

INVERTEBRATE DRIFT PATTERNS IN A REGULATED RIVER: DAMS, PERIPHYTON BIOMASS OR LONGITUDINAL PATTERNS?

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ABSTRACT

Macroinvertebrate drift was sampled at 15 sites along the Tongariro River, New Zealand above and below two hydroelectric dams. Sixty-seven invertebrate taxa were collected in the drift. Trichoptera (31) were the most diverse, followed by Diptera (13), Ephemeroptera (8) and Plecoptera (8). However, chironomidae were the numerically dominant taxa in the drift throughout the river and represented over 80% of all animals collected. Of these, Orthocladinae and Diamesinae were the most abundant. Taxonomic richness declined with distance downstream and peaked at sites with intermediate levels of periphyton biomass. The per cent of Ephemeroptera, Plecoptera and Trichoptera (EPT) was 3–4 times higher in the unregulated section of the river and declined exponentially with both distance downstream and increase in periphyton biomass, but densities were similar along the river. Of the measured environmental variables periphyton biomass was most closely linked with drift community structure. Periphyton biomass was six times higher in the lower section of the river than the upper unregulated section. The autocorrelation between periphyton biomass and distance downstream complicates the interpretation of results. However, because of the distinct differences between above and below dam sections of river in periphyton biomass and the strong link between it and invertebrate drift we suggest that the alteration of flow patterns by the hydroelectric dams and the associated shift in periphyton biomass is the most likely explanation for invertebrate drift patterns in the river. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS: diversity; drift; flow management; flow regulation; hydroelectric dams; macroinvertebrates; periphyton; streams; Tongariro River

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INTRODUCTION

Drift of benthic invertebrates plays a key role in the spatial distribution of stream benthos (e.g. Waters, 1972; Brittain and Eikeland, 1988; Allan, 1995), and is considered to be one of the most important dispersal mechanisms of benthic invertebrates (Mackay, 1992; Allan, 1995). Drifting invertebrates are an important food source for riverine salmonids (e.g. Elliott, 1967; Waters, 1969; Hayes *et al.*, 2000), and are a potential bioassessment tool (Pringle and Ramirez, 1998). Many factors can potentially influence the drift of lotic invertebrates including discharge, current velocity, photoperiod, water chemistry, temperature, benthic densities, predation, life history patterns and sedimentation (Brittain and Eikeland, 1988).

There are also many factors that affect the biodiversity of stream insects in the benthos (Vinson and Hawkins, 1998). These include the availability of periphyton and particulate organic matter as a food source (Townsend, 1981; Jowett and Richardson, 1990; Death, 2002), substrate stability (Death and Winterbourn, 1995; Death, 1996; Townsend *et al.*, 1997) and hydraulic conditions (Jowett *et al.*, 1991; Collier, 1993a,b; Jowett, 2003). These factors can in turn affect the pool of drifting animals.

Altering and controlling flow regimes can have deleterious impacts on lotic ecosystems (Bunn and Arthington, 2002). Dams can cause major deviations from the natural flow regime of downstream reaches (Poff *et al.*, 1997), and can alter discharge volume, water temperature and sediment deposition (Vinson, 2001). Furthermore, stabilization of flow in regulated rivers can induce higher algal production (Lowe, 1979; Williams and Winget, 1979; Petts, 1984; Dufford *et al.*, 1987), and in turn can alter the invertebrate community composition with certain taxa such as chironomids and oligochaetes becoming numerically dominant (Munn and Brusven, 1991). Flow also

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determines habitat structure including substrate composition which can also alter biotic composition. Numerous studies have shown that flow disturbance has a significant effect on benthic communities (e.g. Resh *et al.*, 1988; Vinson and Hawkins, 1998; Lake, 2000; Death, 2002). Furthermore, lotic invertebrates of unregulated streams are likely to have life history traits to survive frequent fluctuations in flow that are characteristic of such rivers (Winterbourn *et al.*, 1981; Winterbourn, 1997). Therefore, it is likely that regulating flow will have a major impact on lotic invertebrates in such rivers (Henriques, 1987). Incorporating flow variability into hydroelectric operations may potentially mitigate some of these effects from dams. Hence, artificial floods can potentially act as an important natural disturbance and return stream communities to a more characteristic composition (e.g. Robinson *et al.*, 2003; Robinson *et al.*, 2004).

Rivers have been adversely impacted by dam construction worldwide. Most large rivers in the Northern Hemisphere have been affected in some way through alteration of the flow regime (Dynesius and Nilsson, 1994). The Tongariro River is an integral part of a large hydroelectric power scheme and has two dams situated on the river. The Tongariro Power Development (TPD) was initialised in 1983 and diverts water from several rivers in the central North Island, including the Tongariro. The river is a major part of a world-famous rainbow trout (*Oncorhynchus mykiss*) fishery (Stephens, 1989; Cryer, 1991) and supports a population of the endangered native blue duck (*Hymenolaimus malacorhynchos*).

Previous studies have suggested that the presence of dams on the Tongariro River has led to a change in the invertebrate communities below the dams as a result of changes in flow altering key variables such as food supply and substrate (Dedual and Collier, 1995; Collier, 2002). However, these studies have only examined potential dam effects with limited spatial replication. This study assesses the effects of both dams by sampling 15 sites down the length of the Tongariro River. We predict that periphyton biomass will increase downstream of both dams because of flow alteration. This will lead to a shift from drifting invertebrate communities with a high proportion of EPT taxa to ones dominated by chironomids and oligochaetes.

METHODS

Study sites

The Tongariro River is the longest tributary of Lake Taupo in the central North Island of New Zealand (Figure 1). The river has a catchment area of 772 km² and receives drainage from the Kaimanawa Ranges in the east and the volcanoes of Tongariro National Park in the west. Water is diverted into the Tongariro River at Rangipo Dam from Lake Moawhango in the Kaimanawa Ranges. The geology of the Kaimanawas is primarily greywacke with ash deposits on the lower slopes whereas the western catchment has geology of predominantly andesite conglomerate. The lower section of the river is flanked by pumice alluvium and andesite deposits. Catchment vegetation is predominantly native southern beech forest (*Nothofagus* spp.) or tussock grassland above c. 500 m asl, with some *Pinus radiata* plantations and pasture at lower elevations. Mean annual rainfall in the upper catchment is 2097 mm per annum.

The Tongariro River has a flow regulated through a hydroelectric scheme comprising two dams (Rangipo Dam and Poutu Intake). Therefore, for the purposes of this study, the river can be considered to consist of three sections: upstream of Rangipo Dam which is called the Waipakihi River (main tributary) and has an unregulated flow regime, the Rangipo reach which is the section below the Rangipo Dam and above the Poutu Intake and the lower Tongariro which is the section of the river below the Poutu Intake. The mean flow of the Waipakihi above Rangipo Dam is approximately 10 m³ s⁻¹. The Rangipo Dam releases a minimum flow of 0.6 m³ s⁻¹ into the river and below the Poutu Intake there is a residual flow of 16 m³ s⁻¹. The lower section of the river near Turangi has a mean flow of 27 m³ s⁻¹. Fifteen sites were sampled: three from the Waipakihi (sites 1–3), 2 from the Rangipo reach (sites 4 and 5) and 10 from the lower Tongariro (sites 6–15).

Sampling protocol

Macroinvertebrate drift was sampled (benthic macroinvertebrates were not sampled) over a 24-h period on one occasion between 3–8 April 2005. Five drift nets (modified from Field-Dodgson, 1985) (dimensions: mouth

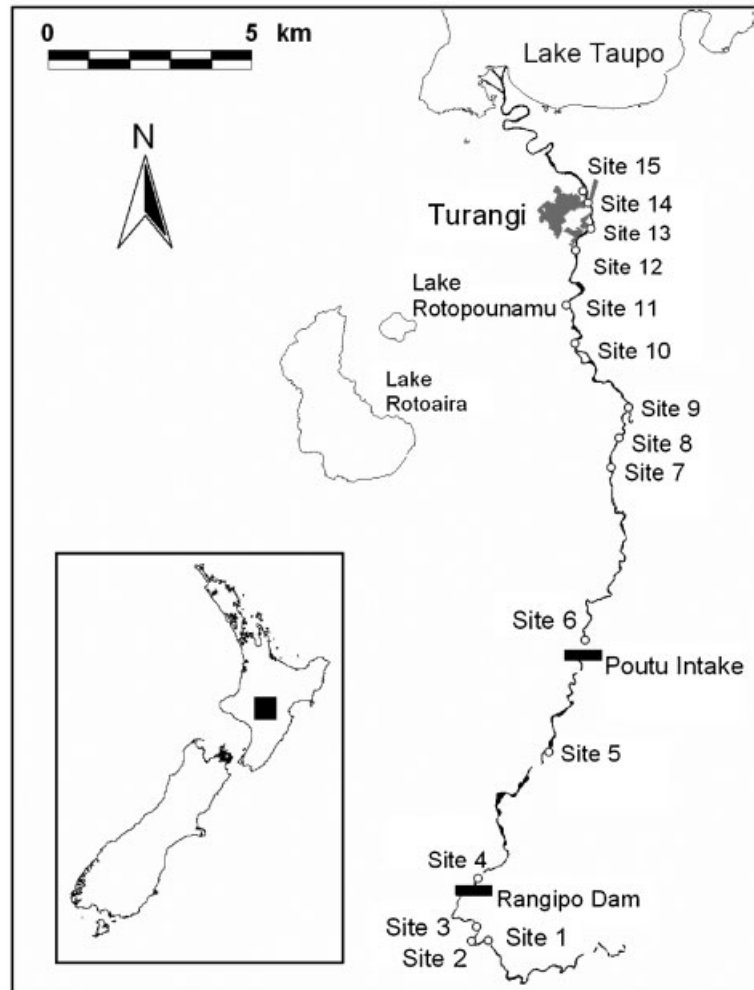


Figure 1. Location of 15 study sites on the Tongariro River

opening = 0.0056 m², mesh = 250 μ m, length = 0.85 m) were placed 10 cm above the substrate at the lower end of riffles in a perpendicular transect across the river where possible. Riffles were selected for sampling as they have been found to produce approximately three times more invertebrates than pool habitat (Buffagni and Comin, 2000).

Samples were preserved in 10% formalin. In the laboratory the samples were washed through 500 μ m and 1 mm Endecott sieves before being identified and enumerated to the lowest possible taxonomic level using available keys (e.g. Towns and Peters, 1996; Winterbourn *et al.*, 2000).

Depth and water velocity were recorded with a Marsh–McBirney flowmate current metre at the mouth of each drift net at the beginning of each 24-h sampling period. Conductivity and temperature were measured using a Eutech instruments ECScan pocket meter. Substrate composition was assessed visually as percentage of silt (<1 mm), sand (1–2 mm), fine gravel (2–20 mm), coarse gravel (20–60 mm), cobble (60–260 mm) and boulder (>260 mm). Flow type of each site was assessed visually as percentage of still, backwater, pool, run or riffle over a 100 m reach.

Periphyton

Periphyton biomass was estimated from measures of chlorophyll *a* from five stones (mean area: 60 cm²) collected randomly from each site. These were kept cool and dark before being frozen. Chlorophyll *a* and

phaeophytin were extracted using 90% acetone at 5°C for 24 h in the dark. Absorbances were read on a Varian Cary 50 conc UV–Visible Spectrophotometer and converted to pigment concentration following Steinman and Lamberti (1996). Stone surface area was estimated following Graham *et al.* (1988) and then halved to correct for the proportion of the stone available for periphyton growth.

Community metrics

Density (individuals m^{-3}), number of taxa, rarefied species richness ($ES(n)$) (Sanders, 1968; Hurlbert, 1971), Simpson's dominance index (λ') (Simpson, 1949), Pielou's evenness index (J') (Pielou, 1975, 1984) and % Ephemeroptera, Plecoptera and Trichoptera (EPT) animals (Lenat, 1988) were calculated on flow corrected abundance data.

Data analysis

Regression (GLM procedure of SAS, 2004) was used to determine the relationship between the above metrics, periphyton biomass and distance downstream. To determine whether communities were similar based on their position in the river, analysis of similarities (ANOSIM) was carried out in PRIMER (Clarke and Warwick, 1994). ANOSIM is a nonparametric procedure that determines whether average similarities between samples within groups are closer than the average similarities of all pairs between groups (Clarke and Warwick, 1994). Taxa contributing to the differentiation between the sections of the river were determined using the similarity percentages (SIMPER) routine (Clarke, 1993), in PRIMER (Clarke and Warwick, 1994).

In order to visualize the relationship between communities in two-dimensional space, ordination was performed using non-metric multidimensional scaling (NMDS) (Kruskal and Wish, 1978) in PRIMER (Clarke and Warwick, 1994) using Bray–Curtis similarities. This is a nonparametric technique which uses ranks of multivariate similarity in a dataset. Principal Component Analysis (PCA) was performed on the environmental variables to determine differences between the habitat at each site and between the three river sections.

To determine the environmental variables that best link with community composition, the BIOENV routine (Clarke and Ainsworth, 1993) was used in PRIMER (Clarke and Warwick, 1994). This calculates the value of Spearman rank correlation coefficients (r_s) between distances in the biotic and environmental resemblance matrices, and calculates r_s for all possible combinations of variables in order to find the best fit.

RESULTS

Physicochemical measures

Conductivity was on average twice as high in the lower Tongariro (mean = 88.5 $\mu s cm^{-1}$) than the Waipakihi (mean = 45.8 $\mu s cm^{-1}$) ($F_{2, 12} = 25.51$, $p < 0.001$; Table I). PCA on the environmental characteristics indicated all variables contributed equally to differences between sites (Figure 2). Sites 1–4, 6 and 13, which had low velocity, shallow riffles with smaller substrates grouped together. High conductivity, chlorophyll *a*, percentage sand and temperature were characteristics of sites downstream. Site 9 had large substrates and high velocity and site 5 had low conductivity and chlorophyll *a*.

Periphyton

Periphyton biomass assessed as chlorophyll *a* ranged from 0.29 (site 5) to 3.23 $\mu g cm^{-2}$ (site 10), and increased with distance downstream ($F_{1, 13} = 15.97$, $p = 0.02$, $r^2 = 0.55$; Figure 3). However, there was no downstream increase in chlorophyll *a* in the lower section of the river ($F_{1, 8} = 1.76$, $p = 0.22$, $r^2 = 0.18$; Figure 3). Chlorophyll *a* was approximately twice as high in the lower Tongariro as the Waipakihi and six times higher than Rangipo reach sites ($F_{2, 12} = 7.56$, $p = 0.007$).

Drift density

The density of invertebrates in the drift ranged from 0.11 (site 4) to 1.16 m^{-3} (site 10). Lower Tongariro sites (0.81 m^{-3}) had a much higher drift density than both the Waipakihi (0.22 m^{-3}) and Rangipo reach (0.28 m^{-3}).

Table I. Physicochemical characteristics measured at 15 sites on the Tongariro River, April 2005

Site	Name	Altitude (m asl)	NZ map easting	Coordinates northing	Depth (cm)	Velocity (m s ⁻¹)	Conductivity (μs cm ⁻¹)	Temperature (°C)
1	Waipakihi 1	880	2 750 463	6 215 777	33	0.90	47.0	12
2	Waipakihi 2	857	2 749 848	6 215 750	22	0.98	44.5	13
3	Waipakihi 3	840	2 750 029	6 216 297	51	0.81	45.8	11
4	Rangipo reach 1	813	2 750 083	6 218 070	29	0.70	88.0	12
5	Rangipo reach 2	672	2 752 681	6 222 733	33	1.03	44.4	11
6	Below Poutu intake	580	2 754 010	6 226 836	32	0.85	86.9	12
7	Puketerata	473	2 754 978	6 233 164	49	0.93	84.7	13
8	Water supply	460	2 755 262	6 234 253	52	0.71	89.0	14
9	Whitikau pool	440	2 755 618	6 235 391	63	1.05	81.8	12
10	Shag pool	417	2 753 630	6 237 745	52	1.22	88.0	12
11	Barlows pool	395	2 753 332	6 239 156	63	0.81	89.6	14
12	Breakfast pool	384	2 753 664	6 241 171	55	0.73	90.5	14
13	Judges pool	380	2 754 240	6 241 990	33	0.97	92.8	13
14	Swirl pool	368	2 754 121	6 242 932	33	0.90	91.1	14
15	Upper Island pool	365	2 753 925	6 243 361	29	0.89	90.7	14

Depth and velocity measurements are means per site ($n=5$).

(Table III). Density increased with increasing periphyton biomass and with distance downstream (Table II; Figure 4). Beneath Rangipo dam large numbers of Cladocera and Copepoda were present in the drift. These were excluded from the analysis as they are lentic invertebrates believed to have been carried in from Lake Moawhango immediately upstream.

Diversity

Mean number of taxa collected per sample ranged from 7 (site 4) to 21 (site 12). The number of taxa increased gradually downstream (Table II; Figure 4(c)) and peaked at intermediate levels of periphyton biomass around $2 \mu\text{g cm}^{-2}$ before declining (Table II; Figure 4(d)). Relationships between diversity indices and both distance downstream and chlorophyll *a* were strengthened if the Rangipo reach sites were removed (Table II). Per cent EPT declined exponentially both downstream (Table II; Figure 4(e)) and with increasing chlorophyll *a* (Table II;

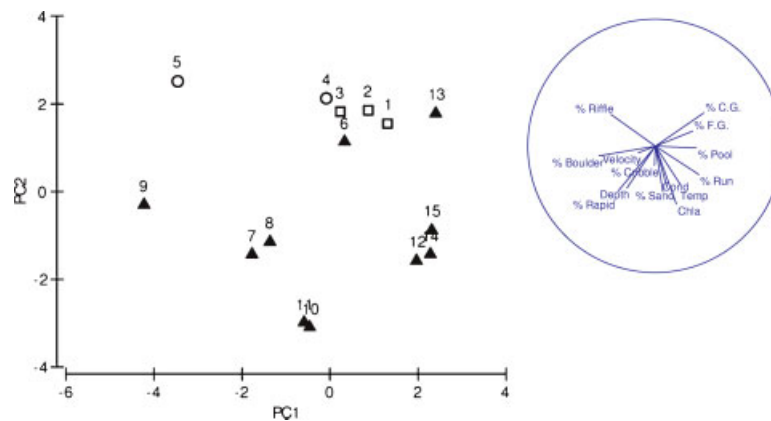


Figure 2. PCA for environmental variables collected from 15 sites along the Tongariro River, April 2005. Axis 1 explained 29.7 and axis 2 26.3% of variation in the data. Vectors demonstrate the direction of increases in environmental variables. □ = Waipakihi River, ○ = Rangipo reach, ▲ = Lower Tongariro. FG = fine gravel, CG = coarse gravel. This figure is available in colour online at www.interscience.wiley.com/journal/rra

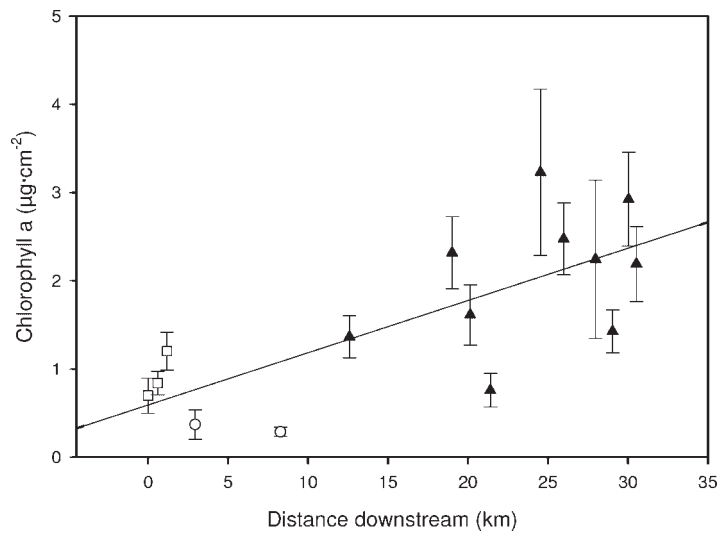


Figure 3. Mean chlorophyll *a* (± 1 standard error) collected on five stones at 15 sites on the Tongariro River, April 2005 as a function of distance downstream. \square = Waipakihi River, \circ = Rangipo reach, \blacktriangle = lower Tongariro. Regression line: $y = 0.59 + 5.92e^{-0.05x}$, $F_{1, 13} = 15.97$, $p = 0.02$, $r^2 = 0.55$

Table II. Results of regression analysis for various diversity indices for drift at 15 sites along the Tongariro River collected April 2005 as a function of (a) distance downstream and (b) chlorophyll *a*

	D.f.	<i>F</i>	<i>P</i>	r^2	Equation
(a) Distance downstream					
Density (m^{-3})	1, 13	64.98	<0.001	0.55	$y = 0.16 + 0.03x$
No. of taxa	1, 13	6.72	0.022	0.34	$y = 13.45 + 0.18x$
ES(100)	1, 13	2.34	0.15	0.15	Non-significant
Excluding Rangipo reach	1, 11	21.51	<0.001	0.66	$y = 17.07 - 0.2x$
%EPT	1, 13	18.88	<0.00	0.59	$y = 32.3e^{-0.05x}$
Excluding Rangipo reach	1, 11	157.76	<0.001	0.93	$y = 39.12e^{-0.06x}$
(b) Chlorophyll <i>a</i>					
Density	1, 13	31.17	<0.001	0.71	$y = 0.12 + 0.32x$
No. of taxa	2, 12	11.06	0.002	0.65	$y = 7.63 + 10.78x - 2.47x^2$
ES(100)	1, 13	0.72	0.41	0.05	Non-significant
Excluding Rangipo reach	2, 10	6.66	0.01	0.57	$y = 21.57 - 7.59x + 1.41x^2$
%EPT	1, 13	3.77	0.07	0.22	Non-significant
Excluding Rangipo reach	1, 11	13.31	0.004	0.55	$y = 54.31e^{-0.75x}$

Table III. ANOVA results testing if diversity indices for drift samples measured in three sections, collected from the Tongariro River, April 2005 differ between the three river sections

	<i>F</i>	<i>P</i>
Density	10.25	0.003
No of taxa	5.04	0.03
ES(100)	12.81	0.001
%EPT	37.25	< 0.001
EPT density	4.26	0.04

For all values d.f. = 2, 12.

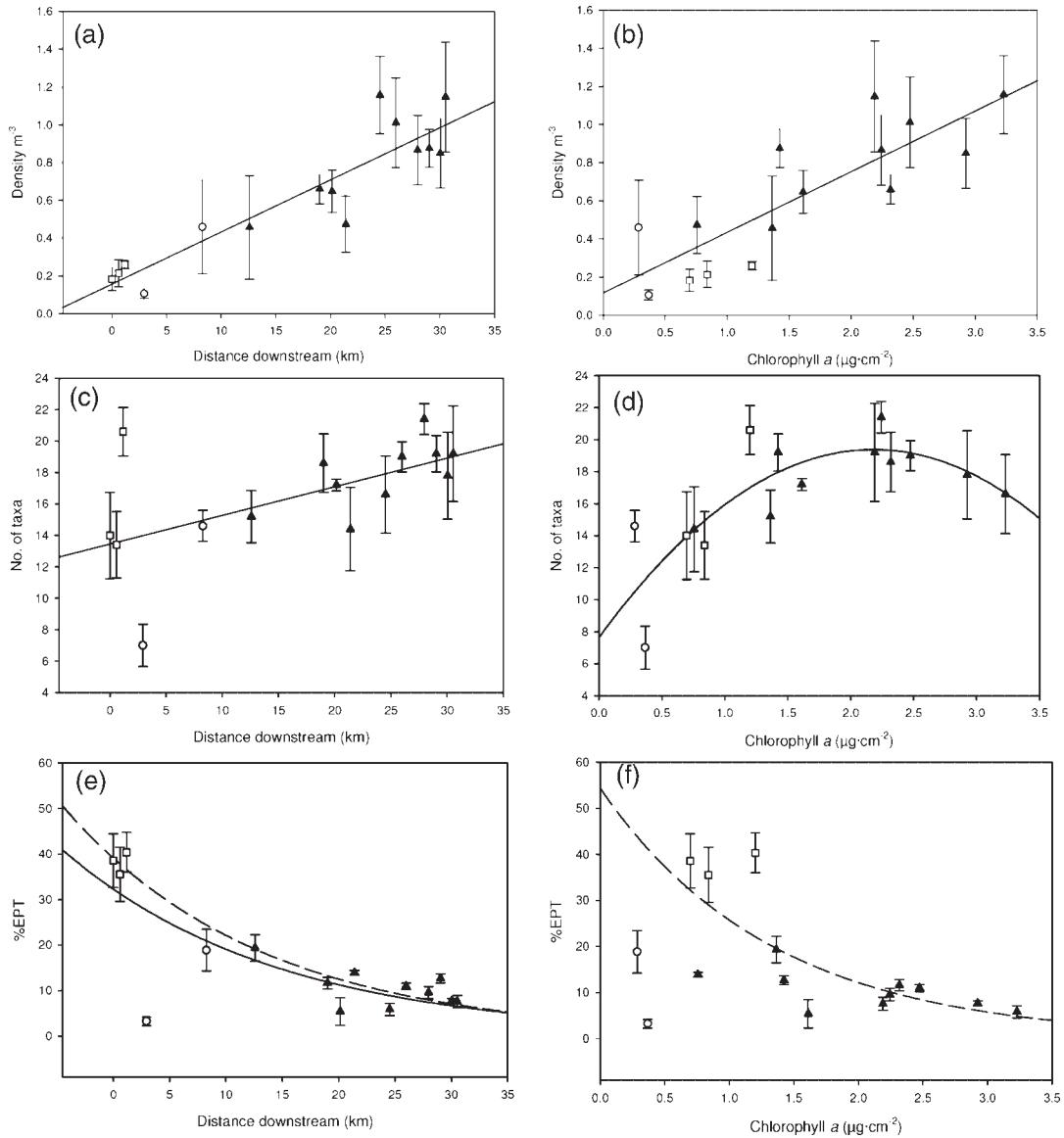


Figure 4. Mean density of drifting macroinvertebrates (± 1 standard error) for 15 sites along the Tongariiro River, April 2005 as a function of (a) distance downstream and (b) chlorophyll *a*, mean number of drifting taxa (± 1 standard error) for 15 sites along the Tongariiro River, April 2005 as a function of (c) chlorophyll *a* and (d) distance downstream, and mean %EPT of drifting macroinvertebrates (± 1 standard error) for 15 sites along the Tongariiro River collected April 2005 as a function of (e) distance downstream and (f) chlorophyll *a*. \square = Waipakihi River, \circ = Rangipo reach, \blacktriangle = lower Tongariiro. Solid regression lines include the two Rangipo reach sites (4 and 5), dashed lines exclude these sites. Regression analysis results are presented in Table II

Figure 4(f). Rarefied species richness declined gradually with distance downstream and as chlorophyll *a* increased (Table II), and was highest in the Waipakihi River (Table III).

Per cent EPT was 3–4 times higher in the Waipakihi River than the remaining sites downstream of the two dams (Table III). However, the density of EPT taxa was only slightly less in the lower Tongariiro than the Waipakihi, with the only major difference being an order of magnitude lower density at site 4 in the Rangipo reach (Table III). Although the percentage of Ephemeroptera was less in the lower Tongariiro than the Waipakihi ($F_{2, 12} = 9.82$, $p = 0.003$), densities were not different between the sections ($F_{2, 12} = 0.58$, $p = 0.58$). Density of plecopterans was approximately 10 times higher ($F_{2, 12} = 40.05$, $p < 0.001$) and per cent plecopterans approximately 16 times higher

($F_{2, 12} = 491.04$, $p < 0.001$) in the Waipakihi than the two flow controlled sections. Relative abundance of trichopterans was more than twice as high in the Waipakihi as in both the Rangipo reach and the lower Tongariro ($F_{2, 12} = 18.11$, $p = 0.002$). However, density of Trichoptera was similar between the Waipakihi and lower Tongariro, with the Rangipo reach sites having 4 times less Trichoptera ($F_{2, 12} = 5$, $p = 0.03$).

Community composition

Sixty-seven taxa were collected from the drift. Trichoptera (31) were the most diverse, followed by Diptera (13), Ephemeroptera (8) and Plecoptera (8) (Figure 5). Chironomidae were the most abundant taxa in the drift throughout the river and comprised over 80% of all organisms found. Differences between river sections were largely attributable to differences in the density of the two chironomid subfamilies Orthoclaadiinae and Diamesinae (Table IV(b)). The Waipakihi River sites were characterized by orthoclads and the stonefly *Zelandoperla* spp., and moderate densities of *Deleatidium* spp. and the algal piercing Hydroptilid *Oxyethira albiceps* (Table IV(b)). Density of *Zelandoperla* was approximately 10 times higher in the Waipakihi River than the other sections ($F_{2, 12} = 55.31$, $p < 0.001$).

Drift assemblages in the Rangipo reach were dominated by the chironomid sub-family, Orthoclaadiinae (Table IV(b)), although density was not different between the three sections ($F_{2, 12} = 3.35$, $p = 0.07$). The lower Tongariro was dominated by the chironomids Diamesinae (Table IV(b); $F_{2, 12} = 10.25$, $p = 0.003$) and Orthoclaadiinae. Caddisflies from the *Hydrobiosis umbripennis* group were approximately 3 times more abundant in the drift in the lower section of the river (Table IV(b); $F_{2, 12} = 4.07$, $p = 0.04$). The mayfly *Deleatidium* spp. was present in moderate numbers in the drift through all sections of the river (Table IV(b); $F_{2, 12} = 0.43$, $p = 0.7$), as was the caddisfly *O. albiceps* (Table IV(b); $F_{2, 12} = 1.28$, $p = 0.3$). Chironomids were 3–4 times more abundant in the lower Tongariro than the Waipakihi and the Rangipo reach ($F_{2, 12} = 11.65$, $p = 0.002$) and increased strongly downstream ($r^2 = 0.83$, $F_{1, 13} = 64.98$, $p < 0.001$) and with increasing chlorophyll *a* ($r^2 = 0.71$, $F_{1, 13} = 31.17$, $p < 0.001$).

NMDS of drifting invertebrate communities produced a two-dimensional plot with low stress (0.05) grouping sites from the Waipakihi River separate from the lower Tongariro (Figure 6). Site 4 communities appeared closer to Waipakihi sites and site 5 communities to sites from the lower section. ANOSIM confirmed a difference in invertebrate communities between the three sections of the river (Table IV(a); $R = 0.848$, $p = 0.001$). However, pairwise differences were only significant between the lower Tongariro and the Waipakihi ($R = 0.96$, $p = 0.003$), and the lower Tongariro and Rangipo reach ($R = 0.728$, $p = 0.03$).

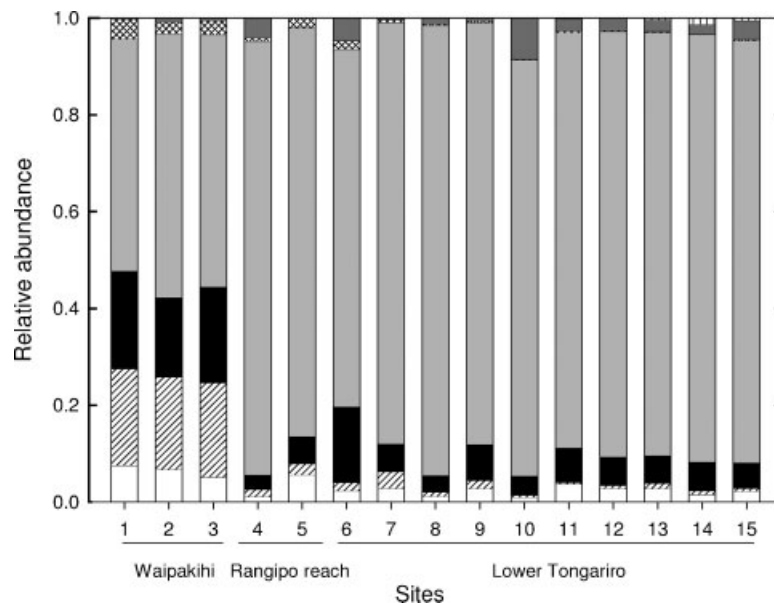


Figure 5. Relative abundances of number of invertebrates in the drift for 15 sites on the Tongariro River, April 2005. Ephemeroptera, Plecoptera, Trichoptera, Diptera, Coleoptera, Nematoda

Table IV. Difference in drift assemblages between the three sections of the Tongariro River collected April 2005; (a) ANOSIM examining differences in drift assemblages between sections of the river, (b) SIMPER showing the taxa contributing to the greatest differentiation between river sections

Group comparisons	<i>R</i>	<i>P</i>	
(a) Comparisons of invertebrate communities			
Waipakihi versus Rangipo reach	0.5	0.1	
Waipakihi versus lower Tongariro	0.96	0.003	
Rangipo reach versus lower Tongariro	0.728	0.03	
Mean density (m ⁻³)			
Taxon	Waipakihi	Rangipo reach	Lower Tongariro
(b) Mean density of the 15 taxa contributing to the greatest per cent dissimilarity between groups			
<i>Orthocladinae</i>	0.074	0.186	0.311
<i>Zelandoperla</i> spp.	0.033	0.004	0.003
Diamesinae	0.008	0.016	0.257
<i>Deleatidium</i> spp.	0.012	0.012	0.017
Tanypodinae	0.012	0.007	0.028
<i>Olinga feredayi</i>	0.005	0	0.002
Elmidae <i>Hydora</i>	0.006	0.004	0.003
<i>Aoteapsyche</i> spp.	0.005	0.003	0.004
<i>Hydrobiosis umbripennis</i> group	0.004	0.001	0.014
<i>Costachorema callistum</i>	0.004	0.004	< 0.001
<i>Austroperla cyrene</i>	0.003	0.001	< 0.001
Oligochaeta	0.001	0.002	0.026
Chironomidae pupae	0.007	0.005	0.064
Chironominae	0.001	0.002	0.028
<i>Oxyethira albiceps</i>	0.013	< 0.001	0.017

BIOENV revealed that distance downstream was the strongest determinant of the multivariate organization of drifting invertebrate communities ($R = 0.82$). With distance downstream removed from the analysis, chlorophyll *a* and conductivity were the best descriptors of drift community structure ($R = 0.6$). Chlorophyll *a* explained 36% of the variation on its own ($p = 0.003$). Within the lower section of the river, BIOENV found chlorophyll *a*, depth and distance downstream were the best descriptors of community structure ($R = 0.71$).

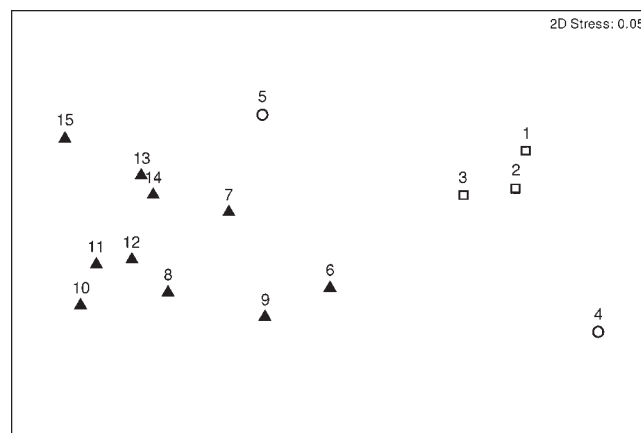


Figure 6. NMDS ordination on invertebrate drift data at 15 sites along the Tongariro River, April 2005. □ = Waipakihi River, ○ = Rangipo reach, ▲ = Lower Tongariro. Numbers indicate group membership. 1. Waipakihi, 2. Rangipo reach, 3. lower Tongariro

DISCUSSION

Designing field experiments or surveys to test the effects of impoundments on rivers is challenging as rivers naturally change as they move downstream and it is difficult to replicate dams in space (Vannote *et al.*, 1980; Downes *et al.*, 2002). Because of this it is difficult to separate the effects of flow regulation and the natural longitudinal patterns in rivers (Ward and Stanford, 1983). However, despite this there is clearly a higher percentage of EPT present in the drift in the unregulated compared to regulated sections of the Tongariro River.

Periphyton

Periphyton biomass was approximately twice as high in the lower Tongariro River as in the unregulated Waipakihi River (upper Tongariro River), and six times higher than in the Rangipo reach. Although periphyton biomass increased between the upper and lower river, this increase was not constant within sections and within the lower section of the river there was no increase (Figure 3). This suggests that the dams are altering periphyton biomass via changes in the flow regime and not simply downstream change. The influence of flow regime on periphyton communities has been widely documented (e.g. Biggs and Close, 1989; Duncan and Blinn, 1989; Stevenson *et al.*, 1996), and periods of constant flow, which can occur below dams, can lead to high levels of biomass (e.g. Lowe, 1979; Petts, 1984; Dufford *et al.*, 1987; Biggs, 2000). Biggs and Close (1989) and Biggs (2000) suggested that the hydrologic regime is as important as nutrients in determining levels of periphyton.

Differences in drift assemblages along the river

Trichoptera was the most diverse taxon in the river, followed by Diptera, Ephemeroptera and Plecoptera. However, Chironomidae was the numerically dominant taxa along the length of the river and represented over 80% of all animals found in the drift. The main difference in drifting invertebrate assemblages between the sections was an increase in the density and relative abundance of chironomids in the regulated sections. Invertebrate communities in the regulated sections of the river were clearly different from those in the unregulated Waipakihi section. The stonefly *Zelandoperla* spp. was approximately 10 times more abundant in the Waipakihi than the remaining sections of the river. Quinn and Hickey (1990) have found that *Zelandoperla* is limited to sites with undeveloped catchments, low nutrients and low periphyton biomass. This decline in *Zelandoperla* below the dams suggests flow regulation is altering a key habitat variable such as periphyton biomass or temperature, which leads to the near exclusion of this invertebrate in the drift.

The chironomids, Orthocladinae and Diamesinae were abundant in the drift throughout the river, but were more abundant in the regulated sections of the Tongariro. Chironomids have been found to be tolerant of river impoundment (Camargo and Voelz, 1998), and are thus often found to proliferate in regulated rivers (Munn and Brusven, 1991). Chironomids are often abundant in the drift simply because they are abundant in the benthos (e.g. Robinson *et al.*, 2002; Hieber *et al.*, 2003). Their increased density in the regulated sections is also likely to be associated with increased periphyton biomass as (Towns, 1981).

Changes in community composition that are often found to result from river regulation such as shifts in functional feeding groups (Brittain and Saltveit, 1989; Camargo and Voelz, 1998; Vallania and Corigliano, 2007) were not found in this study. The main change was a large increase in the density of the algal feeding chironomids. The lack of change between feeding types that often results from river regulation may be partly due to the dams on the Tongariro River being a 'run of the river' hydroscheme with limited storage capacity. This limits the downstream changes in water chemistry and temperature regimes that are associated with reservoirs (especially with hypolimnetic releases) (Saltveit *et al.*, 1994; Ahearn *et al.*, 2005).

Density and diversity of drifting invertebrates

Increased invertebrate drift densities were associated with increases in periphyton biomass in the Tongariro River. Several studies have shown that the reduction of food resources can lead to increases in drift rates (Hildebrand, 1974; Death, 1988; Shearer *et al.*, 2003). The increase in drift density with increased food resources in this study is therefore likely to reflect increases in benthic density, although these were not measured in this study.

The number of drifting taxa peaked at intermediate levels of periphyton biomass suggesting that higher levels of periphyton biomass may be either restricting the presence of some species, such as certain EPT taxa in the river or by lowering the propensity of these species to enter the drift. Once periphyton reaches medium-high biomass ($>1.5 \mu\text{g cm}^{-2}$) in the Tongariro River, the pool of drifting animals becomes increasingly dominated by chironomids. However, no taxa were found to be consistently excluded from the drift at sites with higher levels of periphyton biomass.

Although species richness increased downstream, rarefied richness showed a weak downstream decline suggesting the increase in richness downstream may be due to the passive increase in richness associated with collecting more individuals. The indistinct relationships between different diversity measures and both increasing periphyton biomass and distance downstream makes the differentiation of causal factors difficult.

Ephemeroptera, plecoptera and trichoptera

The proportion of EPT taxa was considerably higher in the drift in the Waipakihi River, with 3–4 times more than in the regulated sections of the river and declined with increasing periphyton biomass. However, density of these taxa only differed slightly between the Waipakihi and the lower Tongariro. Dedual and Collier (1995) also found small numbers of EPT in the benthos and drift of the lower section of the river. Of the EPT taxa, Plecoptera were most affected by the presence of dams with an order of magnitude lower density in the flow regulated sections of the river compared with the Waipakihi.

CONCLUSIONS

There are more invertebrates and taxa, and proportionally fewer EPT drifting in the regulated lower section of the Tongariro River. The below dam increase in periphyton biomass and invertebrate drift along the river suggests that the presence of dams has led to altered periphyton biomass and a shift in the composition of invertebrate drift in the Tongariro River independent of natural downstream changes. The strong relationships between invertebrate drift and chlorophyll *a* make changes in periphyton biomass a likely explanation for differences in drift patterns throughout the river.

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