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Periphyton development in three valley segments of a New Zealand grassland river: test of a habitat matrix conceptual model within a catchment

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With 11 figures and 7 tables in the text

Abstract: We monitored water nutrient concentrations, periphyton biomass, and periphyton cellular nutrient concentrations in run and riffle habitats at sites representative of headwater, mid-catchment and lowland valley segments of a grassland river for two years, and community composition on four occasions during this period, to determine how these communities varied spatially and temporally as a function of downstream changes in hydraulic conditions, flood disturbance regimes and enrichment. Predictions of community biomass and structure were tested under a proposed habitat matrix conceptual model for periphyton. Discharge increased and valley segment slope decreased in a downstream direction as expected from geomorphic models of catchment processes. However, site-specific depths and velocities did not change systematically down the river. Water nutrient concentrations suggested a change from nitrogen limitation of primary production at the headwater site to phosphorus limitation at the lowland site. This was associated with a downstream increase in stream nitrate concentrations, but not phosphorus. However, cellular nutrient concentrations and instream nutrient bioassays suggested either N limitation, or weak N and P limitation, at all sites. In runs, mean monthly chlorophyll-a did not vary significantly ($P > 0.05$) among the three sites, but it did in riffles. The differences in community biomass between run and riffle habitats were more significant than differences among sites. Periphyton community structure in the runs was similar among valley segments during a period of frequent flood disturbances, but during a period of infrequent disturbances communities in the headwater sites were dominated by filamentous cyanobacteria whereas in the mid-catchment and lowland sites they were dominated by nitrogen-fixing cyanobacteria and diatoms. Major differences in community structure occurred in riffles among the sites. Riffle communities at the headwater site were

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dominated by filamentous cyanobacteria and diatoms, whereas at the mid-catchment and lowland sites filamentous green algae and diatoms were dominant, possibly a result of increased nitrate concentrations progressing downstream. Overall, a downstream gradient in nitrate enrichment appeared to control biomass and community composition of the riffle communities, but not the run communities. Strong grazer activity in runs during more hydrologically stable periods at the lowland site appeared to override any response to nutrients and maintained biomass at low levels. Periphyton biomass and community composition was predicted more accurately from the habitat matrix conceptual model based on local habitat factors than by expected downstream gradients in hydraulic conditions and enrichment.

Introduction

Physical conditions change greatly down the course of rivers (VANNOTE et al. 1980, STATZNER & HIGLER 1986). Three main valley segments can often be identified (e.g. BRUSSOCK et al. 1985): (1) a headwater segment, typically with a narrow channel confined in a V-shaped valley, a steep channel gradient (although the local channel profile may be stepped), turbulent flow, and substrata dominated by bedrock, boulders and cobbles; (2) a mid-catchment segment typically with a much broader valley and flood plain development, often including braiding, active channel migration and bank erosion, a moderate channel gradient (with well defined pool-riffle-run sequences), moderate velocities and substrata dominated by cobbles and gravels; and (3) a lowland segment, with a very broad valley and associated floodplain within which the active river meanders as a single thread channel, the channel gradient is low resulting in low water velocities and a finer substrata of gravels and sands which can be active at discharges less than bankfull. The abundance of fine substrata and low relief dampens riffle formation and the bedforms that are created are easily modified by single flood events (BRUSSOCK et al. 1985). Major downstream changes in light and nutrient supply can often be associated with the geomorphic changes (VANNOTE et al. 1980, HOLMES & WHITTON 1981, NAIMAN et al. 1987). In headwater valley segments within forested catchments, extensive riparian shading can occur (e.g. DE NICOLA et al. 1992) and nutrient levels in the streams are usually low (e.g. COOPER & THOMSEN 1988, CLOSE & DAVIES-COLLEY 1990, BIGGS 1995). However, the riparian shading often decreases moving downstream with intensification of landuse and channel widening resulting in greatly increased light levels. This change in landuse can also increase inorganic nutrient supplies (e.g. OMERNIK 1977, HOLMES & WHITTON 1981, CLOSE & DAVIES-COLLEY 1990, BIGGS 1995). In grassland catchments, such progressive changes in light will generally not occur because of limited (or no) riparian shading (e.g. WILEY et al. 1990), and these catchments are often developed for agriculture along much of their length.

We could expect that any broad downstream changes in geomorphology and resource supply should result in systematic and predictable changes in the biomass and composition of periphyton in rivers, such as proposed under the River Continuum Concept (RCC) (VANNOTE et al. 1980). In 1st to 6th Order systems, we could expect that average periphyton biomass should increase downstream and community structure should change from predominantly low profile *R* (ruderal) or *S* (stress) selected taxa to communities dominated by architecturally more complex, nutrient demanding, *C* (competitive) or *C–S* taxa (sensu GRIME 1979, BIGGS et al. 1998). Several studies have attempted to define downstream changes in periphyton biomass and production while testing predictions of the RCC (e.g. MINSHALL et al. 1983, BOTT et al. 1985, NAIMAN et al. 1987, WILEY et al. 1990). However, the results have only partially supported this hypothesis. It is apparent that conditions are often far more heterogeneous in many catchments than allowed for in generalised concepts such as the RCC and periphyton communities may be responding mainly to the local, site specific, conditions. Also, the RCC does not specifically address the effects of flood disturbances which can potentially override, or at least strongly alter, responses by periphyton to variations in light and nutrient resource supply (BIGGS 1995, 1996, PETERSON 1996), and disturbance events can vary greatly in intensity and frequency within catchments (e.g. TOWNSEND et al. 1997a).

In the following study, we present a detailed analysis of within-catchment variations in periphyton development as functions of meso- and macro-scale changes in habitat in a 1st–6th order grassland river system. We wanted to assess whether average periphyton biomass and community structure could change predictably downstream in grassland catchments where headwater forests are now (and historically) absent and in response to reductions in channel gradient (hydraulic conditions), increases in nutrient enrichment associated with intensification of land use (but in the absence of the confounding effects of shading), and variations in disturbance regimes. Through this, we wanted to test the habitat matrix conceptual model of BIGGS et al. (1998) as an alternative predictor of changes in periphyton communities within catchments to the RCC that has a heavy dependency on canopy cover as a driving function.

Kakanui River study area

The study was carried out in the Kakanui River, North Otago, South Island, New Zealand (Fig. 1). The river had three main valley segments based on channel form following the model proposed by BRUSSOCK et al. (1985). The headwater segment (Tables 1, 2) encompassing a V-shaped valley with a stepped pool-riffle channel and dominated by a cobble, boulder and bedrock substrata, extended from the first order rivulets down to the 4th order streams

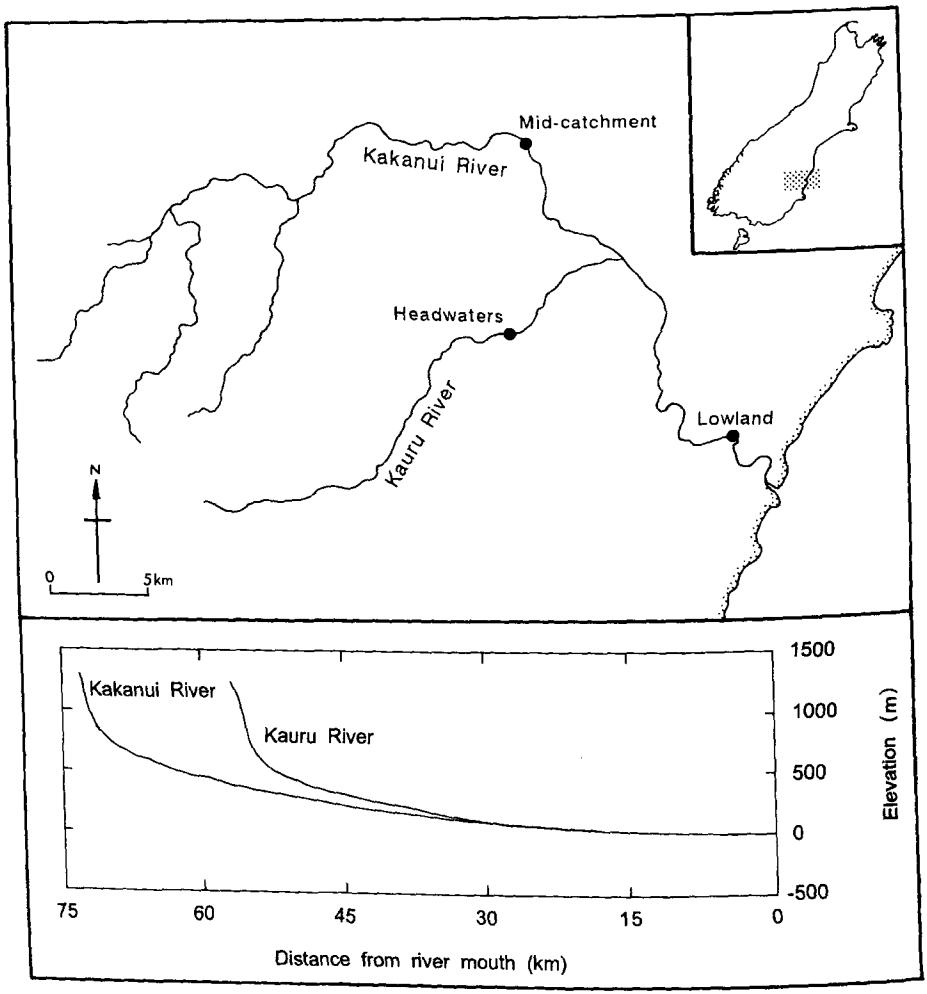

Fig. 1. Map of Kakanui River study area and a longitudinal profile based on elevation.

(Fig. 1). A progressive decrease in channel slope, and an associated increase in the proportion of runs, occurred at the head of the mid-catchment valley segment as the 5th order streams coalesced to form the 6th order river. Here the channel had a weakly armoured bed in the riffles and a strongly armoured bed in the runs with the paved layer dominated by cobbles. This channel surface was rarely moved during floods. Bedrock formed the channel banks along some sections. Approximately half way down this valley segment the river left the confines of the foothills and entered an outwash plain. Areas of Tertiary bedrock intersected the river at various points and created localised hydraulic controls. The bed was dominated by a cobblegravel substratum, with braids in a number of locations. The gradient of the river was reduced still further at

about 5–7 km from the sea where it graded into the lowland valley segment. Here the river became more confined into a single, narrower, meandering channel with a predominantly run structure. Gravels dominated the substratum in the runs and cobbles in the occasional riffle. Much of the channel was highly armoured and the bed appeared very resistant to movement during floods.

The upper catchment was predominantly steep hill-country reaching an altitude of 1500 m and prior to European settlement the vegetation was largely dominated by tall native snow tussock grasslands (WENDELKEN 1976). These have subsequently been oversewn with pastoral grasses for low intensity cattle and sheep grazing. Agriculture intensified in the mid catchment where hills were much lower (historically covered in short native tussock grasses; WENDELKEN 1976) with improved pasture grasses and high stock densities. In the lower catchment (<100 m altitude and historically covered in short native tussock grasses; WENDELKEN 1976) the pastures were even more highly developed (including supplementary irrigation) and supported intensive sheep and cattle grazing, with small areas of intensive horticulture. Much of the upper basin was underlain by schistose rock. However, the lower catchment was an outwash plain underlain by Tertiary sediments. Sites were selected to be representative of these valley segments and to be close to hydrological gauging stations. The headwater site received a small amount of shading from riparian willows (and an adjacent pine-tree plantation) early in the morning and late in the afternoon. Otherwise the sites were largely unshaded.

Materials and methods

Field procedures

Flows were monitored in each valley segment by the local river monitoring authority (Otago Regional Council) using pressure transducer water level recorders. Rating curves were developed based on monthly gaugings which covered a full range of flows. Five periphyton samples were collected on each visit from September 1992 through to June 1994 along each of two separate transects at each site; one from a run habitat and another from a riffle habitat. Sampling on some occasions was missed due to high flows which made access to the river too dangerous. The width of the river at each transect location was divided equally into 5 sections and the depth and velocity at the mid-point of each section was measured using a Gurley current meter and wading rod. The stone beneath each of these points was then lifted from the bed and transported to the bank where material from within a 6 cm diameter circle was scraped off with a scalpel. The five samples from each transect were pooled and returned, chilled, to the laboratory where they were frozen for later analysis.

An additional sampling was carried out at the headwater site 4 days following a major flood on 19th March 1994, then 30, 50 and 70 days after to assess the regeneration dynamics of the communities. Both run and riffle communities were sampled.

Individual regression equations were developed between discharge and mean water velocity for runs and riffles at each sampling site. This allowed discharge to be converted to velocity for the sampling period, and velocity exceedance statistics to be calculated (BIGGS 1995). Coefficients of determination were generally between 0.72 and 0.78.

At the time of each periphyton sampling, a water sample was collected in a sterile 120 ml specimen container and frozen until analysis for soluble nutrients. Temperature and conductivity were measured in the field. Substratum particle size was assessed at each site on one occasion using the Wolman method (MOSLEY 1983). For this assessment, one hundred particles were randomly selected, each from a run and a riffle.

In-stream nutrient enrichment assays were conducted seasonally in runs at the sites during a part of the study period with relatively few flood disturbances (austral summer, 14 February–3 March 1993; autumn, 13–30 April; winter, 22 June–9 July; spring, 24 September–11 October) to precisely determine the nutrient limiting periphyton accrual. A modification of the FAIRCHILD & LOWE (1984) nutrient diffusing substratum method was used and involved deploying five replicate reservoirs of nutrient agar (300 ml) placed in each of four lines within galvanised steel boxes anchored to the river bed (dimensions = 0.6 m × 0.4 m, with an internal frame to hold the reservoirs). Hardened-ashless filters were placed over the tops of the reservoirs for a periphyton colonisation surface and held in place with plastic collars. A flat lid with 2 cm high longitudinal partitions (to maintain parallel flow and prevent diffusion onto neighbouring treatments) was then fixed to the top of the boxes. Holes, the diameter of the reservoir necks, allowed the lid to be seated so that the filter papers were flush with the surface of the lid and exposed to the stream current. This approach was developed as a much more robust alternative to the ‹flower-pot› method for our flood prone study river (BIGGS & LOWE 1994). These samplers were generally deployed for 17 days in each season. At the end of this period, the filter papers were removed and placed directly into a centrifuge tube with 5 ml of 90 % ethanol for extraction of the chlorophyll-a. On one occasion (1993 spring) when periphyton growth rates were high and moving into a flow recession immediately after a spring flood, a second set of substrata was also deployed in the riffles to determine differences in periphyton chlorophyll-a and invertebrate density as an indication of the potential effects of herbivory on biomass differences between riffles and runs. Invertebrates were picked from the filter papers and placed in 40 % formalin for returning to the laboratory. Periphyton chlorophyll-a was assessed as for the seasonal nutrient enrichment assays.

Laboratory procedures

Upon thawing, the periphyton samples from the stone substrates were blended and sub-sampled for analysis of chlorophyll-a and ash-free dry mass (AFDM). Chlorophyll-a was analysed after extraction in boiling 90 % ethanol and reading on a spectrophotometer. An acidification step was used to correct for phaeopigments (SARTORY & GROBBELAAR 1984). The centrifuge tubes with the nutrient diffusing substratum filter papers were placed in a heated (74 °C) water bath for five minutes to boil the ethanol and complete the chlorophyll extraction. Ash-free dry mass (AFDM) was determined

on a subsample of the natural stone community by drying at 105 °C for 24 h and ashing at 400 °C for 4 h. Sub-samples were also analysed for N and P as total Kjeldahl N and total P normalised to AFDM to give mat nutrient concentrations (% N_c, % P_c) as described by Biggs & Close (1989). These analyses included all nutrients sorbed to inorganic particles, organic detritus, and bacteria/fungi. The biomass of invertebrates collected on the spring nutrient diffusing substrata was determined as AFDM. Water samples were thawed and analysed for nitrate – N (NO_3–N) and dissolved reactive phosphorus (DRP) using auto-analyser methods as summarised in Biggs & Close (1989).

Community structure was determined seasonally using an inverted microscope. Aliquots of each sample were scanned at 480× and 780× magnification to identify the dominant taxon based on its contribution to the sample's biovolume (i.e. a visual integration of frequency × size). All other taxa were then rated on an 8 point scale in relation to that of the dominant taxon. If two taxa were co-dominant they were both given a score of 8 (Biggs 1995). Generally one or, at most, three taxa made up approximately 70 % of the community.

Data analysis

The average number of floods per year was determined as the number of events where velocities exceeded 1 m s^{-1} (see Biggs 1995). Velocity intensity (V_{80}) was determined as the 80th percentile velocity from a cumulative frequency distribution of velocities for the 2 year study period. This incorporated flood peaks and their recessions, and was interpreted to be a measure of the intensity of velocity stress at the sites (after Biggs 1995).

Geometric means were calculated for most variables to correct for non-normality in the distribution of data. Single factor and nested analysis of variance were used to test for significance of differences among sites and habitats within sites (using log transformed data where appropriate).

For some analyses and testing of the habitat matrix conceptual periphyton model of Biggs et al. (1998), the two-year dataset was divided into two separate years for each site, and run and riffle habitats, based on the overall frequency of flood disturbances. A relatively low frequency of flood disturbances occurred for the period February to December 1993 (when the in-stream nutrient diffusing substratum assays were carried out), whereas a high frequency of floods occurred July 1992 to February 1993 and January to June 1994 (see later). Data collected from these later two (discontinuous periods) were merged for the biomass analysis. Two sets of samples were analysed for community structure during the period of low flood frequency in 1993, and two sets were analysed from the period of high flood frequency (July 1992–February 1993).

Data from the more detailed sampling carried out at the headwater site before and after the 19th March 1994 flood was analysed using a combination of biomass and relative abundance plots, together with a principal components analysis. Principal component scores were calculated on the pooled run and riffle data, but changes in the location of the communities in principal components space over time (a function of the Factor 1 and Factor 2 co-ordinates) were plotted separately for runs and riffles.

The habitat matrix conceptual model of BIGGS et al. (1998) was tested for both chlorophyll-a and taxonomic community structure (using the separate low and high flood frequency periods for each site and habitat, as defined above). The predicted mean monthly chlorophyll-a for each site, habitat and flood frequency period was calculated by inserting flood frequency (corrected to give an annual frequency for each habitat and time period) and average cellular nitrogen concentrations for the given period in equation (1) of BIGGS et al. (1998). Predicted values of chlorophyll-a were then plotted against observed values to indicate goodness of fit ($N = 12$). For community structure, the functional group that could be expected to dominate the assemblages in each habitat during the given flood frequency period was predicted by ascribing a possible range of values to the axes of Fig. 2 in BIGGS et al. (1998). Flood frequency was given a range of 0–40 events per year and cellular N was given a range of 1–10 % N_c. These ranges were based on data reported by BIGGS (1995) from 15 streams covering a wide spectrum of disturbance frequencies and levels of enrichment and our unpublished studies from elsewhere (see also Fig. 4 of BIGGS et al. 1998). The disturbance frequency boundary separating habitats that were expected to be most suitable for *R* selected taxa was arbitrarily set at >10 events per year. The boundaries for enrichment separating habitats expected to be most suitable for *S*, *C*–*S* and *C* selected taxa were 4 and 7 % N_c. The functional group for the three most common taxa was determined from BIGGS et al. (1998) for each of the samplings and then compared against the functional group predicted to dominate based on disturbance frequency and enrichment.

Results

Hydrology and hydraulics

Average conditions

Mean and median flows increased, and channel gradient decreased moving down the catchment (Table 1). Hydraulic conditions at the time of the site visits displayed the expected differences between runs and riffles, with depths being greater and velocities lower in the runs (Table 2). Variability in velocity during the study period was much less in the riffles than runs.

Among-site differences were found for depth and velocity in the runs, but not necessarily as would be expected from the downstream reductions in overall channel gradient. For example, velocities in the run at the lowland site were highest and these differences were statistically significant (Table 2). This is probably because relative roughness decreased greatly at the lowland run compared with the other sites as indicated by much smaller median sediment particle sizes in relation to mean depth. Hydraulic conditions in the riffles were more similar among the sites with depths averaging 0.15–0.20 m and velocities 0.58–0.69 m/s. Velocities in the riffles did not differ significantly among sites.

Table 1. Summary of general physical and chemical statistics for the study sites ([1] determined from full flow record). ANOVA F values: ** $P<0.01$, *** $P<0.001$, n.s. not significant.

	Site/Catchment Location			ANOVA F
	Headwater	Mid-catchment	Lowland	
Physical				
Distance from sea (km)	36.0	33.0	5.5	–
Slope of reach (%)	1.24	0.38	0.15	–
Mean flow[1] (m^3/s)	1.32	3.19	5.40	–
CV flow	2.86	2.31	3.04	–
Median flow[1] (m^3/s)	0.57	1.68	2.55	–
Chemical				
Temperature (°C)	10.58	10.43	10.63	n.s.
Conductivity (mS/m)	6.2	6.5	9.4	***
NO_3-N (mg/m^3)	35.0	22.0	116.0	**
DRP (mg/m^3)	6.0	5.0	7.0	n.s.
NO_3:DRP	5.14	3.49	17.74	***

Flood flows

The annual frequency of flood events where water velocities exceeded 1 m/s was highest in the riffles at 7.5–11 per year (Table 2), and lowest in the runs, particularly at the mid-catchment site (1.5 per year). The 80% velocity exceedances indicate that the flow regime at the lowland riffle site was the harshest of the environments (Figs. 2, 3, 4). No bed channel re-shaping was observed at the sites except during a major flood in December 1993 when bars were completely altered. This channel re-shaping was particularly pronounced at the lowland site.

As noted earlier, the frequency of flood events was not uniformly distributed over the two year study period. Abnormally low rainfall resulted in few events in the period February to December 1993. Conversely, a high frequency of flood events occurred in July 1992 to February 1993 and January to June 1994 (Figs. 2, 3, 4).

Periphyton

Average standing crop

The overall mean site chlorophyll-a and AFDM did not vary significantly, but there was a significant difference between riffles and runs within sites (Table 3). When differences in standing crop were analysed separately for runs and riffles, chlorophyll-a in the lowland riffle was significantly higher than the other sites (Table 2). Percentage chlorophyll-a did not vary significantly be-

Table 2. Summary of hydraulic and periphyton statistics for the sampling sites. ANOVA F values: * $P<0.05$, ** $P<0.01$, *** $P<0.001$. Statistics with same superscript for a given parameter are not significantly different form each other at $P<0.05$ as evaluated using a post-hoc Tukey test. The periphyton statistics were calculated as geometric means.

		Runs				Riffles			
		Sites			ANOVA	Sites			ANOVA
		Head	Mid	Low	F	Head	Mid	Low	F
Hydraulics									
Depth (m)	$\bar{x}$	0.26^1	$0.50^{1,2}$	0.48^2	***	0.15^1	$0.20^{1,2}$	0.21^2	*
	(%CV)	(40.5)	(22.7)	(17.6)		(33.1)	(37.0)	(35.2)	
Velocity (m/s)	$\bar{x}$	0.30^1	0.19^1	0.33^2	*	0.69	0.58	0.64	n.s.
	(%CV)	(59.5)	(49.9)	(57.4)		(31.0)	(27.0)	(37.4)	
Froude No.	$\bar{x}$	0.20^1	0.08^2	0.15^1	***	0.59^1	0.45^2	0.46^2	**
	(%CV)	(50.8)	(41.7)	(50.5)		(22.8)	(26.8)	(24.4)	
Flood events > 1 m/s (no/y)	$\bar{x}$	6	1.5	7		11	7.5	10.5	–
V_{80} (m/s)	$\bar{x}$	0.44	0.25	0.64		0.85	–	1.04	–
D_{50} (mm)	$\bar{x}$	256	83	46		147	100	35	–
Periphyton									
Chlorophyll-a (mg/m^2)	$\bar{x}$	10.1	17.0	8.6	n.s.	18.0^1	13.7^1	59^2	**
	(%CV)	(88.7)	(48.3)	(83.0)		(76.6)	(31.8)	(16.6)	
AFDM (g/m^2)	$\bar{x}$	6.2	15.1	5.6	n.s.	10.7	14.5	21.6	n.s.
	(%CV)	(84.9)	(50.5)	(56.8)		(84.9)	(27.6)	(17.9)	
% Chlorophyll-a	$\bar{x}$	0.20	0.13	0.21	n.s.	0.21^1	0.12^2	0.30^1	***
	(%CV)	(60.5)	(59.7)	(58.9)		(58.9)	(84.0)	(42.2)	
% P_c	$\bar{x}$	0.29	0.40	0.35	n.s.	0.28	0.27	0.37	n.s.
	(%CV)	(35.6)	(45.8)	(43.7)		(72.8)	(40.4)	(33.6)	
% N_c	$\bar{x}$	3.37	3.81	4.22	n.s.	3.02^1	3.34^1	4.94^2	*
	(%CV)	(28.7)	(14.6)	(21.3)		(85.8)	(23.7)	(11.9)	
$N_c:P_c$	$\bar{x}$	11.8	9.7	12.0	n.s.	10.8	12.5	13.3	n.s.
	(%CV)	(15.6)	(18.1)	(10.9)		(38.4)	(20.8)	(6.8)	

tween run and riffle habitats, but overall mean site values did vary significantly.

Variations in periphyton chlorophyll-a during the year appeared to be controlled more by variations in disturbance frequency than by season (particularly at the headwater site) (Figs. 2, 3, 4). Indeed, chlorophyll-a and AFDM were significantly higher during the period of low flood frequency within each site for both riffles and runs (e.g. nested ANOVA on chlorophyll-a for flood period within site: F – ratio = 10.57, $P<0.001$, $N = 55$ in runs; F – ratio = 12.07. $P<0.001$, $N = 55$ in riffles). A more detailed analysis within sites (Table 4) indicated that the difference in standing crop between flood frequency periods was most pronounced, and highly significant, at the headwater site for

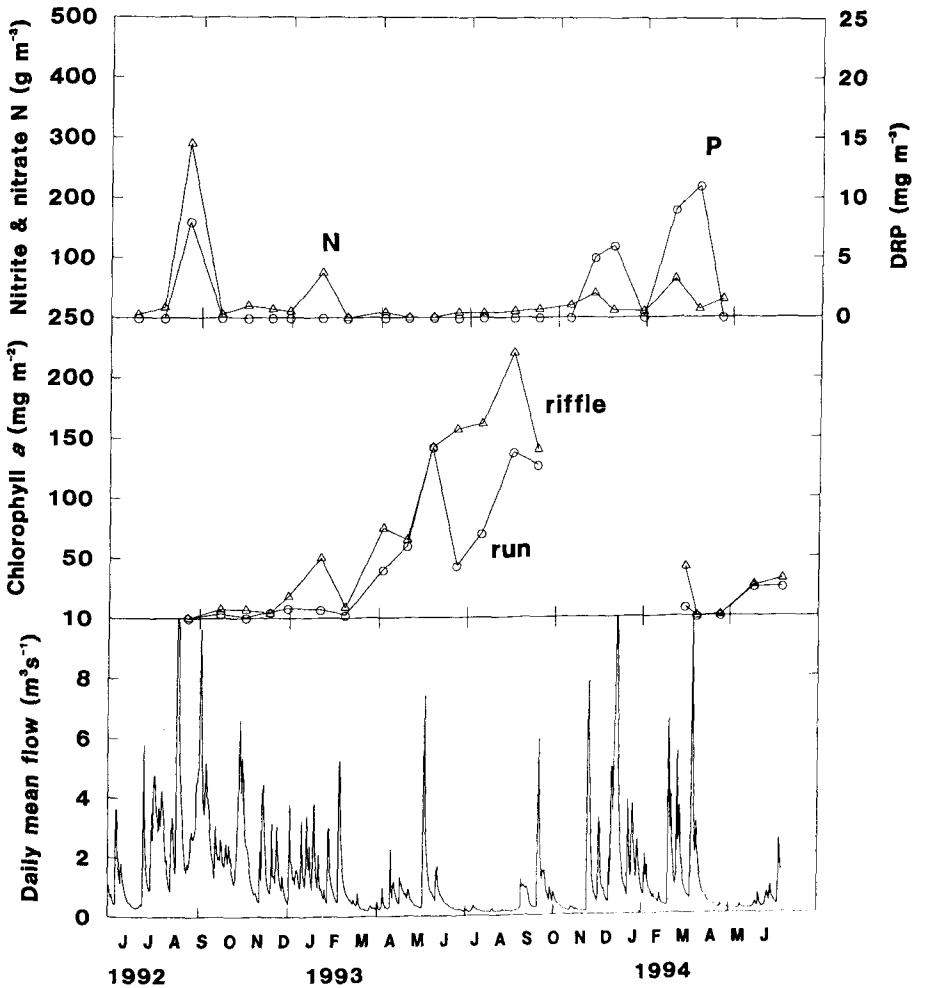

Fig. 2. Temporal fluctuations in water nutrients, periphyton chlorophyll-a and flow at the headwater site (Kauru River) in the Kakanui River catchment.

both run and riffle habitats. Overall, AFDM in the riffles varied most as a function of the flood frequency period. Variability in both chlorophyll-a and AFDM was lower during periods of infrequent flooding.

Community structure

Mean taxonomic richness did not vary significantly among the sites or as a function of runs vs. riffles within sites (Tables 3, 5, 6). When the site data were pooled there was still no difference in richness between riffles and runs. However, there were significant differences as a function of flood disturbance fre-

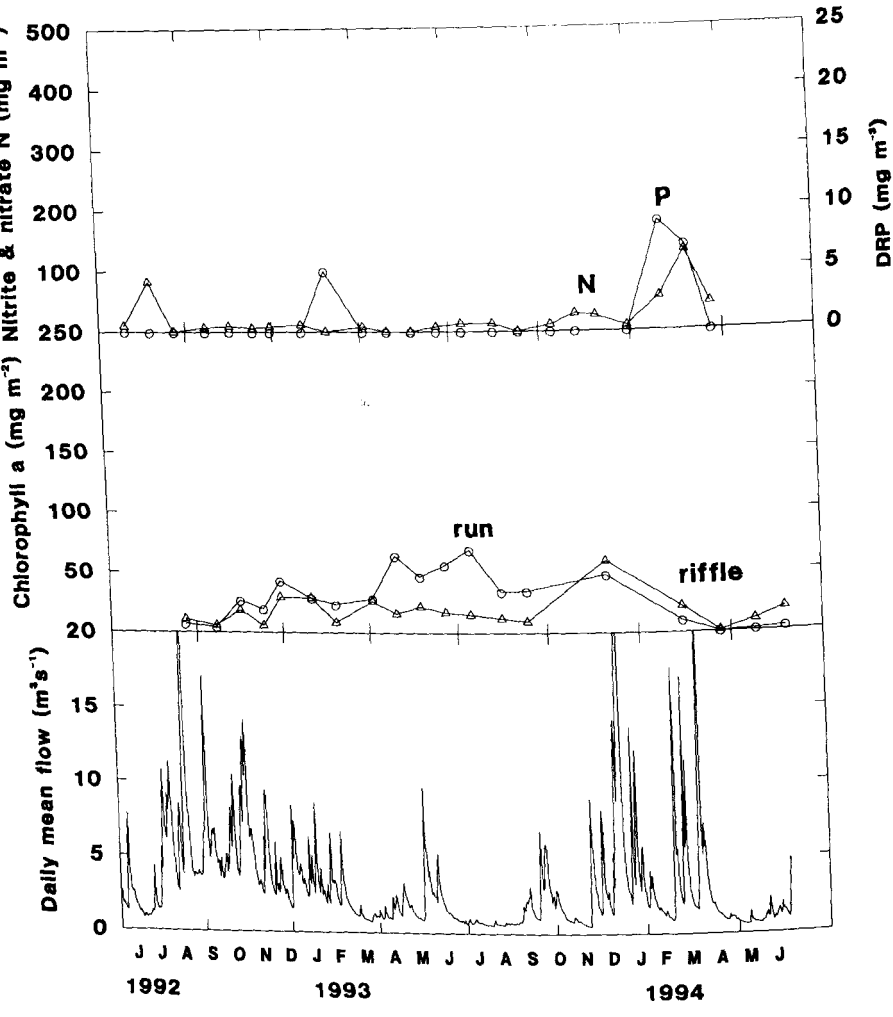

Fig. 3. Temporal fluctuations in water nutrients, periphyton chlorophyll-a and flow at the mid-catchment site, Kakanui River.

quency (Fig. 5). Communities in the period of frequent floods had the lowest richness (13–14 taxa), whereas communities in the more hydrologically stable period had the highest richness (17–18 taxa) (Table 3).

Runs: Periphyton community structure was similar in runs of the three sites during the high flood frequency period (sampled September 1992 and January 1993) (Table 5, Figs. 2–4). The ruederal (*R* selected) diatoms *Gomphoneis minuta* var. *cassieae* KOCIOLEK & STOERMER, *Synedra ulna* (NITZ.) EHR. and *Cymbella kappii* CHOL. were dominant or abundant. However, the three sites had distinctly different communities during the low flood frequency period

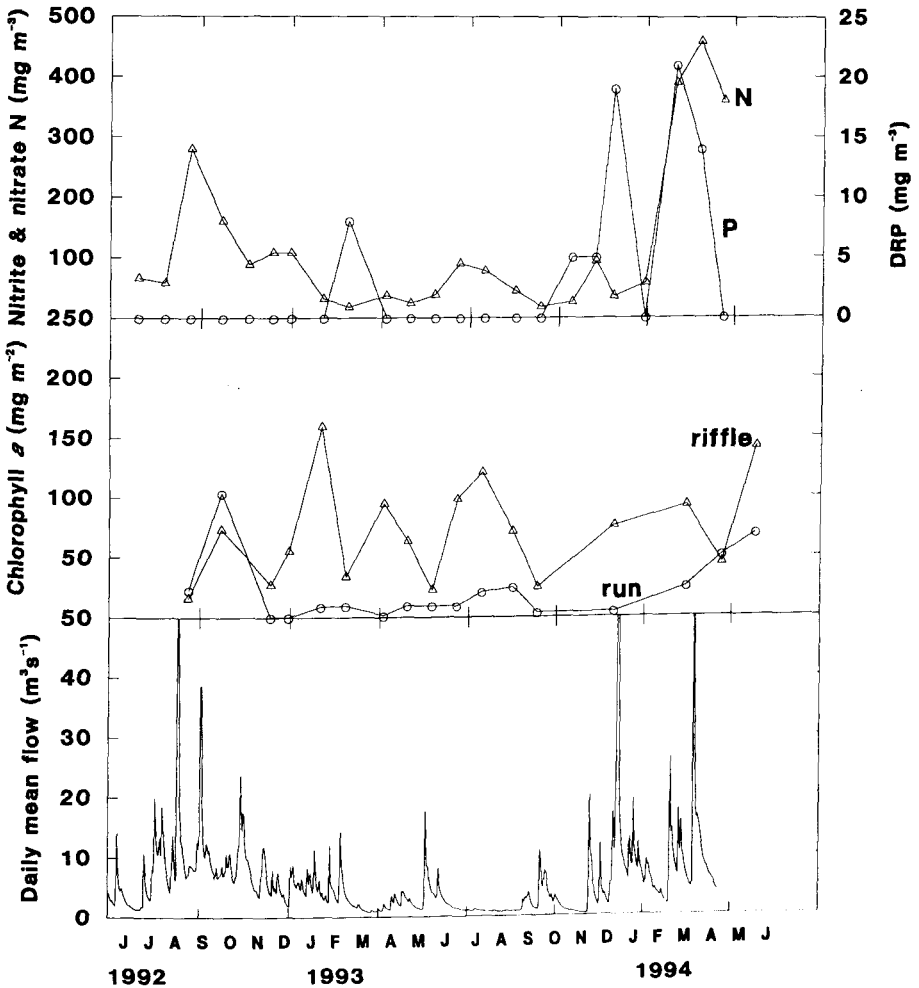

Fig. 4. Temporal fluctuations in water nutrients, periphyton chlorophyll-a and flow at the lowland site, Kakanui River.

(sampled May and August 1993) when considerable biomass accrued. During this period, the headwater site was dominated by stress tolerant (*S* selected) filamentous cyanobacteria *Lyngbya* sp. and *Tolypothrix* sp.; the mid-catchment site was dominated by the diatom *Epithemia sorex* KÜTZ (which contains a nitrogen fixing endosymbiont) and the colonial blue green nitrogen fixer *Nostoc* sp. The lowland site was dominated by *Nostoc* sp. and *Synedra ulna*. The taxa generally formed a thicker, more architecturally complex, community during the low flood frequency period than the tightly adhering, low growing, taxa dominating during the high flood frequency period.

Table 3. ANOVA of three periphyton parameters as a function of site and hydraulic habitat (riffle or run). Chlorophyll-a and AFDM log transformed for the analysis.

Source	Sum of squares	DF	*F*	*P*
1 **Chlorophyll-a**				
Site	5.08	2	0.982	0.378
Habitat {Site}	34.98	3	4.510	0.005
Error	268.84	104		
2 **AFDM**				
Site	6.88	2	2.205	0.115
Habitat {Site}	18.39	3	3.928	0.011
Error	162.30	104		
3 **% Chlorophyll-a**				
Site	0.31	2	12.16	0.000
Habitat {Site}	0.08	3	1.961	0.124
Error	1.322	104		
4 **Taxonomic richness – among sites**				
Site	16.00	2	0.966	0.399
Habitat {Site}	29.50	3	1.188	0.342
Error	149.00	18		
5 **Taxonomic richness – among flood frequency periods**				
Habitat	1.50	1	0.265	0.614
Flood period {Habitat}	102.23	6	17.056	0.036
Error	90.67	16		

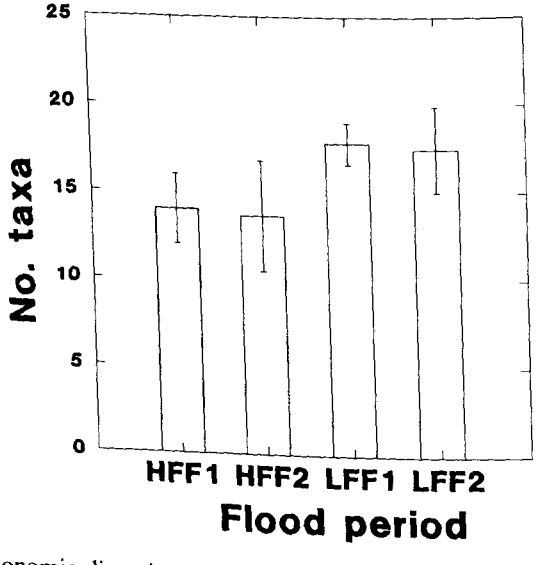

Fig. 5. Mean taxonomic diversity of the pooled site and habitat data sampled on two occasions during the high flood frequency period (HFF) and the low flood frequency period (LFF) (± SE).

Table 4. Comparison of geometric mean chlorophyll-a and AFDM concentrations for runs and riffles between high flood frequency and low flood frequency periods. ANOVA *P* values: *** $P<0.001$, ** $P<0.01$, * $P<0.05$.

Site/Habitat			Runs	Riffles
Chlorophyll-a				
Headwater	- frequent floods	$\bar{x}$	2.0	4.2
		(%CV)	(196)	(145)
	- infrequent floods	$\bar{x}$	60.1	91.2
		(%CV)	(17)	(17)
		ANOVA *P*	***	***
Mid-catchment	- frequent floods	$\bar{x}$	10.7	11.5
		(%CV)	(63)	(50)
	- infrequent floods	$\bar{x}$	23.7	15.6
		(%CV)	(39)	(15)
		ANOVA *P*	n.s.	n.s.
Lowland	- frequent floods	$\bar{x}$	3.2	47.7
		(%CV)	(286)	(16)
	- infrequent floods	$\bar{x}$	11.8	68
		(%CV)	(43)	(17)
		ANOVA *P*	n.s.	n.s.
AFDM				
Headwater	- frequent floods	$\bar{x}$	1.9	4.1
		(%CV)	(151)	(129)
	- infrequent floods	$\bar{x}$	23.0	31.0
		(%CV)	(25)	(26)
		ANOVA *P*	***	**
Mid-catchment	- frequent floods	$\bar{x}$	9.9	9.4
		(%CV)	(52)	(39)
	- infrequent floods	$\bar{x}$	20.6	20.0
		(%CV)	(48)	(14)
		ANOVA *P*	n.s.	*
Lowland	- frequent floods	$\bar{x}$	4.22	14.3
		(%CV)	(120)	(20)
	- infrequent floods	$\bar{x}$	6.1	28.8
		(%CV)	(39)	(11)
		ANOVA *P*	n.s.	**

Riffles: As in the runs, communities in the riffles were markedly different between the period of frequent and infrequent flood disturbances. During the highly disturbed period, *R* selected diatoms tended to dominate the sites (*Diatoma hiemale* (ROTH) HIEB., *Gomphoneis* and *Synedra ulna*), with the *C–S* selected taxa *Spirogyra* sp. also being a dominant on one occasion at the mid-catchment and lowland sites (Table 6). In the less frequently disturbed period, the sites were dominated by filamentous cyanobacteria (*Lyngbya* and *Tolypothrix*) at the headwater site and *C–S* selected filamentous green algae at the

Table 5. Summary of the relative abundance, and associated biomass, of periphyton taxa in runs of the Kakanui River sites. HFF = high flood frequency periods (Sept. 1992, Jan. 1993). LFF = low flood frequency periods (May 1993, Aug. 1993). Functional group classifications are given in brackets after the taxa (following BIGGS et al. 1998): *C*, competitive taxa; *C-S*, competitive-stress tolerant taxa; *S*, stress tolerant; *R*, ruedral ([1], expected functional group based on disturbance frequency and cellular N concentration – see text; [2], recorded functional groups based on the three most common taxa as listed in the preceding table of data).

	Headwater				Mid-catchment				Lowland			
	HFF		LFF		HFF		LFF		HFF		LFF	
1 Taxa												
Chlorophyta												
Ankistrodesmus sp.	0	0	0	0	0	1	1	0	0	0	0	0
Gloeocystis sp.	0	0	0	1	0	0	0	0	0	0	0	0
Mougeotia sp. (*C-S*)	0	0	0	5	0	0	0	0	0	0	0	0
Oedogonium sp. (*C-S*)	0	3	5	0	0	0	0	3	0	0	2	0
Spirogyra sp. (*C-S*)	0	0	2	0	0	0	1	3	0	0	0	0
Stigeoclonium sp. (*C-S*)	0	3	0	0	0	0	0	0	0	0	0	0
Ulothrix zonata (*R*)	0	0	0	0	0	0	0	0	0	0	3	0
Bacillariophyta												
Achnanthidium sp.	0	0	0	1	2	2	0	1	4	0	1	0
Planothridium lanceolatum	3	3	3	1	4	2	2	1	5	3	0	4
Achnanthidium minutissimum (*R*)	3	3	4	2	3	2	2	2	5	3	3	3
Cocconeis sp. (*R*)	1	2	2	3	1	0	1	1	0	4	2	0
Cymbella kappii (*R*)	3	3	4	4	7	4	1	3	7	2	4	4
Cymbella minuta (*R*)	1	3	2	4	4	3	1	2	4	3	3	4
Diatoma sp.	0	2	0	0	0	0	0	0	0	0	0	0
Diatoma hiemale (*R*)	7	0	1	1	0	0	0	0	0	0	0	0
Epithemia sorex (*S*)	0	2	1	1	0	6	8	8	0	0	1	1
Fragilaria vaucheriae (*R*)	1	0	0	0	1	1	0	0	0	0	2	0
Gomphoneis minuta var. *cassieae* (*R*)	8	8	5	5	7	5	2	3	7	8	4	3
Gomphonema sp.	2	1	3	1	0	0	0	0	3	4	3	3
Gomphonema accuminatum	0	0	1	1	0	0	0	0	0	0	0	1
Gomphonema constrictum	0	0	0	0	0	0	0	0	2	0	0	0
Melosira varians (*C*)	3	0	0	0	0	0	0	0	0	0	0	0
Navicula avenacea (*R*)	0	2	6	5	1	5	7	6	0	0	1	1
Navicula cryptocephala (*C-S*)	1	1	0	3	0	3	1	0	0	0	1	1
Rhopalodia novaezelandiae (*S*)	0	0	0	0	0	4	2	4	0	0	0	0
Surirella sp.	0	3	1	2	2	2	2	0	0	0	0	0
Synedra rumpens (*R*)	4	3	3	1	3	3	1	3	3	6	3	5
Synedra ulna (*R*)	6	2	7	7	8	8	1	5	8	5	3	8
Tabellaria flocculosa	1	1	0	0	2	1	1	0	0	0	0	2
Unidentified	0	0	0	0	0	0	1	0	2	1	0	2
Rhodophyta												
Audouinella hermanii (*C-S*)	0	0	0	0	0	0	0	6	0	0	1	0
Cyanobacteria												
Lyngbya sp.	0	0	8	0	0	0	0	6	0	0	4	0
Nostoc sp. (*S*)	0	0	0	0	0	0	0	7	0	0	8	0
Phormidium sp. (*C-S*)	0	0	1	0	0	0	0	3	0	0	1	0
Tolypothrix sp. (*S*)	0	6	0	8	0	0	0	4	0	0	0	0
2 Richness	14	17	18	19	13	16	17	18	11	10	19	14
3 Biomass												
Chlorophyll-a (mg/m^2)	3.7	7.4	143	138	4.6	43	64	69	104	0.1	9.7	21
Ash-free dry mass (g/m^2)	4.1	2.4	75	42	17	36	56	65	33	2.2	6.9	7.7
4 Functional group classification												
Expected[1]	*R*	*R*	*S/C-S*	*S/C-S*	*S/C-S*	*S/C-S*	*S/C-S*	*S/C-S*	*R*	*R*	*C-S*	*C-S*
Recorded[2]	*R*	*R/S*	*?*	*S/R*	*R*	*R/S*	*S/R*	*S*	*R*	*R*	*S*	*R*

Table 6. Summary of the relative abundance, and associated biomass, of periphyton taxa in riffles of the Kakanui River sites. HFF = high flood frequency periods (Sept. 1992, Jan. 1993). LFF = low flood frequency periods (May 1993, Aug. 1993). Functional group classifications are given in brackets after the taxa (following BIGGS et al. 1998): *C*, competitive taxa; *C-S*, competitive-stress tolerant taxa; *S*, stress tolerant; *R*, ruedral ([1], expected functional group based on disturbance frequency and cellular N concentration – see text; [2], recorded functional groups based on the three most common taxa as listed in the preceding table of data).

	Headwater				Mid-catchment				Lowland			
	HFF		LFF		HFF		LFF		HFF		LFF	
1 Taxa												
Chlorophyta												
Ankistrodesmus sp.	0	0	0	0	0	1	1	1	1	1	0	1
Gloeocystis sp.	0	0	0	0	0	0	0	0	0	1	0	0
Mougeotia sp. (*C-S*)	0	0	1	3	0	0	0	8	0	0	3	0
Oedogonium sp. (*C-S*)	0	2	0	5	0	0	0	1	0	0	8	7
Spirogyra sp. (*C-S*)	0	1	0	0	0	8	8	0	0	8	7	0
Stigeoclonium sp. (*C-S*)	3	0	0	0	0	0	0	2	2	0	0	0
Ulothrix zonata (*R*)	3	0	0	0	0	0	0	0	1	0	4	3
Bacillariophyta												
Achnanthidium sp.	0	0	1	2	2	1	0	1	3	0	2	0
Planothridium lanceolatum	3	1	3	4	4	2	2	3	4	2	2	6
Achnanthidium minutissimum (*R*)	2	1	4	3	4	2	3	3	3	2	3	4
Cocconeis sp. (*R*)	1	1	1	1	0	1	1	1	0	1	2	3
Cymbella kappii (*R*)	2	2	3	4	5	3	1	5	8	1	4	3
Cymbella minuta (*R*)	3	1	2	4	3	4	1	1	5	1	4	4
Diatoma sp.	1	0	0	0	0	0	0	0	1	0	0	0
Diatoma hiemale (*R*)	8	0	2	5	1	0	0	0	0	0	0	0
Epithemia sorex (*S*)	0	0	4	5	1	4	5	5	1	0	0	0
Fragilaria vaucheriae (*R*)	0	0	0	0	2	0	0	0	0	0	3	0
Gomphoneis minuta var. *cassieae* (*R*)	8	8	5	5	8	5	8	7	8	0	3	0
Gomphonema sp.	2	0	3	0	0	0	3	2	2	1	4	3
Melosira varians (*C*)	5	0	0	1	0	0	0	0	0	0	0	0
Navicula avenacea (*R*)	0	0	6	2	0	3	3	4	0	0	1	0
Navicula cryptocephala (*C-S*)	0	0	0	1	0	2	1	1	0	1	0	2
Rhopalodia novaezelandiae (*S*)	0	0	0	0	3	3	3	3	0	0	0	0
Surirella sp.	0	0	0	0	1	0	3	2	0	0	0	0
Synedra rumpens (*R*)	4	0	4	7	3	3	1	3	3	3	2	3
Synedra ulna (*R*)	7	1	7	6	7	3	3	8	8	2	7	8
Tabellaria flocculosa	0	0	0	0	1	0	0	0	2	0	0	2
Unidentified	0	0	0	0	0	0	3	5	1	0	0	3
Rhodophyta												
Auduoinella hermanii (*C-S*)	0	0	0	0	0	5	0	0	0	1	1	3
Cyanobacteria												
Lyngbya sp.	0	0	8	0	0	0	6	0	0	0	3	0
Phormidium sp. (*C-S*)	1	0	1	0	0	0	1	1	1	0	0	0
Tolypothrix sp. (*S*)	0	3	0	8	0	0	0	0	0	0	0	3
2 Richness	15	10	16	17	14	16	19	21	17	13	18	16
3 Biomass												
Chlorophyll-a (mg/m^2)	7.4	50	142	220	5.9	29	16	15	73	55	64	121
Ash-free dry mass (g/m^2)	11	55	61	67	18	17	28	20	25	10	28	35
4 Functional group classification												
Expected[1]	*R*	*R*	*S/C-S*	*S/C-S*	*S/R*	*R*	*S*	*S*	*R*	*R*	*C-S*	*C-S*
Recorded[2]	*R*	*R*	*?*	*S/R*	*R*	*C-S/R*	*C-S/R*	*R/C-S*	*R*	*C-S*	*C-S*	*R/C-S*

mid-catchment and lowland site (*Mougeotia* sp., *Oedogonium*, *Spirogyra* sp.), but with ruderal diatoms also being abundant.

Temporal dynamics

Following high flows, cycles of accrual and sloughing occurred at the headwater site, but these became less pronounced progressing downstream (Figs. 2, 3, 4). An accrual sequence in the headwater run from March to June 1994 is replotted at a larger scale in Fig. 6. Prior to the flood on 19 March, chlorophyll-a was low and communities consisted predominantly of diatoms (mostly *Gomphoneis* and *Gomphonema* cf. *angustatum* (KÜTZ.) RABH.). A sampling just 4 days after the flood (at the headwater site only) indicated that most of the chlorophyll-a had been removed by the flood. The little periphyton that was collected contained a variety of diatoms, none of which was clearly more abundant than any other. These included *Gomphoneis*, *Synedra ulna*, *Tabellaria flocculosa* (ROTH) KÜTZ, *Cymbella* sp., *Navicula* sp., *Achnanthidium* sp. A 40–50 day period of re-colonisation followed with peak biomass being reached in the run after approximately 70 days. No major succession of species occurred in the community during redevelopment. Instead *Gomphoneis* resumed its dominance over the entire accrual period, with the other pre-flood taxa also being important. Only *Synedra ulna* and *Cymbella minuta* HILSE ex. RABH increased in abundance relative to the pre-flood sampling.

Conversely, the pre-flood biomass was much higher in the riffle and the flood had a more significant effect in terms of biomass loss (Fig. 7). As with the run, the community was dominated by *Gomphoneis*. However, two filamentous green algae were also abundant (*Oedogonium* sp. and *Spirogyra* sp.). These taxa were completely eliminated from this habitat by the high flows and did not return during the time of the study. Sampling immediately after the flood yielded a variety of diatoms similar to that observed in the run (*Gomphoneis, Cymbella, Synedra ulna, Achmanthidium;* plus *Epithemia* and *Rhoicosphenia curvata* (KÜTZ.) GRUND ex RABH)). As in the run there was a prolonged period of regeneration, but at a lower rate of biomass accrual. *Gomphoneis* also resumed its dominance by the time colonisation was complete.

An analysis of temporal shifts in the first two principal components of the communities over the flood and regeneration period gives a measure of relative structural dynamics of the periphyton as a function of disturbance (Fig. 8). Prior to the flood the run and riffle communities had quite different locations in principal components space reflecting their distinctly different structures such as the high relative abundance of diatoms in the runs (Factor 1) and the high relative abundance of filamentous algal taxa in the riffles (Factor 2). Immediately following the flood both run and riffle communities had a similar composition. By the second post-flood sampling (approx. 30 days following

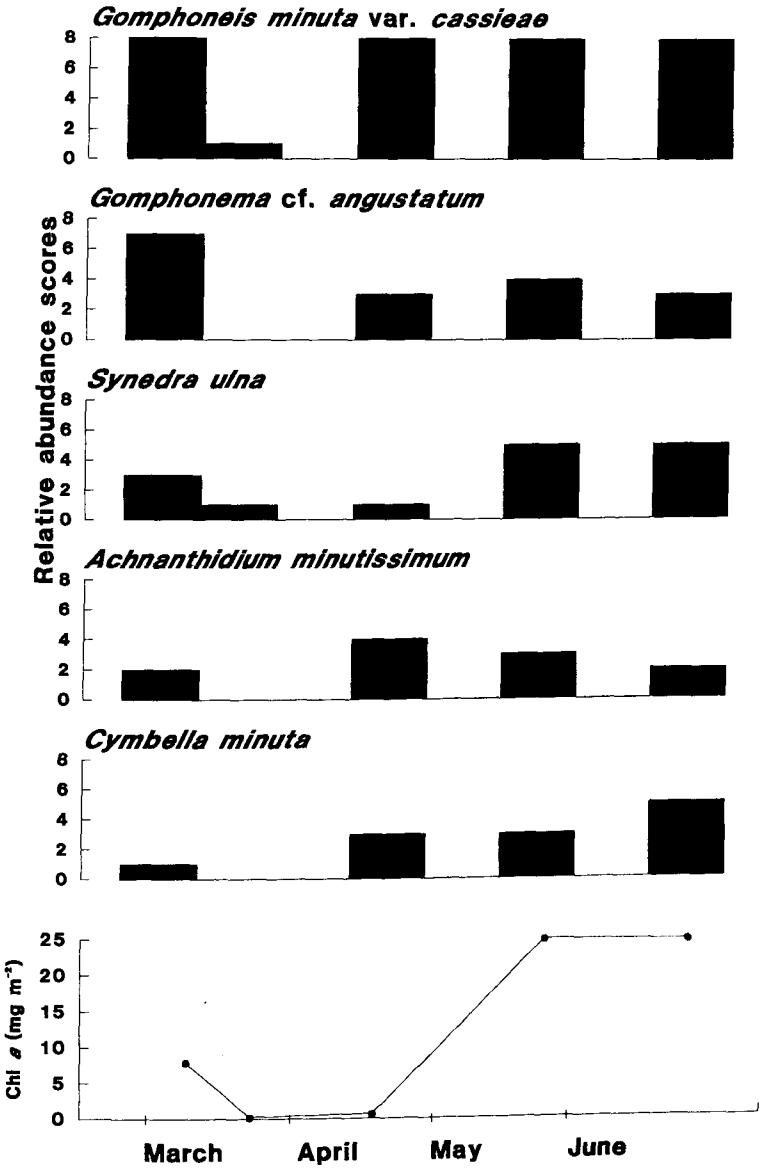

Fig. 6. Chlorophyll-a accrual, and dominant taxa, in a run at the headwater site following a major flood on 19 March 1994. The first column is the sampling 10 days prior to the flood.

the flood), communities in both habitats had regenerated to a state similar to the pre-flood run community (but with a much lower biomass, Figs. 6, 7). However, following this time the run community continued to develop strongly along Factor 1, whereas the riffle community started to separate in

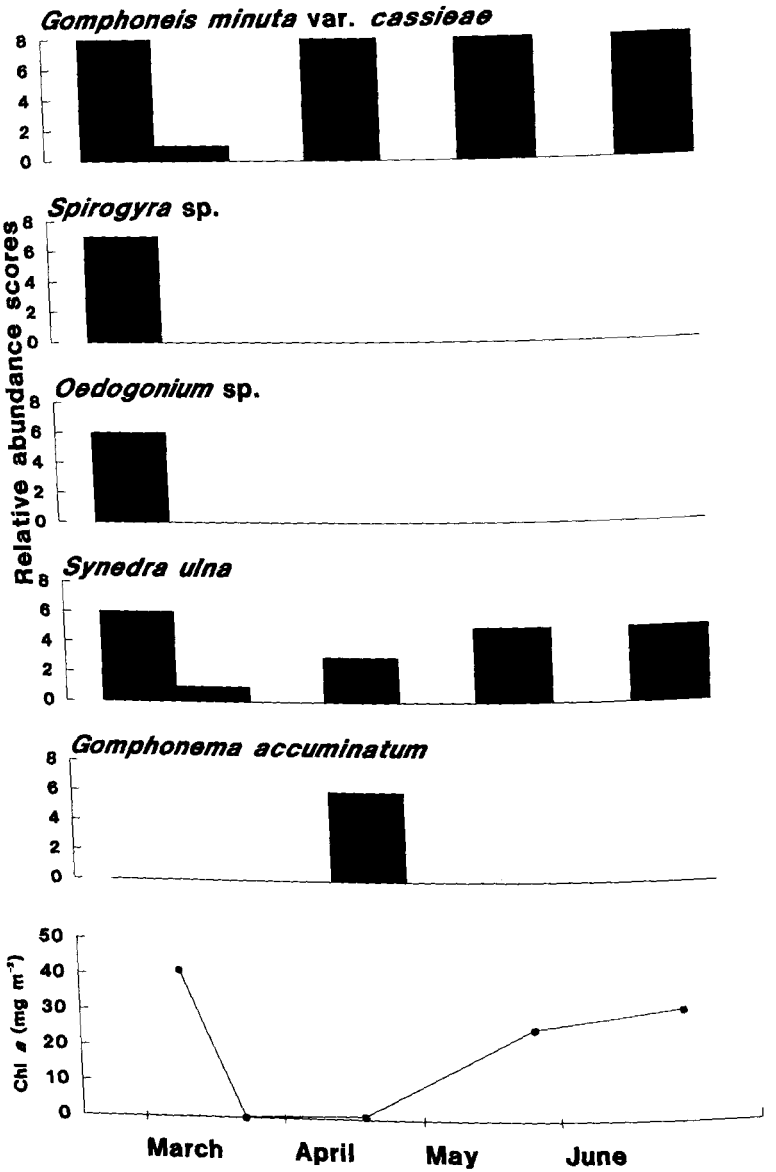

Fig. 7. Chlorophyll-a accrual, and dominant taxa, in a riffle at the headwater site following a major flood on 19 March 1994. The first column is the sampling 10 days prior to the flood.

principal component space and develop more along Factor 2. These results suggested succession away from dominance by a common group of initial colonists and back to a mature "climax" community was taking >30 days.

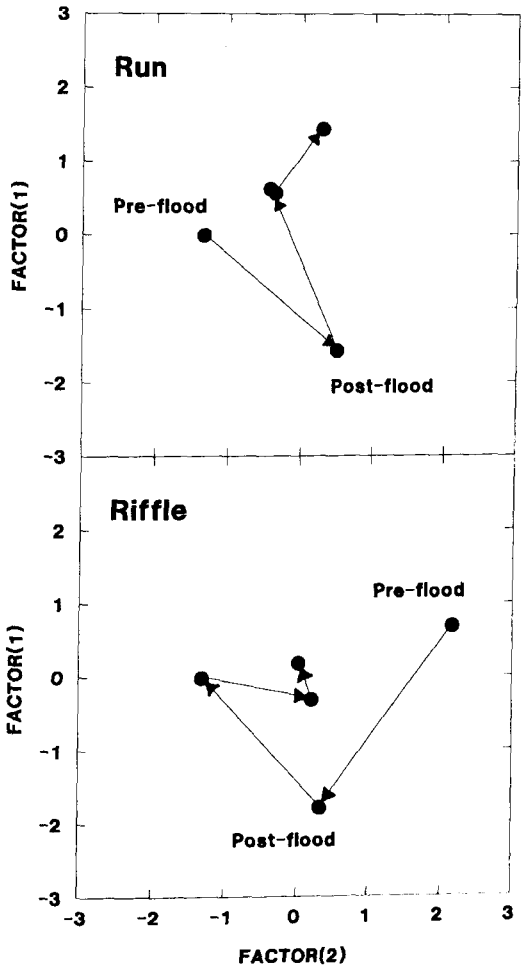

Fig. 8. Shifts in principal component factor scores for run and riffle communities as a result of flood disturbance at the headwater site.

Table 7 lists the relative abundance of common taxa in runs at all three sites 10 days before and 30 days after the same flood. Over this period, the total taxonomic richness of the sites remained largely the same. As noted, *Gomphoneis* had a higher degree of persistence with its position of relative abundance remaining, or increasing, over the flood. The other taxa to have a moderate degree of persistence included *Cymbella kappii* and the branched red alga *Audouinella hermanii* ROTH (DUBY). Taxa which generally decreased in relative abundance with the flood included *Stigeoclonium* sp., *Epithemia* and *Synedra rumpens* KUTZ. Only the headwater site retained the same taxon as a dominant component of the run community after the flood. However, because these re-

Table 7. Summary of relative abundance of common periphyton taxa in runs before (9 March) and after (19 April) the flood on 19 March 1994.

Taxa	Headwater		Mid-catchment		Lowland	
	Before	After	Before	After	Before	After
Chlorophyta						
Oedogonium sp.	0	3	0	3	5	5
Stigeoclonium sp.	0	0	1	0	6	0
Ulothrix zonata	3	0	0	0	0	5
Bacillariophyta						
Planothidium lanceolatum	1	1	2	3	3	3
Achnanthidium minutissimum	2	4	2	3	3	1
Cocconeis sp.	1	3	0	1	1	1
Cymbella kappii	3	3	2	6	6	6
Cymbella minuta	1	3	3	4	8	4
Epithemia sorex	3	0	8	6	0	0
Gomphonema cf. *angustatum*	7	3	3	5	1	2
Gompohonema accuminatum	0	4	0	0	0	0
Gomphoneis minuta var. *cassieae*	8	8	3	5	2	0
Melosira varians	0	1	0	1	3	5
Navicula avenacea	0	0	0	0	1	5
Navicula cryptocephala	1	0	1	3	3	1
Synedra rumpens	2	1	3	2	8	4
Synedra ulna	3	1	1	8	4	7
Rhodophyta						
Auduoinella hermanii	0	2	2	0	5	8
Richness	12	12	12	13	15	14

sults are from pooled replicates it was not possible to test the statistical significance of these differences.

Downstream gradient in enrichment

Nutrient concentrations in the water were generally low at all sites (Table 1), but with higher concentrations of nitrogen at the lowland site. There was generally little temporal variation in water nutrients. The highest concentrations recorded at all three sites were during the prolonged periods of frequent floods (Figs. 2, 3, 4). Ratios of nitrate nitrogen to dissolved reactive phosphorus were <72 (the highest recorded at the lowland site in April 1994), and usually considerably lower. Ratios for the mid-catchment and headwater sites were, with one exception, <4 during the first 14 months of the study.

Cellular nutrient concentrations (Table 2) were low, but with a trend of increasing cellular N moving downstream. $\%N_c$ values were significantly different ($P<0.05$) in the riffles among the sites with the lowland site being much higher than the mid-catchment or headwater sites. There was only one signifi-

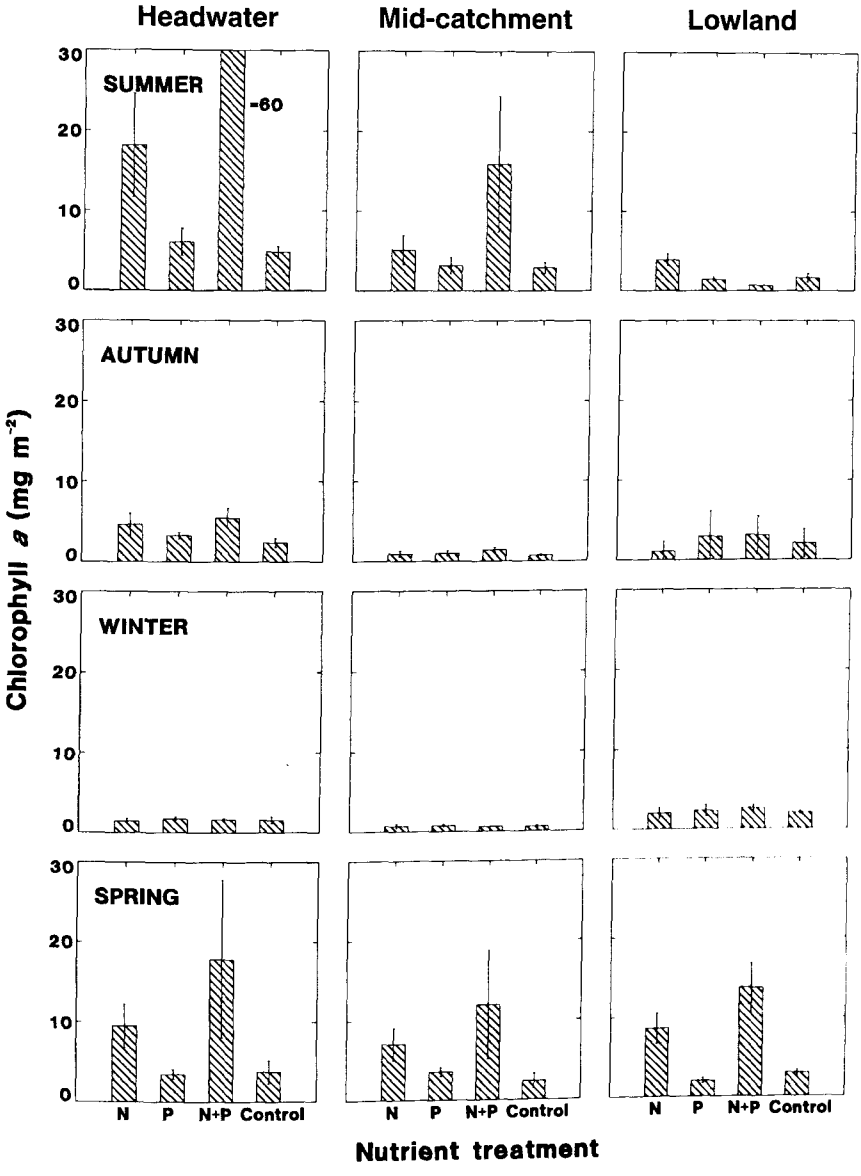

Fig. 9. Summary of seasonal nutrient diffusing substratum assays of nutrient limitation in the runs at each study site, Kakanui River (± SE).

cant difference in cellular nutrients between runs and riffles at the sites. This occurred for % P_c at the mid-catchment site. Over the three sites, the cellular nutrient concentrations suggested that nitrogen was more limiting than phosphorus for periphyton growth (growth limitation for algae can be expected at <0.5 % P_c and <11 % N_c; GERLOFF & FITZGERALD 1976, AUER & CANALE 1982), but that co-limitation could also be occurring. Seasonal in-situ nutrient

assays in the runs at each site during the period with relatively few floods largely confirmed nitrogen limitation at all sites for spring and summer (Fig. 9). In most cases during these two seasons, joint N + P enrichment resulted in a much higher chlorophyll-a concentration than N alone, confirming that not all populations were limited by N. Growth on all control and enriched substrata was very low during autumn and winter, and a significant nutrient response only occurred at the headwater site in autumn. Low water temperatures may have contributed to this very slow growth.

Grazing effects on chlorophyll-a

In spring 1993, during the period of low flood frequency, we incubated nutrient diffusing substrata in both the riffles and runs to compare growth and quantify differences in macro-invertebrate grazer abundance between the habitats which could explain the differences observed in natural substratum biomass. The lowland site had significantly lower ($P = 0.009$, Mann-Whitney U test) chlorophyll-a in the run than riffle on control substrata (Fig. 10). Invertebrate biomass in the lowland run was also significantly higher than on the riffle substrata ($P = 0.005$, Mann-Whitney U test). This invertebrate commu-

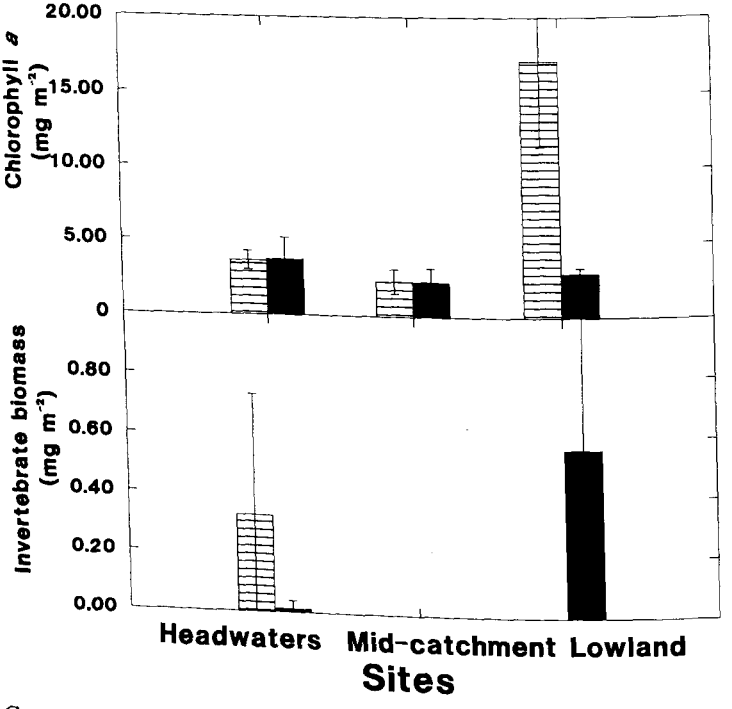

Fig. 10. Comparison of chlorophyll-a and grazer biomass in riffles vs. runs (solid bars) on control nutrient, diffusing substrates (spring 1993) (± SE).

nity was mainly dominated by snails (*Potamopyrgus antipodarum*). Periphyton chlorophyll-a was not significantly different between riffles and runs for the mid-catchment and headwaters sites (i.e. $P>0.05$, Mann-Whitney U tests). There was also a substantial biomass of macro-invertebrate grazers on the riffle substrata at the headwaters site although the difference with runs was not statistically significant. This was mainly composed of caddisfly and mayfly larvae. Our field observations suggested that the snails in the runs at the lowland site were having a major "top-down" effect on periphyton biomass, but that caddisflies and mayflies were not having much effect at the headwater site.

Testing predictions of the periphyton habitat matrix conceptual model

Predicted and observed chlorophyll-a concentrations (separated by habitat, site and flood frequency period) are summarised in Fig. 11. Measured chlorophyll

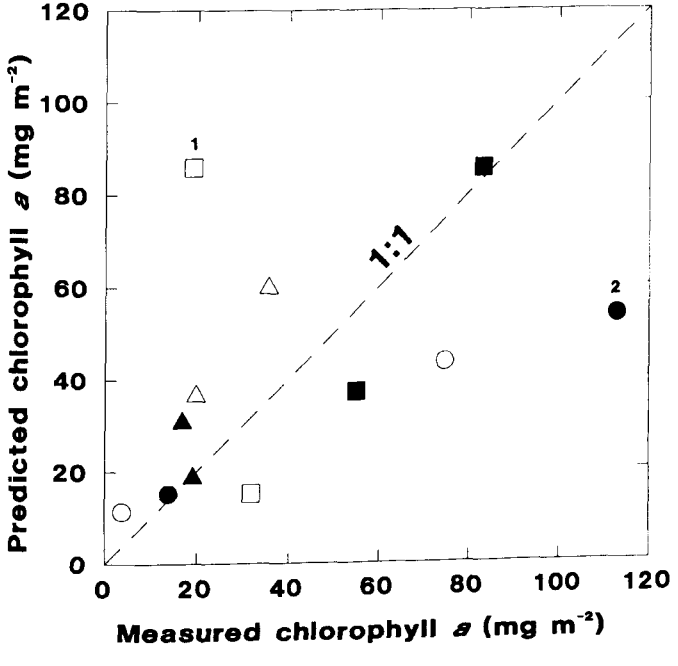

Fig. 11. Measured mean monthly chlorophyll-a vs. that predicted from the habitat matrix conceptual model of BIGGS et al. (1998) for different sites, habitats and flood frequency periods. Circles are the headwater site, triangles the mid-catchment site and squares the lowland sites. Open symbols are runs and closed symbols are riffles. The line of unity along which the points should cluster if there was full agreement between observed and predicted chlorophyll-a is also shown (1 = lowland run, low flood frequency; 2 = headwater riffle, low flood frequency).

values covered a wide range (<5 – >100 mg/m^2 chlorophyll-a), and 10 of the 12 points agreed fairly well with predicted concentrations. Points below the line of unity indicate that the recorded chlorophyll-a concentrations are greater than predicted, whereas points above the line indicate that predicted chlorophyll-a concentrations were higher than recorded. Overall, predicted chlorophyll tended to be higher than observed. There were two major outliers. Firstly, the lowland run during the period of low flood disturbance frequency had a much lower chlorophyll-a concentration than predicted (denoted by "1" above the point on Fig. 11). This discrepancy appeared to be due to high grazing activity (see preceding section) which was not accommodated in the original empirical formulation of the chlorophyll equation (Eq. 1 of BIGGS et al. 1998). Conversely, the headwater riffle during the period of low flood frequency had much higher chlorophyll-a than predicted (denoted by "2" above the point on Fig. 11). We cannot explain this difference. The correlation between observed and predicted was significant ($r = 0.721$, $P = 0.012$) if the low flood frequency, lowland run, point (which we believe to be strongly affected by grazing) is not included in the correlation.

The functional group dominating both run and riffle habitats could be ascertained on all four samplings at the mid-catchment and lowland sites, and on three of the samplings at the headwater site (Tables 5, 6). The dominant taxa at the headwater site on one occasion during the high flood frequency period was a short, sessile *Lyngbya* sp. which was not given a functional group designation by BIGGS et al. (1998). Overall, the functional group recorded as partially or totally dominating agreed reasonably with the expected functional group (based on disturbance frequency and cellular nutrient concentrations) (section 4 of Tables 5, 6). Thus, the stream periphyton habitat matrix conceptual model performed well as a predictor of functional group of the dominant taxa for different combinations of disturbance and enrichment.

Discussion

We expected that mean water depths and enrichment should increase, and velocities should decrease from headwaters to lowland sites in the study river. However, we found that changes in mean site hydraulics for both runs and riffles did not conform to these expected changes. While runs and riffles at the headwater site were significantly shallower, there were no general trends between the mid-catchment and lowland sites. Indeed, mean run velocities were highest in the lowland valley segment. Broadscale changes in catchment slope, and the aggregation of tributary inflows, were only resulting in partial changes in hydraulic conditions at the scale of an individual sampling transect. Conversely, the degree of enrichment did increase moving doenstream. Concentra-

tions of nitrate in the water were 3.5-fold higher at the lowland site than the headwater site. The local habitat constraints for periphyton growth were therefore far more complex than was initially predicted from a simple channel form-catchment enrichment model such as the River Continuum Concept.

However, the communites did develop in a predictable way as a function of both local disturbance and nutrient supply constraints. Based on the habitat matrix conceptual model of BIGGS et al. (1998), we would predict that the average biomass of periphyton should be higher at more enriched, lower disturbance sites and that the structure of these communities should be dominated by high profile, nutrient-demanding, taxa. We could also predict the converse of this at more disturbance-prone, unenriched sites. There was reasonable agreement with the model predictions in all respects except chlorophyll-a concentrations in the runs at the lowland site (see below).

In an earlier study, BIGGS & LOWE (1994) surveyed periphyton biomass and physical/nutrient characteristics of eight sites on this river during summer low flows (February 1992). They found that the snail *Potamopyrgus antipodarum* was able to track areas of high periphyton production on nutrient diffusing substrata placed in runs. Grazing by these animals prevented significant increases in run periphyton biomass of the lowland section of the river. The results of our present study, and those of BIGGS & LOWE (1994) strongly suggest that the deviation of chlorophyll-a in the runs at the lowland site during the period of low flood frequency from that predicted using the habitat matrix conceptual model was due to high grazing activity by *Potamopyrgus*. Based on the difference between observed and predicted (Fig. 11), we estimate that snail grazing may have reduced mean periphyton chlorophyll-a in the runs of the lowland site during the period of stable flows by approximately 80 %. While BIGGS et al. (1998) recognise that such intense snail grazing could be an important modifier of the empirical predictions of their model in habitats with low disturbance frequency, the magnitude of this was not quantified.

We found that there was no statistically significant difference in periphyton chlorophyll-a for both riffles and runs between times of high and low frequency of flood disturbance events at the mid-catchment and lowland sites, whereas there was a significant difference at the headwater site (Table 4). At the headwater site, almost half the bed in the run and almost one fifth in the riffle was bedrock. However, the remaining bed was unarmoured and appeared to be very mobile during floods. Such bed movement will be destructive for both the periphyton (BIGGS & CLOSE 1989) and the invertebrates (SCRIMGEOUR & WINTERBOURN 1989, TOWNSEND et al. 1997b). When flows stabilise again, periphyton recolonisation and accrual is likely to be much faster for periphyton than invertebrates (SCRIMGEOUR & WINTERBOURN 1989, POWER 1992) resulting in significant biomass development which is largely unconstrained by grazing. At the mid-catchment and lowland sites bed mate-

rials were moderately coarse (Table 2), channel slopes were lower, and the bed well armoured. The result of this is that only the most severe of floods (e.g. December 1994) is likely to have re-worked the bed. Thus, snails and other less mobile grazers at these lower sites will be much less affected by the smaller floods, and could consequently maintain grazing pressure on periphyton whether flows are variable or not. It appears that periphyton communities in both runs and riffles at the headwater site are abiotically (or 'bottom-up') controlled for much of the year through flood disturbance and nutrient limitation during the interflood periods. However, this appears to switch in the runs of the lowland site to biotic control during periods of low flood frequency.

The mid-catchment and lowland communities in the runs sampled in May 1993 were dominated by *R* selected taxa on several occasions when *S* or *C–S* taxa were expected. This deviation from expected may have also been a result of grazing which can maintain communities at early seral stages (i.e. dominated by *R* selected taxa) (STEINMAN 1996). *Synedra ulna* was the dominant taxon at both the sites on these occasions. For the three sampling occasions that were clearly not predicted correctly in the riffles (Table 5), there was a greater preponderance of taxa thought to require higher levels of enrichment (BIGGS et al. 1998) than was expected from the cellular nitrogen data. This may indicate that the nominated division between *S* and *C–S* groups (4 % N_c) may be too high.

Periphyton communities in runs of all three sites were dominated by a similar group of diatoms when flood disturbance frequency was high. However, during the period of low flood frequency, the headwater communities became dominated by filamentous cyanobacteria/diatoms, while communities in the mid-catchment and lowland sites were dominated by both nitrogen fixing cyanobacteria and diatoms. In the riffles, however, there was a clear separation between headwater communities and the other sites. While the headwater site was dominated by diatoms (high flood frequency) and cyanobacteria (low flood frequency), the mid-catchment and lowland valley segments were dominated more by filamentous green algae and diatoms (regardless of flood frequency). These changes in riffle communities among valley segments most closely reflected the differences in depth (and probably shear stress) and nitrogen enrichment among the sites. However, for the runs hydraulic conditions did not change systematically down the catchment and even though there was progressive enrichment downstream, community differences were generally not as large as for the riffles.

We expected to observe successional changes from *R* selected taxa to *S* or *C–S* taxa at the headwater site following the intense March 1994 flood (as depicted in Fig. 3 of BIGGS et al. 1998). However, such systematic changes did not occur. In the riffle, the green filamentous taxa *Spirogyra* and *Oedogonium* were common or abundant prior to the disturbance, but were not recorded as

part of the relict community following the flood and never reappeared for the remainder of the study. Instead, the *R* selected taxa (particularly *Gomphoneis*) grew rapidly and monopolised the substrata for months after the flood disturbance. Periphyton communities of temperate streams are often dominated by diatoms in spring, which give way to cyanobacteria in summer and patchy growths of green filamentous algae in late summer (e.g. MARKER 1976, POWER 1992). Had the regeneration period extended into summer at the headwater site then perhaps we may have recorded a succession through to *S* or *C–S* selected filamentous dominants.

Conclusions

In this study we found that the hydraulic conditions did not follow a sequence of decreasing velocity and increasing depth for the three sites located down the catchment. This was particularly apparent in the runs and was unexpected. The river was much more heterogeneous in slope (at the scale of tens of meters) than was expected from the general catchment profile. However, there was an increase in levels of enrichment at the most downstream site associated with intensification of landuse. Our results suggest that it is incorrect to assume that overall channel gradient will reflect micro- and meso-scale hydraulic habitat conditions and enable a generalised periphyton response to be predicted from broadscale changes in catchment morphology. Instead, the interaction of flood disturbance frequency and level of enrichment at a given point in the catchment better explained spatial and medium-term temporal variations in periphyton biomass and community composition in the catchment.

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