stream ("Kerosene Creek"), and an unnamed stream near the Waiotapu tourist area. Additional samples were collected from Waikokomuka Stream, a non-geothermal stream, to provide a cool site comparison, and the sinter terraces at Orakeikorako.

The diversity of biota was typically low in the geothermally influenced streams. Biota were found to respond to gradients in environmental and habitat conditions within and between geothermal fields.

The spatial distributions of the dominant algal groups appeared to be consistent with previous studies of algae in geothermal habitats, with temperature and chemical composition (e.g., pH and sulphide concentrations) important in determining distribution. Cyanobacteria (e.g., *Mastigocladus laminosus*, *Oscillatoria* sp.) were typically found at high temperatures and only in non-acidic, low sulphide streams. At cooler, acidic sites, or at sites containing high sulphide concentrations, other groups of algae dominated (e.g., diatoms).

Macroinvertebrates recorded in this survey were typically those that had been recorded in geothermally influenced sites previously. One exception, however, was the first New Zealand wild record of the exotic gastropod mollusc *Melanoides tuberculata* at Golden Springs. This species is likely to have been released from tropical aquaria.

Temperature was the dominant factor determining the community composition and abundance of macroinvertebrate species within and between geothermal fields. Decrease

in pH was associated with a significant decrease in invertebrate taxa richness, and molluscs were restricted only to non-acidic sites. Some variation in macroinvertebrate composition and abundance appears to be related to substrate type. Covariance of substrate types with other important environmental factors (e.g., sand and gravel substrates typically occurred at cooler sites and bedrock or boulder substrates at low pH), however, confuses this relationship, and we suggest substrate relationships be examined further at sites with similar environmental conditions.

The presence of invasive species (*Melanoides tuberculata* and the Guppy, *Poecilia reticulata*) at Golden Springs also may have strong effects on the composition of native geothermal invertebrate faunas at these sites.

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1. INTRODUCTION

On a world scale, the Taupo Volcanic Zone contains a high concentration of geothermal waters in a relatively small area. Other geothermal areas with large numbers of geothermal waters include the United States (Yellowstone National Park), Iceland, Japan and the former Soviet republics (Vincent & Forsyth, 1987). The landscape and water bodies overlying most geothermal fields are characterised by zones of high temperature and unusual pH conditions (Vincent & Forsyth, 1987). Within the Taupo Volcanic Zone the influence of geothermal activity on water-bodies varies widely, with waters between fields ranging in temperature and pH from hot and alkaline to cold and acidic, with all ranges of variability in between. Within each geothermal system, conditions are also often highly variable as conditions in streams generally change down their lengths. Water temperatures, in particular, tend to decrease in a downstream direction as the geothermal influence wanes (Vincent & Forsyth, 1987; Pritchard, 1991).

The biodiversity of these unusual habitats is typically low, as species occurring here commonly need to be adapted to extremes in temperature, pH or toxicant levels (Vincent & Forsyth, 1987). In response to these conditions, however, a unique indigenous aquatic biota has evolved. This biota includes a few species or varieties only found in geothermal habitats, notable occurrences of species more commonly found in tropical or subtropical climates, and common stress-tolerant species (for example, see Winterbourn (1968); Vincent & Forsyth (1987). Collectively, this biota possesses high conservation, genetic, and scientific values.

To date, most ecological studies of biota in geothermal waters, and in particular the macroinvertebrates, have focussed on basic descriptions of the presence of biota within these systems, commonly noting the temperature or pH at which the taxa were recorded. These studies have generally been undertaken at discrete geothermal locations examining, for example, the occurrences of taxa within and along single streams or within individual lakes. For algae, the factors determining distribution are better known than for other biota, with water temperature, pH and sulphide concentrations being the most important determinants (e.g., Stockner, 1967; Castenholz, 1976; Lamberti & Resh, 1985). For macroinvertebrates, less is known about the quantitative responses of communities to gradients in the underlying geothermal resource, or whether the factors determining distribution within habitats are also those responsible for distribution patterns observed between habitats. In addition, it is known from studies of cool-water stream biota, for example invertebrates, that distribution patterns can be influenced by a number of environmental factors, including landuse, current velocity, substrate type, shade and water depth (e.g., Collier, 1995; Death, 2000; Quinn, 2000). Whether the same factors influence the community composition and abundance of biota within and between geothermal streams is unknown.

The aim of this report is to provide information to address some of these questions. Because the Taupo Volcanic Zone contains a large number of diverse geothermal waters it provides an ideal setting to examine distribution gradients with respect to environmental gradients.

Specifically, this report aims to:

- describe the algal and invertebrate communities in a variety of geothermal habitats with a particular emphasis on running water and spring habitats;
- measure community changes along geothermal stress gradients, and;
- examine the significant habitat and environmental factors influencing the diversity and distribution of aquatic geothermal biotic communities.

Here, we define geothermal waters as those in which thermal or chemical (i.e., pH) conditions are influenced by natural volcanic activity. The main focus of the study is to examine the responses of macroinvertebrates to gradients in stream habitats, with algae examined of secondary importance and at lower taxonomic resolution.

A better knowledge of the significant attributes in geothermal ecosystems will allow resource managers to focus effort on the important environmental features of these systems, measure changes in ecosystem health, and develop appropriate tools and indicators for monitoring. This knowledge is required to predict the effects of changes in the geothermal fields on the biota.

2. METHODS AND SAMPLING SITES

2.1 Site locations and field methodology

Samples were collected from a number of geothermal habitats in the Taupo Volcanic Zone. (Figures 1-4). Sites were selected in association with Environment Waikato staff to represent a broad range of environmental conditions, including pH, temperature and other habitat attributes. They comprised mainly geothermal spring fed or influenced streams; Otamakokore Stream (Waikite Valley), Golden Springs, Waipuwerawera Stream, Hakereteke Stream ("Kerosene Creek"), and an unnamed stream near the Waiotapu tourist area (see Figures 1-4). Additional samples from cold (non-geothermally influenced or with extremely reduced influence) streams were also collected from Waikokomuka Stream, which flows into Hakereteke Stream, and Otamakokore Stream after convergence with several other non-geothermally influenced streams. Samples were also collected from the sinter terraces at Orakeikorako to examine algal and invertebrate species composition, but were not included in analyses with the other sites due to the terraces comprising a distinct (i.e., non-stream) habitat where different collection methods needed to be employed.

For macroinvertebrates, a semi-quantitative survey of the 20 stream sites was undertaken using kick sampling (250 µm mesh). At each site a consistent three-minute sampling effort was used along a 30 m reach. Waipuwerawera Stream, previously sampled by Winterbourn & Brown (1967) and James (1985), was also sampled using kick sampling with a 500 µm mesh for future comparison with these previous studies. This stream has cooled since the initial sampling by Winterbourn & Brown due to drawoff of geothermal fluid for industrial purposes (James, 1985).

A visual estimation of the coverage of benthic algal species was made, and samples were collected for identification by taking substrate scrapings. Duplicate samples were collected at each site, with one preserved (Lugols Iodine) and one kept alive. Taxa were identified by Vivienne Cassie-Cooper (Landcare Research, Hamilton) or Cathy Kilroy (NIWA, Christchurch) and the dominant taxa noted from each sample.

Chemical (temperature, conductivity, dissolved oxygen, pH) and habitat (water depth, stream width, stream velocity, substrate type, shade, bank height, bank erosion) factors were recorded at each site. Chemical factors were recorded by taking mid-stream spot measurements using YSI 30 conductivity, YSI 60 pH, and YSI 95 dissolved oxygen meters. Stream velocity was measured using a Montedoro PSM2A flow velocity meter, generally at three points across each of three transects along the reach. Habitat factors were recorded at five transects along each reach. Water depth was recorded as the maximum depth across each transect. Other variables were generally visually estimated on a zero to 100% scale. Macroinvertebrates were identified to the lowest taxonomic level practical (usually species), and algae to a higher level (usually genera).

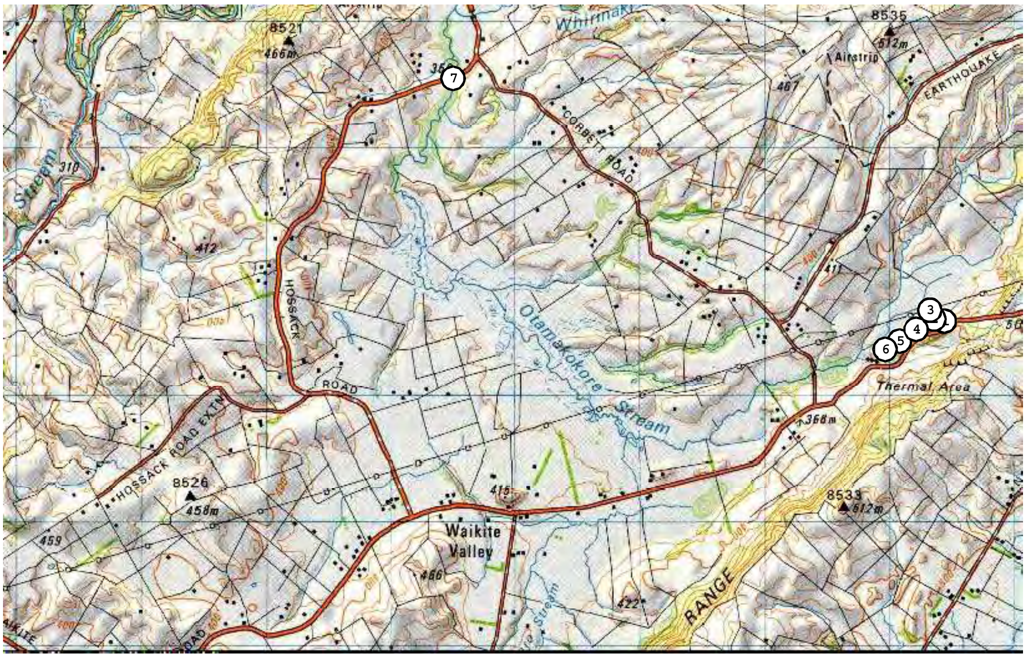

Figure 1. Map showing location of Otamakokore Stream sites.

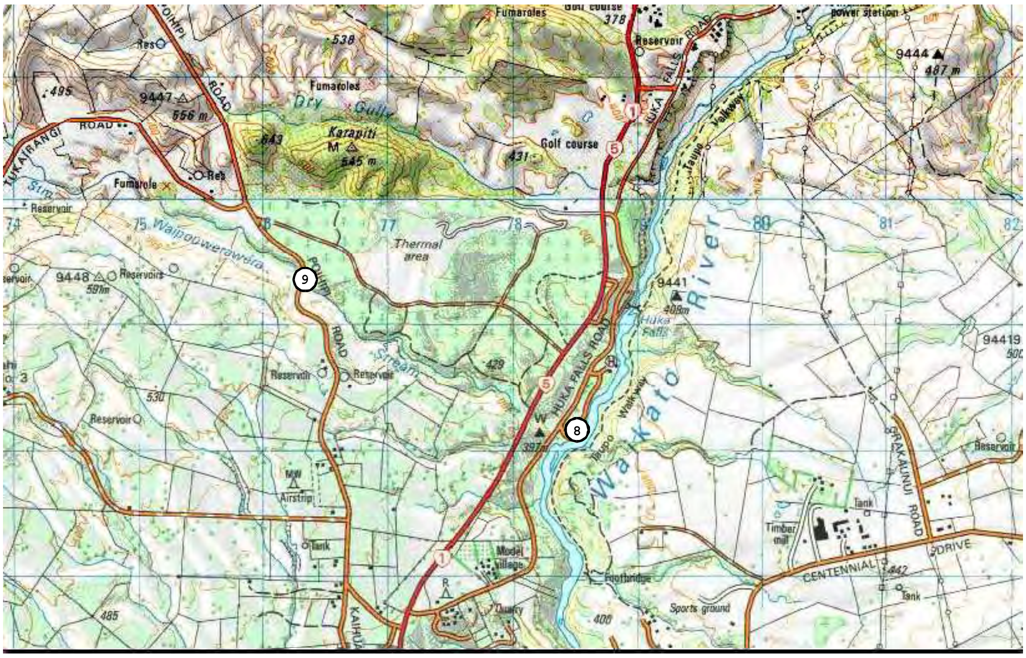

Figure 2. Map showing location of Waipuwerawera Stream sites.

Figure 3. Map showing location of Golden Springs sites.

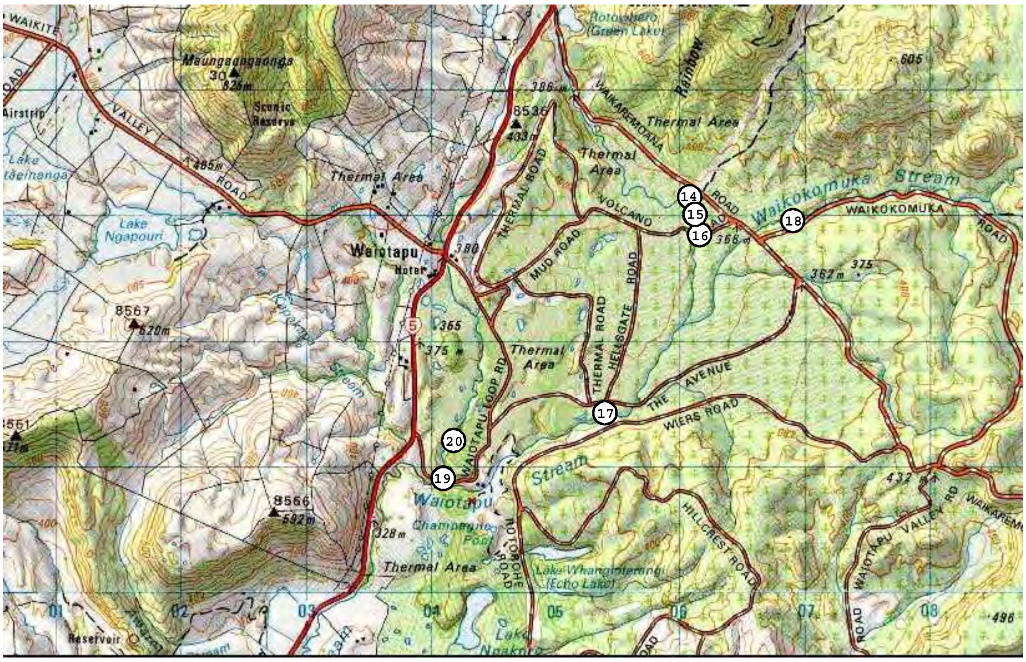

Figure 4. Map showing location of stream sites on Hakereteke Stream (14-17), Waikokomuka Stream (18) and an unnamed Waiotapu Stream (19-20).

2.2 Analyses of responses of invertebrates to environmental gradients

Relationships between macroinvertebrate taxa richness, pH and temperature were examined using linear regression analysis using log (x+1) transformed data (SYSTAT, version 9, SPSS Inc., Chicago, U.S.A.).

Mulitdimensional scaling (MDS) and Canonical correspondence analysis (CCA) were used to elucidate patterns in macroinvertebrate community composition. MDS is a method akin to Cluster analysis, in that the resulting diagram is constructed using a similarity matrix based on species composition between sites. However, MDS has advantages over Cluster analysis in situations where species respond to gradients in environmental conditions, rather than forming different communities based on distinct environmental conditions. MDS produces a two-dimensional map that attempts to satisfy all the conditions imposed by a similarity matrix. Samples are thus distributed on the map such that those with similar composition are found close together, and samples with dissimilar composition are distributed far apart from one another (Clarke & Warwick, 1994). CCA is an ordination technique that is used to infer environmental factors that are important in determining the distribution of species between sites. CCA is used when species show unimodal response patterns in relation to underlying environmental variables. The results of CCA are presented on an ordination diagram. The position of the sites and species on the ordination diagram indicate the association between species and samples, and their distance from the centre of the ordination the strength of their association. Environmental variables with the longest arrows on the ordination plot are those most strongly associated with the variations in species composition (Ter Braak, 1987).

For multivariate analyses, species were removed that occurred only at single sites. Sites were removed from the analyses in which a total of less than ten invertebrates were recorded in the modified dataset. Sites 5, 8, 19 and 20 were thus removed from analyses (see Appendix 1). In CCA, dissolved oxygen values from two sites on Otamakokore Stream could not be recorded due to high temperatures. Data for these sites were replaced with average oxygen values from upstream and downstream sites on Otamakokore Stream. MDS was based on the Bray Curtis similarity coefficient calculated on the log (x+1) transformed abundances of macroinvertebrate taxa to downweight the effects of dominant species. This was to ensure that the results of the ordination not only reflect the abundance differences of the dominant species between sites but also those less abundant. CCA was performed on species abundance data log (x+1) transformed to downweight the effects of dominant species. Some of the environmental variables were log (x+1) transformed to improve normality of the data. All environmental data was standardised to zero mean and unit variance to remove the influence of different scales of measurement. Some of the measured environmental variables were removed from the ordination because of covariability with other environmental factors revealed in an exploratory ordination. MDS and CCA were performed using the Primer Routines in Multivariate Research statistical package (PRIMER, Primer-E Ltd., Plymouth, U.K.) and CANOCO 4.0 (Centre for Biometry Wageningen, Netherlands), respectively.

To further explore the optimum conditions for abundant species along the dominant environmental gradient, and to enable prediction of the effects to invertebrates of changes to this gradient, we used weighted averaging (WA) regression techniques. WA provides a value that is an estimate of the optima of a species unimodal response curve to the variable of interest. A weighted average is taken of the environmental data, in which values are weighted proportional to the species abundance, i.e.:

$$u = (y_1x_1+y_2x_2+\ldots+y_nx_n)/(y_1+y_2+\ldots y_n)$$

where,
u is the weighted average (= the estimate of the optimal conditions for that species).
$y_1, y_2, \ldots y_n$ are the abundances of a species at sites 1, 2, … n.
$x_1, x_2, \ldots x_n$ are the values of environmental variables at sites 1, 2, … n.

3. RESULTS

3.1 Habitat conditions

A range of habitat conditions was recorded in the survey that could potentially affect the distributions of invertebrates and algae. Temperature and pH varied widely (Figure 5). Waikokomuka Stream, which had no geothermal influence, had the lowest temperature recorded. The bottom site sampled from Otamakokore Stream (site 7), after convergence of several cold-water streams, had the most similar temperature conditions to Waikokomuka Stream and thus had little, if any, influence of geothermal activity on temperature at this point. Waipuwerawera Stream (sites 8 and 9) and the lower site from Hakereteke Stream (site 17) also appeared to have limited geothermal influence. The remaining sites all had greatly elevated temperatures (>25 °C) compared with non- or minimally-geothermally influenced streams in the area. pH varied widely among sites, with non- or minimally-geothermally influenced streams in the range of 5 to 8. At the other sites pH was as low as 3.0 and up to 9.1. Temperature in general lowered with distance sampled downstream (e.g., Golden Springs). Otamakokore Stream was a notable exception to this pattern with several points of reheating occurring along the sampled length, as indicated by the non-sequential distribution of sites in Figure 5.

Averages of habitat conditions based on the groupings in Figure 5 are given in Table 1, and a complete list of measurements is given for all sites in Appendix 2.

Conductivity was typically high in the geothermal stream sites reaching a maximum stream average of 1237.5 µS/cm at the unnamed stream at Waiotapu. By comparison, typical conductivity of New Zealand streams in rivers is around 100 µS/cm (Close & Davies-Colley, 1990). Dissolved oxygen concentrations were typically lower in more heated streams, although measurements of oxygen saturation showed that all of the sites except Golden Springs were > 85% saturation. The sites represented a range of stream sizes, depths and water velocities (Table 1).

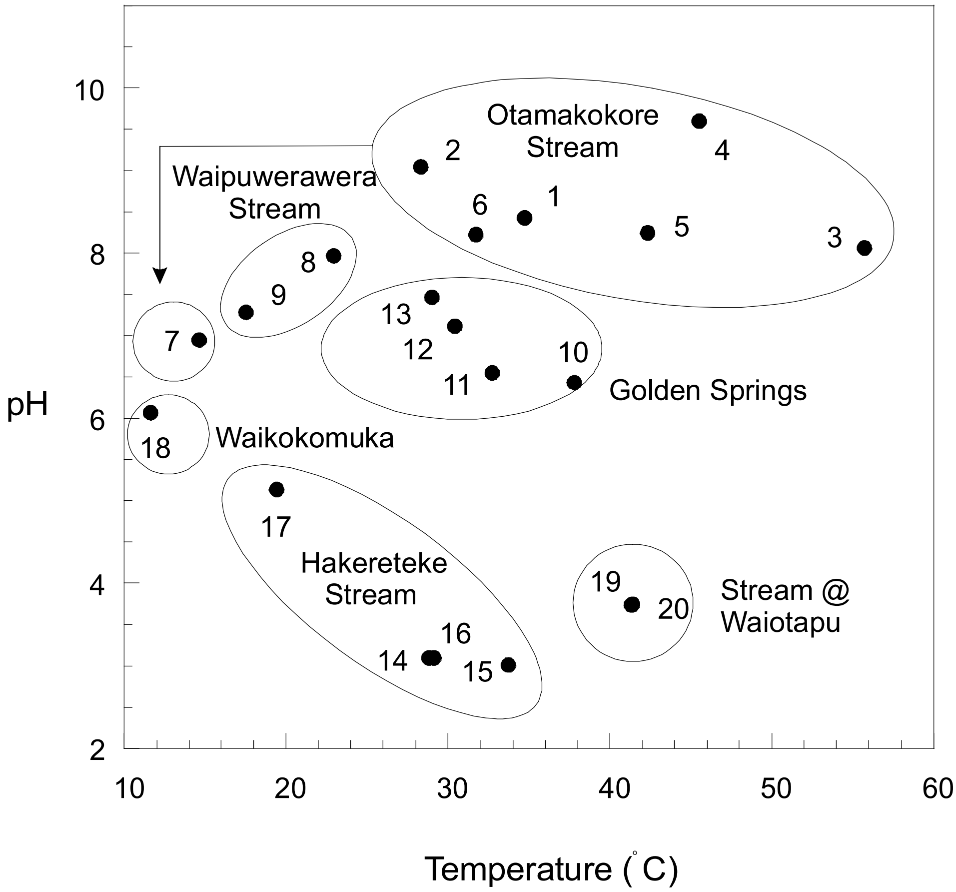

Figure 5. Temperature and pH recorded from 20 stream sites with various levels of geothermal influence in the Taupo Volcanic Zone (see Figures 1-4 for site numbers).

The Orakeikorako terraces ranged in temperature conditions, with spot measurements taken of 53.6, 25.3, 14.7 °C at sites in close proximity (all within 2 m of one another). Other variables were relatively similar between sites, with pH averaging 8.6 and conductivity 1502.8 µS/cm (@ 25 °C). The hottest site was from within a small channel and the two cooler sites were small shallow pools of standing water.

Table 1. Average physico-chemical and habitat variables from 20 stream sites with various levels of geothermal influence in the Taupo Volcanic Zone (ordered from warmest to coolest).

	Sites	Temperature (°C)	pH	Conductivity (µS/cm @ 25 °C)	Dissolved oxygen (mg/L)	Oxygen saturation (%)	Stream velocity (m/s)	Channel depth (m)	Channel width (m)
Stream at Waiotapu	19-20	41.4	3.75	1237.5	6.06	96.6	0.32	0.31	3.39
Otamakokore Stream	1-6	39.7	8.60	955.4	6.89	109.0	0.21	0.17	1.38
Golden Springs	10-13	32.5	6.90	816.8	4.58	61.9	0.24	0.37	1.99
Hakereteke Stream	14-16	30.5	3.07	720.7	7.03	93.9	0.53	0.58	2.99
Waipuwerawera Strm	8-9	20.2	7.63	131.4	8.73	86.5	0.52	0.26	1.45
Hakereteke Stream	17	19.4	5.14	301.4	8.25	90.0	0.53	0.85	4.46
Otamakokore Stream	7	14.6	6.95	300.2	7.97	78.5	0.71	1.03	3.26
Waikokomuka Strm	18	11.6	6.07	115.3	10.30	94.7	0.41	1.14	1.52

3.2 Algal composition

A list of the algal species recorded from substrate scrapings from the geothermal sites is given in Table 2. In Otamakokore Stream the cyanophyte *Mastigocladus* dominated at sites between 45.3 to 55.7 °C, and the cyanophytes *Oscillatoria* sp., *Phormidium* ?*laminosum* and the diatom *Epithemia* sp. between 31.7 °C and 42.3 °C. At Golden Springs *Oscillatoria* sp. also dominated (32.7 - 37.7 °C). The chlorophyte ?*Gloecystis* sp. dominated the algae in Hakereteke Stream, and in the unnamed stream at Waiotapu, only the diatom *Nitzchia* sp. was recorded. At Orakeikorako, the cyanophyte ?*Leptolyngbya* dominanted.

3.3 Faunal composition

A list of invertebrate species recorded in the sites is listed in Table 4. All samples were collected with a 250 µm mesh kicknet, except samples 8b and 9b from Waipuwerawera Stream, which were collected using a 500 µm mesh for future comparison with historical records (James, 1985). Regression analyses (Figure 6) indicted that taxa richness significantly increased with increasing pH (R^2 = 0.33; F = 8.996; P = 0.008), but no significant relationship existed for temperature (R^2 = 0.16; F = 3.533; P = 0.076).

Table 2. Algae species recorded from thermal habitats in the Taupo Volcanic zone. P = present. D = dominant.

	Otamakokore Stream	Golden Springs	Hakereteke Stream	Stream at Waiotapu	Orakeikorako
Class Cyanophyceae/Cyanobacteria					
?Aphanocapsa sp.					P
?*Calothrix* sp.					P
Dichothrix sp.					P
?Leptolyngbya sp.					D
Mastigocladus laminosis	D				
Oscillatoria sp.	D	D			
Phormidium ?laminosum	D				
Phormidium/ Lyngbya sp.	P	P			
?Phormidium sp.					P
Class Diatomophyceae/ Bacillariophyceae					
?Achnathes sp.	P				
Cymbella/ Encyanema	P				
Epithemia sp.	D				
Eunotia serpentina	P				
Eunotia sp.	P	P			
Gomphonema sp.			P		
Mastogloia sp.	P				
Melosira sp.	P				
Navicula sp.	P				
Neidium sp.	P				
Nitzschia ?linearis	P				
Nitzschia sp.	P			D	P
Pinnularia sp.	P				P
Pinnularia ?microstauron		P			
Rhopaloidia sp.	P				P
Rhopaloidia gibberula (= R. rupestris)	P				
Surirella sp.	P				
Surirella ?robusta	P				
Surirella ?teneta	P				
other pennate diatoms		P			
Class Chlorophyceae					
Chlamydomonas ?sphagnicola (resting stages)			P		
?Gloeocystis sp.			D		P
Class Euglenophyceae					
Euglena sp.			P		

Table 3. Macroinvertebrate species recorded from geothermal and non-geothermal habitats in the Taupo Volcanic zone. P = present.

sites	Otamakokore 1	Otamakokore 2	Otamakokore 3	Otamakokore 4	Otamakokore 5	Otamakokore 6	Otamakokore 7	Waipuwerawera 8a	Waipuwerawera 9a	Waipuwerawera 8b	Waipuwerawera 9b	Golden Springs 10	Golden Springs 11	Golden Springs 12	Golden Springs 13
Odonata															
Ischnura aurora	P		P			P									
Procordulia grayi								P							
Xanthocnemis zealandica															
Ephemeroptera															
Austroclima sepia															
Coloburiscus humeralis									P		P				
Zephlebia dentata									P		P				
Plecoptera															
Acroperla trivacuata															
Trichoptera															
Husonema alienum											P				
Hydrobiosis gollanis															
Hydrobiosus umbripennis															
Oecetis unicolor															
Oeconesus maori															
Olinga feredayi															
Orthopsyche fimbriata									P						
Orthopsyche thomasi									P		P				
Pycnocentria funerea									P		P				
Triplectides cephalotes															
Triplectides obsoletus															
Coleoptera															
Antiporus sp.														P	P
Hydrophilidae	P	P	P		P	P						P	P		
Lancetes lanceolatus		P		P		P									
Liodessus plicatus	P	P		P							P	P	P	P	
Ptilodactylidae															
Diptera															
Austrosimulium sp.							P								
Chironomus sp. A?		P	P	P											
Chironomus zelandicus															
Empididae															
Ephydrella thermarum			P	P											
Eriopterini spp.															
Limonia sp.				P											
?Naonella sp.							P								
Nothodixa sp.						P									
Orthoclad sp.															
Polypedilum sp.															
Tanyderidae															
Tanytarsus ?funebris	P	P	P			P									
Cricotopus sp.							P								
Crustacea															
Ostracoda															
Paranephrops planifrons															
Mollusca															
Lymnaea tomentosa					P					P					
Melanoides tuberculata														P	P
Physa sp.							P			P				P	
Glyptophysa variabilis				P									P		
Potamopyrgus antipodarum							P		P	P					
Gyraulus corinna										P					
Gyraulus kahuica														P	
Acari				P	P	P									
Oligochaeta															
Eiseniella sp.						P		P	P	P	P				
Tubificidae							P				P				
Hirudinea							P							P	P

Table 3. Macroinvertebrate species recorded from thermal and non-thermal habitats in the Taupo Volcanic zone (continued). P = present.

sites	Hakereteke 14	Hakereteke 15	Hakereteke 16	Hakereteke 17	Waikokomuka 18	@ Waiotapu 19	@ Waiotapu 20	Orakei-Korako	Orakei-Korako	Orakei-Korako
Odonata										
Ischnura aurora										
Procordulia grayi										
Xanthocnemis zealandica				P						
Ephemeroptera										
Austroclima sepia					P					
Coloburiscus humeralis					P					
Zephlebia dentata					P					
Plecoptera										
Acroperla trivacuata					P					
Trichoptera										
Husonema alienum										
Hydrobiosis gollanis					P					
Hydrobiosus umbripennis					P					
Oecetis unicolor				P						
Oeconesus maori					P					
Olinga feredayi					P					
Orthopsyche fimbriata										
Orthopsyche thomasi										
Pycnocentria funerea										
Triplectides cephalotes				P						
Triplectides obsoletus					P					
Coleoptera										
Antiporus sp.										
Hydrophilidae										
Lancetes lanceolatus										
Liodessus plicatus									P	P
Ptilodactylidae					P					
Diptera										
Austrosimulium sp.					P					
Chironomus sp. A?	P	P	P	P					P	P
Chironomus zelandicus						P				
Empididae				P						
Ephydrella thermarum								P	P	P
Eriopterini spp.					P					
Limonia sp.										
?Naonella sp.				P				P		
Nothodixa sp.										
Orthoclad sp.						P				
Polypedilum sp.			P	P	P					
Tanyderidae					P					
Tanytarsus ?funebris								P	P	P
Cricotopus sp.										
Crustacea										
Ostracoda					P					
Paranephrops planifrons					P					
Mollusca										
Lymnaea tomentosa										
Melanoides tuberculata										
Physa sp.										
Glyptophysa variabilis										
Potamopyrgus antipodarum										
Gyraulus corinna										
Gyraulus kahuica										
Acari										
Oligochaeta										
Eiseniella sp.										
Tubificidae										
Hirudinea										

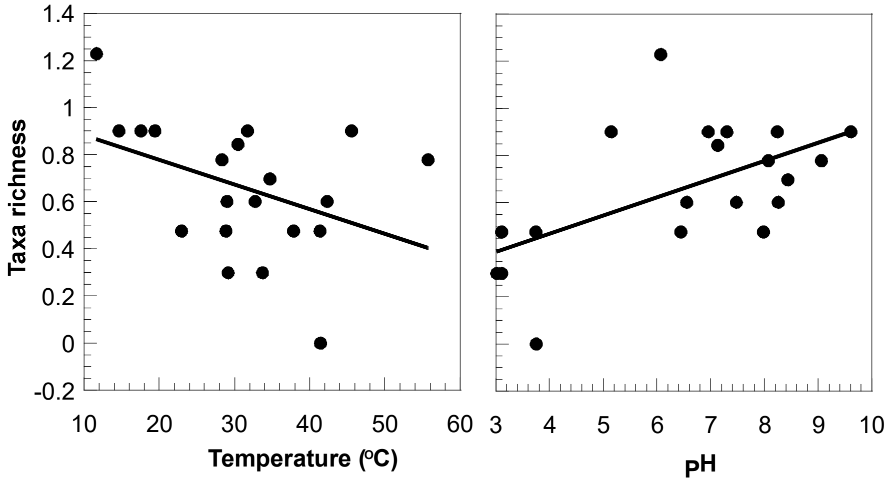

Figure 6. Log (x+1) taxa richness from 20 stream sites with various levels of geothermal influence in the Taupo Volcanic Zone against temperature and pH.

3.4 Macroinvertebrate community dynamics

MDS was used to find natural groupings of samples based on species composition and abundance and to detect changes in community composition that may occur along environmental gradients. The MDS ordination (Figure 7) revealed that the composition of macrofauna from samples within each stream were often more similar to one another than those from the other streams as indicated by the discrete groupings of samples. Thus, each stream can be distinguished from one another based on the composition of the invertebrate communities. However, it is apparent that gradients in macroinvertebrate composition occurred along environmental gradients. Sites closer to the bottom of the ordination in each stream are generally upstream or warmer sites, with composition changing as the sites become cooler downstream, towards the top of the ordination. The two coldest sites in the ordination (Waikokomuka and Waipuwerawera Streams) were distributed closely to one another, indicating that Waipuwerawera Stream has a similar species composition to that of non-geothermal streams. Of the more geothermally influenced sites, the macroinvertebrate composition in Hakereteke Stream was more similar to that in Otamakokore Stream and dissimilar to that in Golden Springs, and vice versa. The low stress value of the MDS (0.06) indicates that this diagram provides a good representation of the similarity relationships between sites.

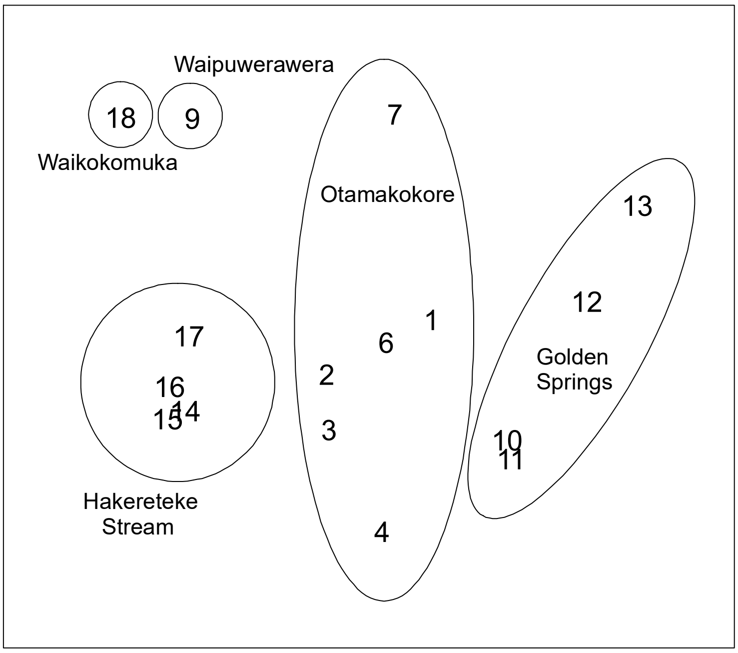

Figure 7. Ordination diagram based on MDS of macrofaunal composition from 16 stream sites with various levels of geothermal influence in the Taupo Volcanic Zone. Numbers correspond to site numbers (see Figures 1-4). Stress = 0.06.

CCA was used to detect the environmental variables important in determining the patterns in community composition found in MDS. Samples were distributed similarly in the CCA (Figure 8) as they were in the MDS ordination, allowing us to have confidence in the representation given by CCA, and that the measured environmental variables examined adequately explains species distribution. Samples from the cooler sites occurred to the right side of the ordination (i.e., sites 18, 9 and 7). The warmest sites from Otamakokore Stream occurred on the left hand side of the ordination and towards the top (sites 4, 3 and 2), separating Hakereteke Stream samples (top middle) and Golden Springs samples (bottom left).

Species most strongly associated with the cooler sites were *Coloburiscus humeralis, Zephlebia dentata, Austrosimilium* sp*., Potamopyrgus antipodarum* and *Eisniella* sp. *Chironomus* sp. A was most strongly positively associated with the Hakereteke Stream samples. Taxa associated with Otamakokore Stream were *Ephydrella thermarum*, Acari and *Lancetes lanceolatus*. Species associated most strongly with Golden Springs samples were *Antiporus* sp., *Physa* sp., *Melanoides tuberculata* and Hirudinea.

Temperature explained the largest proportion of variability in macroinvertebrate composition and abundance among sites (lambda A = 0.59, P = 0.01). Temperature was strongly associated with Axis 1, the axis that explains the most variation in community composition. Samples from the warmest sites are distributed on the left hand side of the ordination, intermediate temperatures sites in the middle, and the

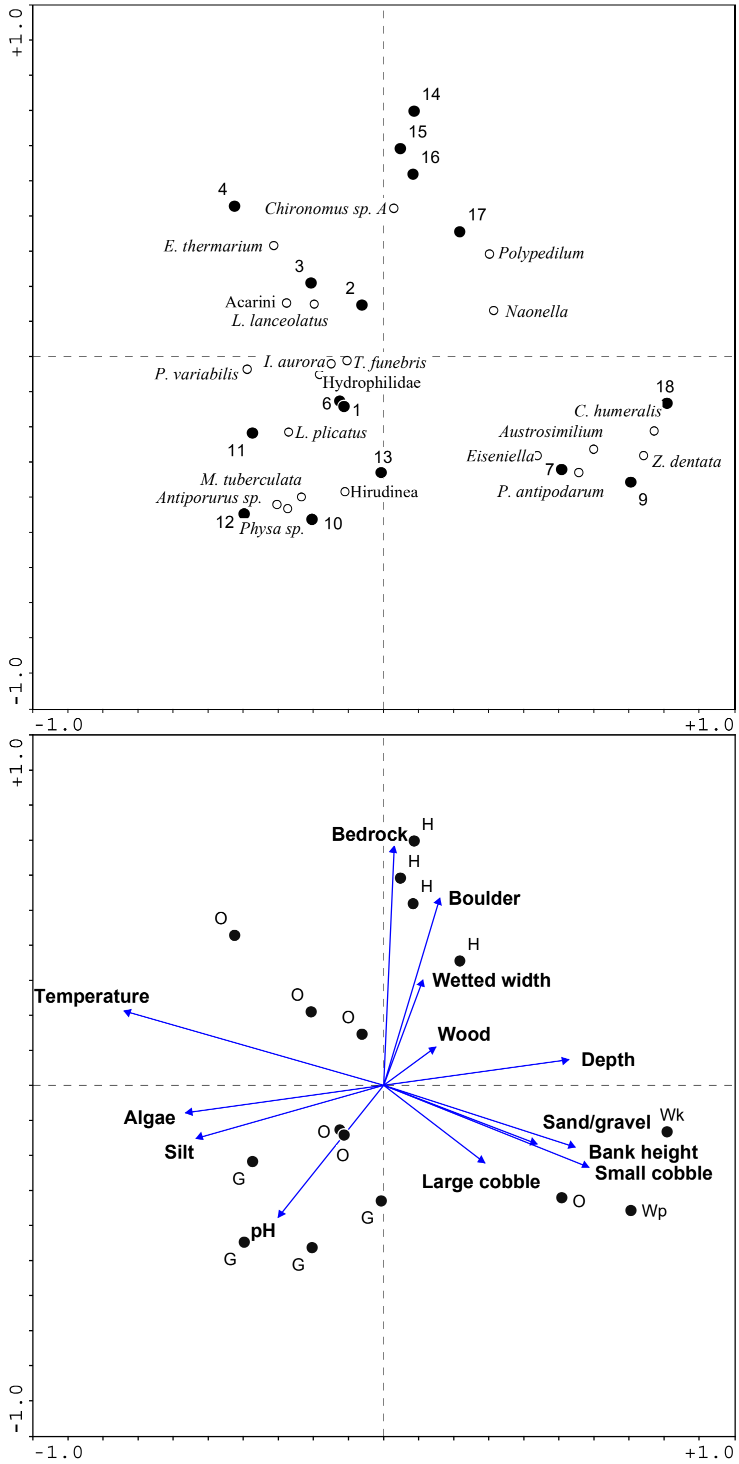

Figure 8. Ordination biplots based on CCA of macrofaunal composition from 16 stream sites with various levels of geothermal influence in the Taupo Volcanic Zone. The site (closed circles) and species (open circles) biplot is above, and the site and environmental variables (arrows) biplot is below. Numbers correspond to site numbers (see Figures 1-4). Eigenvalues for axes 1 and 2 = 0.791 and 0.719 respectively. H = Hakereteke; O = Otamakokore; G = Golden Springs; Wk = Waikokomuka; Wp = Waipuwerawera.

coolest sites on the right hand side of the ordination. Other environmental variables influencing the observed patterns on this axis were algae and silt, both strongly negatively associated with Axis 1, and water depth, % sand & gravel, bank height and % small cobble, all strongly positively associated with Axis 1. This indicates that in the current study, those sites with the highest temperatures were generally more silty and had more luxuriant algal growths, while cooler streams tended to have sand & gravel or small cobble substrates with higher banks. Some of the variation along Axis 1, and therefore between hot and cold streams, may not be entirely due to temperature *per se,* but also to unrelated physical habitat factors that co-vary with temperature. The variation along Axis 2, and thus the factors indicated as being important for distinguishing the three most geothermally influenced streams (Hakereteke Stream, Otamakokore Stream and Golden Springs), was related to substrate (i.e., % bedrock and % boulders were both strongly positively associated, and pH, strongly negatively associated with Axis 2). Thus, species abundant in Hakereteke Stream (e.g., *Chironomus* sp. A) are likely to be associated with harder substrates and lower pH, and those in Golden Springs with high pH and less stable, silty substrates.

Weighted average optima and tolerances of macroinvertebrate species from the current study are given in Figure 9. Weighted average species optima concur with the distributions found in CCA. Ephemeroptera, *Austrosimilium* sp. and *Potamopyrgus antipodarum* had low temperature optima, while at higher temperatures Coleoptera Diptera and Mollusca generally dominated.

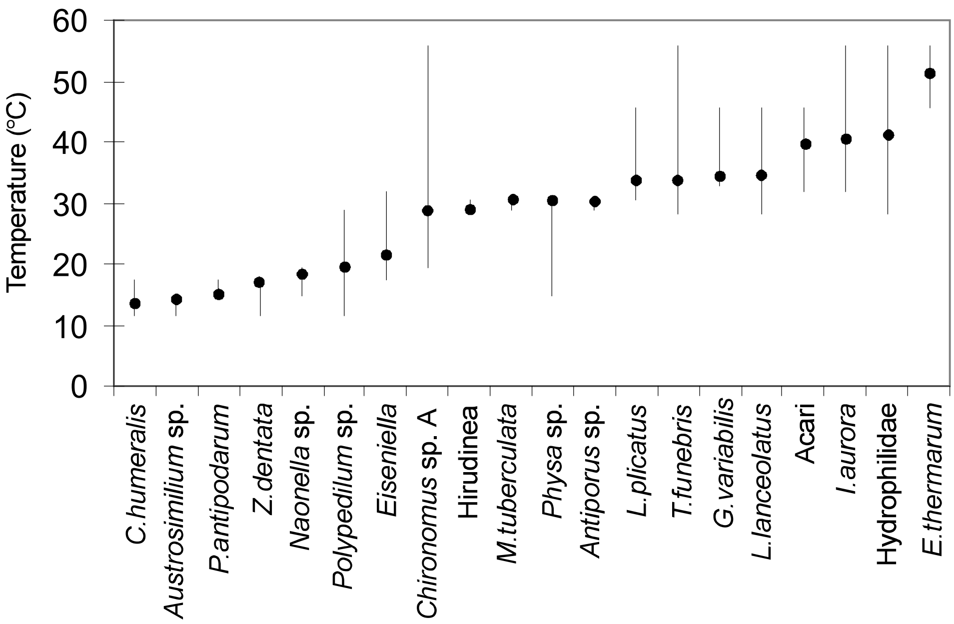

Figure 9. Weighted average optima (dots) and maximum and minimum (bars) temperatures recorded for dominant species.

4. DISCUSSION

4.1 Algal composition

The factors determining the major distribution patterns of algae within and between geothermal habitats are already fairly well understood, with the dominant factors being temperature, pH and sulphide concentrations (Stockner, 1967; Castenholz, 1976; Lamberti & Resh, 1985; Brock, 1985). Within individual streams, temperature gradients are often prevalent. Cyanobacteria are able to grow at higher temperatures than any other algal group, although this group is not successful in acidic waters, whereas diatoms generally dominate in cooler waters (Stockner, 1967; Brock, 1985). Thus, in the alkaline Otamakokore Stream the cyanobacteria *Mastigocladus laminosus* was seen to dominate at higher temperatures, and as the stream cooled diatoms (e.g., *Epithemia*) became more important. Lamberti & Resh (1985), similarly, recorded cyanophytes as dominating at high temperatures (41-52 °C) and diatoms at lower temperatures in Little Geyser Creek, California, U.S.A. In the neutral to alkaline Golden Springs, the cyanobacteria *Oscillotoria* sp. dominated (32.7-37.8 °C, pH 7.3-8.0), and on the sinter terraces at Orakeikorako the cyanophytes ?*Leptolyngbya* and *Dichothrix* sp. were prevalent. In the highly acidic Hakereteke Stream (29.1-33.7, pH 3.0-3.1) and the stream near Waiotapu (41.3-41.1 °C, pH 3.7), however, cyanophytes were notably absent, and chlorophytes and diatoms dominated. Brock & Brock (1970) have noted that cyanobacteria do not grow below pH 4.8 and this may partly explain their absence from Hakereteke Stream. In addition to pH, Castenholz (1976) believes the concentration of soluble sulphide to be among the most important factors determining the distribution of thermophilic algae between habitats. In New Zealand, *Mastigocladus laminosus*, for example, is sensitive to sulphide concentrations over 0.15 mg/L (Castenholz, 1976). Of the streams where cyanophytes were absent, the water content of Hakereteke Stream is likely to have its waters dominated by sulphate-chloride, as is the case in Lake Rotowhero, and at the stream near Waiotapu the waters are likely to have an acid sulphate chemistry, as this predominates in the waters in the Waiotapu area (Mongillo & Clelland, 1984). By contrast, Golden Springs is acid-bicarbonate, Orakeikorako neutral-chloride, and the Waikite Valley neutral sodium-chloride-bicarbonate in composition (Mongillo & Clelland, 1984). Hot alkaline springs in New Zealand are commonly dominated by *Mastigocladus* and *Oscillotoria* (e.g., Winterbourn, 1973b; Cassie & Cooper, 1989).

4.2 Macroinvertebrate richness, composition and abundance

Taxa richness in the sites surveyed was typically low, except in Waikokomuka Stream which had no geothermal influence. Significant relationships between taxa richness and temperature, however, were not observed in the present study, although this may partly reflect the paucity of sites sampled at each temperature extreme (i.e., at cool-water temperatures and at those greater than 50 °C). Lamberti & Resh (1985), for example, found macroinvertebrate species richness to decrease from 15 at 27 °C to zero at 45 °C at Little Geysers Creek, California, U.S.A. In our study the relationship was also affected by one site, in Otamakokore Stream (site 3), where we recorded five invertebrate species at the extremely high temperature of 55.7 °C. Macroinvertebrates are typically not recorded at temperatures above 50 °C (Vincent & Forsyth, 1987; Pritchard, 1991). In addition, we also recorded four species at 53.6 °C at Orakeikorako (Site 18). At both sites we suspect that species may perhaps not have been living in the water at this temperature, but rather living in microhabitats where temperature was significantly cooler. In Otamakokore Stream, for example, although the temperature of the main channel was high there may have been cooler refuges for taxa along the stream reach, possibly near the banks where water flow is slower. Alternatively, the stream fauna collected here may be more tolerant to temperature than previously recorded. A significant positive relationship was found between pH and taxa richness, suggesting that acidity is a strong influence on the distribution of species in the habitats.

Taxa recorded in geothermally influenced streams were in general typical of those recorded in similar habitats previously in New Zealand. Most of the taxa recorded are common taxa of “natural” streams that can tolerate high temperatures or unusual pH. Fauna recorded from the more greatly geothermally influenced sites are discussed below.

Odonata

Ischnura aurora was recorded from Otamakokore Stream at temperatures between 31.7 and 55.7 °C (pH 8.07-8.43). However, at the site with the highest temperature it was unlikely to have been sampled from the direct heated channel, at least alive. Instead it may have been sampled from a cooler microhabitat along the side of the stream, or as it drifted from a cooler site upstream. This species has been previously been recorded at 34.0 °C in Waipahihi Stream (Winterbourn & Brown, 1967) and at 29.5 °C and pH 3.1 from Lake Rotowhero. This species is a recent immigrant from Australia (Rowe, 1987), where it is commonly found in freshwaters at higher temperatures (Vincent & Forsyth, 1987).

Xanthocnemis zealandica was recorded only at the lowest site on Hakereteke Stream where geothermal influence was reduced (19.4 °C, pH 5.14). It has also been recorded previously in Hakereteke Stream by Forsyth (1983). However, he recorded it at a site upstream from our sites, and above the concentration of springs that feed it with warm water, but below the confluence with the Lake Rotowhero outlet (13 °C). This species has also been recorded in the geothermally influenced Waipahihi Stream by James (1985) at a temperature of 24.5 °C, and at a relatively neutral pH. *X. zealandica* is common and widespread in its distribution in New Zealand (Rowe, 1987), and the temperature at which it was recorded here is not above what might normally be expected in summer in a typical lowland stream. Vincent & Forsyth (1987) note that this species can live at temperatures little higher than summer littoral temperatures.

Trichoptera

The Leptoceridae *Oecetis unicolour* and *Triplectides cephalotes* were recorded at the lowest site at Hakereteke Stream (19.4 °C, pH 4.14). Both have been recorded previously from Opal Lake (Forsyth & MacKenzie, 1981). This lake has ambient temperatures, but is highly acidic (pH 4), similar to the conditions in which they were recorded from here.

Coleoptera

Liodessus plicatus was recorded at Otamakokore Stream, Waipuwerawera Stream, Golden Springs and Orakeikorako (17.5-53.6, pH 6.44-9.6), and *Antiporus* sp. was recorded in Golden Springs (29.0-30.4 °C, pH 7.12-7.47). These species are common inhabitants of non-geothermal habitats, although both have been recorded previously in Lake Rotowhero at 34 °C and pH 3.1 (Forsyth & McColl, 1974). *L. plicatus* has also been recorded from the Lake Rotowhero outlet stream (23 °C), the Hakekerete Stream below the confluence of Lake Rotowhero (13 °C) (Forsyth, 1983), and from warm pools in the Rotorua area (Ordish, 1966).

Lancetes lanceolatus was recorded in Otamakokore Stream (28.3-45.5 °C, pH 8.29-9.05) and Hydrophilidae were recorded at Otamakokore Stream (28.3-55.7 °C, pH 8.07-9.05) and Golden Springs (32.7-37.8 °C, pH 6.44-6.55). Neither *Enochrus* species or *Rantus pulverosis* were recorded in our study despite having previously been found in geothermal influenced waters in the region (e.g., Forsyth & McColl, 1974).

Diptera

Ephydrella thermarum was recorded from Otamakokore Stream (45.5-55.7 °C, pH 8.1-9.6) and Orakeikorako (14.7-53.6, pH 8.16-8.92). This species is a common dweller in thermal waters, including at Waimangu between 34 and 43 °C (Winterbourn, 1969a), the Parakiki Stream outflowing from Lake Rotokawa (temperature unrecorded) (Forsyth, 1977), and the Copland River warm springs in the South Island at 32 °C (Winterbourn, 1973b). Winterbourn (1968) gives temperature ranges for *Ephydrella* species in thermal waters between 28 and 47 °C, and occurrences from Waipahihi Stream, Ketetahi Springs, Orakeikorako, Waimangu Valley, and Ohinemutu.

Limonia sp. and *Nothodixa* sp. were recorded in Otamakokore Stream (45.5 °C, pH 9.6 and 31.7°C, pH 8.23, respectively), and Empididae were recorded at the bottom site in Hakereteke Stream (19.4 °C, pH 5.14). *Limonia* is recorded fairly commonly from geothermal waters, e.g., Waimangu, Mokai and Waipahihi Stream (Vincent & Forsyth, 1987).

Chironomids were diverse and often abundant in the habitats sampled. *Chironomus zealandicus* was recorded from the stream near Waiotapu (41.4 °C, pH 3.75). This species is a common representative in geothermal waters and can tolerate extreme acidity. For example, Forsyth (1977) recorded it in abundance in Lake Rotokawa at pH 2.1, and Forsyth & McColl (1974) in Lake Rotowheri at pH 3.1. *Chironomus* sp. A was recorded from Otamakokore Stream (28.3-55.7 °C, pH 8.07-9.6), Hakereteke Stream (19.4-33.7 °C, pH 3.1-5.14) and Orakeikorako (14.7-25.3 °C, pH 8.72-8.92).

Tanytarsus funebris was recorded in high abundance at Otamakokore Stream (28.3-55.7 °C, pH 8.07-9.5) and Orakeikorako (14.7-53.6 °C, pH 8.16-8.92). *T. funebris* has previously been recorded in a variaety of geothermal waters (e.g., Hall of Fame Stream, Wairaki and South Lake, Rainbow Mountain) at temperatures up to 36 °C and pH 5 (Vincent & Forsyth, 1987). At both sites where we collected this species we recorded higher temperatures, although we cannot discount that these animals may have inhabited cooler microhabitats within the stream. An unidentified *Tanytarsus* species has been recorded previously at Orakeikorako at 36 °C and pH 5 (Vincent & Forsyth, 1987). *Polypedilum* sp. was recorded from Hakereteke Stream (1.4-28.8 °C, pH 3.1-5.4).

Unidentified orthoclads were recorded from the stream near Waiotapu, (41.3 °C, pH 3.74) and *Naonella* sp. was recorded from the bottom site at Hakereteke Stream (19.4 °C, pH 5.14) and Orakeikorako (53.6, pH 8.16). Unidentified orthoclads have previously been recorded from Waipapa Stream, Orakeikorako and Hirunui River Springs (Stark et al., 1976; Vincent & Forsyth, 1987).

Other insect taxa

Hemipterans were absent from all sites. Pritchard (1991) considers Hemipterans to be one of the most representative taxa of geothermal waters, particularly the Saldidae and Coroxidae. Their absence is, however, likely to be a reflection of the habitats sampled, with standing waters not being a focus of this survey. Both *Sigara* (Corixidae) and *Saldula stoneri* (Saldidae) are known from geothermally heated lakes in the Taupo volcanic zone (Winterbourn, 1968; Winterbourn et al., 2000). Ephemeroptera and Plecoptera were also rare in the geothermally influenced waters, with only *Coloburiscus* and *Zephlebia* being found in the minimally influenced Waipuwerawera

Stream. Quinn et al. (1994) found *Zephlebia dentata* to have a 96 hour LT_{50} of 23.6 °C, and it is thus intolerant of high temperatures.

Mollusca

Molluscs were found at Waipuwerawera Stream, Otamakokore Stream and Golden Springs, but not in the more acidic Hakereteke Stream or the stream at Waiotapu. These streams both had pH levels below 6, an acidity that Vincent & Forsyth (1987) consider to be the greatest molluscs can tolerate due to dissolution of their carbonate shells.

Lymnaea tomentosa (or *L. columella*) was recorded from Otamakokore Stream (42.5 °C) and Waipuwerawera Stream (17.5 °C). Winterbourn & Brown (1967) and James (1985) recorded this species at 24.5 and 18.5 °C from Waipuwerawera Stream and at 35 °C and 25 °C in Waipahihi Stream, respectively.

Physa sp. was recorded from Otamakokore Stream (14.6 °C), Waipuwerawera Stream (22.9 °C) and Golden Springs (30.4 °C). This species has been recorded previously in Waipuwerawera at temperatures up to 33.5 °C (Winterbourn & Brown, 1967) and 24.5 °C (James, 1985). *Glyptophysa variabilis*, recorded in Otamakokore and Golden Springs, has apparently not been noted previously in thermal streams. However, Winterbourn (1973a) notes that misidentifications of this species have occurred in the past, and it may thus have been previously referred to as *Physa* sp.

Potamopyrgus antipodarum was recorded from Waipuwerawera Stream at 17.5-22.9 °C and at the coolest site in Otamakokore Stream at 14.6 °C. James (1985) recorded *Potamopyrgus* at temperatures up to 24.5 °C in Waipuwerawera Stream. Winterbourn (1968) noted this species up to 28 °C in various North Island thermal waters, and Winterbourn (1973b) up to 28 °C in the Copland River Springs, South Island. Experiments conducted by Winterbourn (1969b) indicated that 28 °C represents the temperature at which the activity of this snail is first curtailed, although Quinn et al. (1994) report a 96 hour LT_{50} at 32.4 °C.

Gyraulus corinna was recorded in Waipuwerawera Stream at 17.5 °C and *G. kahuica* in Golden Springs at 29 °C. These species have apparently not been recorded in geothermally influenced streams previously.

A gastropod mollusc matching the description of *Melanoides tuberculata* (Brown, 2001; Pointier & Marquet, 1990) was recorded from Golden Springs at temperatures of 29.0 °C and 30.4 °C. This is a common snail in tropical aquaria worldwide, originating from the Middle East and East Africa, which has now established wild populations widely throughout the tropics (Pointer & Delay, 1995). *Melanoides* has become naturalised in many locations, including North America (Brown, 2001), South

America (Pointier et al., 1994; De Marco, 1999) and French Polynesia (Pointier & Marquet, 1990). It has also been recorded in thermal springs in Morocco (Laamrani et al., 1997). This is apparently the first record of it having become naturalised in New Zealand. Golden Springs also contains naturalised populations of the Guppy (*Poecilia reticulata*), a tropical fish, and it seems likely that *Melanoides* was released into the stream from a tropical aquarium. As with the Guppy, *Melanoides* may perhaps not be able to spread outside of geothermally heated streams due to an inability to survive outside of warmer temperatures, but its impact on native invertebrate communities at this site is not known.

Other non-insect taxa

Hirudinea (leeches) were recorded at Golden Springs. Leeches have been recorded in geothermal waters by Forsyth (1977) from Lake Rotokawa, a cold but acidic lake. Another annelid recorded was *Eiseniella* from Otamakokore Stream (31.7 °C, pH 8.23) and Waipuwerawera Stream (17.5-22.9 °C, pH 7.29-7.97).

Acari were recorded from Otamakokore Stream (31.7-45.5 °C, pH 8.2-9.6).These have not yet been identified, but several species have been previously recorded from Orakeikorako and Hirunui River Springs (Brock & Brock, 1971; Stark et al., 1976).

Fish

Two fish species were sampled incidentally. The Guppy, *Poecilia reticulata*, was recorded at sites 11 and 12 at Golden Springs, and the Mosquitofish at site 9 from Waipuwerawera Stream. *Poecilia* is a released captive aquarium fish that has been recorded in this area previously. It was once also present in Waipahihi Stream, although apparently cannot survive outside of thermal areas year round due to cool winter temperatures (McDowall, 2000).

4.3 Patterns in community composition

From the examination of macroinvertebrate distribution patterns in the streams it appears that species are affected by a range of environmental conditions. CCA indicated that temperature was a dominant gradient determining the distribution of species among and within the streams. This is hardly surprising given its influence on the biology of animals, and because it was recorded over such a wide range in the current study. At cooler sites more typical stream fauna occurred, for example Ephemeroptera taxa (e.g., *Coloburiscus humeralis* and *Zephlebia dentata*), *Austrosimilium* sp. and *Potamopyrgus antipodarum*. At higher temperatures Diptera (e.g., *Ephydrella thermarum*) and Coleoptera (e.g., *Lancetes lanceolatus*) dominated.

Different species have different optima and tolerance ranges to temperature, largely determined by the temperature specific enzyme systems of each species (Pritchard, 1991). It has thus long been noted that different groups of biota have markedly different tolerances to water temperature, and that this can often result in an abrupt zonation of species (Vincent & Forsyth, 1987). However, gradients in other factors that co-vary with, or are caused by, temperature changes, such as increased algal abundances (as indicated by its high loading along the same axis), changes in algal composition, and the presence or absence of predators, are also likely to have lead to change in composition along this gradient.

Some of the variation along this gradient must also be attributed to substrate conditions, with the cooler sites sampled being generally dominated by small cobble and sand & gravel, while the warmer streams had predominantly silt or bedrock substrates. We suggest that in similar future research that samples be stratified among substrate types where possible. It also seems apparent that the distribution of animals is caused by substrate independently of the temperature gradient (with bedrock strongly positively associated with Axis 2 in the CCA). Macroinvertebrate communities from non-geothermal streams are also influenced by substrate size (Quinn & Hickey, 1990; Death, 2000).

Substrate size also covaried with pH. For example, Hakereteke Stream had predominiantly bedrock and boulder substrates, and also extremely high acidity (< pH 6), whereas Golden Springs, with its lack of these hard substrates was more alkaline (> pH 6). However, the absence of Mollusca (*M. tuberculata, Physa* sp., *G. variabilis* and *P. antipodarum*) from Hakereteke Stream and the unnamed stream at Waiotapu is likely to be caused mostly by low pH, due to dissolution of their carbonate shells by the acidity (Vincent & Forsyth, 1987) than substrate type. However, if pH alone was the most important factor causing variation in community composition along this gradient we would expect Golden Springs to have a more similar species composition to Hakereteke Stream than to Otomokokore Stream. Clearly, several physico-chemical factors interact to determine community composition at a site.

An additional factor that may have caused the species composition differences between Golden Springs and Hakereteke Stream is the presence of exotic species released from tropical aquaria in Golden Springs. *Melanoides tuberculata* may change habitat conditions (for example, due to their peculiar burrowing activities) in such a way that populations of other species are reduced (or enhanced), or similarly, it may reduce some species abundances by direct competition for resources. A stronger force influencing community composition here, however, may be the presence of the predatory Guppy (*Poecilia reticulata*) which is known to feed on a range of small insects and crustaceans (McDowall, 2000). Invertebrate fauna in New Zealand geothermal habitats would normally be free of predation pressure from fish.

Landuse is a dominant driving factor determining the distribution of macroinvertebrates in cold water streams (Quinn, 2000). However, it is difficult to predict the effects, if any, of landuse on the streams in the current study. Much of the water in Golden Springs and Otamakokore Stream would have been derived directly from spring fed water rather than land runoff, despite both streams originating in rural catchments. Hakereteke Stream may perhaps have the greatest influence from rural landuse due to draining water from farmland prior to having geothermal inputs from Lakes Rotowhero and from within the stream itself.

Unique chemical compositions of the geothermal waters in Golden Springs, Otamakokore Stream and Hakereteke Stream, that have variable toxic effects on invertebrate species, may also have lead to some of the variation in community composition between sites.

Changes in the optima and tolerances of species to temperature (Figure 9) provide a basis for developing predictions of likely changes in species composition should changes occur in water temperature due to, for example, industrial use of geothermal resources. It must be noted, however, that species collected here were from a limited number of sites, and that species were commonly restricted to a small number of samples. It is apparent from comparisons of the fauna with other studies (e.g., as in Section 4.2) that tolerances of many taxa are far wider than were recorded here. Estimates of species temperature optima from this study should therefore be used with some caution. Knowledge of the relationships of fauna with substrate and pH must also be taken into account if predicting what the resulting changes in species composition will be. However, it is apparent that at cooler temperatures (< 20 °C) typical cold water invertebrates such as Ephemeroptera taxa (e.g., *Coloburiscus humeralis* and *Zephlebia dentata*) will be most likely to dominate invertebrate communities. Above temperatures of 20 and 35 °C, Diptera, Coleoptera and Mollusca are most likely to dominate. At the higher temperatures, only a limited fauna will be recorded with the likely presence of *Ephydrella thermarum.*

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