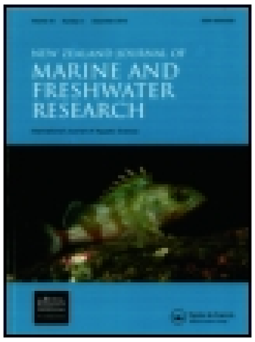

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Magnitude of effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers

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Abstract Data from runs in 88 rivers throughout New Zealand, and a comparison between areas of contrasting substrate size in the Mohaka River, were used to investigate the influences of physical factors on benthic macroinvertebrates. Substrate size preferences were more clearly demonstrated by the comparison of different substrates in the Mohaka River than between runs in the 88 rivers. Taxonomic richness and densities of most collector-browsers were highest on small cobble–boulder substrates. However, filterers and a facultative shredder showed strong preferences for large cobbles and boulders and an undescribed orthoclad showed a strong preference for sand. Among the 80 stony-bedded rivers, those exposed to maximum flows of < 5×, 5–10×, and 10–20× their median flow during 6 weeks before sampling had similar taxonomic richness, densities, and biomass. In contrast, rivers that had experienced maximum flows of > 20× their median flows had markedly lower median taxonomic richness, density, and biomass than less-flooded rivers. Among the 51 stony, "non-flooded" sites, those with 1–30% of their catchments developed to improved pasture had similar community composition to, but higher total biomass than those with < 1% development. However, sites with > 30% catchment development (median = 70%) differed significantly ($P < 0.1$) from those with less developed catchments: the former had lower diversity, taxonomic richness, numbers of ephemeropteran, plecopteran, and trichopteran species (EPT), and had lower biomass of species that are sensitive to changes in water quality related to eutrophication; they had higher biomass of species that are associated with an abundance of periphyton. Trout biomass was also c. 3-fold lower than in the rivers with lesser-developed (1–30%) catchments.

Keywords benthic invertebrates; aquatic insects; water quality; surveys; sediments; floods; enrichment; periphyton; land use; agriculture

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INTRODUCTION

Multivariate analyses of invertebrate communities in runs in 88 New Zealand rivers in relation to environmental factors have recently been carried out (Quinn & Hickey 1990). The results indicated that factors related to the degree of catchment development as fertilised pasture have a marked effect on community composition. Substrate size and recent flooding also emerged as important influences on invertebrate abundance and taxonomic richness.

Previous studies have indicated that invertebrate abundance increases with substrate size up to cobble size, then decreases at boulder and bedrock sizes (see Minshall (1984) for review). This relationship applied to the mayfly *Deleatidium* spp. in the Waingawa River, an unstable river in New Zealand (Jowett & Richardson 1990), but the substrate size preferences of other New Zealand taxa have not been studied in detail.

Studies by Irvine (1985), Sagar (1986), Scrimgeour et al. (1988), and Scrimgeour & Winterbourn (1989) have shown that major floods can substantially reduce taxonomic richness, invertebrate biomass, and densities in New Zealand rivers. These studies provide preliminary indications of the magnitude of floods required to substantially affect invertebrates, but there is a lack of information on the effects of various levels of flooding in different river types from which hypotheses on the mechanisms involved can be developed and evaluated.

Several North American studies indicate that agricultural catchment development causes marked changes in river invertebrate communities, with the loss of enrichment-sensitive species (Dance & Hynes 1980; Lenat 1984, 1988). Winterbourn (1986) has described several processes by which catchment development could affect New Zealand stream communities and Allen (1959) reported changes in the fauna of a stream following agricultural development. However, despite the development of 36% of New Zealand's land area to improved pasture (Rutherford et al. 1987), quantitative information on the influences of a range of levels of catchment development on common New Zealand river taxa, and a general description or understanding of the effects of development on community characteristics, were not available.

The present paper uses data from the 88-river study, and a comparison of communities in areas having different particle size in one of these rivers, to attempt to quantify the magnitude of the influences of these selected factors on invertebrates. The analysis emphasises the threshold levels at which physical factors have a strong influence on invertebrate community characteristics (i.e., total density and biomass; taxonomic richness; biomass of taxonomic/ feeding groups; and densities of common taxa).

METHODS

Sampling

A survey was conducted of invertebrates present in a narrow range of current velocity and depth conditions (10–90% ranges = 0.42–0.65 m s^{-1} and 0.30–0.54 m, respectively) in 88 rivers throughout New Zealand (Quinn & Hickey 1990). This dataset was augmented by an investigation of substrate size effects on invertebrate communities in one of the rivers, the Mohaka River, which had high densities of a wide range of common taxa and a diversity of habitats.

In the 88 river survey, seven 0.1 m^2 Surber samples (250 μm mesh nets; substrates disturbed to c. 0.1 m depth) were collected from each site on one occasion under baseflow conditions (below median flow) during autumn 1987. These samples were combined in the field to give a single sample per site for analysis. Surficial sediment composition was also visually assessed as the percentage cover by the following size class categories (after Minshall 1984, table 12.2): silt (Si, < 0.063 mm); sand (Sa, 0.063–2 mm); gravel (G, 2–64 mm); small cobbles (SC, 64–128 mm); large cobbles (LC, 128–256 mm); boulders (B, 256–330 mm); and bedrock (R). To aid statistical analysis of the substrate data, field size assessments were transformed into a single substrate index (SI, mm) by summing the mid-point values of the size classes weighted by their proportional cover (bedrock was assigned a nominal size of 400 mm for these calculations). Macrophyte cover only exceeded 5% at three of the sites and macrophytes were not included in the areas sampled except at the Hoteo River. Details of the sampling and sorting procedures and the related environmental data, and a description of the sites are given by Quinn & Hickey (1990).

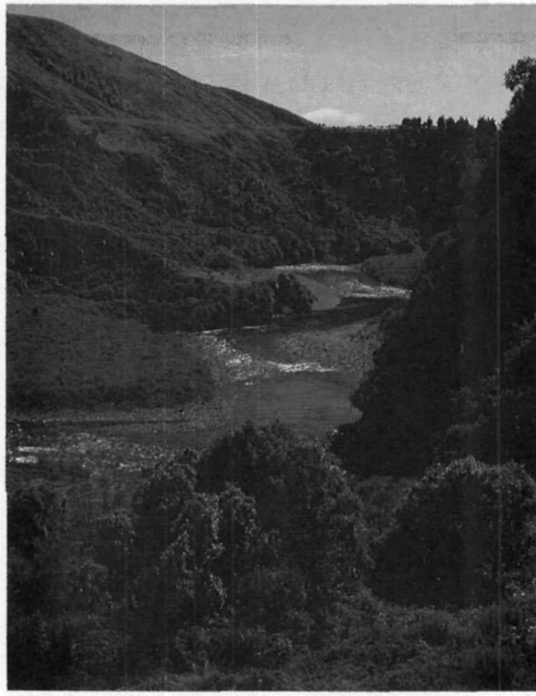

Fig. 1 Mohaka River, in the vicinity of the study area. *Photo: C. W. Hickey*

Substrate size effects were further investigated in the Mohaka River at a site 10 km upstream of State Highway 5 (NZMS1 N114 029745; 176° 36′E 39° 12′S) (Fig. 1) under baseflow conditions (flow = 23.6 $m^3 s^{-1}$ cf. median = 29.7 $m^3 s^{-1}$) on 24 February 1988. Four replicate 0.1 m^2 Surber samples (500 μm mesh nets) were collected from areas dominated by each of the sediment classes listed above, except silt and bedrock which were not present. The gravels were further divided into small and large classes (i.e., SG, 2–32 mm and LG, 33–64 mm, respectively). Depth and current velocity (at 0.6 × depth) were measured with an electromagnetic current meter (Montedoro-

Whitney Model PVM-2A) and matched as closely as possible between sampling sites.

The Mohaka River at this site is at 320 m elevation, is 40 m wide, has forest and scrub over 78% of its catchment (the remainder is mostly improved pasture), and relatively low flow variability (coefficient of variation = 0.90; mean annual flood/median flow ratio = 7.74 (based on 30 years' continuous data); cf. median values of 1.54 and 36.5 respectively for the 88 study rivers).

Analysis

The effects of substrate size, recent flooding, and catchment development were investigated by comparing the invertebrate communities between rivers grouped in 4–6 range classes with respect to these environmental variables (Table 1). The class boundaries were selected to reflect thresholds for effects apparent in bivariate plots of invertebrate parameters versus environmental factors, and to include at least nine rivers in each class. Where appropriate, rivers known to be strongly affected by confounding factors (such as small substrate size and flooding) were excluded from these analyses. Differences in environmental and biotic factors between classes were investigated by comparing ranked values using non-parametric ANOVA and Tukey's multiple comparisons (Conover & Iman 1981).

Table 1 Acronyms for environmental factors investigated.

Acronym	Full description
CHLa	Water column chlorophyll *a* (mg m^{-3})
CVFLOW	Coefficient of variation of flow
DEVEL	% cover of catchment by improved pasture
DO	Dissolved oxygen (g m^{-3})
ELEV_S	Site elevation above sea level (m)
MAXTEMP	Mean annual temperature + half mean winter-summer range (°C)
MEANF	Mean flow (m^3 s^{-1})
MEDF	Median flow (m^3 s^{-1})
PAFDW	Periphyton ash-free dry weight (g m^{-2})
PCHLa	Periphyton chlorophyll *a* (mg m^{-2})
pH	$-\log [H^+]$
SLOPE_S	River slope in vicinity of site, from 1:50 000 or 1:63 000 scale maps (m m^{-1})
SI	Substrate visual particle size index (see text)
TKN	Total Kjeldahl nitrogen (mg m^{-3})
TP	Total phosphorus (mg m^{-3})
TSS	Total suspended solids (mg m^{-3})
TURB	Turbidity with Hach 2100A meter (NTU)

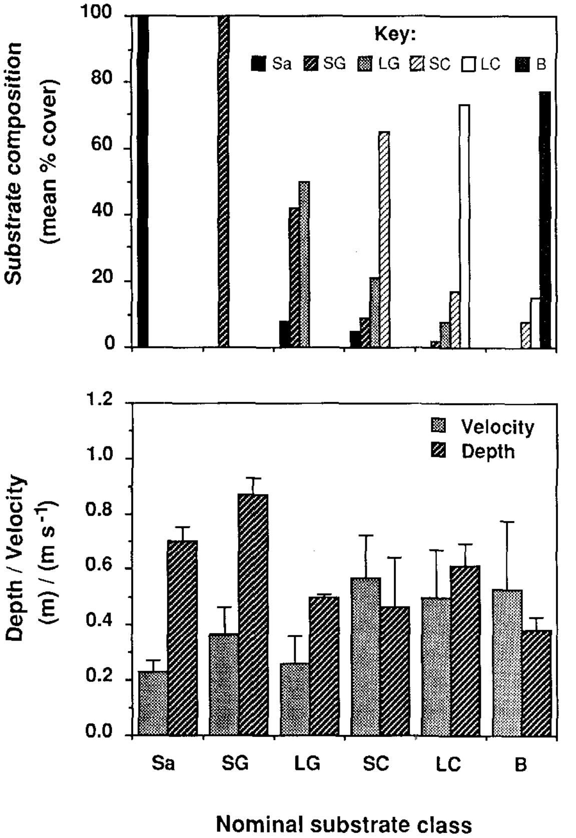

Fig. 2 Substrate composition, current velocities, and depths amongst the patches catagorised as sand (Sa), small gravel (SG), large gravel (LG), small cobble (SC), large cobble (LC), and boulder (B) sampled for invertebrates in the Mohaka River (bars represent median values and the whiskers represent approximate 95% confidence intervals (1.58× interquartile range/$\sqrt{n}$) for comparison of medians (from Velleman & Hoaglin 1981).

RESULTS

Substrate size effects

Mohaka River studies

The physical conditions at the sites of contrasting substrate size sampled in the Mohaka River are shown in Fig. 2, and Fig. 3 displays invertebrate community characteristics and the densities of the 15 most common taxa in these sites. It was not possible to exactly match the conditions of velocity and depth between the patches of contrasting substrate in the Mohaka River (Fig. 2), because these factors are closely related. However, neither current velocity nor depth were significantly correlated with total

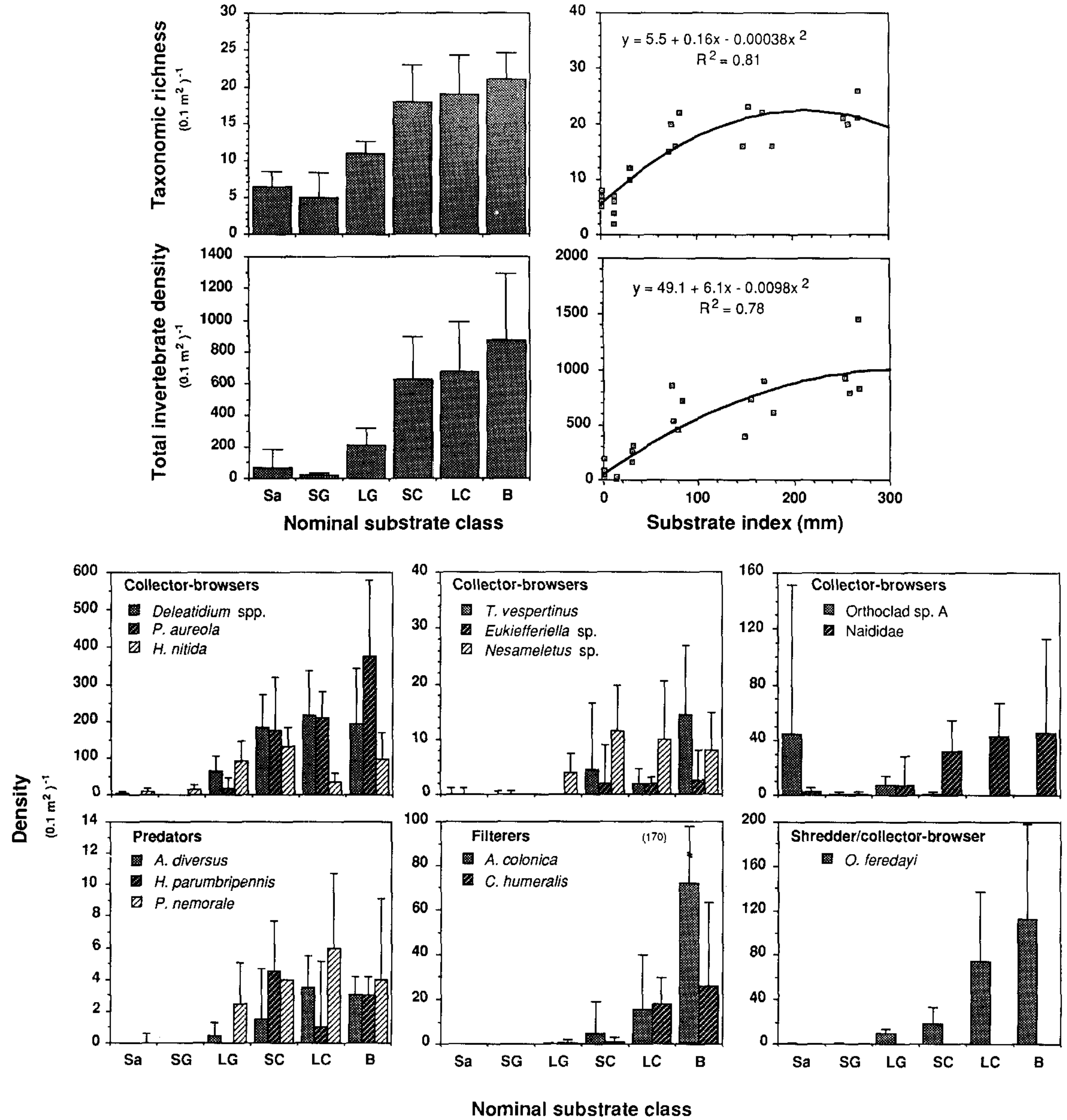

Fig. 3 Comparisons of median invertebrate taxonomic richness, total densities, and the densities of the 14 common taxa amongst patches of contrasting substrate in the Mohaka River (substrate classes as in Fig. 2; whiskers represent approximate 95% confidence intervals).

invertebrate density ($r_s = 0.11$ and -0.31, respectively; $P > 0.05$) and nor was taxonomic richness ($r_s = 0.25$ and -0.41, respectively; $P > 0.05$): this applied to 17 samples collected from cobbly areas in the Mohaka River having velocities and depths covering the range of values (0.2–0.6 m s^{-1} and 0.4–1.0 m respectively, Fig. 2) considered in the substrate comparison (authors' unpubl. data). Therefore, these factors were unlikely to have been important in producing the very marked differences in invertebrate community structure observed over the range of substrate sizes (Fig. 3).

Taxonomic richness and total densities were least in patches of sand and small gravel in the Mohaka River (where SI < 30 mm) (Fig. 3). Small cobble, large cobble, and boulder substrates had high densities and taxonomic richness, whereas large gravel substrates were intermediate. Polynomial models relating total invertebrate density and taxonomic richness to substrate size in the Mohaka River accounted for most of the observed variation ($R^2 = 0.78$ and 0.81, respectively), indicating the important influence of substrate size on these community characteristics (Fig. 3).

The distributions of many of the 14 taxa that were common in the Mohaka River (Fig. 3) indicated pronounced substrate preferences. Only the undescribed orthoclad showed a preference for sand, where it accounted for most of the total density (Fig. 3). In contrast, the distributions of all other collector-browsers indicated preferences for larger, gravel-boulder substrates. *Hydora nitida* was present on all substrate types but was most abundant on gravels, cobbles, and boulders, where it was relatively evenly distributed. *Deleatidium* spp. and *Nesameletus* sp. were most abundant and evenly spread over small and large cobbles and boulders. These mayflies were scarce or absent in areas of sand and small gravel, but moderately abundant in large gravel. The distributions of Naididae, the chironomids *Eukiefferiella* sp. and *Tanytarsus vespertinus*, and the cased caddis *Pycnocentrodes aureola* indicated strong preferences for cobble and boulder substrates; the latter two species were particularly abundant on boulders. The distributions of the filterers (i.e., the mayfly *Coloburiscus humeralis* and the caddis *Aoteopsyche colonica*) and the facultative shredder (*Olinga feredayi*) indicated strong preferences for large cobbles and particularly boulders. The predators *Archichauliodes diversus* and *Psilochorema nemorale* were scarce or absent from sand and small gravels and most abundant on cobbles and boulders. *Hydrobiosis parumbripennis* only occurred among cobbles and boulders (Fig. 3).

88 -river comparison

Figure 4 shows the distributions of both invertebrate community level parameters and the 14 most frequently occurring taxa in the 88-river dataset in relation to substrate size. It identifies the rivers according to their degree of recent flooding. Both the number of taxa and total invertebrate densities were significantly lower ($P < 0.05$) in eight rivers where sand and/or silt covered 39–98% of the bed (SI < 30mm) than in rivers with coarser substrates in the 88-river dataset (Fig. 4). The upper boundary of the range of total density and taxonomic richness values did not differ markedly with SI between c. 30 and 180 mm (Fig. 4). Taxonomic richness was intermediate (6–19 taxa per 0.7 m^2) in rivers where > 50% of the surficial substrate was bedrock (i.e., at three of the five sites with SI > 250 mm: Fig. 4). Total densities were high at one of the bedrock sites, where chironomids and the gastropod *P. antipodarum* were abundant (6300 m^{-2} and 3600 m^{-2}, respectively), but were only moderate (1000–2400 m^{-2}) at the other two sites. Predator densities were very low at the bedrock-dominated sites except in the Waipapa River where the bedrock had many holes, grooves, and fissures.

Effects of recent flooding

Flooding effects were investigated by comparing invertebrate communities in relation to the level to which the maximum flow in the 6 weeks before sampling exceeded the median flow in 80 of the 88 rivers with stony beds. Continuous flow data for each site were obtained from the National Hydrometric Archive (TIDEDA: Walter 1987). This analysis assumed that the communities present in the flooded rivers would otherwise have been similar to the remaining non-flooded rivers. This assumption is supported by:

(1) the 680× higher total density at the Kauaeranga River following a period of relatively stable flows in summer, than in this survey after a flood of c. 60× the median flow (Quinn & Hickey 1990); and

(2) substantially higher (i.e., 1.5, 10, and 24-fold) total densities recorded on other occasions, following periods of relatively stable flows in autumn, at three other sites that were exposed to recent floods exceeding 20× their median flow in this study (authors' unpubl. data).

The eight rivers in which sand and silt covered much of the bed (SI < 30 mm) were excluded from the analysis to eliminate the apparent confounding effect on invertebrates of fine sediments. A 6-week period was chosen because this is approximately half the time that Scrimgeour et al. (1988) found was required for the invertebrate biomass and species richness to reach a relatively steady state following a scouring flood (45× median flow) in the Ashley River. This indicated that the invertebrate communities were likely to have substantially recovered from the effects of floods that occurred over 6 weeks before sampling.

Initially, communities were separated into five flooding classes containing similar numbers of sites (i.e., max. flow < 5×, 5 –10×, 10–20×, 20–60×, and

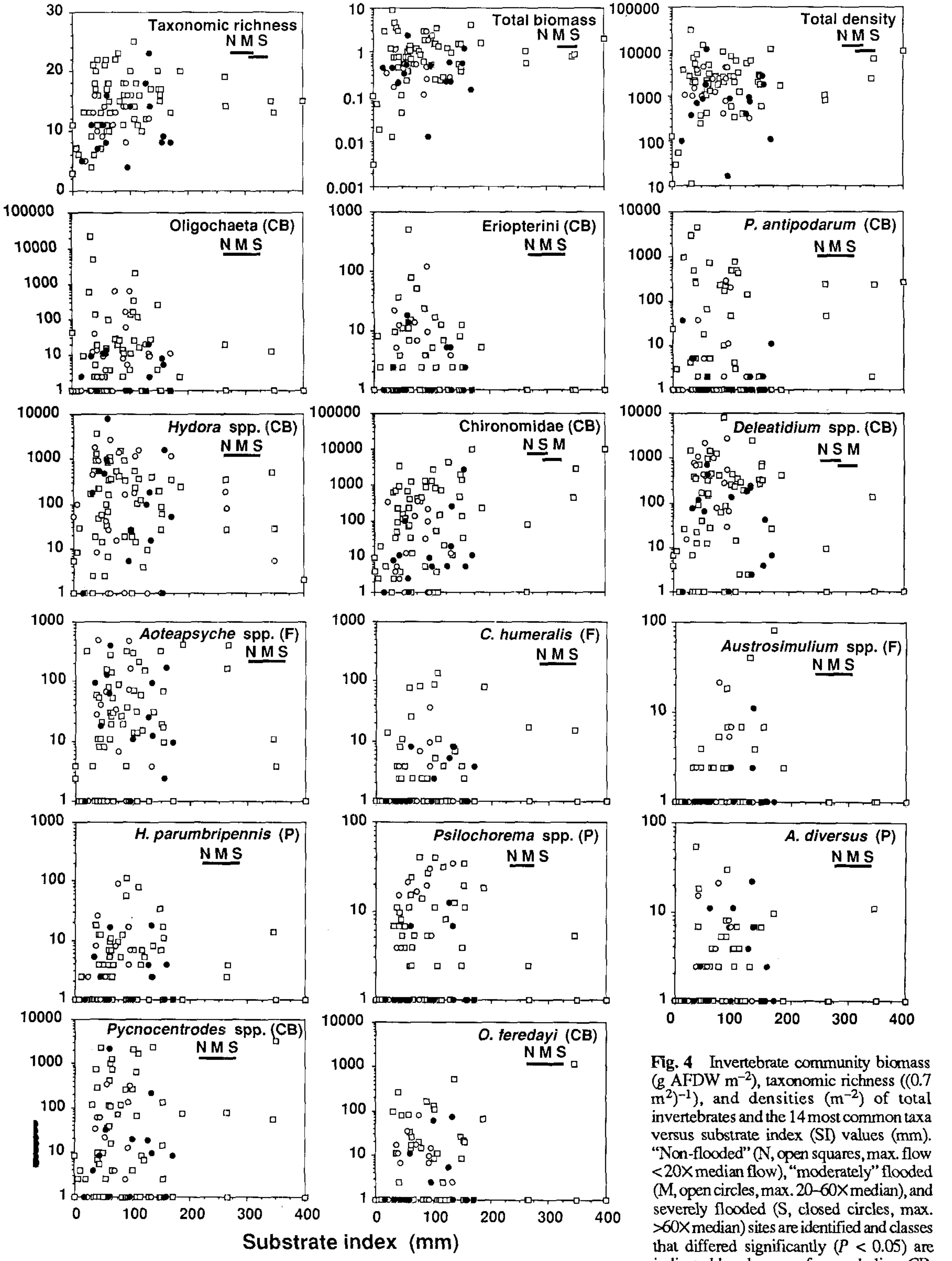

Fig. 4 Invertebrate community biomass (g AFDW m^{-2}), taxonomic richness ($(0.7\ m^2)^{-1}$), and densities (m^{-2}) of total invertebrates and the 14 most common taxa versus substrate index (SI) values (mm). "Non-flooded" (N, open squares, max. flow <20× median flow), "moderately" flooded (M, open circles, max. 20–60× median), and severely flooded (S, closed circles, max. >60× median) sites are identified and classes that differed significantly ($P < 0.05$) are indicated by absence of an underline. CB, collector-browsers; P, predators; F, filterers.

> 60× median flow) and compared. However, the former three classes of sites did not differ significantly ($P > 0.05$) in their community level characteristics (i.e., density, biomass, and taxonomic richness), suggesting that at these states of flow the threshold for marked impacts on the invertebrate communities had not been reached. Consequently, the 54 sites that had not experienced flows exceeding 20× their median flows were classified as "non-flooded" and compared with the 14 "moderately" flooded (max. flow 20–60× median) and 12 "severely" flooded (max. flow > 60× median) sites.

The moderately flooded and severely flooded sites had significantly ($P < 0.05$) fewer taxa than the non-flooded sites (medians = 13.5 and 10 cf. 16 taxa, respectively) and lower median total invertebrate biomass (by 39 and 62.5% respectively) and median total density (by 52 and 49%, respectively: Fig. 4, Table 2). Of the 14 most common taxa, only Chironomidae, *Deleatidium* spp., and *Psilochorema* spp. showed significant differences in density between the non-flooded and either of the flooded site classes (Fig. 4). Both the densities of chironomids and the biomass of periphyton (as chlorophyll *a*) were much lower at the moderately and severely flooded sites than at the non-flooded sites (c. 18-fold, Table 2). *Psilochorema* density differed little between the non-flooded and moderately flooded sites, but was markedly lower at the severely flooded sites. On the other hand, *Deleatidium* had significantly higher median density at the moderately flooded sites than at either the non-flooded or severely flooded sites. However, the median biomass of collector/browsing Ephemeroptera (of which *Deleatidium* spp. comprised on average 93% of the density) was similar at the non-flooded and moderately flooded sites, indicating that the high densities in the moderately flooded sites resulted from larger numbers of early instar larvae.

The predominance of high densities of *O. feredayi*, *Pycnocentrodes* spp., and *C. humeralis* at non-flooded sites (Fig. 2) indicates that these species may have been sensitive to flooding, although their densities did not differ significantly ($P > 0.05$) between the flooded and non-flooded sites. In contrast, the results do not indicate any effects of moderate or severe flooding on *Hydora* spp., *Aoteapsyche* spp., *H. parumbripennis*, or *A. diversus*.

Effects of catchment development

A subset of the 88-river dataset was used to investigate the influence of catchment development to improved pasture (DEVEL) on invertebrate taxonomic richness, biomass, and taxonomic/feeding groups. To minimise the influence of environmental factors other than those associated with DEVEL, rivers were excluded that had silty/sandy beds (SI < 30mm), moderate–severe recent flooding (flow > 20× MEDF in 6 weeks before sampling), significant upstream effluent discharge, or received geothermal inputs, or urban run-off. This left 51 rivers that were divided into the following four classes: < 1% DEVEL ($n = 16$); 1–10% DEVEL ($n = 14$); 10–30% DEVEL ($n = 12$); and > 30% DEVEL ($n = 9$). Invertebrate community level characteristics, the biomasses of taxonomic/feeding groups, and environmental factors (Table 1) were then compared between the classes (Fig. 5 and 6). Median flows did not differ significantly between these classes ($P > 0.05$; median MEDF 7–11.5 $m^3 s^{-1}$).

Differences were most marked between the > 30% DEVEL class and the remaining, less-developed, classes (Table 3). The former had significantly lower ($P < 0.1$) median values of diversity, taxonomic richness, numbers of ephemeropteran, plecopteran,

Table 2 Median values of factors that differed significantly (non-parametric ANOVAs; $P < 0.1$) between rivers grouped according to their degree of flooding in the 6 weeks before sampling (see Tables 1 and 3 for key).

	Flood class		
	< 20MEDF	20–60MEDF	> 60MEDF
Number of rivers	54	14	12
Taxonomic richness ($(0.7\ m^2)^{-1}$)	16	13.5	10
Total invertebrate density (m^{-2})	2231	1360	838
Total invertebrate biomass (g AFDW m^{-2})	0.933	0.449	0.473
Ephemeroptera CB (g AFDW m^{-2})	0.124	0.104	0.036
Deleatidium spp. (m^{-2})	207	493	68
Psilochorema spp. (m^{-2})	2.8	7.8	0
Chironomidae (m^{-2})	152	7.9	9.3
PCHLa (mg m^{-2})	30.2	2.4	6.7

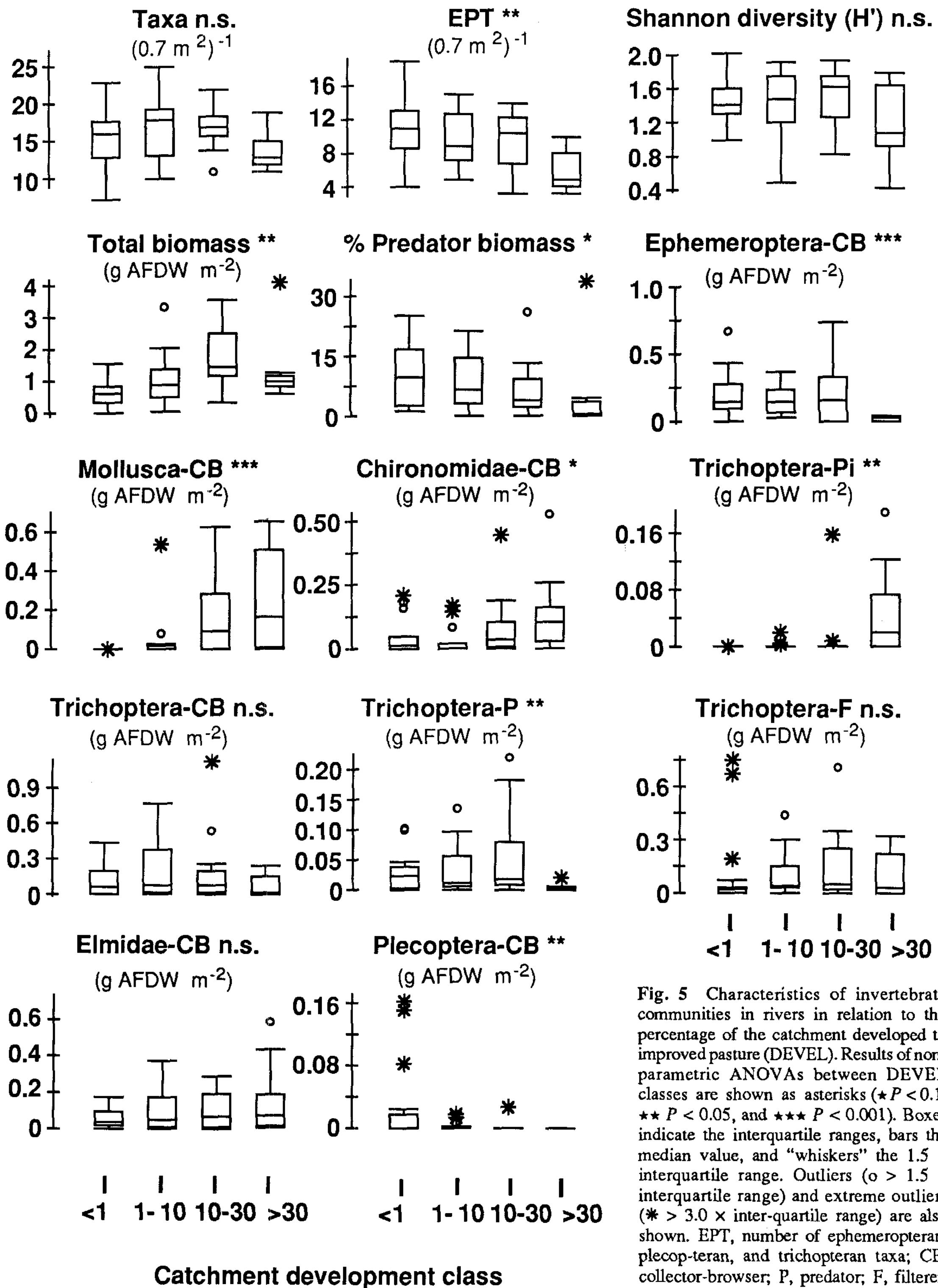

Fig. 5 Characteristics of invertebrate communities in rivers in relation to the percentage of the catchment developed to improved pasture (DEVEL). Results of non-parametric ANOVAs between DEVEL classes are shown as asterisks (⋆ $P < 0.1$; ⋆⋆ $P < 0.05$, and ⋆⋆⋆ $P < 0.001$). Boxes indicate the interquartile ranges, bars the median value, and "whiskers" the 1.5 × interquartile range. Outliers (o > 1.5 × interquartile range) and extreme outliers (✱ > 3.0 × inter-quartile range) are also shown. EPT, number of ephemeropteran, plecop-teran, and trichopteran taxa; CB, collector-browser; P, predator; F, filterer; Pi, algal piercer.

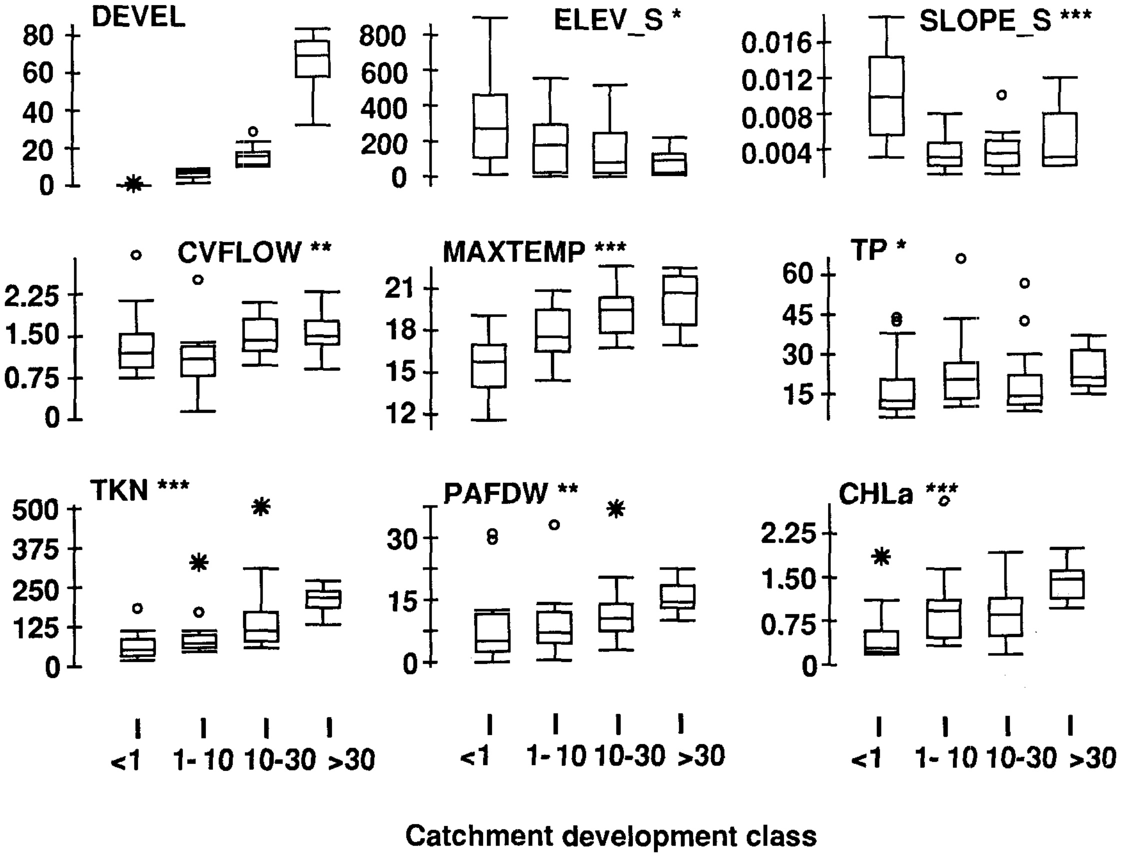

Fig. 6 Comparison of environmental characteristics in rivers classified according to the percentage of their catchments developed as improved pasture (DEVEL) (for description key see Table 1 and Fig. 5).

and trichopteran species (EPT), predator/total biomass ratios, and biomasses of predatory Trichoptera and collector-browsing Ephemeroptera and Plecoptera (Fig. 5, Table 3). In contrast, they had significantly higher ($P < 0.1$) biomasses of algal piercing Trichoptera and collector-browsing chironomids and molluscs (Fig. 5, Table 3). Biomass of collector-browsing and filtering Trichoptera and collector-browsing Elmidae did not differ significantly between the DEVEL classes (Fig. 5).

The variation in environmental factors listed in Table 1 that differed significantly ($P < 0.1$) among the four DEVEL classes is also shown in Fig. 6 and the median values for the > 30% DEVEL and combined ≤ 30% DEVEL classes are summarised in Table 3. Flow variability (CVFLOW), temperature, nutrients (TKN and TP), periphyton, and water column algal concentration all showed a general increase with DEVEL (Fig. 6). Site elevation and slope did not differ markedly between the 1–10%, 10–30%, and > 30% DEVEL rivers (Fig. 6), indicating that these factors were not important in producing the differences in invertebrates observed between these classes. Turbidity and the concentration of suspended solids were uniformly low (at least at baseflow) in all classes (e.g., median turbidity = 1.0 and 2.5 NTU in the < 1 and > 30% DEVEL classes, respectively).

DISCUSSION

Effects of substrate size

Invertebrate preferences for substrate size were shown much more clearly by the Mohaka River study than the 88-river comparison (Fig. 3 and 4), reflecting the greatly reduced sources of variation in the single river study. Nevertheless, the 88-river dataset provides a broader perspective on the range of taxonomic richness, biomass, and species densities that can be expected to occur over the full range of substrate sizes encountered in New Zealand rivers of the size range covered (10–90 percentile range of median flow = 0.5–32 $m^3 s^{-1}$). The 88-river data also provide preliminary indications of substrate preferences of some taxa that were uncommon in the Mohaka River (i.e., *P. antipodarum,* and Eriopterini).

The relationships between invertebrate density and taxonomic richness observed in this study are generally consistent with those of previous investigations: both increase as substrate size increases from sand to cobbles and then decline with further increases to bedrock (Minshall 1984; Jowett & Richardson 1990). However, in the Mohaka River total densities and taxonomic richness were slightly higher among boulders than cobbles (Fig. 3).

Several processes are important in determining invertebrate substrate size preferences in a given river: species are expected to respond differently to substrate depending on their feeding mode, water quality requirements, and biotic interactions. The current velocity required to disturb a substrate particle increases with particle diameter above the silt–sand range (Carson & Griffiths 1987; Ashworth & Ferguson 1989). Thus larger particles provide a more stable habitat for both periphyton and invertebrates. Larger substrates also trap and retain more coarse particulate organic matter (Rounick & Winterbourn 1983; Webster et al. 1987), which probably accounts for the strong preference of the facultative shredder *Olinga feredayi* for large cobbles and boulders in the Mohaka (Fig. 3). In contrast, the smaller interstitial spaces of gravel beds are expected to retain more fine particulate organic matter (Parker 1989) which may account for the greatest abundances of detrital-feeding oligochaetes and Eriopterini in rivers having gravel–small cobble beds (Fig. 4).

Increased water turbulence with increased bed roughness is expected to reduce the thickness of the "boundary layer", i.e., the low-velocity region that exists just above the stone surfaces (Smith 1975; Davis 1986). This increases the exchange of dissolved gases, nutrients, and organic matter between the bulk

Table 3 Median values of invertebrate community and environmental variables that differed significantly (non-parametric ANOVAs; * $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$; **** $P < 0.001$) between sites having < 30 and > 30% of their catchment in improved pasture (i.e., DEVEL) (EPT, number of ephemeropteran, plecopteran, and trichopteran taxa; CB, collector-browsers; P, predators; Pi, algal piercers).

	Median values DEVEL class			
Variable	≤ 30%	> 30%	Increase	Sign. level
DEVEL (%)	6.8	69.6		
Number of sites	42	9		
Invertebrates				
EPT ($(0.7\ m^2)^{-1}$)	10.5	5	–52%	***
% predator biomass	6.9	0.7	–10-fold	**
Shannon diversity (H')	1.45	1.09	–33%	*
Taxonomic richness ($(0.7\ m^2)^{-1}$)	16.5	13	–21%	*
Ephemeropt–CB (mg AFDW m^{-2})	156	5	–32-fold	****
Trichoptera–P (mg AFDW m^{-2})	20.5	3.5	–6-fold	***
Megaloptera–P (mg AFDW m^{-2})	3	0	–∞	**
Plecoptera–CB (mg AFDW m^{-2})†	12.6	0	–∞	*
Plecoptera–P (mg AFDW m^{-2})†	20.6	0	–∞	**
Trichoptera–Pi (mg AFDW m^{-2})	0	21.9	∞	****
Mollusca–CB (mg AFDW m^{-2})	0	167	∞	**
Chironomid–CB (mg AFDW m^{-2})	9	105	12-fold	*
Environmental				
CHLa (mg m^{-3})	0.5	1.5	3-fold	****
TKN (mg m^{-3})	80	220	2.7-fold	****
MAXTEMP (C)	17.4	20.7	19%	***
PAFDW (gAFDW m^{-2})	7.7	14.7	2-fold	***
PCHLa (mg m^{-2})	21	40.2	2-fold	*
TP (mg m^{-3})	14	22	1.7-fold	*

† Mean values given where median = 0 in both classes; see Table 1 for other abbreviations

flow and the stone surfaces and interstitial water—influencing both periphyton (Hickey 1988) and invertebrates (Statzner 1981). Hence, at a given current velocity, the coarser substrates are expected to provide more suitable habitat for:

(1) invertebrates having high oxygen requirements, such as some Plecoptera, Ephemeroptera, and Trichoptera (Nebeker 1972; Wiley & Kohler 1980; Williams et al. 1987); and

(2) for periphyton growth where nutrient concentrations are sufficiently low to be limiting (Riber & Wetzel 1987).

This is consistent with the general increase in collector-browsing ephemeropteran and trichopteran species (i.e., *Deleatidium* spp., *Nesameletus* sp., and *P. aureola*) with substrate size in the Mohaka River (Fig. 3).

The greater bed stability and exchange of water between the bed and water column in areas of larger substrates is also expected to favour these as habitat for filter-feeding invertebrates. This contention is supported by the increase in maximum densities of *Austrosimulium* spp. with substrate size up to large cobbles and the occurrence of maximum densities of *C. humeralis* (that filters interstitial water: Wisely (1961)) at sites among the 88 rivers with small to large cobble beds (Fig. 4). Furthermore, *C. humeralis* and *A. colonica* showed strong preferences for large cobbles and boulders in the Mohaka River (Fig. 3). Orth & Maughan (1983) also observed that simuliid larvae had a strong preference for turbulent habitats. Rougher substrates cause greater small-scale variability in stone-surface current velocities (Davis 1986); gravel–boulder-sized beds provide a more complex three-dimensional habitat than do silty, sandy, and bedrock areas (Minshall 1984). Both result in a greater range of micro-habitats and more refuges from predation by other invertebrates, fish (Brusven & Rose 1981), and birds (Pierce 1979, 1986), and from scouring during high flows (Williams & Hynes 1974; Cowie 1980). This habitat diversity and the presence of refuges are expected to contribute to the greater taxonomic richness and invertebrate biomass and densities in rivers with gravel to cobble/boulder-dominated beds (Fig. 3 and 4).

Mosses can greatly enhance invertebrate abundance in stony streams by providing shelter, sites for periphyton growth and detritus accumulation, and material for case construction by larval insects (Suren 1988). The moderately high invertebrate biomass (3.039 g AFDW m^{-2}) at one predominantly silty bedded river (Hoteo, SI = 20, Fig. 4), where the sample included vascular hydrophytes, indicates that these can also enhance invertebrate abundance in silty and sandy rivers.

Effects of recent flooding

The comparison of the invertebrate communities between rivers exposed to recent floods of different size in relation to their median flows supports the findings of Sagar (1986) and Scrimgeour et al. (1988) that major floods can cause substantial reductions in taxonomic richness, and total invertebrate biomasses and densities in New Zealand rivers. Furthermore, the comparison has indicated the degree of flooding generally required in New Zealand rivers to substantially reduce the total abundance and taxonomic richness of invertebrates inhabiting runs at baseflow, and the relative sensitivities to loss in floods of the common taxa.

The results indicate that generally flood flows need to exceed c. 20× the median flow to have significant effects on invertebrate abundance and taxonomic richness c. 3–4 weeks after a flood event (Fig. 4). This is consistent with the previous findings: McLay (1968) reported that invertebrate densities recovered to pre-flood levels 3 weeks after a 5-fold increase in flow in the Kakanui River; Scrimgeour et al. (1988) reported that flows in the Ashley River of 5–9× median flow did not result in significant reductions in invertebrate biomass or taxonomic richness, whereas both were reduced to a very low level following a flood of 45× median flow. By contrast, Irvine (1985) observed that a 5-fold increase in flow resulted in 72–90% reductions in densities of the invertebrates that were probably resident in sloughed-off periphyton. Both Chironomidae and the periphyton that they commonly inhabit (Towns 1981; Irvine 1985) occurred at much lower densities (c. 18- and 7-fold lower, respectively) at moderately and severely flooded sites (i.e., flow > 20× median) than at the non-flooded sites (i.e., flow < 20× median). This indicates that periphyton-associated invertebrates are likely to be particularly susceptible to loss in floods. This is consistent with the observation that abundance of chironomid in the drift is more closely related to the current/discharge regime than abundance of other macroinvertebrate groups (Brittain & Eikeland 1988).

Differences in invertebrate body shape and flexibility can also be expected to influence the effects of flooding on individual species. The gastropod *P. antipodarum*, the cased caddisflies *Pycnocentrodes* spp. and *O. feredayi*, and the erect, rigid-gilled mayfly *C. humeralis* all generally had their highest densities at non-flooded sites (max.

flow < 20× median). In contrast, the dorso-ventrally flattened *Deleatidium* spp. and *A. diversus*, the thin, fusiform *Hydora* spp., and the free-living caddisflies (especially retreat-building *Aoteapsyche* spp.) all appeared to be less affected by high flows (Fig. 4). This supports the view that these more streamlined and/or flexible-bodied species are better able to resist being washed away (Statzner 1981, 1988) or can seek refuge from high currents, for example by retreating deeper into the substrate (Bishop 1973; Hynes 1974; Poole & Stewart 1976) or to their fixed shelters.

Deleatidium spp. appeared to be particularly well adapted to withstand or recover from moderately high flows: its median density was significantly higher ($P < 0.05$) at the moderately flooded sites (493 m^{-2}) than at either the non-flooded (207 m^{-2}) or severely flooded sites (68 m^{-2}). However, the median biomass of collector/browsing Ephemeroptera (of which *Deleatidium* spp. comprised on average 93% of the density) was similar at the non-flooded and moderately flooded sites (0.124 and 0.104 g AFDW m^{-2}, respectively). This indicates that the high densities at the moderately flooded sites were brought about by larger numbers of early-instar larvae. Therefore, the recent moderate floods had affected *Deleatidium* densities but the populations were rapidly recovering—probably as a result of subsequent oviposition and egg hatching. This is consistent with the frequent dominance and abundance of *Deleatidium* in rivers having beds that are often disturbed by floods (Winterbourn 1981; Winterbourn et al. 1984; Sagar 1986; Scrimgeour et al. 1988), and with its rapid recovery following a flood in the Kakanui River (McLay 1968).

The physical characteristics of river channels and beds also influence the threshold ratio of flow to median flow at which invertebrates are severely affected. Channel slope, cross-sectional shape, and bed roughness together determine the relationship (usually a power law) between current velocity and flow (Bovee & Milhous 1978), whereas the size of the dominant bed particles, and their degree of imbrication (armouring), determine the threshold current velocity for mass movement of the bed (Carson & Griffiths 1986; Ashworth & Ferguson 1989). The availability of refuges to which the invertebrates can retreat during high flows probably also influences persistence and stability of invertebrates in a particular river exposed to flood flows. Potential refuges include: stable, deep, gravels; low-velocity areas around stable boulders; and side braids and "dead zones".

The comparison of invertebrates at sites exposed to different levels of flooding has provided indications of both susceptible species and the magnitude of flooding impacts. This information should assist in the design and interpretation of future ecological studies and biomonitoring programmes. It also provides guidance on the likely effects of various flows in regulated rivers.

Effects of catchment development to improved pasture

The lower taxonomic richness, diversity, percentage predator biomass, and biomass of enrichment-sensitive groups (i.e., Plecoptera, predatory Trichoptera, and Ephemeroptera: Hynes 1960, Winterbourn 1981) at sites having > 30% of their catchments developed to improved pasture (i.e., DEVEL > 30%) (Fig. 5, Table 3) indicate that factors associated with catchment development have important influences on invertebrate communities in New Zealand rivers. These findings are generally consistent with previous observations of catchment development effects reported by Allen (1959), Dance & Hynes (1980), and Lenat (1984, 1988). They are particularly important for New Zealand where c. 36% has been developed as improved pasture (Rutherford et al. 1987).

The causal links between the degree of catchment development and the invertebrate fauna are expected to be complex because of the large number of environmental factors that vary with catchment development to improved pasture. These include:

(1) increased nutrient inputs (e.g., Wilcock 1986) leading to increased periphyton biomass (e.g., Biggs & Price 1987; Biggs 1988) and consequent changes in the benthic micro-habitat, as well as increases in diurnal fluctuations in pH and dissolved oxygen (Quinn & Gilliland 1989);

(2) increased inputs of sediment (e.g., Dons 1987) and pesticides (e.g., Willis & McDowall 1982);

(3) increased light (where development involves removal of riparian shade vegetation) with consequent higher temperatures (Beschta & Taylor 1988); and

(4) increased flow variability (Dons 1987).

We found a general increase in flow variability (CVFLOW), temperature, nutrients (TKN and TP), periphyton, and water column algal concentration with increasing DEVEL (Fig. 6). Although environmental influences that are not directly associated with catchment development may have contributed to the increases in these factors, the increases are consistent with trends expected with catchment development. Insufficient pH and dissolved oxygen measurements precluded the evaluation of catchment development effects on these factors. Turbidity and the concentration of suspended solids did not appear to be important factors (at least at baseflow), being uniformly low relative to criteria for protection of aquatic life (Lloyd 1987) in all classes. Nevertheless, because higher sediment inputs at high flows are expected in pastoral than forest catchments (Wilcock 1986), sediment effects cannot be discounted.

For some taxonomic/feeding groups, changes in their food supply may provide an explanation for the differences in their biomass between rivers having > 30% DEVEL and those in the lower DEVEL classes. For example, the greater biomass of algal-piercing Trichoptera (mainly *Oxyethira albiceps*) at the > 30% DEVEL sites is consistent with the greater availability of their benthic algal food. Similarly, the increased concentrations of algae in the water column (Fig. 6, Table 3) may account for the tolerance of filter-feeding Trichoptera to increased DEVEL. However, the feedback expected in the interaction between periphyton and grazing invertebrates (e.g., Jacoby 1987; Hill & Knight 1987, 1988; Winterbourn & Fegley 1989) results in a variety of possible explanations for the lower biomass of collector-browsing Ephemeroptera and Plecoptera, and the higher periphyton biomass at the more developed sites. At least two processes could account for this, either individually or in concert. If other factors (e.g., flow variability, elevated temperatures, and higher sediment inputs) reduce the biomass of these relatively intolerant taxa in rivers with more developed catchments, the resultant reduction in grazing pressure should allow greater periphyton build-up. Alternatively, if higher nutrient concentrations, temperatures, and (possibly) light levels at the more developed sites are responsible for the build-up of periphyton, the resulting abundant periphyton will reduce the amount of relatively clean substrate preferred by the dominant Ephemeroptera (*Deleatidium* spp.: Winterbourn et al. 1984). Thick periphyton growths are also expected to reduce the mass transfer of metabolites between the water column and the bed, thereby reducing the suitability of the interstitial habitat for species with high oxygen requirements such as some Ephemeroptera (Nebeker 1972; Wiley & Kohler 1980). Moreover, the diurnal cycles of photosynthesis and respiration of periphyton can produce fluctuations in dissolved oxygen and pH (Quinn & Gilliland 1989) that are unfavourable for species with high oxygen requirements and low tolerance of high pH. Clearly, there is a need for carefully designed experimental studies to develop an understanding of the processes producing the differences in invertebrate communities identified among rivers with different levels of catchment development in this broad survey.

Although the > 30% DEVEL class had lower median values of taxonomic richness and biomass of predatory Trichoptera, collector-browsing Ephemeroptera, and Plecoptera, total invertebrate biomasses were similar to the 1–10 and 10–30% DEVEL classes and 1.6 fold higher than in the < 1% DEVEL class (Fig. 5). Nevertheless, the loss of large "behavioural drifting" (*sensu* Waters 1965) stoneflies and mayflies and their replacement by small chironomids and algal piercing caddisflies, and net spinning caddisflies and snails (that occur less in the drift than mayflies and stoneflies (McLay 1968; Brittain & Eikeland 1988)) would be expected to reduce the feeding efficiency of larger, drift-feeding fish, such as adult trout (Bachman 1984; Wilzbach & Hall 1985).

To evaluate this hypothesis, the biomass of trout (assessed by drift-diving: Jowett 1990) was compared amongst the four DEVEL classes for 44 of the stony (SI > 30 mm) study rivers for which trout data were available. Other factors that differed between the classes (Fig. 6) may have also influenced trout biomass, but this comparison showed that median trout biomass was c. 3-fold lower in the eight rivers with > 30% DEVEL than in the other rivers (eight in the 10–30% DEVEL class, 16 rivers in the 1–10% DEVEL class—Fig. 7). Notably, the median ratio of trout biomass to total invertebrate biomass was 2-fold lower ($P < 0.05$) in the > 30% DEVEL rivers than in the ≤30% DEVEL rivers (Table 4). This trend in relation to trophic structure was also apparent in the percentage predator biomass (Fig. 5) and the invertebrate to periphyton biomass ratios (Table 4). This indicates lower efficiency of energy transfer between the primary producer, primary consumer, and predator trophic levels in the rivers with more developed catchments.

With development to pasture, marked impacts on the community composition of river invertebrates do not appear to occur until a large proportion of the catchment of moderate-sized rivers (median MEDF c. 8 $m^3 s^{-1}$) is developed (i.e., > 30% DEVEL class where median DEVEL = 70%). Development of 1–10 and 10–30% of the catchment appears to increase invertebrate biomass without causing any reduction in taxonomic richness, diversity, or loss of the potentially more sensitive ephemeroptera, trichopteran

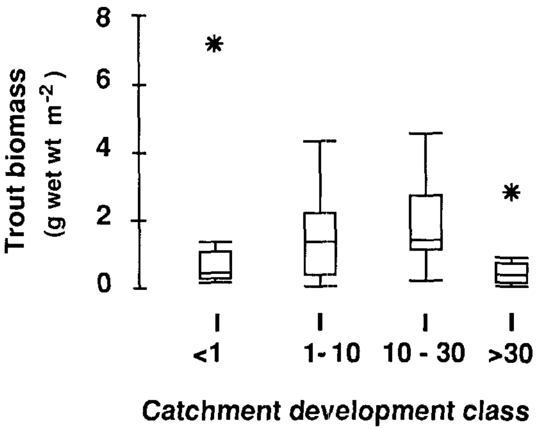

Fig. 7 Comparison of trout biomass among 44 stony-bedded rivers in relation to the percentage of the catchment developed to improved pasture (for description key see Fig. 5).

and plecopteran species. However, the analysis was limited by the relatively small number of sites in the dataset having > 30% DEVEL. The addition of further sites, covering the > 30–100% DEVEL range, should allow a more detailed description of the effects on invertebrates of various levels of development. Furthermore, to provide a sound basis for prediction of the effects on invertebrate communities of agricultural development in specific cases, studies of the likely processes involved are also required. Our results indicate that these should include both direct effects of suspended sediment, flow variability, and temperature, and indirect effects via changes in periphyton in response to increases in nutrients, light, and temperature.

Table 4 Periphyton, invertebrate, and trout biomass ratio comparisons (non-parametric ANOVA) between sites having ≤ 30 and > 30% catchment development as improved pasture. The invertebrate/trout comparison assumes trout AFDW = wet weight × 0.25 and is based on 44 stony sites (SI > 30mm).

DEVEL class	Median values ≤ 30%	Median values > 30%	Sign. level
Biomass ratios			
Periphyton/invertebrates	7.9	15.3	$P < 0.01$
Invertebrates/trout	2.7	6.0	$P < 0.05$

CONCLUSIONS

Our findings support several hypotheses on factors influencing benthic invertebrates in rivers. These in particular warrant further investigation in more intensive surveys and/or experimental studies :

(1) Substrate size
- That cobble-boulder substrates are preferred by most collector-browsers.
- That boulders substrates are preferred by filterers (possibly owing to their stability, large interstitial spaces, and the turbulent near bed flows they produce) and by shredders (possibly owing to their retentiveness of coarse particulate organic matter).

(2) Floods
- That species that construct fixed shelters and those having flexible, streamlined, bodies are more resistant to flooding effects than species having erect and/or inflexible bodies.
- That, in general, flood flows in New Zealand rivers need to exceed median flows by > 20× to substantially reduce invertebrate densities and taxonomic richness 3–4 weeks after the flood.
- That invertebrates that inhabit periphyton growths have lower resistance to flooding effects than those that occur on clean stones and within the bed possibly because periphyton generally sloughs at lower velocities than are required to move the bed.

(3) Catchment development to improved pasture
- That very low and low levels of catchment development (1–10 and 10–30%, respectively) increase invertebrate biomass without substantially changing community type; moderate–high levels (c. 70%) reduce invertebrate taxonomic richness and the biomass of species that are sensitive to changes in water quality related to eutrophication, but increase the biomass of species that are associated with an abundance of periphyton.
- That the replacement of larger "behaviourally drifting" invertebrates by smaller species, and those that occur less in the drift at sites with moderate–highly developed catchments, reduces the available food supply for trout, and hence trout biomass.

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