

Microhabitat preferences of benthic invertebrates and the development of generalised *Deleatidium* spp. habitat suitability curves, applied to four New Zealand rivers

IAN G. JOWETT

Freshwater Fisheries Centre
Ministry of Agriculture and Fisheries
P. O. Box 8324, Riccarton
Christchurch, New Zealand

JODY RICHARDSON

Fisheries Research Centre
Ministry of Agriculture and Fisheries
P. O. Box 6016, Rotorua, New Zealand

BARRY J. F. BIGGS

Hydrology Centre
DSIR Marine and Freshwater
Department of Scientific and Industrial Research
P. O. Box 22-037, Christchurch, New Zealand

CHRISTOPHER W. HICKEY

JOHN M. QUINN

Water Quality Centre
DSIR Marine and Freshwater
Department of Scientific and Industrial Research
P. O. Box 11-115, Hamilton, New Zealand

Abstract Microhabitat preferences of 12 benthic invertebrate taxa were investigated in four New Zealand rivers. Most taxa showed significant habitat preferences. Generally, taxa were more abundant in water less than 0.75 m deep and in gravel or coarser substrates, and no taxa showed a clear preference for fine substrate (sand and fine gravel) or deep water. *Coloburiscus humeralis*, *Zelandoperla* spp., and *Aoteapsyche* spp. preferred coarse substrate and water velocities of more than 0.75 m s⁻¹, whereas *Nesameletus* spp. and *Pycnocentrodus* spp. were associated with similar substrate but lower water velocities (0.2–0.8 m s⁻¹). Naididae preferred low (< 0.3 m s⁻¹) water

velocities, *Potamopyrgus antipodarum* and Chironomidae low to moderate velocities (0.0–0.75 m s⁻¹), and all three were associated with a broad range of substrates. *Deleatidium* spp., *Olinga feredayi*, Hydrobiosidae, and *Aphrophila neozelandica* were found in a wide range of habitats. Velocity, depth, and substrate suitability curves developed for *Deleatidium* in each of the four rivers also demonstrated the broad habitat tolerances of this genus. Generalised suitability curves formed by enveloping, rather than averaging, curves from each of the rivers performed favourably when compared to models based on suitability curves developed for each river individually. Correlations between *Deleatidium* abundance and the joint suitability function, calculated from the generalised velocity, depth, and substrate curves, were significant but poor ($r = 0.44$ – 0.69) in each of the four rivers. The intercepts of the linear relationships between *Deleatidium* abundance and the joint preference factor were not significantly different from zero for three of the four rivers, suggesting that the preference functions are applicable to in-stream flow assessments.

Keywords instream habitat; modelling; *Deleatidium* spp.; incremental methodology; habitat suitability function; microhabitat preference; benthic invertebrate

INTRODUCTION

The in-stream flow incremental methodology (IFIM) has encouraged study of in-stream habitat suitability functions for aquatic species (e.g., Gore & Judy 1981; Moyle & Baltz 1985; Morin et al. 1986; Raleigh et al. 1986) with the expectation that changes in in-stream habitat with flow (as predicted by IFIM hydraulic modelling) will result in changes to species abundance. This expectation has never been tested experimentally, either for fish or benthic invertebrates (Morhardt 1986; Orth 1986). Even the existence of a general relationship between abundance and the index of habitat suitability, weighted usable area (WUA), has been questioned (Mathur et al. 1985; Scott & Shirvell

1987). However, statistically significant relationships between benthic invertebrate abundance and habitat suitability have been demonstrated in the rivers where suitability functions have been derived (Orth & Maughan 1983; Morin et al. 1986; Jowett & Richardson 1990). Benthic invertebrate densities have also been related to more complex hydraulic parameters, such as Froude number (Statzner 1981; Orth & Maughan 1983), Reynolds number, and boundary layer terms (Statzner et al. 1988).

Deleatidium spp. (Ephemeroptera: Leptophlebiidae) are some of New Zealand's most widespread and common species of benthic invertebrates, and are important food for fish (Sagar & Eldon 1983; McLennan & MacMillan 1984) and black stilts (Pierce 1986). Habitat suitability functions were derived for *Deleatidium* from data collected on the Waingawa River (Jowett & Richardson 1990). Only about 25% of the variation in *Deleatidium* abundance was explained by depth, velocity, and substrate. Five other variables, including calculated bottom velocity, were considered, but the only variable related to *Deleatidium* abundance was periphyton biomass, with invertebrate densities higher in areas with light algal coatings. Jowett & Richardson (1990) suggested that the distribution and abundance of *Deleatidium* is influenced by colonisation and a large element of chance, especially in rivers such as the Waingawa, where in-stream conditions are frequently

altered by floods and substrate movement. They recommended that suitability functions derived from the Waingawa River be compared with those derived from other rivers to develop a generally applicable set of functions for New Zealand.

In this study, water velocity, depth, and substrate preferences of several benthic invertebrate taxa are examined. Habitat suitability functions for the most numerous taxon, *Deleatidium*, are derived for each of four rivers. Generalised suitability functions are then derived from the river-specific functions and the predictive ability of the generalised functions tested for each of the four rivers.

METHODS

Data collection

The four rivers (Clutha, Mangles, Mohaka, and Waingawa Rivers) differ in size, source, and flow regime (Table 1) and all have cobbles and gravels as their predominant substrates (Table 2).

The Clutha River, a large lake-fed river in the South Island, was sampled between its source, Lake Wanaka, and Cromwell, 30 km down stream, in March 1980, February 1981, and August 1981. Three invertebrate samples were collected from each of 35 shallow riffle locations with a 0.06 m² Surber sampler. The net mesh size was 0.25 mm. Water depth and

Table 1 General information about the sampling sites. Flow and temperature data from the Water Resources Database (DSIR Marine and Freshwater, Christchurch).

River	Latitude (S)	Longitude (E)	Mean flow (m ³ s ⁻¹)	Flow variability (cv)	Mean annual water temperature (°C)
Clutha	44°54'	169°18'	195	0.50	12.0
Mangles	41°49'	172°26'	10	1.27	11.7
Mohaka	39°10'	176°38'	40	0.90	12.1
Waingawa	40°51'	175°31'	11	1.62	11.3

Table 2 Percentage substrate composition (B, boulder; C, cobble; G, coarse gravel; F, fine gravel; S, silt) and mean values and range of water velocities, depths, and substrate indices (defined in text) at sampling points.

	No. of samples	Substrate %					Velocity (m s ⁻¹)			Depth (m)			Substrate index		
		B	C	G	F	S	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
Clutha	105	7	30	45 ^a	18	0.12	0.75	1.62	0.20	0.41	0.70	4.2	5.09	6.3	
Mangles	68	1	81	14	3	0.10	0.57	1.55	0.07	0.54	1.55	5.0	5.78	6.4	
Mohaka	80	5	52	29	8	0.10	0.53	1.50	0.19	0.60	1.50	3.0	5.40	6.8	
Waingawa	81	22	28	41	7	0.14	0.66	1.27	0.05	0.42	1.20	4.0	5.62	6.9	

^a Coarse gravel and fine gravel combined

mean water column velocity (at 0.6 of the depth from the surface) were measured at each sampling point with a current meter on a calibrated rod. Visual estimates of the substrate composition (%) were made for each riffle location using the modified Wentworth particle size scale (Bovee & Milhous 1978): sand (0.06–2 mm nominal diameter), gravel (2–64 mm), cobble (64–256 mm), and boulder (>256 mm).

The other three rivers were not lake-fed and thus had more variable flows (Table 1). Invertebrate samples were collected in March 1988 from 68 sampling points on the Mangles River and 80 points on the Mohaka River using a 0.1 m² Surber sampler with a 0.5 mm mesh net. Water depth and velocity were recorded as in the Clutha River. Sampling points were stratified so that they included combinations of depths from 0.1 to 1.5 m and velocities from 0.1 to 1.5 m s⁻¹. Visual estimates of substrate composition were made at each sampling point using the same particle size scale, except that the gravel substrate category was divided into fine gravel (2–32 mm) and gravel (32–64 mm). In the Mohaka, where a greater range of substrate types was encountered, additional stratified samples were taken from substrates ranging from predominantly sand to predominantly boulder in depths of 0.4–1.0 m and velocities of 0.2–0.6 m s⁻¹.

The Waingawa River, a tributary of the Ruamahanga, was sampled at 81 points (bedrock sites were excluded from this analysis) in November 1986. Details of data collection were given by Jowett & Richardson (1990). Water depth and velocity were measured as in the other rivers. Substrate composition was estimated at each sampling point with a particle size scale of sand, fine gravel, gravel, cobble, boulder, and bedrock (solid rock surfaces). Invertebrates were collected in a 0.25 m² Surber sampler with a 0.35 mm mesh net. A higher proportion of boulder substrate was sampled at this site than at the other three rivers (Table 2).

Sampling was carried out in different months, different years, and with mesh sizes varying from 0.25 mm to 0.5 mm. Samples in deeper water were collected using SCUBA and the same sampling procedures as for shallower samples. Winterbourn (1985) considered that the poorly synchronised life-histories of many benthic invertebrates in New Zealand mean that larvae are present most of the time although there may be changes in abundance. In the present study, between-river differences in sampling protocols may have influenced abundance, especially the abundance of small invertebrates such as chironomids and oligochaetes.

Data analysis

Each of the 334 invertebrate samples was sorted into 12 of the more abundant species or family groups and the number of individuals counted. Habitat preferences of each taxon were determined by comparing the mean values of the habitat utilised by that taxon, weighted by the number of invertebrates in the taxon, with those of the river itself at each sampling site (Jowett & Richardson 1990). Habitat preferences were considered to exist when the mean value of the habitat variable occupied by that taxon differed significantly from the mean of the variable in that river. Differences in sample means were tested by a Mann-Whitney *U* test. A similar analysis of habitat preferences was made by comparing invertebrate abundances in all four rivers with water velocities, depths, and substrate at each sampling point. The data were plotted after scaling by dividing invertebrate abundance in each river by the maximum abundance in that river. This eliminated the tendency for data from a river with high invertebrate numbers to obscure the preferences in a river with lower abundance.

Jowett & Richardson (1990) investigated methods of deriving and combining habitat suitability curves for *Deleatidium*. They found curves fitted by eye and exponential polynomial functions generally fitted best, and models formed by multiplying independent functions for water velocity, depth, and substrate performed as well as more complicated multivariate models. In this study, exponential polynomials were fitted and stream-specific habitat suitability curves derived for each river. Joint habitat suitability functions (JSF) were formed by multiplying together the velocity, depth, and substrate suitability values. Substrate measurements were converted to a single index by summing weighted substrate percentages (Jowett & Richardson 1990). The weighting values were a slightly modified form of the original IFIM substrate codes (Bovee 1982) to allow for a fine-gravel category:

$$\begin{aligned} \text{Substrate index} = & 0.08 \text{ bedrock}\% + 0.07 \text{ boulder}\% \\ & + 0.06 \text{ cobble}\% + 0.05 \text{ coarse gravel}\% \\ & + 0.04 \text{ fine gravel}\% + 0.03 \text{ sand}\%. \end{aligned}$$

Two dimensionless hydraulic variables, Reynolds number (*Re*) and Froude number (*Fr*), were calculated from mean depth (*D*) and mean velocity (*V*) at each sampling point:

$$Re = V \times D / \text{kinematic viscosity of water}$$

$$Fr = V / (g D)^{0.5}$$

where *g* is the acceleration due to gravity. Reynolds number is a measure of turbulence and the Froude number describes the nature of the flow (from tranquil

to rapid). Relationships between *Deleatidium* abundance and Reynolds and Froude numbers were examined to determine whether they were useful measures of habitat suitability.

Generalised habitat suitability curves were derived in two ways, both subjective. Smooth curves were drawn as approximate averages of the stream-specific exponential curves, with their maximum values (suitability value of 1) as the average of the stream-specific curves. The second method enveloped smoothed data from each of the rivers. Smoothed values of *Deleatidium* abundance (y-axis) were calculated along the x-axis (independent variable) from a weighted average of nearby values of abundance. This is known as locally weighted scatterplot smoothing (Wilkinson 1988). The smoothed curves for each river were standardised so that maximum curve ordinates were equal to unity and generalised curves drawn so they enveloped the maxima of the smoothed data and the majority of the smoothed data points. Habitat suitability and JSF values at each data point were calculated. The values were then correlated with *Deleatidium* abundance to assess the predictive ability of the different suitability curves, JSFs, and methods of derivation.

RESULTS

Invertebrate abundance and in-stream habitat

Mean (\pm SD) invertebrate density per square metre ranged from 1140 ± 681 in the Waingawa River to 5421 ± 3061 in the Mangles River (Table 3). Overall, *Deleatidium* was the most numerous taxon, particularly in the Waingawa where it comprised 75% of

all invertebrates. However, in the Clutha River, chironomids were almost twice as numerous as *Deleatidium*, and in the Mangles River there were almost equal numbers of *Aoteapsyche* spp. and *Deleatidium*. Between-river comparisons of abundance were complicated by the use of different mesh sizes in three rivers. In the samples analysed in this study, oligochaetes and chironomids were the smallest invertebrates and comparisons of numbers of these may be significantly biased. For example, in 13 samples taken from a first-order alpine stream, 69.5% of chironomids and 17% of *Deleatidium* caught in a 0.25 mm mesh sieve passed through a 0.5 mm mesh sieve (A. M. Suren, DSIR Marine and Freshwater pers. comm.). This could explain the high numbers of chironomids collected in the Clutha River. However, taxa other than Chironomidae and Naididae were larger and less subject to bias. *Deleatidium* abundance was highest in the two rivers where the largest mesh size was used and lowest in the river where the smallest mesh size was used.

Many of the taxa demonstrated significant habitat preferences (Table 4, Fig. 1). Usually significant preferences were consistent between rivers, i.e., a preference either for values greater than the mean of the sampling points or for values less than the mean. Consistent velocity preferences were found in three or all of the rivers for 4 of the 12 taxa, substrate preferences for 5 of the 12, and depth preferences for one taxon. When all data were analysed together, mean velocity, depth, and substrate, weighted by the number of individuals of the taxon at each sampling point (Table 5) were often significantly different from

Table 3 Mean numbers (m^{-2}) and coefficients of variation of the predominant invertebrate taxa in each river.

	Clutha	Mangles	Mohaka	Waingawa
<i>Deleatidium</i> spp.	603 (0.8)	1325 (0.4)	1312 (0.7)	851 (0.6)
<i>Coloburiscus humeralis</i>	59 (2.4)	180 (2.1)	77 (1.8)	1 (3.9)
<i>Nesameletus</i> spp.	2 (3.1)	65 (1.1)	44 (1.2)	34 (2.6)
<i>Zelandoperla</i> spp.	1 (5.4)	32 (2.6)	4 (3.0)	4 (1.9)
<i>Pycnocentroides</i> spp.	109 (1.8)	916† (0.8)	594† (1.6)	12 (2.8)
<i>Olinga feredayi</i>	108 (1.0)	566 (0.6)	335 (1.2)	18 (3.6)
<i>Aoteapsyche</i> spp.	164 (1.9)	1333 (1.4)	298 (1.7)	1 (2.3)
Hydrobiosidae	45 (1.2)	48 (0.6)	61 (0.9)	18 (0.8)
Chironomidae	1330 (1.7)	118 (1.0)	376 (1.9)	17 (1.4)
<i>Aphrophila neozelandica</i>	16 (3.3)	27 (2.6)	24 (1.9)	3 (2.5)
<i>Potamopyrgus antipodarum</i>	343 (1.7)	38 (2.7)	9 (5.3)	0
Naididae	169 (2.6)	173 (1.6)	298 (1.7)	0

†*P. aureola*

Table 4 Significance that mean values of velocity, depth, and substrate utilised by each taxon, weighted by the number of individuals, are greater (+) or less (-) than those of the sampling sites in the Clutha (Cl), Mangles (Ma), Mohaka (Mo), and Waingawa (Wa) Rivers. Dot indicates no significant difference; -, + $P < 0.05$; —, ++ $P < 0.01$; —, +++ $P < 0.001$.

Taxon	Velocity				Depth				Substrate			
	Cl	Ma	Mo	Wa	Cl	Ma	Mo	Wa	Cl	Ma	Mo	Wa
<i>Deleatidium</i> spp.	++	.	+	++	.
<i>Coloburiscus humeralis</i>	.	+++	+++	.	.	—	—	—	+++	+++	+++	.
<i>Nesameletus</i> spp.	.	—	.	—	.	++	.	—	.	.	++	+++
<i>Zelandoperla</i> spp.	+++	+++	+++	+++	+++	+++
<i>Pycnocentroides</i> spp.	—	—	.	++	.	+++	+++
<i>Olinga feredayi</i>	—	.	.	—	—	.	.	—	.	.	+++	+++
<i>Aoteapsyche</i> spp.	+++	+++	+++	.	—	—	—	+++	+++	+++	.	.
Hydrobiosidae	.	.	+++	+++	.	++	.
Chironomidae	—	.	—	.	.	—	—	.	+++	.	.	+++
<i>Aphrophila neozelandica</i>	—	+++	+++	.	++	.	—	.	++	+++	+++	+++
<i>Potamopyrgus antipodarum</i>	—	—	—	.	.	.	—
Naididae	—	—	—	.	.	.	—	.	.	—	.	.

the mean velocity, depth, and substrate index of the sampling points (0.64 m s^{-1} , 0.48 m , and 5.46 , respectively). However, different sampling protocols, species composition and abundance, and ranges of substrates and depths sampled in each river may introduce some bias into Table 5, particularly the predominance of cobble substrate in the Mangles River and lack of samples in water deeper than 0.7 m in the Clutha River. The bias was minimised to some extent by excluding the samples taken in sand in the Mohaka River from the comparison.

Coloburiscus humeralis, *Zelandoperla* spp., *Aoteapsyche*, and *Aphrophila neozelandica* preferred high-velocity water with a weighted mean velocity of more than 0.85 m s^{-1} (Table 5). In contrast, *Nesameletus* spp., Chironomidae, *Potamopyrgus antipodarum*, and Naididae preferred lower-velocity water with weighted mean velocities of 0.60 m s^{-1} or less and did not occur in high numbers in water velocities of more than 0.85 m s^{-1} . *Pycnocentroides* and *Olinga feredayi* also had low weighted mean velocities, but were present over a wider range of velocities (Fig. 1). *Nesameletus* and *P. antipodarum* preferred velocities of less than 0.5 m s^{-1} , Chironomidae less than 0.75 m s^{-1} , whereas Naididae clearly preferred velocities less than 0.3 m s^{-1} . *Deleatidium* and Hydrobiosidae showed broad velocity preferences (Fig. 1).

Generally, taxa were more abundant in water depths of less than about 0.75 m , but *Deleatidium*, *Nesameletus*, *O. feredayi*, Hydrobiosidae, and Naididae were also relatively abundant in deeper water (Fig. 1).

Many taxa preferred the coarser substrates (Table 4, Fig. 1). Two of the three mayfly taxa (*C. humeralis* and *Nesameletus*) and the stonefly genus (*Zelandoperla*) preferred cobble-sized or larger substrate (substrate index ≥ 6), whereas the other mayfly genus (*Deleatidium*) was abundant in substrates ranging from gravel to boulder (substrate index 4–7). Two of the four caddisfly taxa (*Pycnocentroides* and *Aoteapsyche*) were most abundant in coarse (cobble-sized or larger) substrate, whereas *O. feredayi* and Hydrobiosidae were abundant in gravel as well as the coarser substrates. Two taxa (*P. antipodarum* and Naididae) were abundant in gravel-sized or finer substrate.

Table 5 Means of velocity, depth, and substrate index, weighted by the number of individuals at each sampling point in all four rivers and significance level that the weighted mean was different from the mean of the sampling points. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Taxon	Velocity (m s^{-1})	Depth (m)	Substrate index
<i>Deleatidium</i> spp.	0.69*	0.48	5.62***
<i>Coloburiscus humeralis</i>	0.94***	0.40***	5.90***
<i>Nesameletus</i> spp.	0.46***	0.56**	5.86***
<i>Zelandoperla</i> spp.	1.17***	0.50	5.93***
<i>Pycnocentroides</i> spp.	0.60*	0.42***	5.82***
<i>Olinga feredayi</i>	0.58**	0.53*	5.70***
<i>Aoteapsyche</i> spp.	0.97***	0.43**	5.85***
Hydrobiosidae	0.73***	0.44*	5.62***
Chironomidae	0.60*	0.39***	5.42
<i>Aphrophila neozelandica</i>	0.86***	0.47	5.74***
<i>Potamopyrgus antipodarum</i>	0.59**	0.43**	5.11***
Naididae	0.37***	0.46	5.42

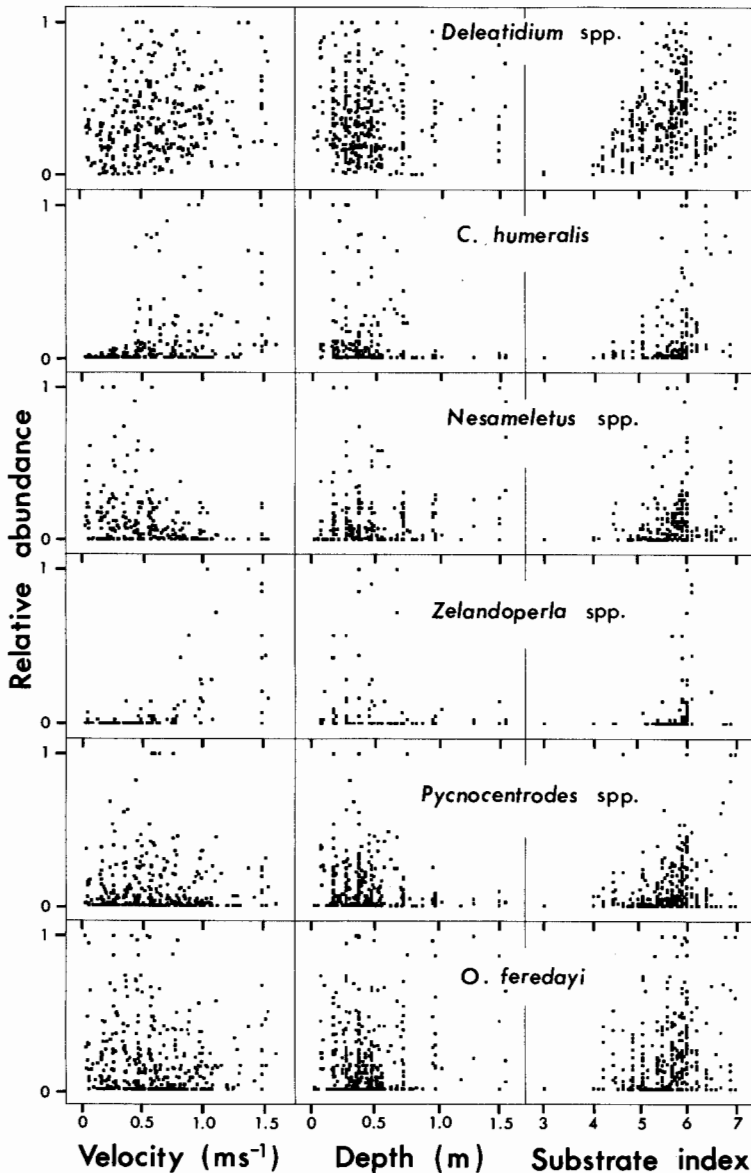


Fig. 1 Comparison of relative invertebrate abundance (density of taxon at a sampling point divided by the maximum density sampled in that river) with water velocity, depth, and substrate index at 334 sites in all four rivers.

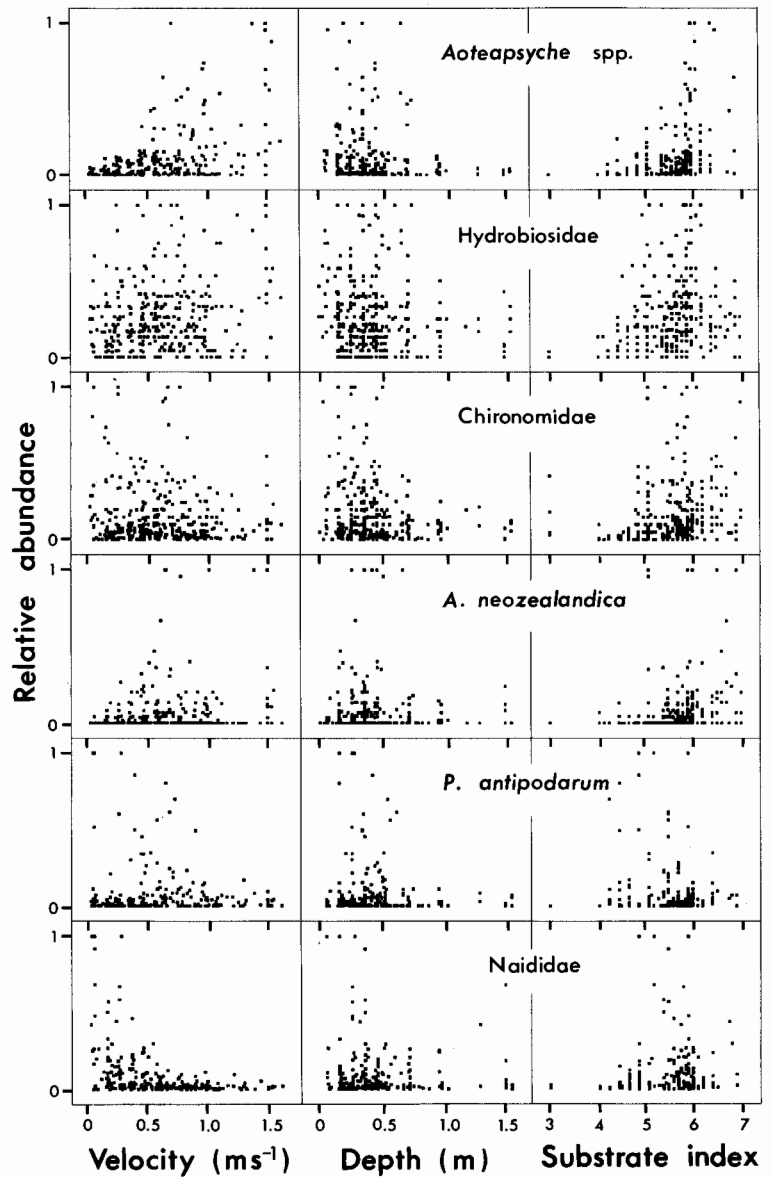
Modelling *Deleatidium* abundance

Stream-specific curves

Exponential velocity suitability curves developed for each river had well-defined optima at water velocities ranging from 0.9 m s^{-1} in the Waingawa River to 1.29 m s^{-1} in the Clutha River (Fig 2A). Locally weighted smooth curves of velocity suitability had similar shapes, and in three of the four rivers, optimum

velocities were equal to the highest sampled (Fig. 2B). Substrate suitability curves showed more variation among rivers than did velocity (Fig. 2C, 2D), but all showed optimum substrate to be gravel-sized or larger. Not all rivers contained boulder substrate (Table 2), making any decline in preference with larger substrate difficult to define. The relationship between *Deleatidium* abundance and substrate was not significant in the Clutha River,

Fig. 1 (continued)



where substrate composition was estimated as an average for each riffle rather than at the sampling point and gravel was not divided into fine and coarse categories.

Locally weighted smooth curves for depth (Fig. 2F) indicated invertebrate densities were highest in the shallowest water sampled in all rivers except the Waingawa. Depth suitability curves for the Mangles and Mohaka Rivers showed a high preference for

shallow (< 0.5 m) water, as indicated by the locally weighted curves, whereas curves for the Clutha and Waingawa Rivers each showed optimum depths at about 0.4 m (Fig. 2E). Depth curves for the Mangles River (Fig. 2E, 2F) were concave unlike those of the other rivers. In the Mangles River, seven samples were collected in depths greater than 1.0 m. The average velocity at these points was greater than at equivalent sampling points in either the Waingawa

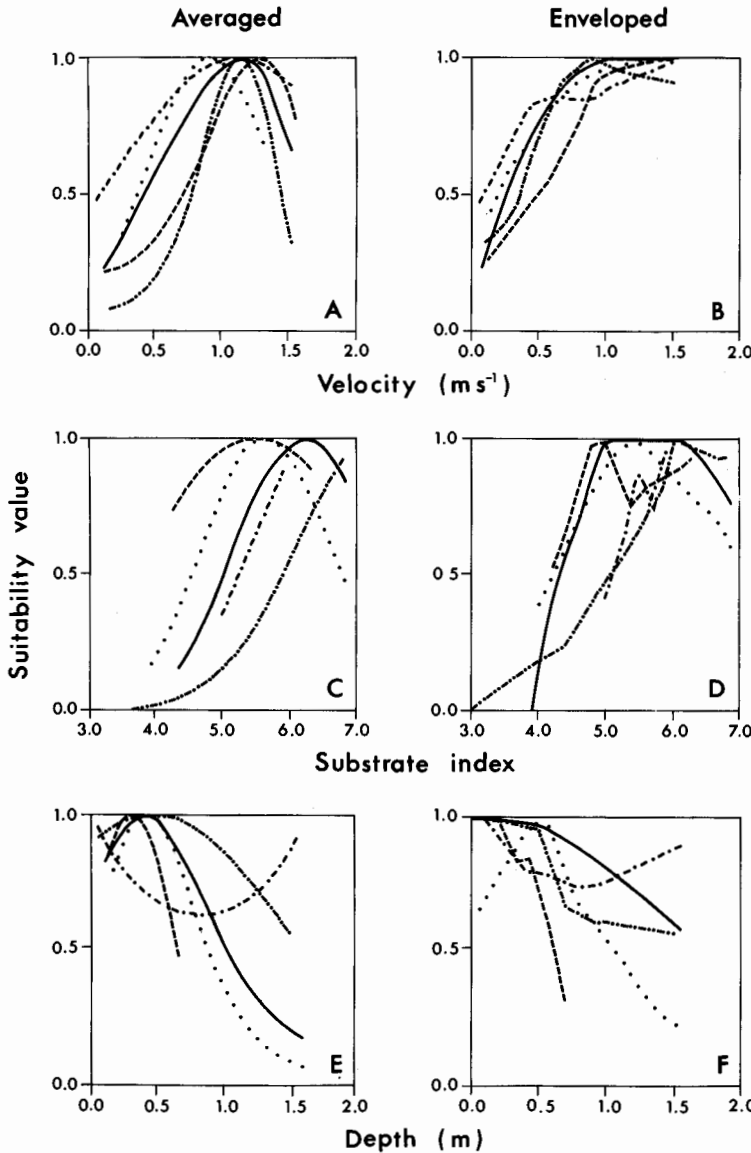


Fig. 2 Comparison of *Deleatidium* suitability curves for the Clutha (dashed line), Mangles (dash and one dot), Mohaka (dash and two dots), and Waingawa (dotted line) Rivers. Solid lines are generalised *Deleatidium* suitability curves based on averages of stream-specific exponential curves (A, C, E) and on enveloping locally weighted smooth curves (B, D, F).

and Mohaka Rivers resulting in an apparent increase in abundance with depth.

Interpretation of curves was complicated by interrelationships between substrate, water depth, and velocity and was not completely eliminated by stratified sampling. Stratified sampling of water depth and velocity, as adopted in the Mangles and Mohaka Rivers, may have improved correlations with abundance, especially for the Mohaka River where

Table 6 Pearson correlation coefficients (r) between pairs of variables: water depth (D), velocity (V), and substrate index (S). * $P < 0.05$.

River	N	S,V	S,D	D,V
Clutha	105	-0.033	-0.227*	-0.041
Waingawa	81	0.246*	-0.250*	0.246*
Mangles	68	0.538*	-0.060	-0.144
Mohaka	80	0.341*	-0.185	-0.086

stratified sampling of substrate was carried out as well. In the Clutha and Waingawa Rivers, substrate size was inversely related to water depth, whereas in the other two rivers substrate size was positively correlated with water velocity (Table 6).

Generally, either the velocity or substrate suitability curves were better single variable predictors of *Deleatidium* abundance than depth (Table 7A). Velocity suitability curves were the best predictors for the Clutha and Mangles, whereas substrate suitability curves were best for the Waingawa and Mohaka Rivers, where the range of substrate sampled was greatest.

When suitability curves for each river were combined by multiplication into a single joint suitability function (JSF), correlation coefficients increased for all rivers except the Waingawa (Table 7A). Correlation coefficients for each river increased as flow variability decreased, although the correlation between r and flow variability was not significant at the 95% level ($r = 0.937$, $P = 0.063$). The predictive ability of JSFs developed for one river was generally poorer when applied to each of the other three rivers. For example, the stream-specific JSF for

the Clutha River, when applied to the other three rivers, resulted in 13–40% lower correlation coefficients than those derived from each river's stream-specific JSF.

Exponential polynomial relationships between *Deleatidium* abundance and Reynolds number were significant for only two rivers, whereas significant exponential polynomial relationships between *Deleatidium* abundance and Froude number existed for all four rivers and were better than those for Reynolds number in all cases (Table 7A). Froude number was highly correlated with velocity ($r = 0.885$, $P < 0.001$) and relationships between them and *Deleatidium* abundance were similar.

Generalised curves

When the stream-specific exponential velocity, depth, and substrate curves (Fig. 2A, 2C, 2E) were averaged, the predictive ability of these curves (Table 7B) was generally worse than the individual stream-specific curves. For instance, the averaged depth curve was a poor predictor ($r = 0.034$) of *Deleatidium* abundance in the Mangles River where the stream-specific depth curves were concave unlike the other curves (Fig.

Table 7 Correlation coefficients (r) between *Deleatidium* numbers and habitat suitability indices calculated from (A) stream-specific exponential polynomials (broken lines in Fig. 2A, 2C, 2E), (B) generalised curves derived by averaging graphically the stream-specific exponential polynomials (solid line in Fig. 2A, 2C, 2E), and (C) generalised curves fitting graphically as an envelope to locally weighted smooth curves (solid line in Fig. 2B, 2D, 2F). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Habitat suitability model	Clutha River	Waingawa River	Mangles River	Mohaka River
A. Stream-specific curves				
Velocity	0.493***	0.310**	0.464***	0.467***
Depth	0.219*	0.401***	0.297*	0.198*
Substrate	0.116	0.487***	0.264*	0.530***
Reynolds number	0.361***	0.199	0.267*	0.097
Froude number	0.516***	0.374***	0.590***	0.572***
Joint suitability function				
Velocity \times depth \times substrate	0.575***	0.452***	0.479***	0.572***
B. Averaged curves				
Velocity	0.436***	0.296**	0.405***	0.573***
Depth	0.226*	0.363***	0.034	0.264**
Substrate	0.050	0.179	0.320**	0.366***
Joint suitability function				
Velocity \times depth \times substrate	0.296**	0.141	0.306**	0.317**
C. Enveloped curves				
Velocity	0.433***	0.309**	0.524***	0.529***
Depth	0.221*	0.337**	0.025	0.242*
Substrate	0.188	0.448***	0.067	0.519***
Froude number	0.406***	0.359***	0.570***	0.582***
Joint suitability functions				
Velocity \times depth \times substrate	0.470***	0.443***	0.492***	0.688***
Froude number \times substrate	0.395***	0.446***	0.570***	0.666***

2E). When averaged curves were combined into a single JSF, all performed poorly compared with their counterpart stream-specific JSFs.

Curves formed by enveloping the locally weighted smoothed data (Fig. 2B, 2D, 2F) generally performed only slightly better than the averaged curves for velocity and substrate and worse for depth (Table 7C). However, when combined into a JSF, the ability of this single model to predict *Deleatidium* abundance exceeded that of individually fitted JSFs for the Mangles and Mohaka Rivers, was similar to the Waingawa JSF, and poorer than the Clutha River JSF. This enveloped velocity, depth, and substrate JSF explained between 20 and 25% of the variation in *Deleatidium* abundance in all four rivers (Table 7C).

The generalised Froude number suitability curve (not shown but similar to Fig. 2B) predicted *Deleatidium* abundance in the Mangles, and Mohaka Rivers (Table 7C) better than any of the stream-specific or generalised curves based on either velocity, depth, or substrate. When combined into a JSF with substrate suitability, this model predicted *Deleatidium* abundance better than the enveloped velocity, depth, and substrate JSF in two rivers and worse in two (Table 7C).

Three of the four linear regression models of *Deleatidium* abundance based on the enveloped velocity, depth, and substrate JSF (Table 7C) had intercepts which were not significantly different from zero ($P < 0.05$). Analysis of covariance showed that slopes of the Clutha and Waingawa River models were similar ($F = 0.60$, $P = 0.44$) and different from that of the Mohaka River model ($F = 9.31$, $P < 0.001$) (Fig. 3). The Mangles River model was the only one with a significantly non-zero but positive intercept. However, when the regression was forced through zero, its slope was similar to that for the Mohaka. In contrast, models using stream-specific and Froude number/substrate JSFs were less realistic. Three of the four stream-specific models (Table 7A) and two Froude number/substrate models (Table 7C) had significantly non-zero intercepts. All Froude number/substrate model intercepts were negative, giving unrealistic predictions of *Deleatidium* abundance for some values of JSF.

DISCUSSION

Habitat preferences

Many species of benthic invertebrates demonstrate preferences and adaptations for particular substrates

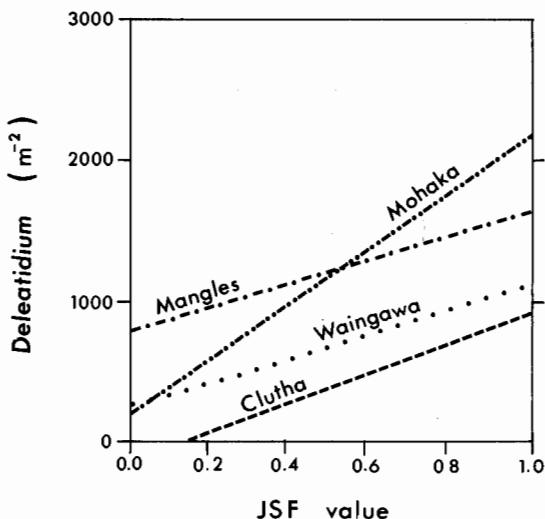


Fig. 3 Comparison of regression equations for *Deleatidium* abundance using the enveloped velocity, depth, and substrate joint suitability function (Table 7C).

or water velocities (Hynes 1970; Minshall 1984). One of the earliest discoveries in insect-substrate relationships was that most (but not all) taxa showed individual preferences for different substrate types and that the preferences differed (Minshall 1984). In this study, we found that when data from all rivers were compared, significant substrate preferences were exhibited by most taxa. Generally taxa preferred coarser substrate, with a weighted mean substrate index of greater than 5.5 (i.e., more than 50% cobble-sized or larger substrate), although some taxa (particularly Chironomidae, *P. antipodarum*, and Naididae) were also abundant in gravel and finer substrate. No taxa demonstrated any clear preference for finer substrates, confirming the view that large substrate was generally more productive than small (Minshall 1984).

Water velocity is interrelated with substrate which makes it difficult to separate the effects of the two. However, the determination of velocity preferences was less subject to bias than substrate because similar ranges of velocity were sampled in each of the rivers. Three taxa (*C. humeralis*, *Zelandoperla*, and *Aotea-psyche*) that demonstrated a preference for high water velocities were also associated with coarse substrate. Conversely, the taxa which preferred low water velocities (Naididae, *P. antipodarum*, and Chironomidae) had low weighted mean substrate indices (Table 5) and were present in

a broad range of substrates. The stronger relationships of these taxa with velocity suggests that, for these taxa, velocity is more important than substrate. *Nesameletus* was also associated with low water velocity but preferred coarse substrates, in contrast to the other three low-velocity taxa. The taxa could be broadly classified into four groups; low to moderate velocity ($< 0.75 \text{ m s}^{-1}$) and broad substrate preferences (Chironomidae, *P. anti-podarum*, and Naididae), moderate velocity ($0.20\text{--}0.80 \text{ m s}^{-1}$) and coarse substrate preferences (*Pycnocentroides* and *Nesameletus*), high velocity ($> 0.75 \text{ m s}^{-1}$) and coarse substrate preferences (*C. humeralis*, *Zelandoperla*, and *Aoteapsyche*), and broad velocity and substrate preferences (*Deleatidium*, *O. feredayi*, Hydrobiosidae, and *A. neozelandica*). These are consistent with known associations of New Zealand benthic invertebrates with velocity and substrate (Allen 1959; Winterbourn 1981; Pridmore & Roper 1985).

In-stream flow-habitat models

Deleatidium, one of the most common genera of benthic invertebrate in New Zealand rivers (Winterbourn 1987; Quinn & Hickey 1990) did not generally demonstrate significant habitat preferences (Table 4) and it was expected that flow-habitat models of abundance would be relatively inaccurate. Hence, the following discussion concentrates on the method rather than the accuracy of the models.

Suitability functions derived from different rivers are often influenced by the range of habitats over which the data are collected and interpretation is complicated by the relationships between hydraulic variables (Bovee 1986; Orth 1986). Thus, it is advantageous to collate data from several different rivers into one set of suitability curves.

It has been suggested that habitat preferences should be derived for each study river (Gore & Nestler 1988). However, we found that functions formed using enveloped data from four rivers performed almost as well as stream-specific functions, and very much better than functions developed for one river and applied to another. Orth & Maughan (1983) found significant relationships between Froude number and five benthic invertebrate species. They also found significant relationships ($r = 0.33\text{--}0.78$) between velocity, depth, and substrate joint preference factors and logarithmically transformed biomass for 10 species of benthic invertebrate, and the intercepts of all relationships were not significantly different from zero. We found that *Deleatidium* abundance was related to Froude number but, when

combined with substrate, was not as good a predictor of *Deleatidium* abundance as the enveloped velocity, depth, and sub-strate JSF. The intercepts of in-stream models using enveloped velocity, depth, and substrate JSFs were closer to zero than models using either stream-specific or Froude number/substrate suitability functions, although slopes differed from river to river (Fig. 3).

Conder & Annear (1987) tested relationships between in-stream habitat (WUA) and trout standing crop both within streams and between streams and concluded that a relationship between WUA and standing crop may exist, but that it was likely to be unique for each stream. We found three different linear relationships between *Deleatidium* abundance and habitat suitability in the four rivers tested. Different sampling protocols may have resulted in differences in abundance between rivers; however, other factors, besides depth, velocity, and substrate, also influence species distribution and abundance (Bovee 1982; Orth 1987). Jowett & Richardson (1990) associated the occurrence of light algal coatings with higher densities of *Deleatidium* and Quinn & Hickey (1990) found that *Deleatidium* density was negatively correlated with indicators of water enrichment and high periphyton biomass.

Unique relationships between invertebrate abundance and habitat suitability for particular rivers validate IFIM application. However, because relationships differ from river to river and because other factors influence abundance, it is erroneous to assume that comparisons of in-stream habitat (WUA) between different rivers will necessarily reflect *Deleatidium* abundance.

The extension of the study of *Deleatidium* distribution to an additional three rivers confirmed the broad habitat preferences observed by Jowett & Richardson (1990) in the Waingawa River. The generalised velocity, depth, and substrate JSF developed by enveloping curves from four rivers performed as well as stream-specific functions in predicting relative densities and with an accuracy similar to those in other in-stream flow-habitat models for benthic invertebrates (Orth & Maughan 1983; Morin et al. 1986). Therefore, the generalised JSF appears to represent the range of in-stream conditions utilised by *Deleatidium* in larger New Zealand gravel-bed rivers and to be a useful indicator of habitat suitability. Similar functions and predictive models could be developed for other taxa, with an expectation of more accurate results for those taxa which demonstrated stronger habitat preferences than *Deleatidium*.

ACKNOWLEDGMENTS

This work was partly funded by the Department of Conservation. We thank Mike Winterbourn and the anonymous referee for their useful comments on this manuscript.

REFERENCES

- Allen, K. R. 1959: The distribution of stream bottom faunas. *Proceedings of the New Zealand Ecological Society* 6: 5-8.
- Bovee, K. D. 1982: A guide to stream habitat analysis using the instream flow incremental methodology. United States Fish and Wildlife Service, Cooperative Instream Flow Group, *Instream flow information paper* 12. 248 p.
- 1986: Developments and evaluation of habitat suitability criteria for use in the instream flow incremental methodology. United States Fish and Wildlife Service, Cooperative Instream Flow Group, *Instream flow information paper* 21. 235 p.
- Bovee, K. D.; Milhous, R. 1978: Hydraulic simulation in instream flow studies: theory and techniques. United States Fish and Wildlife Service, Cooperative Instream Flow Group, *Instream flow information paper* 5. 131 p.
- Conder, A. L.; Annear, T. C. 1987: Test of weighted usable area estimates derived from a PHABSIM model for instream flow studies on trout streams. *North American journal of fisheries management* 7: 339-350.
- Gore, J. A.; Judy, R. D. 1981: Predictive models of benthic macroinvertebrate density for use in instream flow studies and regulated flow management. *Canadian journal of fisheries and aquatic sciences* 38: 1363-1370.
- Gore, J. A.; Nestler, J. M. 1988: Instream flow studies in perspective. *Regulated rivers: research and management* 2: 93-101.
- Hynes, H. B. N. 1970: The ecology of running waters. Toronto, University of Toronto Press. 555 p.
- Jowett, I. G.; Richardson, J. 1990: Microhabitat preferences of benthic invertebrates in a New Zealand river and the development of in-stream flow-habitat models for *Deleatidium* spp. *New Zealand journal of marine and freshwater research* 24: 19-30.
- Mathur, D.; Bason, W. H.; Purdy, E. J.; Silver, C. A. 1985: A critique of the instream flow incremental methodology. *Canadian journal of fisheries and aquatic sciences* 42: 825-831.
- McLennan, J. A.; MacMillan, B. W. H. 1984: The food of rainbow and brown trout in the Mohaka and other rivers of Hawke's Bay, New Zealand. *New Zealand journal of marine and freshwater research* 18: 143-158.
- Minshall, G. W. 1984: Aquatic insect-substratum relationships. In: Resh, V. H.; Rosenberg, D. M. ed. *The ecology of aquatic insects*, pp. 358-400. New York, Praeger Publishers.
- Morhardt, J. E. 1986: Instream flow methodologies. Electric Power Research Institute, California. 123 p.
- Morin, A.; Harper, P.-P.; Peters, R. H. 1986: Microhabitat-preference curves of blackfly larvae (Diptera: Simuliidae): A comparison of three estimation methods. *Canadian journal of fisheries and aquatic sciences* 43: 1235-1241.
- Moyle, P. B.; Baltz, D. M. 1985: Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. *Transactions of the American Fisheries Society* 114: 695-704.
- Orth, D. J. 1986: In defense of the instream flow incremental methodology. *Canadian journal of fisheries and aquatic sciences* 43: 1092-1093.
- 1987: Ecological considerations in the development and application of instream flow-habitat models. *Regulated rivers: research & management* 1: 171-181.
- Orth, D. J.; Maughan, O. E. 1983: Microhabitat preferences of benthic fauna in a woodland stream. *Hydrobiologia* 106: 157-168.
- Pierce, R. J. 1986: Foraging responses of stilts (*Himantopus* spp.: Aves) to changes in behaviour and abundance of their riverbed prey. *New Zealand journal of marine and freshwater research* 20: 17-28.
- Pridmore, R. D.; Roper, D. S. 1985: Comparison of the macroinvertebrate faunas of runs and riffles in three New Zealand streams. *New Zealand journal of marine and freshwater research* 19: 283-291.
- Quinn, J. M.; Hickey, C. W. 1990: Characterisation and classification of benthic invertebrates in 88 New Zealand rivers in relation to environmental factors. *New Zealand journal of marine and freshwater research* 24: 387-409.
- Raleigh, R. F.; Zuckerman, L. D.; Nelson, P. D. 1986: Habitat suitability index models and instream flow suitability curves: brown trout, revised. *U. S. Fisheries and Wildlife Service biological report* 82(10.124). 65 p.
- Sagar, P. M.; Eldon, G. A. 1983: Food and feeding of small fish in the Rakaia River, New Zealand. *New Zealand journal of marine and freshwater research* 17: 213-226.
- Scott, D.; Shirvell, C. S. 1987: A critique of the instream flow incremental methodology with observations on flow determination in New Zealand. In: Kemper, B.; Craig, J. F. ed. *Regulated streams: advances in ecology*, pp. 27-43. New York, Plenum Press.
- Statzner, B. 1981: A method to estimate the population size of benthic macroinvertebrates in streams. *Oecologia* 51: 157-161.

Statzner, B.; Gore, J. A.; Resh, V. H. 1988: Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society* 7: 307–360.

Wilkinson, L. 1988: Sygraph. Systat Inc., Evanston, IL. 922 p.

Winterbourn, M. J. 1981: The use of aquatic invertebrates in studies of stream water quality. *In: Standing biological working party of the Water Resources Council, a review of some biological methods for*

the assessment of water quality with special reference to New Zealand. Part 2. *Water and Soil technical publication* 22: 5–16.

———1985: Sampling stream invertebrates. *In: Pridmore, R. D.; Cooper, A. B. ed. Biological monitoring in freshwaters. Water and soil miscellaneous publication* 83: 241–258.

———1987: Invertebrate communities. *In: Viner, A. B. ed. Inland waters of New Zealand, DSIR Bulletin* 241: 167–190.