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Abstract   Identifying the environmental factors influencing biotic patterns in large rivers will assist with extrapolating biological monitoring results to broader scale conclusions about river condition. In the present study, we collected macroinvertebrates and physico-chemical data at 47 shallow-water (<1-m deep) sites, including nine sites at major tributary junctions, during summer along the lower Waikato River, North Island, New Zealand. Macroinvertebrate communities were dominated by a few relatively abundant and widespread taxa. Upper site samples were characterised by high relative abundances of Diptera, but the significance of this group declined further downstream where Crustacea became more dominant. Overall, more taxa (36) were found at tributary junctions than at mainstem sites within four hydrogeomorphic zones (22–31 taxa per zone). Significant differences among faunal groups identified in a cluster analysis on relative abundance data were detected for the percentage of wood sampled, and for water conductivity which increased downstream at mainstem sites and was high at some junction sites. Non-metric multidimensional scaling of percentage abundance data revealed differences in community composition among zones,

and among some mainstem and tributary junction sites. Geographic position (easting and northing) was significantly correlated with taxa richness and community evenness (Pielou) at mainstem sites (excluding tributary junctions), reflecting an increase in sample diversity and less equitable taxonomic dominance with distance down river. Overall, these results point to an interplay between habitat patchiness and successional and hydrogeomorphic processes influencing macroinvertebrate community composition in the lower Waikato River. Such multiscale variations need to be accounted for in the design of invertebrate biomonitoring programmes if they are to represent the ecological condition of large river environments.

INTRODUCTION

Large rivers are iconic features of many landscapes yet, compared with wadeable systems, relatively little is known about factors influencing their function or the structure and composition of their biological communities. Penultimate river sections can integrate environmental conditions over large spatial scales by reflecting the cumulative effects of activities in extensive upstream catchments, while at the same time naturally interacting with lowland alluvial floodplains (Puckridge et al. 1998; Tockner & Stanford 2002). Such interactions lead to a tight interplay between landscape condition and morphology, hydrodynamics and degree of connectivity in unmodified settings (deDrago et al. 2004). Within-channel complexity can be high in large rivers owing to features such as transverse asymmetry across the channel (Bournaud et al. 1998), and the occurrence of islands, side-arms, slack-water areas, and large tributary junctions (Thorp 1992; Cellot 1996; Schiemer et al. 2001; Kiffney et al. 2006). It has been proposed that transitions among hydrogeomorphic patches along with hydrological

retention characteristics regulate biological diversity in large rivers (Thorp et al. 2006).

Globally, large rivers have undergone significant anthropogenic modification over the last few hundred years through a combination of large-scale changes. Activities have included desnagging operations to facilitate navigation (Harmon et al. 1986), impoundment and flow regulation for hydroelectricity generation (Ligon et al. 1995), truncation of floodplain interactions for flood control purposes (Bayley 1991; Kroon & Ansell 2006), and the introduction and spread of alien species that often proliferate in these environments (Thorp & Casper 2003; Tempero et al. 2006). These ecosystems present a number of challenges for ecologists intent on assessing the effects of anthropogenic modifications and documenting biological patterns. Not least among these challenges are the inaccessibility of deep and fast-flowing habitats using conventional sampling techniques, and the intensity of sampling potentially required to represent the scale and complexity of large river environments. Attempts to deal with these challenges have involved the use of artificial substrates (Boothroyd & Dickie 1989), dredges (Bournard et al. 1998), and grab (Thorp 1992), core (Boubée 1977), or air-lift (Carter 2000; Neale et al. 2006) samplers to collect invertebrate faunas in difficult-to-access habitats. Others have restricted sampling to near-shore areas using kick nets (e.g., Reece & Richardson 2000) where most aquatic invertebrate production is considered to occur (Thorp & Delong 1994).

Many of the anthropogenic impacts on large rivers described above have also occurred in the Waikato River, New Zealand's longest river, where extensive regulation of flows for hydroelectricity generation and flood prevention has occurred, along with other pressures associated with agricultural and urban development (Chapman 1996). Nevertheless, water quality of the river has improved considerably since the 1950s, with dissolved oxygen, pH and ammonia generally considered "excellent" for ecological purposes (Smith 2006). Studies conducted to date using a range of different sampling methods have contributed to a broadscale understanding of spatial and temporal patterns in macroinvertebrate community composition along the Waikato River (e.g., Davenport 1981; Carter 2000; Taylor 2001). However, more intensive sampling is required to identify the spatial scale over which these patterns occur, both longitudinally and among habitats, to help provide a basis for extrapolating the results of biological monitoring to broader scale conclusions about river condition. In the present study, we used a spatially-stratified approach to assess macroscale (hydrogeomorphic zone and position along the channel), mesoscale (habitats within zones), and microscale (e.g., among substrate types) variations in macroinvertebrate community composition along the lower Waikato River. Our specific aims were to: (1) assess whether hydrogeomorphic zonation or a longitudinal gradient in community composition occurs based on macroscale features and measures of spatial location; and (2) determine the significance of different mesoscale and microscale habitats for the diversity and composition of the fauna.

MATERIALS AND METHODS

Study area

The Waikato River drains a catchment area of 14 260 km^2 or 12% of the area of New Zealand's North Island (ew.govt.nz). Its flow originates on the eastern flank of Mt Ruapehu at 2797 m a.s.l., and then enters the Tongariro River before passing through Lake Taupo. From the lake, the river has cut a path through an ignimbrite plateau to create a high gradient middle section that supports eight hydroelectric dams. Along this section the river falls 340 m over 188 km to the lowest dam at Karapiro (Fig. 1), falling a further 40 m to Port Waikato 140 km downstream. Land use along this lower section is predominantly agricultural with several urban centres present, the largest of which is Hamilton with a population of 185 000 (2005 figures, www.stats.govt.nz), and where mean annual rainfall and air temperature are 1082 mm and 13.6°C, respectively (www.ew.govt.nz; www.metservice.com). Median river discharge at Hamilton is 254 m^3.s^{-1}, increasing to 403 m^3.s^{-1} at Mercer (Fig. 1) (Environment Waikato unpubl. data). Chapman (1996) noted at the time that the river provided drinking water for over 30 communities and around 30% of New Zealand's electricity generation, and the catchment supported over 5.6 million cows, beef cattle and sheep, in addition to over 340 000 humans. Several introduced fish are widespread in the lower Waikato River system including rudd (*Scardinius erythrophthalmus*), tench (*Tinca tinca*), goldfish (*Carassius auratus*), and koi carp (*Cyprinus carpio*), which are abundant (Hicks et al. 2005; Tempero et al. 2006).

For sampling purposes in the present study, the lower Waikato River was divided into four zones of similar length (22 to 33 km) based on known geomorphic and hydrological differences (Fig. 1).

Fig. 1 Location of sampling sites in four zones (boundaries indicated by bars) along the lower Waikato River, New Zealand.
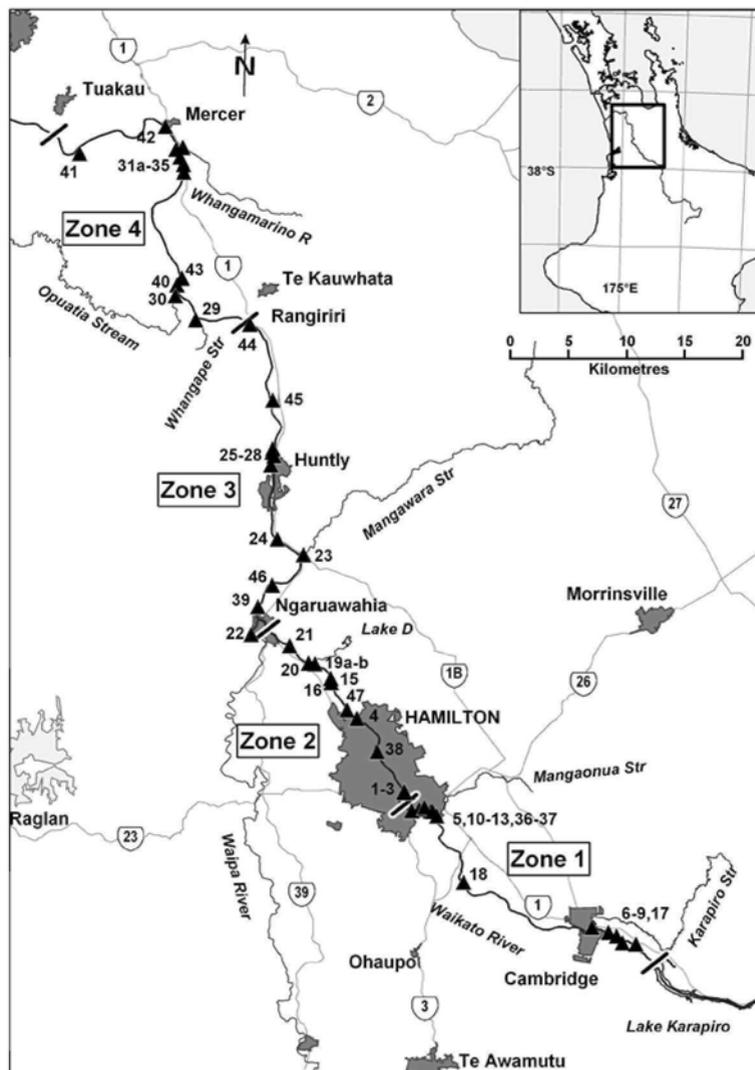
Zone 1—Karapiro to Hamilton City

This narrow incised section has steep littoral zones and is frequently constrained by vertical ignimbrite walls. Adjacent land use is predominantly agricultural. Regulated flows create variable water levels which mainly affect depth rather than wetted width owing to the incised channel.

Zone 2—Hamilton City to Ngaruawahia

The channel is less incised, with extensive willow fringes and some gently-shelving gravel beaches which are exposed to varying degrees during water level fluctuations. Macrophyte beds occur in permanently submerged littoral areas.

Zone 3—Ngaruawahia to Rangiriri

The Waipa River enters the Waikato River at Ngaruawahia where it increases mean flow by 25%, dampening flow fluctuations and markedly increasing water turbidity downstream (Smith 2006). Downstream of Ngaruawahia, the river becomes constricted as it flows through the Taupiri Cut, and then broadens into what was originally a floodplain area with several riverine lakes. Stop-banking and other flood control works now limit floodplain interactions. Extensive willow fringes are evident as well as grassy banks that are grazed by livestock. Macrophyte beds are more prevalent in this stretch and there are occasional shallow mid-channel bars.

Zone 4—Rangiriri to Tuakau

The river becomes constricted in parts as it moves through low hills towards the coast. Occasional islands are present and the bed largely comprises mobile, duning sand (Davenport 1981). River margins are fringed with willows and macrophyte beds grow in areas of fine sediment. The flow is tidally-influenced along much of this zone but is not affected by saline intrusion (Environment Waikato unpubl. data).

A total of 47 sites in these zones was sampled between 7 and 25 February 2005 at accessible locations determined by proximity to roads, tracks and boat ramps, and the steepness of river banks. Similar numbers of sites occurred in each zone (n = 10–14). Nine sites were at major tributary junctions (Fig. 1): Karapiro (Site 17, zone 1), Mangaonua (Site 10, zone 1), Waikere (Sites 19a and 19b, zone 2), Waipa (Site 22, zone 3), Mangawara (Site 23, zone 3), Whangape (Site 29, zone 4), Opuatia (Site 30, zone 4), and Whangamarino (Site 33, zone 4). All tributaries are 5th–6th order except for Waikere Stream which is mapped as 3rd order and drains several lakes.

Environmental measurements

Water temperature (0.1°C) and conductivity (0.1 mS.m^{-1}) were measured at the time of sampling with WTW Cond. 340i or YSI 3200 meters. Visual assessments were made of water velocity (none, very slow (<0.1 m.s^{-1}), slow (0.1–0.2 m.s^{-1})), degree of overhead shade (insignificant, partial, significant) and percentage substrate composition (inorganic, macrophyte, wood, roots) in the sampling area. In addition, the size distribution of inorganic particles sampled was assessed visually according to the following size classes based on median diameter: sand/silt (<2 mm), gravel (2–64 mm), cobble (>64–256 mm), and boulder (>256 mm) (which was generally associated with bank stabilisation).

Macroinvertebrate sampling and processing

Invertebrates were sampled from a range of habitat types within 1 m depth from the water surface. Habitats included littoral shelves, rock faces, islands/sandbars, side channels, banks/beaches, and coves/backwaters at locations that were adjacent to true right or left banks, mid-river (at least 10 m from either bank), or at junctions with major tributaries. Samples were collected by sweeping a D-frame net (0.5 mm mesh) through vegetation, brushing wood, and disturbing benthic substrates upstream for 2–5 min depending on habitat availability. A 0.5 mm

mesh net size is widely used for biomonitoring in New Zealand (Stark et al. 2001), but can be expected to under-represent some small taxa such as early instar chironomids and Collembola.

Samples were stored in c. 70% isopropanol and subsequently rinsed thoroughly over a 0.5 mm sieve, and large organic material was discarded after being visually inspected for invertebrates. The remaining sample was spread evenly on a 300 mm □ 400 mm tray marked with 100 mm □ 100 mm grids, and one grid square was selected randomly. All organisms present in that square were removed and counted, and this process was repeated until counts exceeded 200 individuals or the whole sample had been processed (range = 0–702 individuals). The remaining sample was scanned for rare species, which were recorded separately. Identifications were made using standard keys (principally Winterbourn 1973; Chapman & Lewis 1976; Winterbourn et al. 2000). Indeterminate species in some hemipteran, coleopteran and dipteran groups were verified by professional taxonomists, and any taxa considered non-aquatic were excluded from analyses. Taxa comprising the category "other" were mostly Collembola, Hemiptera, Coleoptera, and Acarina.

Statistical analysis

Invertebrate data from samples with total numbers exceeding 20 (n = 42) were converted into percentages to enable comparison of community composition among samples. Absolute abundances were not analysed because the number collected was affected by sampling effort and we wanted to compare community composition among sites. Rare species were allocated a value of 0.5. Cluster analysis was performed using the group-average method on a Bray-Curtis similarity matrix to identify sample groupings based on percentage composition (McCune & Grace 2002). The cluster analysis was also conducted on presence-absence data but the resulting dendrogram (not shown) yielded few distinguishable groups. Non-metric multidimensional scaling (NMDS) was also performed on a Bray-Curtis similarity matrix to explore associations between species relative abundance and sample distribution in multi-dimensional space (Clarke 1993). Biplots with a cut-off of P = 0.2 were used to define associations between sample and species distributions (McCune & Mefford 1999). Differences between the four zones, locations (left or right bank, mid-river, tributary junction), habitats (littoral shelves, rock faces, islands/sandbars, side channels, banks/beaches, coves/backwaters), and shade and

current velocity classes were conducted using Multi-Response Permutation Procedures (MRPP) (McCune & Mefford 1999). This procedure is a non-parametric method that does not require assumptions of multivariate normality or homogeneity of variances. MRPP was conducted using the Euclidean distance measure with the natural weighting method n/sum(n). The distance matrix was rank-transformed to help correct for any loss of sensitivity owing to increased community heterogeneity (i.e., the null hypothesis was no difference in average within-group rank of distances).

Spearman correlations were used to explore relationships between NMDS scores for ordination axes 1–3, and the environmental parameters measured including easting and northing based on the New Zealand Map Grid (NZMG) to indicate spatial position. The NZMG is a metre co-ordinate system with its origin at 41°S and 173°E, such that the land area of New Zealand is fitted into a rectangle of 1.0 million metres □ 1.5 million metres, consistent with a mapping scale of 1:50 000 (Department of Lands and Survey 1973). Correlation analysis was also used to relate environmental variables to the relative abundance of common taxa (occurring in >20 samples), and to taxa richness and Pielou eveness for all mainstem sites (i.e., excluding major tributaries) where invertebrates were found. The significance of Spearman coefficients was assessed at $P < 0.05$ using the False Discovery Rate to adjust for multiple comparisons (FDR; Garcia 2003; McBride 2005). Kruskal-Wallis tests were used to assess differences in environmental parameters among the cluster groups identified and among zones. All multivariate analyses were conducted with PC-Ord v.5 (McCune & Mefford 1999). Kruskal-Wallis and Spearman rank correlation tests were conducted using Systat v.11 (Systat Software, Inc., California, United States).

RESULTS

Environmental parameters

Most samples were taken from littoral shelves ($n = 33$) followed by side-channels ($n = 6$), or rockfaces, islands/sandbars, banks/beaches or coves/backwaters ($n = 1–4$ each). Three samples were taken from shallow gravel bars in mid-river (samples 13, 28, and 35), and the remainder were on the true left ($n = 17$) or right ($n = 18$) banks of the main channel or at tributary junctions ($n = 9$). Macrophytes comprised 50% (± 6.2 SE) of substrates sampled on average, followed by wood (20% ± 3.9), roots

(mainly willow; 9% ± 3.3), and rocks (combined gravel, cobbles, and boulders) or sand/silt (12% ± 4.7 and 9% ± 3.2, respectively). Conductivity at the sampling sites ranged from 13.4 to 25.6 mS.m^{-1}; on the main river, values were <17.0 mS.m^{-1}, whereas four of the nine confluence sites had conductivities >20.0 mS.m^{-1}. Measured water temperatures ranged from 18.5 to 29.2°C. Highest spot temperatures were recorded in slow-moving water along littoral shelves in zones 1 and 2.

Of the physico-chemical variables measured, only conductivity was significantly correlated with geographic location of mainstem sites ($r_s = 0.51$ with northing, $P < 0.01$, $n = 38$), largely reflecting higher conductivity below the Waipa confluence. There was a significant effect of zone on conductivity ($H = 10.84$, d.f. = 3, $P < 0.05$), as well as on the percentage of wood ($H = 9.47$, d.f. = 3, $P < 0.05$), roots ($H = 7.98$, d.f. = 3, $P < 0.05$), and macrophytes ($H = 12.82$, d.f. = 3, $P < 0.01$) sampled. Wood and roots were poorly represented at zone 3 sites, whereas macrophytes represented relatively little of the substrates sampled in zone 1 and made the greatest contribution in zone 3 samples.

Invertebrate communities

A total of 63 taxa was collected in all samples (see Fig. 2 for taxa in samples containing more than 20 individuals), with an average of 9 taxa (± 0.6 SE) and a maximum of 22 taxa per sample. Macroinvertebrate communities were dominated by a few abundant and widespread taxa. Eight taxa were found in more than 20 samples and were represented by 100 or more individuals. They were in order of total abundance: the amphipod *Paracalliope* sp. (all samples), the chironomid *Tanytarsus* (35), various indeterminate oligochaete species (Oligochaeta, 22), *Xanthocnemis zealandica* (23), the shrimp *Paratya curvirostris* (22), a *Cricotopus* chironomid (26), the limpet *Ferrissia neozelanica* (23), and the hydroptilid trichopteran *Oxyethira albiceps* (28). The introduced snail *Physa acuta* and the native hydrobiid *Potamopyrgus antipodarum* were collected at more than 20 sites but in relatively low numbers overall (Fig. 2). Forty-seven taxa were found in fewer than 5 samples. These infrequently-encountered taxa included 10 Diptera taxa, 8 Hemiptera, 7 Coleoptera, and 4–5 each of Crustacea, Trichoptera, and Collembolla taxa (retained by the 0.5 mm mesh net). The tubificid oligochaete *Branchiura sowerbyi* was found in three samples in zones 2 and 4.

Zone 1 samples were characterised by high relative abundances of Chironomidae and other
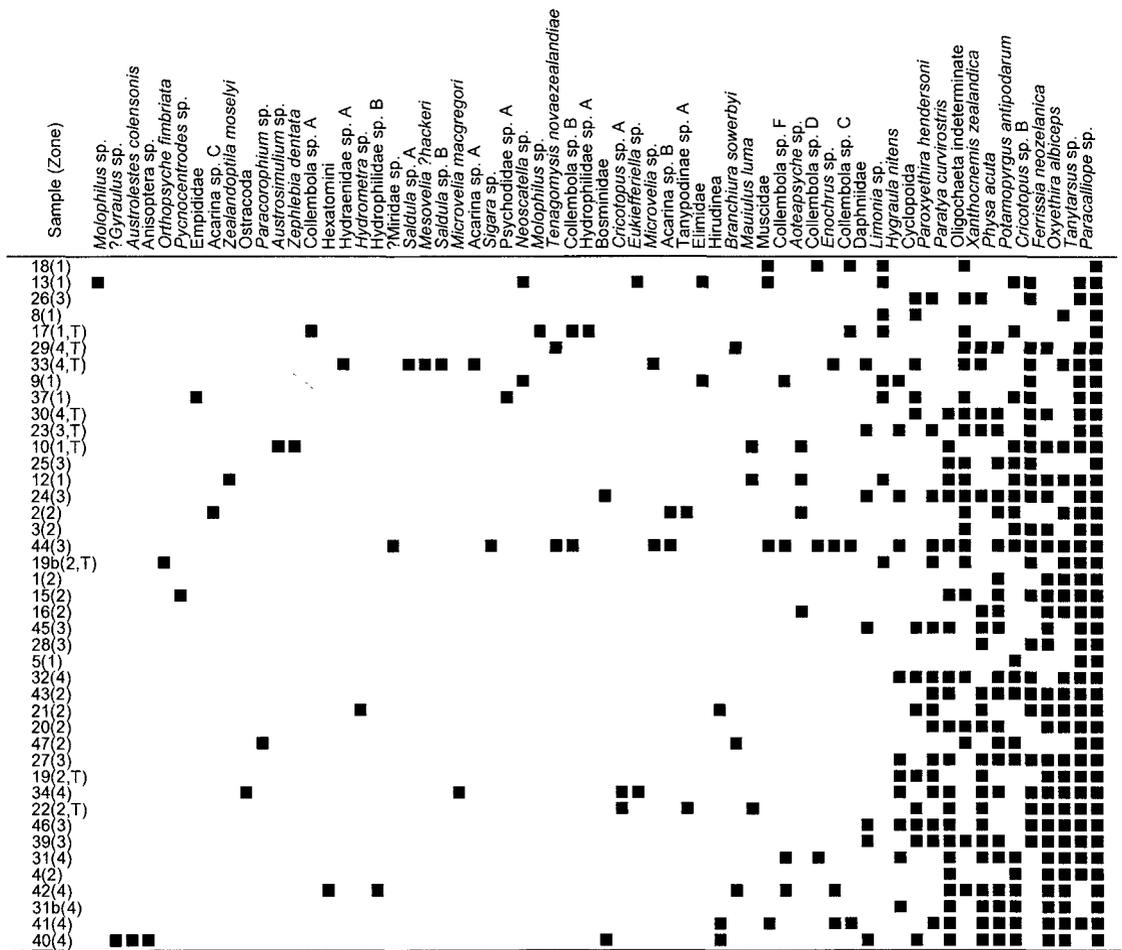
Fig. 2   Ordered matrix of taxa occurrence (dark squares) in 42 samples (>20 individuals/sample) from the lower Waikato River, New Zealand. Sites are ordered by the location along axis 1 of the NMDS ordination. (T, tributary junction.)

Diptera (mainly *Limonia* sp.), but the significance of these groups declined further downstream where Crustacea became more dominant (Fig. 3A). Zone 1 also had relatively high abundances of Odonata and "other" invertebrates (mainly Elmidae). Mollusca comprised >5% of total numbers collected in zones 3 and 4. The fauna at major tributary junctions (all sites combined) was dominated by Chironomidae and Crustacea, mainly *Paracalliope* (Fig. 3A). There were 22–31 taxa overall in each zone, with most taxa found in the most downstream zone and least in zone 2. Overall more taxa (36) were found at tributary junctions compared with mainstem sites in any of the zones. However, no pattern was evident in the relative contribution of taxa among different groups between mainstem and junction sites (Fig.

3B). Similar numbers of infrequently-encountered taxa were found in samples from tributaries, and left or right banks (20–22). For the mainstem sites, most of these taxa were found in zone 4 (16) followed by zones 1 (14), 3 (11), and 2 (9).

Classification and ordination of samples

Cluster analysis of percentage abundance data distinguished four groupings at 30% information remaining (Fig. 4). Most zone 2 and 4 mainstem sites (90–100%) occurred in group A, whereas group D comprised three out of eight zone 1 sites. Tributary sites occurred in groups A, B, and C, and constituted half the sites in group B. Conductivity was highest in cluster groups B and C (Table 1). Group D samples were largely collected from wood, whereas roots
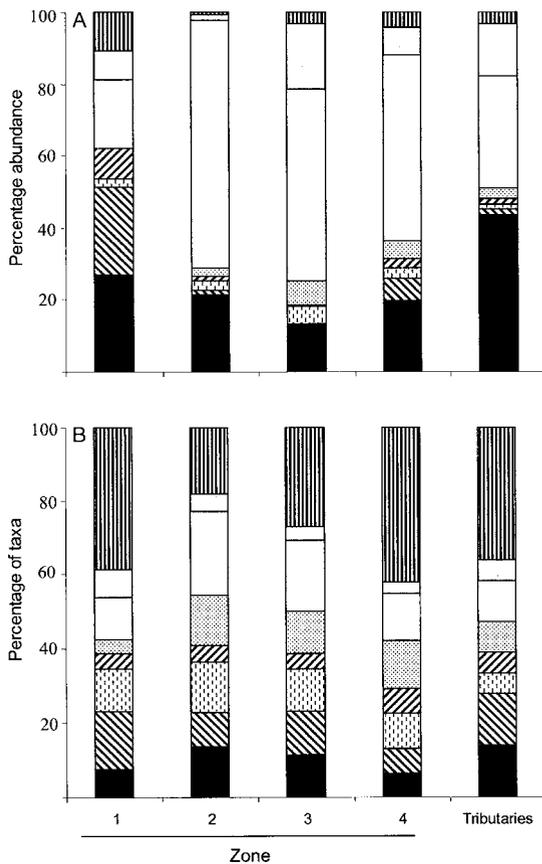
Fig. 3 Composition of major invertebrate groups for: **A**, percentage abundance and **B**, percentage of taxa in samples collected at mainstem sites along four zones (1–4) and at major tributary junctions of the lower Waikato River, New Zealand ("Other", mostly Collembola, Hemiptera, Coleoptera, and Acarina.)

☷ Other
☐ Oligochaeta
☐ Crustacea
▨ Mollusca
▨ Odonata
▥ Trichoptera
▨ Other Diptera
■ Chironomidae

made up 17–21% of substrates sampled on average at group A and B sites, but were absent from the other groups. The percentage of stones (gravels and larger) in the sampling area was highest for group A, but low or absent in other samples. Macrophytes constituted substantial percentages (>44%) of substrates in group A–C samples (Table 1). Kruskal-Wallis tests indicated significant differences among cluster groups in conductivity ($H = 9.14$, d.f. = 3, $P < 0.05$) and the percentage of wood sampled ($H = 10.44$, d.f. = 3, $P < 0.05$).

The percentage abundance NMDS provided a 3-dimensional solution with a low stress value of 0.08. The first two axes of this ordination accounted for 82% of the variation (axis 1 = 61%, axis 2 = 21%). Biplots indicated that sites dominated by *Paracalliope* occurred to the far right of the ordination, whereas samples towards the bottom left of the ordination (mostly tributary junctions) were dominated by *Tanytarsus* (Fig. 5). Samples occurring towards the top left of the ordination were characterised by higher relative abundances of Oligochaeta, *Limonia*, and Collembola, although the length of the biplot arrows indicates that those associations were not as strong as for the other taxa.

MRPP indicated a significant separation among zones ($A = 0.11$, $P < 0.01$), with zone 2 being significantly different from zone 1 ($A = 0.22$, $P < 0.001$) and zone 4 ($A = 0.06$, $P < 0.05$). This difference was also significant when tributary sites were excluded from the analysis. Global comparisons among locations or habitats, and among current velocity or shade classes were not significant ($P > 0.05$), although pairwise comparisons between samples collected on the true right bank of the main river and at major confluences were ($A = 0.18$, $P < 0.05$). When tributary and mid-river sites were omitted, there was no difference between samples collected on the true left or right banks for both percentage abundance and presence-absence data.

Relationships with environmental variables

Axis 1 scores of the ordination were significantly correlated with geographic position ($r_s = -0.53$ and 0.47 for easting and northing, respectively, $P < 0.05$ following adjustment for FDR, $n = 42$), suggesting a general shift in community composition with progression down the river. Axis 2 scores were correlated with spot water temperature ($r_s = -0.35$, $P < 0.05$, $n = 40$) and axis 3 scores with ambient conductivity ($r_s = -0.56$, $P < 0.001$, $n = 36$). The temperature and conductivity correlations were conducted separately on reduced data sets owing to missing values and were not adjusted for FDR.

When mainstem samples were considered alone (i.e., excluding tributary junction sites), correlations suggested higher proportions of *Paratya*, *Physa*, *Potamopyrgus*, and *Ferrissia*, and greater taxonomic richness and lower community evenness with distance down the river (i.e., higher northing and lower easting values indicate progression downstream) (Table 2). However, the relative abundance relationships were highly variable and often driven by a few high density outliers. Neither water temperature nor
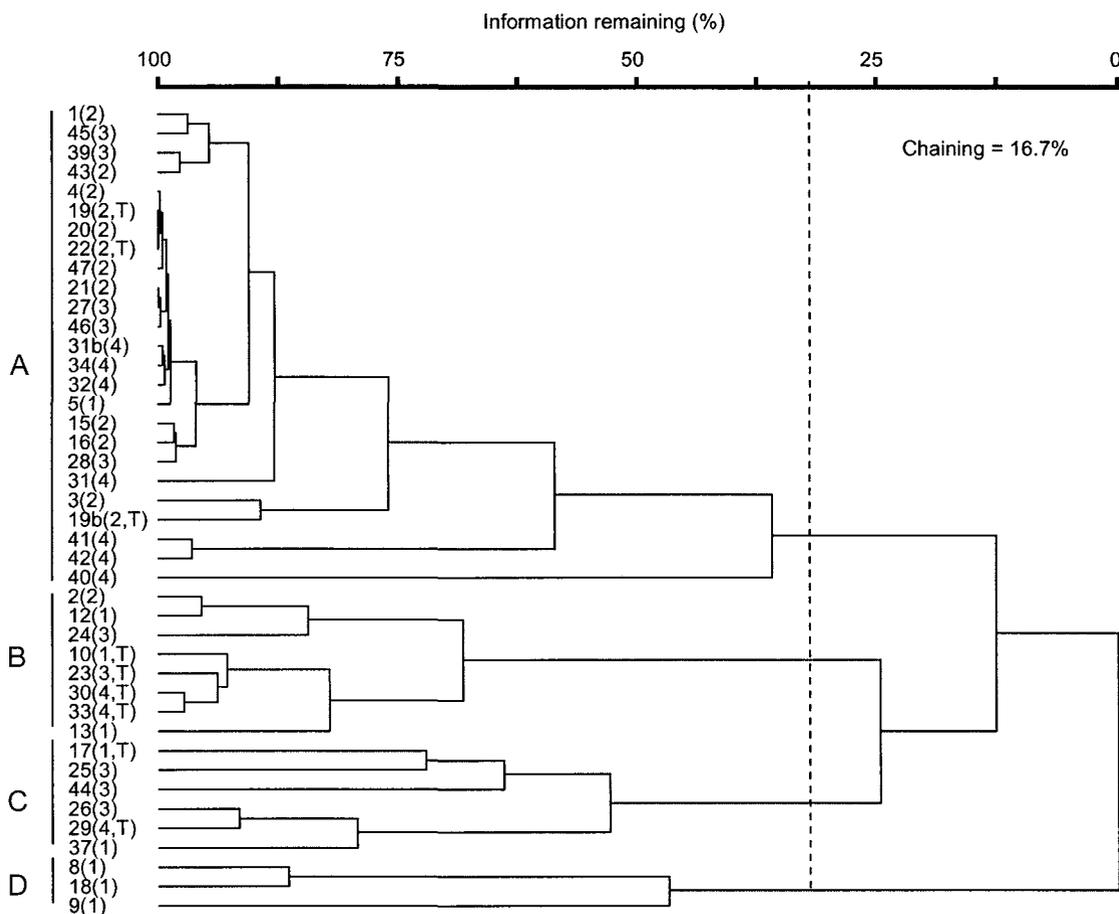
Fig. 4 Cluster dendrogram (Bray-Curtis similarity, group average linkage) of macroinvertebrate faunas (percentage composition) in 42 samples collected in four zones (1–4) and at tributary junctions (T) along the lower Waikato River, New Zealand. Dashed line indicates level of similarity at which four cluster groups (A–D) were distinguished.

Table 1 Mean (SE) environmental parameters measured in four groups identified in cluster analysis of percentage abundance macroinvertebrate data (Bray-Curtis similarity, group average linkage). Higher values for current and shade classes infer faster water and more shade.

| | Cluster group | | | |
	A	B	C	D
Temperature (°C)	23.5 (0.2)	23.2 (0.8)	25.2 (0.9)	23.9 (1.4)
Conductivity (mS.m^{-1})	15.8 (0.1)	18.4 (1.3)	18.0 (1.6)	15.3 (0.4)
Current velocity class	1.7 (0.2)	1.4 (0.2)	1.5 (0.2)	2.0 (0.5)
Shade class	1.7 (0.2)	1.9 (0.3)	1.3 (0.3)	2.0 (0.0)
% wood	18.1 (4.8)	24.3 (8.0)	1.7 (1.7)	73.3 (21.9)
% roots	17.3 (5.4)	20.6 (6.2)	0.0	0.0
% stones	15.2 (7.1)	0.0	0.0	1.7 (1.7)
% sand/silt	4.4 (4.0)	3.8 (3.8)	10.0 (6.3)	13.3 (13.3)
% macrophytes	44.9 (8.9)	51.3 (15.0)	88.3 (7.5)	11.7 (9.3)
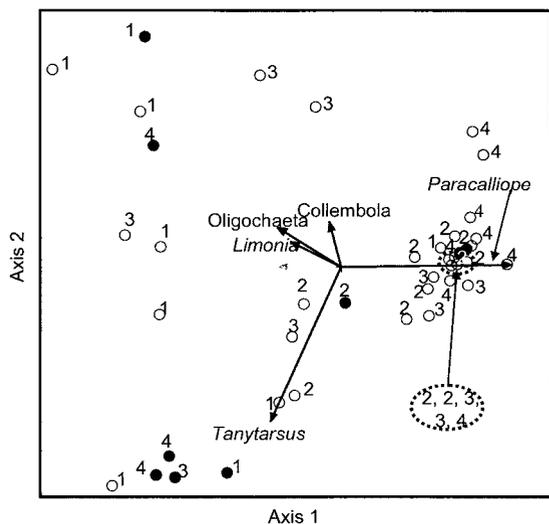
Fig. 5 NMDS ordination plot of percentage abundance data for macroinvertebrate samples from mainstem (open circles) sites and major tributary junctions (closed circles) in four zones (1–4) of the lower Waikato River, New Zealand. Biplot arrows indicate associations between taxa and ordination axes; the angle and length of the line indicate the direction and strength of the relationship.

conductivity were significantly correlated with taxa richness or Pielou evenness, but relationships with relative abundance suggested higher proportions of Oligochaeta in samples where the water was warmer and relatively more snails where conductivity was higher. *Paratya* relative abundances tended to be higher where more macrophytes and less stony substrates (boulders-gravels combined) were sampled (Table 2). Similarly, *Physa* tended to be relatively more abundant in samples with more macrophytes, and *Potamopyrgus* and *Ferrissia* less abundant in samples with more stones. Taxa richness was also significantly and inversely related to the percentage of stony material sampled.

DISCUSSION

Macroscale biotic patterns

The shallow-water macroinvertebrate fauna was taxonomically similar along the mainstem of the lower Waikato River, but there was some suggestion of a longitudinal pattern. The relationships detected with geographic position (easting and northing) suggest macroscale clinal changes in community composition and diversity with distance down the river, although there was considerable variability among samples. The downstream increase in mainstem sample richness was paralleled by a decline in evenness, reflecting increasing relative abundances of some common taxa in the lower river. However, zonal characteristics also seemed to influence macroinvertebrate community composition

Table 2 Spearman correlation coefficients for relationships between percentage abundance of taxa present in >20 samples, taxa richness and evenness versus measured environmental parameters (physicochemical variables with no significant correlations have been omitted) at mainstem sites. Coefficients highlighted in bold are significant at $P <$ 0.05. Probability values for habitat and location variables ($n = 37$) were adjusted for the False Discovery Rate whereas temperature and conductivity were unadjusted owing to missing values ($n = 35$ and 30, respectively).

	Easting	Northing	Temp.	Conductivity	%macrophytes	%stones
Paratya curvirostris	**−0.78**	**0.81**	−0.12	0.29	**0.44**	**−0.45**
Oligochaeta	0.06	−0.02	**0.42**	0.26	0.26	0.03
Xanthocnemis zealandica	0.14	−0.12	−0.18	−0.24	−0.30	0.19
Physa acuta	**−0.68**	**0.74**	−0.04	**0.40**	**0.49**	−0.34
Potamopyrgus antipodarum	**−0.69**	**0.66**	0.01	**0.47**	0.22	**−0.42**
Cricotopus sp.	−0.02	0.01	0.15	0.16	0.09	0.03
Ferrissia neozelanica	**−0.61**	**0.58**	−0.07	0.26	0.38	**−0.45**
Oxyethira albiceps	−0.41	0.38	−0.11	−0.15	0.22	−0.22
Tanytarsus sp.	0.23	−0.21	0.17	−0.00	0.02	0.17
Paracalliope sp.	−0.39	0.40	−0.21	0.19	0.18	−0.36
Taxa richness	**−0.65**	**0.63**	−0.10	0.16	0.34	**−0.46**
Pielou evenness	**0.48**	**−0.45**	0.13	−0.28	−0.16	0.37

independently of longitudinal succession, supporting the tenet that hydrogeomorphic processes are important in regulating species distributions and biocomplexity in large rivers (Thorp et al. 2006).

In a seasonal study carried out along the upper and lower Waikato River, Carter (2000) reported spatial and temporal interactions in the richness of aquatic invertebrates in combined suction and sweep samples. Communities in the lower Waikato River were dominated numerically by *P. antipodarum* or oligochaetes, reflecting the predominance of benthic sediments in suction samples. Davenport (1981) reported 17–28 taxa from multi-plate substrates deployed in the lower river over one year, but no pattern with distance downstream, although he did observe higher diversity in the lower river in general compared with two sites in the upper Waikato River. The absence of longitudinal richness patterns in previous studies may partly reflect that those sites did not extend as far down river and sampling was not as spatially intensive as in the present study. Although a similar longitudinal richness pattern was not evident in these previous studies, richness values relativised by the mean recorded at a site were similar at comparable locations (data not shown) suggesting some congruence between studies despite different sampling methods and target habitats.

Similar invertebrate groups have been found to dominate large rivers in North America, although the order of dominance varies among studies. Chironomidae dominated near-shore samples in large river sites around British Columbia, Canada, where diversity was low compared to coastal rainforest and arid grassland streams (Reece & Richardson 2000). Tubificid oligochaetes, amphipods, chironomids, and molluscs (bivalves) were common in a freshwater tidal section of Hudson River, eastern New York (Strayer et al. 2006), whereas oligochaetes, molluscs (clams), and chironomids were dominant in grab samples from mud, sand or gravel in the Ohio River sampled by Thorp (1992), who avoided larger substrates and wood. deDrago et al. (2004) concluded that benthic communities in the lower Paraguay River occur in predictable, habitat-specific communities, and hypothesised the existence of a species-poor, sand-adapted assemblage of invertebrates in large neotropical rivers.

Influence of mesoscale and microscale factors

In the present study, tributary junction samples contained more taxa overall and communities tended to be more heavily dominated by Chironomidae than any of the mainstem zones. Although high diversity at tributary junctions may partly reflect longitudinal succession in community structure, tributaries are known to create spatial discontinuities that enhance physical heterogeneity and biotic diversity around their junctions with larger mainstem rivers (Kiffney et al. 2006; Rice et al. 2006; Grant et al. 2007). The higher conductivities measured at some tributary junctions suggests that they could contribute to localised increases in ionic (potentially nutrient) concentrations which may influence plant growth in littoral areas, and/or deliver organic carbon derived from the lake and wetland catchments that some drain, thereby providing localised enhancement to trophic resources in the main river. Some overseas studies have indicated effects on large river invertebrate communities of other discontinuities such as islands (Thorp 1992) or variations between different banks reflecting differences in algal biomass, coarse sediments and bottom heterogeneity (Bournaud et al. 1998). Neither of these mesoscale factors (islands or banks) nor other mainstem channel habitat types were identified as important influences on macroinvertebrate communities in the present study, although their apparent lack of influence may partly reflect the predominance of littoral-shelf samples.

In Ohio River, United States, abundances of benthic species were negatively correlated with water depth and current velocity and strongly influenced by sediment particle size and the presence or absence of macrophytes (Thorp 1992). The limited range of flow environments sampled and their coarse characterisation may have limited our ability to detect relationships with hydraulic parameters. Taxonomic richness was highest in Ohio River on gravel and where filamentous algae or vascular plants were present, and lowest on coarse sand (Thorp 1992). Substrate type was also related to invertebrate community composition in grab samples from habitat units that reflected sediment composition and configuration in the Hudson River (Strayer et al. 2006). The inverse relationship between percentage stony material sampled and taxa richness in the present study may partly reflect variable water levels influencing species distributions on littoral shelves where most coarse material occurred, or differences in sampling efficiency among different substrate types. The association between wood and *Limonia* abundance in zone 1 is consistent with known habitat preferences of species in this genus (Winterbourn et al. 2000). Habitat patchiness reflecting variations in organic and inorganic substratum characteristics appears important at the local scale in the lower Waikato River, and interacts with geographic and

hydrogeomorphic factors to influence shallow-water macroinvertebrate community composition.

Implications for biomonitoring

The use of macroinvertebrates to monitor the condition of large river environments requires practical approaches that provide clear and consistent results to accurately represent the ecological condition of study reaches. Thorp & Delong (1994) emphasised the importance of local algal production and direct leaf litter inputs from riparian vegetation as key energy sources fuelling macroinvertebrate productivity in large rivers with constricted channels, although they later recognised the significance of algal-grazer and decomposer pathways driven by autochthonous primary production (Thorp & Delong 2002). Thus sampling shallow-water habitats in the photic zone at river edges might be expected to access the main sites of invertebrate species aggregation, although deep mid-river and shallow littoral faunas may be different (Neale et al. 2006). In recognition of the apparent productivity of littoral areas of large rivers, macroinvertebrate sampling of shallow, near-shore habitats similar to most of those investigated in the present study has now been integrated into large river bioassessment practices in the United States (Flotemersch et al. 2006).

From the present study it is clear that macroinvertebrate sampling designs for monitoring large rivers will need to account for potential sources of variability brought about by microscale (substrate heterogeneity), mesoscale (location of tributaries), and macroscale (longitudinal position and hydrogeomorphic features) factors. Flotemersch et al. (2006) found that sampling both banks at six transects provided representative estimates of macroinvertebrate community composition on major tributaries of the Ohio River. Although this approach would not provide an accurate representation of invertebrate community structure across the entire channel, it does enable comparisons of data along sections of river, especially if multiple littoral samples are integrated over the site of interest as suggested by Flotemersch et al. (2006). Compositing multiple samples will also assist with acquiring sufficient invertebrate numbers to fulfil the requirements of any fixed-count procedures that may be used to process samples, as densities can be low in some habitats (Reece & Richardson 2000; this study).

Strayer et al. (2006) argued that defining macroinvertebrate habitats at the spatial scale of dominant controlling processes will improve the ability to extrapolate results from localised sampling. Understanding the spatial scale over which organisms are responding to environmental gradients and discontinuities, such as the extent of tributary junction influence, will be important for interpreting the results of large river monitoring in New Zealand. Moreover, the interplay between geographic and hydrogeomorphic patterns suggested by the present study indicates that monitoring sites should be stratified spatially to capture macroscale variations in community structure and composition. Although our sampling was conducted over a short period in summer to facilitate comparisons among many sites, other research has highlighted apparent temporal variations in communities in the lower river (Carter 2000). Defining the interaction between season and physical factors in determining macroinvertebrate distribution and abundance will enable the timing of monitoring to be appropriately targeted. Development of large river bioassessment protocols will require testing and validation of these issues to ensure that interpretations reflect ecological condition rather than differences brought about by natural gradients, hydrogeomorphic features, discontinuities, and the physical heterogeneity of habitats in near-shore areas of large rivers.

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