



Macroinvertebrate drift-benthos trends in a regulated river

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With 6 figures and 6 tables

Abstract: Downstream drift plays a fundamental role in the spatial distribution and community structure of lotic macroinvertebrates. We sampled both benthic and drifting macroinvertebrates at 15 sites, in three sections of river with varying flow alteration along the Tongariro River, New Zealand. Our objectives were to examine whether (i) benthic and drift density were linearly related throughout the river, (ii) the presence of dams affected the propensity of macroinvertebrates to drift, and (iii) drift propensity was related to benthic periphyton biomass or natural longitudinal patterns down the river. More taxa were collected from the drift than the benthos, although drift and benthic samples were generally taxonomically similar, despite some structural differences. Nonetheless, differences were evident between the major groups when assessing density and relative abundance links between the benthos and drift. The presence of dams did not affect the propensity of macroinvertebrates to drift on the whole, nor was propensity affected by periphyton biomass or distance from source. These results suggest that although altered periphyton biomass in downstream sections in the Tongariro River is altering the composition of benthic and drifting macroinvertebrates, drift propensity is unaffected. However, some deviations from linear relationships between benthic and drift density are evident suggesting these links may be taxon specific.

Key words: benthic, drift, flow regulation, hydroelectric dam, invertebrate, New Zealand, Tongariro River.

Introduction

Muller (1954) described the downstream drift of lotic macroinvertebrates as simply a consequence of living in running water to which these organisms responded through the evolution of upstream adult flight. Other pioneering research hypothesised that drift is a function of the extent that carrying capacity of a stream is exceeded and is thus a means of removing excess production (Waters 1966). Drift of macroinvertebrates has been a widely studied theme of lotic ecology for decades (e.g. Waters 1965, Brittain & Eikeland 1988, Gibbins et al. 2010) and it is of fundamental importance to the structure and function of lotic ecosystems

(Allan & Castillo 2007). Drift has several crucial functions such as being a means of recolonising denuded downstream habitats and structuring benthic invertebrate communities (Waters 1972, Ríos-Touma et al. 2012), a food source for drift feeding fish (Elliott 1967a, Hayes et al. 2000), and a potential biomonitoring tool (Pringle & Ramirez 1998).

Drift rates can be induced voluntarily and/or be influenced by several biotic and abiotic processes (Brittain & Eikeland 1988, Allan & Castillo 2007). Drift rates can also respond to short term fluctuations in environmental influences such as increased sediment (Gomi et al. 2010), velocity (Gibbins et al. 2010), and bed disturbance (Gibbins et al. 2007). Moreover,

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presence of predatory fish can alter drift activity of invertebrates (Ramirez & Pringle 1998, McIntosh et al. 2002), and is likely to have led to the evolution of diel periodicity of drift (Flecker 1992). Drift density can be a function of benthic densities (McLay 1968, Siler et al. 2001) but can also be independent of the benthos (Waters 1972, Graesser 1988). This benthos-drift link has received considerable attention since the classic drift studies of Waters (1972) and Elliot (1967b) which suggested drift rates are mostly density independent, with greatest rates coming with pupation and emergence events. However, others have documented drift as being influenced by density dependent mechanisms including competition and predation with other benthic organisms (e.g. Kohler 1985).

Damming and regulating rivers is common worldwide (Nilsson et al. 2005). Flow regulation can alter river ecosystems by modifications to such factors as the natural flow regime, channel planform, habitat and sediment dynamics (Ward & Stanford 1983, Ligon et al. 1995, Poff et al. 1997). This can have knock-on effects to the biota living downstream of dams (Vinson 2001, Bunn & Arthington 2002), including benthic (Vinson 2001, Bredenhand & Samways 2009) and drifting (Tonkin et al. 2009) macroinvertebrates. As drift rate can be strongly related to food resource levels (Richardson 1991, Hinterleitner-Anderson et al. 1992, Siler et al. 2001), dams may indirectly alter invertebrate drift rates through reduced habitat and food availability (Hay et al. 2008).

The Tongariro River has had its flow altered through damming for hydroelectric generation, and consists of two downstream regulated sections and one upstream unregulated section. Tonkin et al. (2009) found that drift density differed significantly between the three sections of the Tongariro River with regard to dam position. Moreover, they found strong relationships between community metrics of drifting macroinvertebrates and both periphyton biomass and distance from source. Thus, they conclude that changes to invertebrate drift were likely through changes in periphyton biomass downstream of the dams as suggested by previous studies on both benthic and drifting macroinvertebrates on the Tongariro River (Quinn & Vickers 1992, Dedual & Collier 1995, Collier 2002).

The current paper builds on the work of Tonkin et al. (2009) to assess relations between drift and benthic densities and establish whether spatial variability in drift propensity corresponds to altered flow regimes. Specifically, our objectives were to examine whether (i) the density and relative abundance of macroinvertebrates in the drift were reflecting those found in the

benthos, (ii) the presence of hydroelectric dams was affecting the propensity of macroinvertebrates to drift (the number of animals in the drift in relation to benthos), and (iii) drift propensity was related to benthic periphyton biomass or more related to natural downstream patterns. We hypothesise that, when considering the whole community, macroinvertebrate drift composition and density will be a linear function of that found in the benthos and thus drift propensity will not be affected by dam presence or other factors such as periphyton biomass or distance from source.

Methods

Study sites

The Tongariro River (catchment area = 772 km²; upper catchment mean annual rainfall = 2097 mm p.a.) is the longest tributary of Lake Taupo, central North Island, New Zealand and drains both the Kaimanawa Ranges and the volcanoes of Tongariro National Park (Fig. 1). Water is diverted into the Tongariro River at Rangipo Dam from Lake Moawhango in the Kaimanawa Ranges. Geology of the two catchments differs with the Kaimanawa Ranges consisting of primarily greywacke with ash deposits whereas the Tongariro National Park catchment consists primarily of andesite conglomerate. Downstream sections of the river consist primarily of pumice alluvium and andesite deposits. Southern beech forest (*Nothofagus* spp.), or tussock grassland above c. 500 m a.s.l., are the dominant vegetation throughout the catchment, with some *Pinus radiata* plantations and pasture at lower elevations.

As a result of damming and hydroelectric energy generation, the Tongariro River can be divided into three contrasting sections. These three sections, resulting from two dams (Rangipo Dam and Poutu Intake) consist of: the Waipakihi River upstream of Rangipo Dam (main tributary; mean flow = 10 m³ s⁻¹; hereafter referred to as upper river) has an unregulated flow regime, the mid river section which is the section below the Rangipo Dam and above the Poutu Intake (residual flow downstream of Rangipo Dam = 0.6 m³ s⁻¹), and the lower section which is the section of the river below the Poutu Intake (residual flow = 16 m³ s⁻¹). The lower section of the river near Turangi has a mean flow of 27 m³ s⁻¹. We sampled 15 sites in this study: three from the upper river (sites 1–3), two from the middle section (sites 4 and 5) and ten from the lower section (sites 6–15) (Fig. 1).

Sampling protocol

We performed sampling during the period of 3–8 April 2005. This represents the late summer, early autumn season in New Zealand with relatively dry weather patterns, and thus river flows during this period are relatively stable. Consequently, no major floods occurred in the weeks prior to sampling.

Physicochemical variables

The dams in this river are operated in a 'run-of-river' nature and thus it was concluded that flow characteristics would be

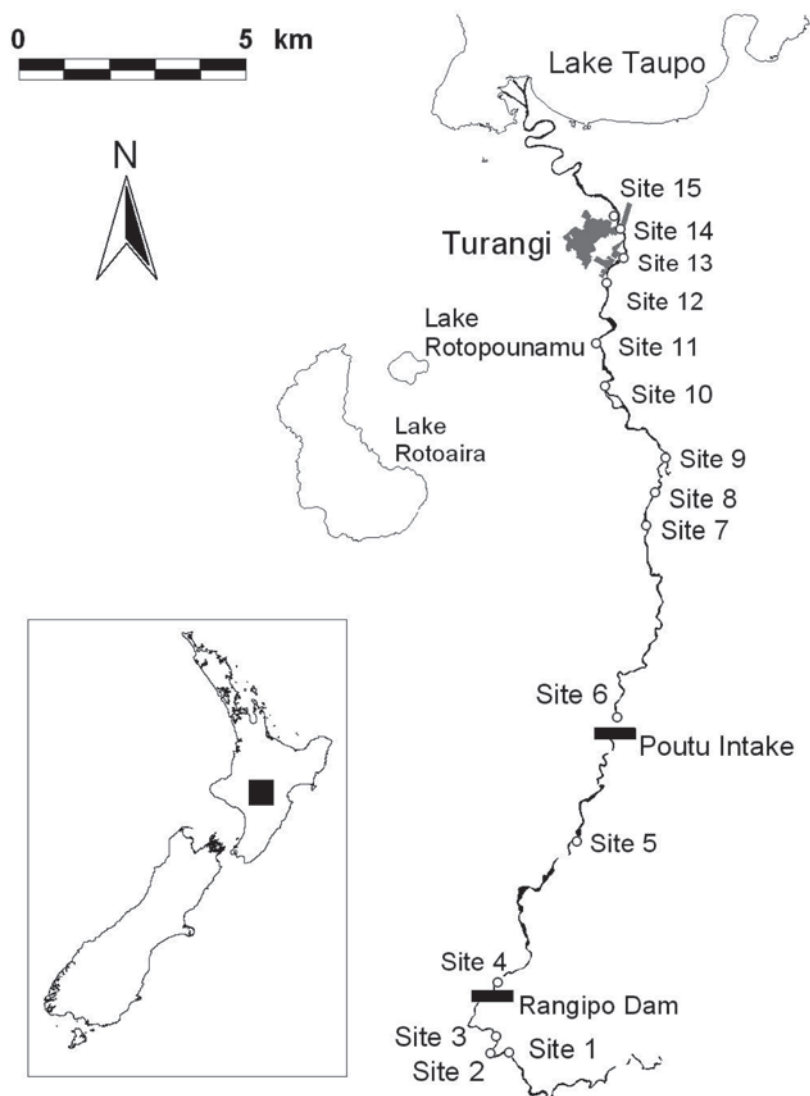


Fig. 1. Location of 15 sites on the Tongariro River, New Zealand, sampled for drifting and benthic macroinvertebrates between 3–8 April, 2005 (map reproduced from Tonkin et al. 2009).

consistent during the 24 hour period of sampling. Thus, at the beginning of each 24 hour sampling period, we recorded depth and water velocity at the mouth of each drift net using a Marsh-McBirney flowmate current meter. We spot measured conductivity and temperature using a Eutech instruments EC-Scan pocket meter. We visually assessed substrate composition 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), throughout the ~100 m study reach. We visually assessed flow type along the ~100 m study reach at each site as percentage of still, backwater, pool, run or riffle. See Tonkin et al. (2009) for a table summarising these physico-chemical variables.

Macroinvertebrates

We took five benthic macroinvertebrate samples from random locations within riffles (~100 m long) using a 0.1 m^{-2} Surber sampler (250 μm mesh) on one occasion between 3–8 April 2005. We sampled macroinvertebrate drift concurrently over a 24-hour period using five drift nets (modified in dimension from

Field-Dodgson 1985) (dimensions: mouth width = 10.4 cm, mouth depth = 5.4 cm, length = 85 cm, mesh = 250 μm), placed 10 cm above the substrate. We positioned these at the lower end of riffles in a perpendicular transect across the river where possible and installed them independently from each other.

We preserved samples in 10% formalin, and in the laboratory, washed samples through 0.5 and 1 mm Endecott sieves before identifying and enumerating to the lowest possible taxonomic level using available keys (e.g. Towns & Peters 1996, Winterbourn et al. 2000). Groups that are difficult to identify such as chironomids were only taken to sub-family level. We did not include drifting terrestrial invertebrates and emergent adult aquatic insects in the analysis. We pooled benthic samples and converted densities to m^2 , and converted drift densities to the number of animals per m^3 . The propensity to drift was the number of animals in the drift (per m^3) divided by the number of animals in the benthos (per m^2) multiplied by 100. Taxonomic richness of the drift was the number of taxa collected over the 24 hour period for all five drift nets. Similarly, richness of benthic samples was the number of taxa present in all five samples per site.

Periphyton

We estimated periphyton biomass from measures of chlorophyll-*a* from five stones (mean area: 60 cm²) collected randomly from each site which were kept cool and dark before being frozen. We extracted chlorophyll-*a* and phaeophytin using 90 % acetone at 5 °C for 24 h in the dark. We used a Varian Cary 50 conc UV-Visible Spectrophotometer to read absorbances and assessed pigment concentration using methods outlined in Steinman & Lamberti (1996). We corrected pigment concentration for stone surface area using methods by Graham et al. (1988) and then halved due to only half the stone being exposed for periphyton growth.

Statistical analysis

We used principal component analysis (PCA) on normalized environmental variables to reduce the number of dimensions of environmental data using Primer v6 (Clarke & Gorley 2006). To assess whether periphyton biomass and drift propensity differed between the three sections of river with regard to dam positions, we used one-way Analysis of Variance (ANOVA) in R 2.13.1 (R Development Core Team 2012) and we used linear regression to assess whether periphyton biomass changed in a longitudinal pattern downstream using R 2.13.1 (R Development Core Team 2012). To assess the relationship between both relative abundances and densities of benthic against drifting macroinvertebrates, we used simple linear regression in R 2.13.1 (R Development Core Team 2012). We used regression to assess whether drift propensity of all taxa and the major taxonomic groups (and some abundant individual taxa) was related to periphyton biomass and distance from source, as well as whether these groups could be predicted by the remaining environmental variables using the first two principal components of the PCA.

We correlated Bray-Curtis resemblance matrices for log ($x+1$) transformed abundance data for benthic and drifting macroinvertebrates using Spearman rank correlations, and determined significance with the nonparametric Monte Carlo permutation procedure RELATE (Somerfield & Clarke 1995) in Primer v6 (Clarke & Gorley 2006). We tested for differences between structure of both drift and benthic data separately in the three sections of river using the nonparametric procedure Analysis of Similarities (ANOSIM) (Clarke 1993) in Primer v6 (Clarke & Gorley 2006), by determining whether average similarities between samples within groups are more closely related than similarities of all pairs between groups (Clarke & Warwick 1994). To visualise any structural differences between benthic and drift datasets, we carried out a non-metric multi-dimensional scaling (NMDS) ordination (Kruskal & Wish 1978) on relative abundance data of combined drift and benthic data using Bray-Curtis similarity. We tested for differences between these data (factors: drift/benthos and river position) using two-way crossed ANOSIM in Primer v6.

Results

Physicochemical variables

The first two components of principal component analysis (PCA) explained 56.1 % of variation in the environmental data (PC1: 29.7 %; PC2: 26.3 %; Table 1).

Table 1. Eigenvector loadings on the first two principal components (PC's) of a PCA on environmental variables collected from 15 sites in the Tongariro River, New Zealand, 3–8 April, 2005.

Variable	PC1	PC2
Conductivity	–0.092	–0.325
Temperature	–0.198	–0.305
% Pool	–0.320	–0.013
% Run	–0.341	–0.224
% Riffle	0.349	0.25
% Rapid	0.293	–0.354
% Boulder	0.444	–0.077
% Cobble	0.007	–0.152
% C.G.	–0.38	0.262
% F.G.	–0.291	0.12
% Sand	–0.058	–0.361
Chlorophyll- <i>a</i>	–0.164	–0.457
Depth	0.224	–0.329
Velocity	0.136	–0.052

PC1 was structured heavily by physical factors associated with higher gradient sites, with positive loadings of percent boulders in the substrate, and percent riffle and rapid habitat. Percent fine and coarse gravels, and percentage of run habitat were negatively loaded on PC1. PC2 was largely structured by water chemistry variables and chlorophyll-*a* (Table 1). Conductivity, temperature, chlorophyll-*a* and depth were negatively associated with PC2, as were percent rapid and sand. Coarse gravel and riffle habitat were positively loaded on PC2 (Table 1).

Periphyton

Periphyton biomass, assessed as chlorophyll-*a*, increased with distance from source ($F_{1, 13} = 15.97$, $p = 0.002$, $R^2 = 0.55$). The lower section had periphyton biomass approximately twice as high as the upper section and six times greater biomass than sites in the middle section between the two dams ($F_{2, 12} = 7.56$, $p = 0.007$). Biomass ranged from 0.29 $\mu\text{g cm}^{-2}$ at site 5 to 3.23 $\mu\text{g cm}^{-2}$ at site 10.

Community composition

Seventy taxa were collected from the benthos and the drift. Forty eight taxa were collected from the benthos and 63 taxa from the drift. Diptera was the numerically dominant taxon throughout the river in both the benthos and drift averaging 72 % composition across all sites for the benthos and 79 % for the drift (Fig. 2). This was largely attributable to densities of chironomids which made up on average 70 % of benthic communities and 78 % of the drift. The main difference

Fig. 2. Benthic (a) and drift (b) densities for macroinvertebrates collected from 15 sites on the Tongariro River, New Zealand between 3–8 April, 2005. Shading and symbols represent the main orders/groups collected. Upper, middle and lower refer to sections of the river in relation to the two dams.

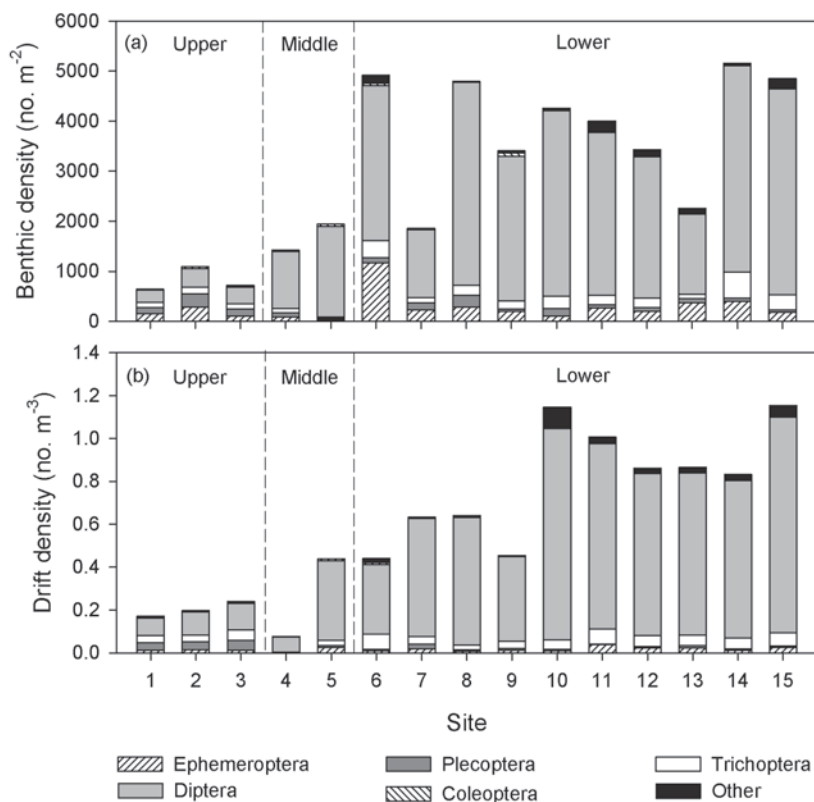


Table 2. Results of linear regression analysis of (a) percent composition and (b) density of drifting against benthic macroinvertebrates collected from 15 sites in the Tongariro River, New Zealand, 3–8 April, 2005. Degrees of freedom = 1, 13. Terms are included in equations only if they are significantly different from zero. NS = Non-significant relationship at $\alpha = 0.05$.

Taxa	<i>F</i>	<i>p</i>	<i>R</i> ²	Equation
(a) % composition				
Ephemeroptera	0.56	0.47	0.04	NS
Plecoptera	153.45	<0.0001	0.92	$y = -1.46 + 0.96x$
Trichoptera	30.39	<0.0001	0.70	$y = -0.32 + 1.29x$
Diptera	82.48	<0.0001	0.86	$y = 27.06 + 0.73x$
Coleoptera	6.23	0.03	0.32	$y = 0.37 + 0.64x$
Other	1.45	0.25	0.10	NS
(b) Density				
All taxa	13.08	0.003	0.50	$y = 0.15 + 0.0002x$
Ephemeroptera	0.05	0.82	0.004	NS
Plecoptera	3.85	0.07	0.23	NS
Trichoptera	4.48	0.05	0.26	$y = 0.03 + 0.00007x$
Diptera	20.04	0.0006	0.61	$y = 0.1 + 0.0002x$
Coleoptera	1.20	0.29	0.09	NS
Other	2.80	0.12	0.18	NS

between the three sections of the river was an increase in the density of dipterans in both the benthos and drift in the lower section (Fig. 2).

For the benthic data, Trichoptera (18) were the most taxonomically rich, followed by Diptera (10), and both Ephemeroptera (7) and Plecoptera (7). For

the drift data, Trichoptera (29) were again the most taxonomically rich with eleven more taxa than found in the benthos. Diptera were the next most diverse (12), followed by Ephemeroptera (8) and Plecoptera (7). Seven taxa that were present in the benthos were not collected in drift samples, whereas 22 taxa that

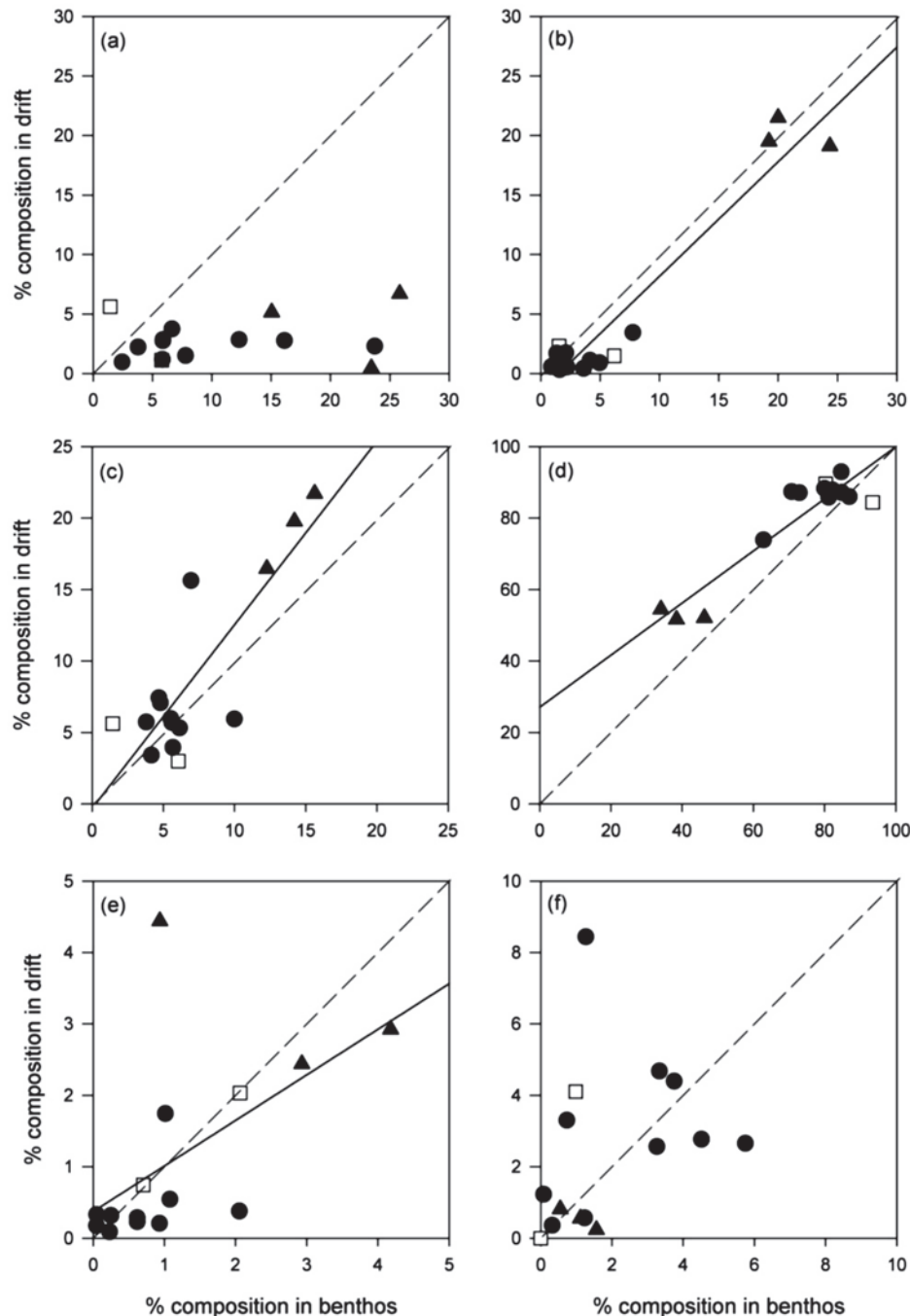


Fig. 3. Percentage contribution to the drift as a function of percentage contribution to the benthos for (a) Ephemeroptera, (b) Plecoptera, (c) Trichoptera, (d) Diptera, (e) Coleoptera, and (f) all other taxa, collected from 15 sites in the Tongariro River, New Zealand, 3–8 April, 2005. Closed triangles = upper river, open squares = middle section, closed circles = lower river. Dashed line represents a 1:1 ratio. Solid lines are displayed where a significant linear relationship exists at $\alpha = 0.05$. See Table 1 for results of linear regression.

were present in drift samples were not in the benthos at any sites.

While only identified to sub-family level, Orthocladiinae (benthos: 870 individuals m^{-2} ; drift: 0.27 individuals m^{-3}) and Diamesinae (benthos: 1127 indi-

viduals m^{-2} ; drift: 0.18 individuals m^{-3}) were the most abundant groups across both sample types, followed by the mayfly *Deleatidium* spp. (benthos: 249 individuals m^{-2} ; drift: 0.02 individuals m^{-3}). Those taxa found in one but not both of the two sample types (i.e.

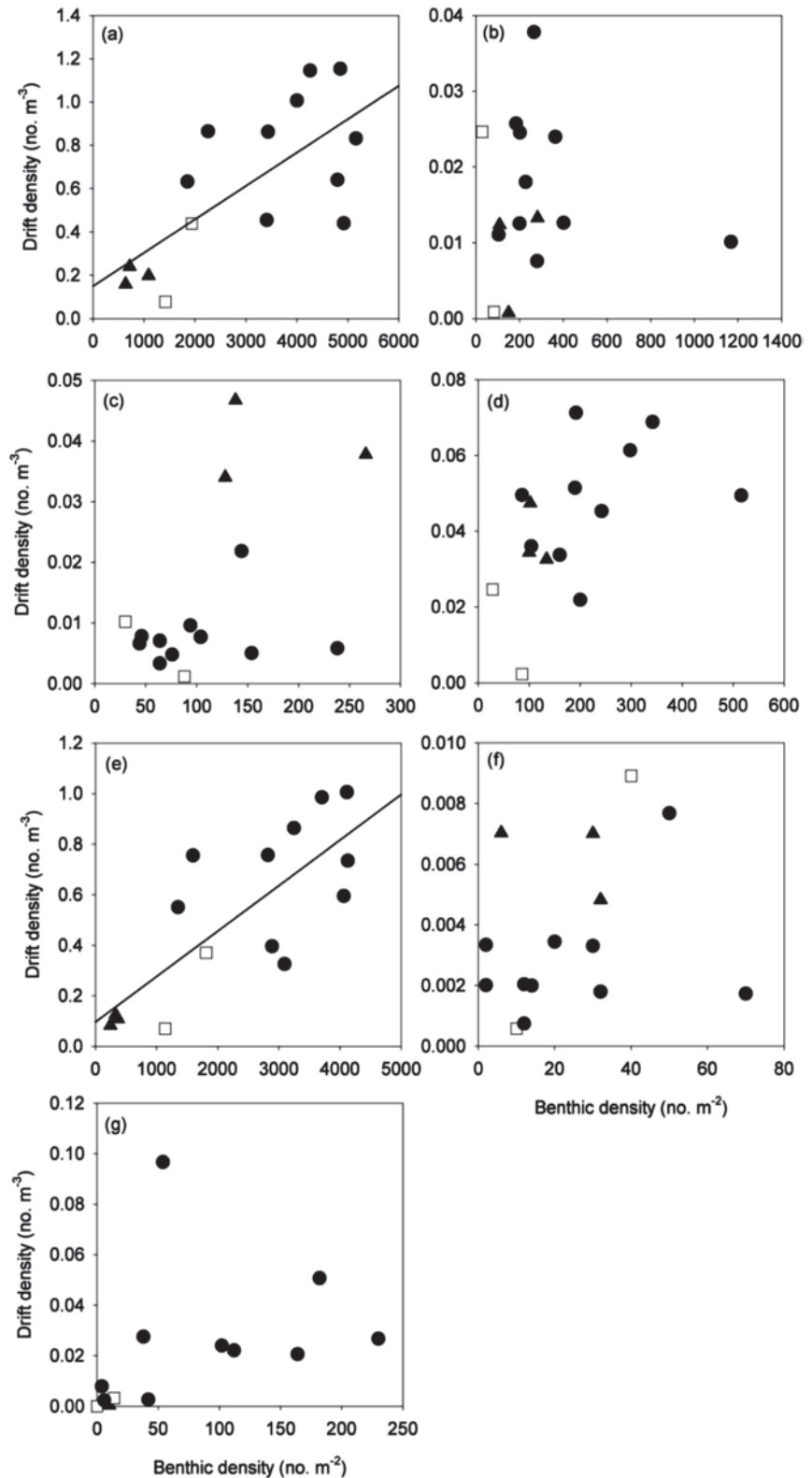


Fig. 4. Drift density as a function of benthic density for (a) All taxa, (b) Ephemeroptera, (c) Plecoptera, (d) Trichoptera, (e) Diptera, (f) Coleoptera, and (g) all other taxa, collected from 15 sites in the Tongariro River, New Zealand, 3–8 April, 2005. Closed triangles = upper river, open squares = middle section, closed circles = lower river. Solid lines are displayed where a significant linear relationship exists at $\alpha = 0.05$. See Table 1 for results of linear regression.

benthos or drift) were always in low densities where they were present. The most abundant taxa found in the benthos but not in the drift was the predatory

stonefly *Stenoperla prasina* which was only found at 3 sites, in the upper and middle sections, with the highest density being 4 individuals m⁻². The cased caddis-

fly *Hudsonema amabile* was the species with highest densities in the drift that wasn't present in any benthic samples (0.0003 m^{-3}), and were only found in sites from site 10 down river.

The density of benthic macroinvertebrates ranged from 640 individuals m^{-2} at site 1 in the upper section to 5160 individuals m^{-2} at site 14 in the lower section. Drift density ranged from 0.08 individuals m^{-3} at site 4 immediately downstream of Rangipo Dam to 1.15 individuals m^{-3} at site 15 in the lower section. The pooled taxonomic richness of the benthos at each site ranged from 16 taxa at site 5 in the middle section to 31 taxa at sites 12 and 14 in the lower section. Pooled richness in the drift ranged from 14 taxa at site 4 to 33 taxa at site 12 in the lower section of the river.

Drift vs benthos

Over the 24 hour period sampled, ephemeropterans demonstrated a low propensity to enter the drift with a much lower contribution to the drift than found in the benthos (Fig. 3; Table 2). Plecoptera exhibited a near 1:1 ratio of drift to benthos proportions and a strong linear relationship was present between the two, whereas dipterans were found to be in higher proportions in the drift than the benthos (Fig. 3; Table 2). Trichoptera exhibited a strong increase in drift ratio with increasing benthic proportion, with a higher propensity to enter the drift in the three upper river sites, and were around a 1:1 ratio in the remainder of sites (Fig. 3; Table 2).

Overall densities of all taxa in the benthos and drift were linearly linked with drift density increasing according to benthic density (Fig. 4; Table 2). However, the only major group to also display a relationship between benthic and drift densities was Diptera (Fig. 4; Table 2). Removing Diptera from the 'all taxa' data, removed any relationship between drift and benthic density ($R^2 = 0.12$, $F_{1,13} = 1.69$, $p = 0.22$). There was no relationship between the number of taxa collected from the drift over the 24 hour period to that found in the benthos at each site ($R^2 = 0.10$, $F_{1,13} = 1.51$, $p = 0.24$; Fig. 5).

Drift propensity

The propensity to drift did not differ between the three sections of river for all taxa or any of the major groups (Table 3). Furthermore, drift propensity for all

Table 3. Results of one-way Analysis of Variance (ANOVA) testing for differences in the propensity to drift of macroinvertebrates between the three sections of river with regard to dam location collected from 15 sites in the Tongariro River, New Zealand, 3–8 April, 2005. Degrees of freedom = 2, 12.

Taxa	F	p
All taxa	0.92	0.42
Ephemeroptera	3.58	0.06
Plecoptera	3.70	0.06
Trichoptera	0.76	0.49
Diptera	2.08	0.17
Coleoptera	0.31	0.74
Other	0.60	0.57

Table 4. Results of linear regression analysis of propensity to drift of macroinvertebrates as a function of (a) periphyton biomass (chlorophyll-*a*) and (b) distance from source collected from 15 sites in the Tongariro River, New Zealand, 3–8 April, 2005. Degrees of freedom = 1, 13. No relationships were significant at $\alpha = 0.05$.

Taxa	F	p	R ²
(a) Chlorophyll-<i>a</i>			
All taxa	1.36	0.26	0.10
Ephemeroptera	1.03	0.33	0.07
Plecoptera	3.45	0.09	0.21
Trichoptera	1.41	0.26	0.10
Diptera	0.52	0.48	0.04
Coleoptera	0.99	0.34	0.07
Other	3.19	0.10	0.21
(b) Distance from source			
All taxa	0.61	0.45	0.04
Ephemeroptera	0.12	0.73	0.01
Plecoptera	3.98	0.07	0.23
Trichoptera	0.30	0.59	0.02
Diptera	0.06	0.81	0.004
Coleoptera	<0.01	0.96	0.0002
Other	0.87	0.37	0.07

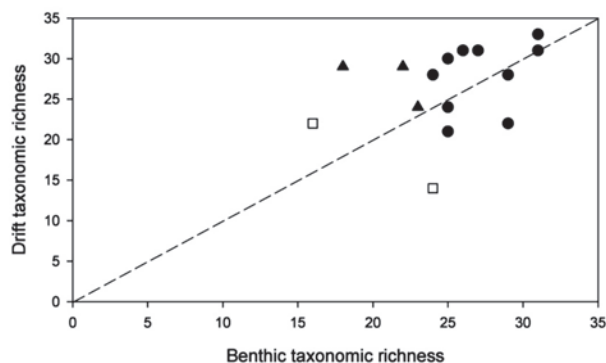


Fig. 5. Number of taxa collected over a 24 hr period as a function of benthic density collected from 15 sites in the Tongariro River, New Zealand, 3–8 April, 2005. Closed triangles = upper river, open squares = middle section, closed circles = lower river. Dashed line represents a 1:1 ratio. See text for results of linear regression.

taxa combined or any of the major groups was not related to chlorophyll-*a* or distance from source (Table 4). Likewise, there was no relationship between either chlorophyll-*a* or distance from source and the three most numerous taxa: *Deleatidium* spp. (chlorophyll-*a*: $R^2 = 0.08$, $F_{1,13} = 1.08$, $p = 0.32$; distance from source: $R^2 = 0.02$, $F_{1,13} = 0.21$, $p = 0.66$), Diamesinae (chlorophyll-*a*: $R^2 = 0.0008$, $F_{1,13} = 0.009$, $p = 0.92$; distance from source: $R^2 = 0.01$, $F_{1,13} = 0.18$, $p = 0.68$), or Orthoclaadiinae (chlorophyll-*a*: $R^2 = 0.25$, $F_{1,13} = 4.25$, $p = 0.06$; distance from source: $R^2 = 0.09$, $F_{1,13} = 1.29$, $p = 0.28$).

The only taxonomic group to respond to either of the principal components was Plecoptera, which increased linearly along PC2 (Table 5). This was reflected by the most abundant stonefly, *Zelandoperla* sp., increasing linearly with PC2 ($R^2 = 0.44$, $F_{1,13} = 9.58$, $p = 0.009$, $y = 0.01 + 0.004x$). *Deleatidium* spp. did not respond to either PC1 ($R^2 = 0.18$, $F_{1,13} = 2.94$, $p = 0.11$) or PC2 ($R^2 = 0.06$, $F_{1,13} = 0.78$, $p = 0.39$). Moreover, Diamesinae (PC1: $R^2 = 0.13$, $F_{1,13} = 1.97$, $p = 0.18$; PC2: $R^2 = 0.008$, $F_{1,13} = 0.11$, $p = 0.75$) and Orthoclaadiinae (PC1: $R^2 = 0.03$, $F_{1,13} = 0.42$, $p = 0.53$; PC2: $R^2 = 0.12$, $F_{1,13} = 1.77$, $p = 0.21$) did not respond to either PC.

Multivariate structure

Multivariate structure of log ($x+1$) transformed abundance datasets for both the benthos and drift exhibited similar patterns (RELATE $\rho = 0.56$, $p = 0.002$). There were clear differences between the three sections of river for both the benthos and drift, and ANOSIM confirmed these differences (Fig. 6; Table 6). However, for both the benthos and drift, there was no pair-wise difference between the upper and middle sections (Table 6). When combining both the benthos and drift using relative abundance data, NMDS indicated clear differences between invertebrate relative abundance in the benthos and drift (ANOSIM $R = 0.268$, $p = 0.01$), but differences were stronger between the three sections of river (ANOSIM $R = 0.756$, $p = 0.001$).

Table 5. Results of linear regression analysis of propensity to drift of macroinvertebrates as a function of (a) principal component (PC) 1 and (b) PC2 collected from 15 sites in the Tongariro River, New Zealand, 3–8 April, 2005. Degrees of freedom = 1, 13. NS represents no significant relationship at $\alpha = 0.05$.

Taxa	<i>F</i>	<i>p</i>	<i>R</i> ²	Equation
(a) PC1				
All taxa	0.6	0.45	0.04	NS
Ephemeroptera	3.19	0.1	0.2	NS
Plecoptera	0.65	0.43	0.05	NS
Trichoptera	0.81	0.39	0.06	NS
Diptera	1.36	0.26	0.09	NS
Coleoptera	0.002	0.97	0.0001	NS
Other	0.32	0.58	0.03	NS
(b) PC2				
All taxa	0.18	0.68	0.01	NS
Ephemeroptera	0.81	0.39	0.06	NS
Plecoptera	5.03	0.04	0.28	$y = 0.01 + 0.003x$
Trichoptera	2.34	0.15	0.15	NS
Diptera	0.004	0.95	0.0003	NS
Coleoptera	2.27	0.16	0.15	NS
Other	3.57	0.08	0.23	NS

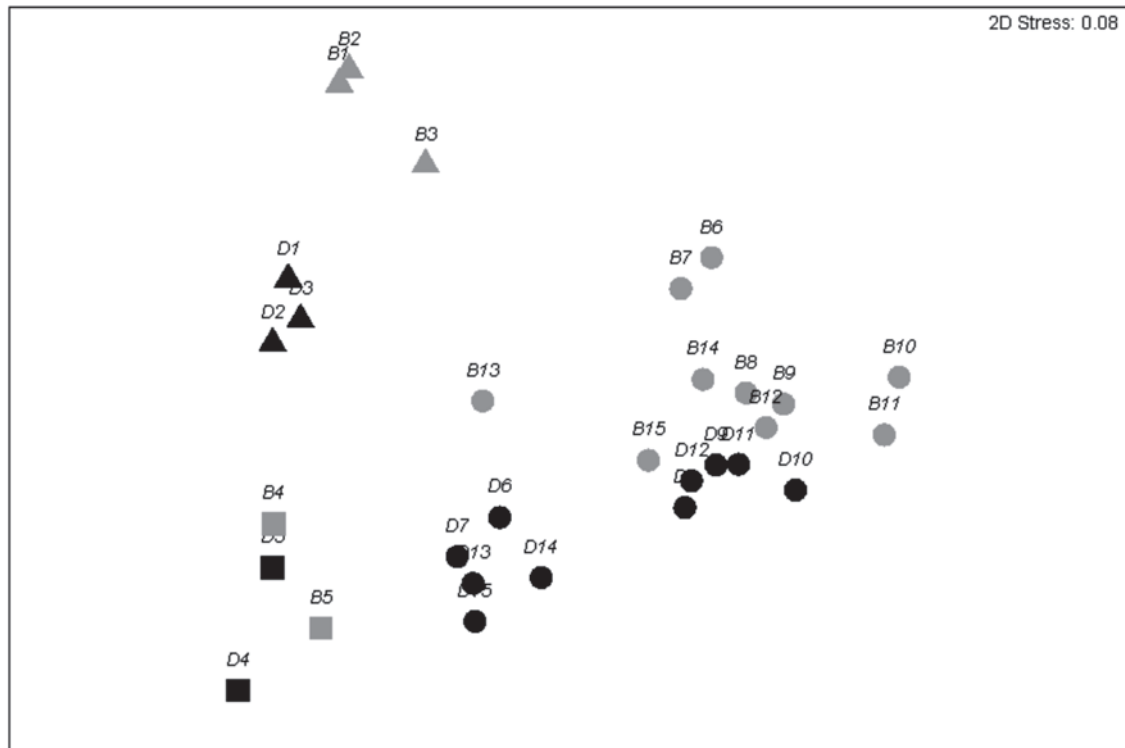


Fig. 6. Non-metric multidimensional scaling ordination on relative abundance drift and benthic data collected from 15 sites in the Tongariro River, New Zealand, 3–8 April, 2005. Samples are coded relative to their position in the river and whether they are drift or benthic. Black symbols represent drift data and grey symbols represent benthic data. Triangles = upper river, squares = middle section, circles = lower river. Sites are labeled in order of their position in the river (site 1 is the uppermost site and 15 the furthest downstream). Benthic samples are labeled with the prefix B and drift with D. 2D stress: 0.08.

Table 6. Results of one-way Analysis of Similarities (ANOSIM) testing for differences in benthic and drifting macroinvertebrate multivariate structure individually between the three sections of river with regard to dam location collected from 15 sites in the Tongariro River, New Zealand, 3–8 April, 2005. **(a)** Log ($x+1$) transformed abundance data, **(b)** percent composition data. Overall = Global ANOSIM between three sections; the remaining analyses are pairwise differences between the three river sections: upper, middle and lower.

Group comparisons	Benthos		Drift	
	<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>
(a) Abundance				
Overall	0.87	0.001	0.90	0.001
Upper – Middle	0.75	0.100	0.50	0.100
Upper – Lower	0.97	0.003	1.00	0.003
Middle – Lower	0.80	0.015	0.79	0.015
(b) % composition				
Overall	0.94	0.001	0.85	0.001
Upper – Middle	1.00	0.100	1.00	0.100
Upper – Lower	0.93	0.003	0.91	0.003
Middle – Lower	0.94	0.015	0.75	0.015

Discussion

Drift-benthos relationships

We found clear differences in both benthic and drifting macroinvertebrates between the three sections of river

subject to differing levels of flow alteration. However, the main differences were between the lower section of river and the remaining two sections (middle and upper), with no pairwise difference between the middle and upper sections. This lack of difference be-

tween the upper and middle sections is likely to be a function of the small number of sites sampled in these sections, three and two sites respectively, limiting the ability to draw inferences from these data. Previous studies on the Tongariro River conclude that shifts in invertebrate communities downstream of the dams were likely caused through changes in benthic periphyton biomass (Quinn & Vickers 1992, Dedual & Collier 1995, Collier 2002). However, riverine biota downstream of dams can be affected through a multitude of factors including changes to temperature, velocity, sediment and habitat (Vinson 2001, Bunn & Arthington 2002).

The dams on the Tongariro River now operate in a 'run-of-river' manner due to infilling of the reservoirs, which limits downstream effects such as changes in temperature regimes and water chemistry typically experienced with large reservoirs (Ahearn et al. 2005). Despite this, it appears the flow alteration in the Tongariro River is enough to alter downstream periphyton and drift density (Tonkin et al. 2009), but not propensity as in this study. It is possible that invertebrate assemblages are influenced by the input of hypolimnetic water which is diverted into the Tongariro River, above Rangipo Dam, from the Moawhango Dam in a neighbouring catchment. Hypolimnetic water can alter the dissolved oxygen and temperature regimes of rivers downstream of dams (e.g. Saltveit et al. 1994, Cereghino & Lavandier 1998), thereby affecting invertebrate communities. Nonetheless, a recent study found the construction of a small run-of-river dam in China altered downstream algal assemblages, with more pronounced effects revealing themselves 2–3 years post construction (Wu et al. 2009).

Overall multivariate structure of the benthos and drift was strongly linked when comparing abundance data, with similar differences in composition between the three sections of river. Conversely, relative abundance data revealed clear differences between the multivariate structure of the benthos and drift, although there were strong linear relationships between the drift and benthos for many of the taxa assessed. Patterns were somewhat driven by Diptera, which dominated both the benthos and slightly more the drift, and when removed, there was no direct univariate relationship between densities of the remaining groups of taxa in the drift and benthos.

The relative abundance of dipterans was greatest in the flow regulated sections of the river, as is often the case (Munn & Brusven 1991, Camargo & Voelz 1998). Diptera are often particularly common in the drift but this is usually a simple function of their abun-

dance in the benthos (Robinson et al. 2002, Hieber et al. 2003). Chironomids from the two sub-families Orthocladiinae and Diamesinae were largely responsible for the dominance of Diptera. Chironomids have been shown to be passive drifters (Elliott 1971), often reflecting current velocity (Brittain & Eikeland 1988). Consequently they may drift for longer distances than more active drifters, especially in large high velocity rivers such as the Tongariro with velocity ranging between 0.7–1.22 m s⁻¹ at the study sites.

We expected mayflies to dominate the drift (Brittain & Eikeland 1988, Allan & Castillo 2007), but found a consistently low percent composition despite benthic increases. The most abundant mayfly in this study, *Deleatidium* spp., exhibited no linear link between the benthos and drift, and the propensity of *Deleatidium* to drift was not related to periphyton biomass, distance from source or any environmental variable. *Deleatidium* have been found to dominate the drift in previous New Zealand studies but their drift may depend on their life stage (Sagar & Glova 1992a, Sagar & Glova 1992b), which we did not assess here. These studies and other previous New Zealand studies have found correlations between densities of macroinvertebrates in the drift and benthos (e.g. McLay 1968, Sagar & Glova 1992b), but Graesser (1988) found no such correlation in three flood-prone Westland streams. Furthermore, when assessing the full pooled community of invertebrates, Shearer et al. (2003) found no correlation between benthic and drift densities, but did at the order level with pooled Ephemeroptera, Diptera and Trichoptera, when combining multiple rivers.

While benthic and drift samples were often similar in composition, there were some departures from linear trends, especially when considering raw densities for individual groups except dipterans. Considerably more taxa were collected in the drift than the benthos, with comparable richness and ratio to a similar study on the nearby Manganuiateao River (Collier & Wakelin 1992). While many factors could potentially explain some of the benthos-drift differences we found (Brittain & Eikeland 1988), one likely influence is that the source of drift is different to the benthic sampling location. Drift can come from long distances and various habitats upstream, especially in larger rivers (Waters 1965, Brittain & Eikeland 1988, Gibbins et al. 2010), thus although drift was collected from riffles, it wasn't limited to riffle-dwelling species. For instance, the caddisfly *Hudsonema amabile* and the mayfly *Amelotopsis perscitus*, which tend to favour slower flowing stream edges, were collected in the drift but not the benthos.

Despite differences in benthic and drifting macroinvertebrates between the three sections, drift propensity was not affected by the presence of dams and altered flow regimes; nor was it affected by periphyton biomass or distance from source. Evidence suggests emigration rates are highly affected by food resource levels; with a reduction in drift rates when resources increase (Richardson 1991, Hinterleitner-Anderson et al. 1992, Siler et al. 2001) and greater drift when resources are low (Kohler 1985, Siler et al. 2001) or patchy (Townsend & Hildrew 1976). Still, drift and benthic density, given the linear link between the two, did increase with increasing periphyton biomass (Tonkin et al. 2009); a pattern also found in benthic communities of surrounding catchments (Tonkin & Death 2012, Tonkin et al. 2012).

The method used here to calculate propensity, dividing drift density by benthic density, may have resulted in considerable 'noise' in the data (Downes 2010), reducing the chance of finding strong links. Moreover, the two predictors, periphyton biomass and distance from source, were autocorrelated which complicates interpretation. However, we used both because periphyton biomass formed three distinct groups in relation to the three river sections rather than a simple linear relationship with distance downstream (Fig. 3 in Tonkin et al. 2009).

While the variability of drift rates we found may be reflecting factors such as resource patchiness, pooling samples across riffles is problematic for identifying these factors. Drift itself is highly patchy and can fluctuate significantly both spatially and temporally (Neale et al. 2008). Often this patchiness is at smaller spatial scales such as reach and patch units, but less so between streams (Boyero & Bosch 2002, Shearer et al. 2003, Neale et al. 2008, Leung et al. 2009), and considerable differences have even been found between drift nets centimetres apart (Downes & Keough 1998), but it may simply be a reflection of benthic patchiness (Downes et al. 1993, Lake 2000).

To more wholly evaluate drift propensity patterns and whether propensity is affected by food supply, we would need finer-scale and more comprehensively replicated long-term sampling, rather than one-off 24 hour samples. In fact, night-time sampling could provide more insight into density dependent drift patterns as drift tends to be more behaviourally oriented to avoid predation rather than the more constant diurnal involuntary drift (Flecker 1992). Even so, given flow remained constant during the sampling period as these dams do not hydropeak, drift sampling was comparable between the regulated and unregulated sections.

Long-term sampling would not only provide more insight into seasonal drift patterns, as seasonal fluctuations in drift are common in temperate regions (Brittain & Eikeland 1988, Sagar & Glova 1992b, Shearer et al. 2002), but also into drift response to changing periphyton biomass. Despite this, clear density independent drift events such as large synchronized emergence events should be less common in New Zealand than elsewhere due to the lack of seasonality and poorly synchronized life cycles in aquatic insects (Winterbourn et al. 1981).

Management implications

Finding more taxa present in the drift suggests drift could be a potential biomonitoring tool as it can capture additional information on riverine biota otherwise overlooked by benthic sampling only (Pringle & Ramirez 1998). However, it is likely better as a complementary measurement to benthic sampling (Pringle & Ramirez 1998). Our data indicate that drift does not necessarily represent the full benthic community standing crop for all species as different taxa have varying propensity to drift (Brittain & Eikeland 1988). Due to factors such as the extra processing time and costs involved with drift compared to benthic samples, drift is often overlooked as a sampling method. Consequently, Shearer et al. (2003) assessed benthos-drift density links in multiple rivers to evaluate whether benthic data could be extrapolated for use as an estimate of drift for models of drift feeding fish (Hayes et al. 2000). Unfortunately with both density dependent and independent factors controlling drift, a general benthos:drift ratio appears unattainable (Shearer et al. 2003).

The high proportion of dipterans in both the drift and benthos matches that found in a previous study on the lower Tongariro River (Dedual & Collier 1995), which found that while Diptera were the most commonly consumed prey type by juvenile rainbow trout (*Oncorhynchus mykiss*), they were not the preferred choice. Drift is a vital means of energy transfer to higher trophic levels such as drift feeding salmonids (Hayes et al. 2000), and can structure behavioural patterns of drift feeding fish (Giroux et al. 2000, Hansen & Closs 2005); thus is crucial to the Tongariro River which supports an important rainbow and brown (*Salmo trutta*) trout fishery (Stephens 1989).

Conclusions

While the presence of dams, and resulting differences in flow regimes, are clearly correlated with both drifting and benthic macroinvertebrates in the Tongariro River, the actual propensity of macroinvertebrates to drift did not differ between the sections. As hypothesized, drift propensity was not linked with benthic periphyton biomass or longitudinal trends down the river, indicating density dependent behavioural responses to changes in habitat or food supply may not be occurring. However, detecting and fully assessing these effects would require more long term seasonal sampling. Links between benthic and drifting macroinvertebrates were variable, with some taxa exhibiting linear links between relative abundance in the benthos and drift, but drift composition was largely representative of the benthos. However, the dominance of Diptera throughout the river swamped any clear patterns in the overall data. These results suggest that while flow regulation on the Tongariro River may be affecting macroinvertebrate communities through altered periphyton biomass, with the exception of some taxon-specific responses, it doesn't appear to affect the propensity to drift. We suggest more long-term experiments on behavioural drift in non-hydropeaking regulated rivers would be a fruitful area of research to elucidate any impacts regulation may have.

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