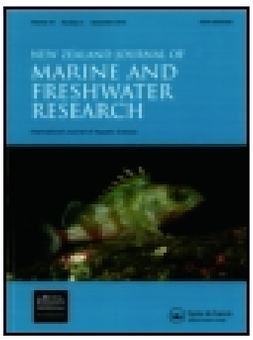

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# Responses of two trophic levels to patch enrichment along a New Zealand stream continuum

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**Abstract** We carried out a benthic survey and two experiments in runs at eight sites down the Kakanui River (South Island, New Zealand) during summer low flows, to investigate the interaction between nutrients, periphyton, and macro-grazers. Benthic periphytic biomass was generally low (< 20 mg $m^{-2}$ chlorophyll *a*) at most sites, but high densities of macro-grazers (mainly snails) were observed at six of the eight sites. Chlorophyll *a* and cellular P concentrations were generally higher on artificial substrates in the first- to third-order tributaries, compared with downstream. Macro-grazer densities (mainly snails) were also highest in the second- and third-order tributaries. Enrichment of patches with N and P did not translate into significant increases in chlorophyll *a* concentrations. Instead there was a general increase in macro-grazers, and an increase in the relative abundance of *Cocconeis placentula*. In a second experiment, the chlorophyll *a* level was five-fold higher on the substrates where macro-grazers were excluded and there was no significant response of chlorophyll *a* to nutrient addition on these substrates. On the grazed substrates, densities of snails and caddis-larvae were two-fold higher with N+P enrichment. These experiments provided evidence for a tight coupling between first and second trophic levels, and strong grazer control of periphyton, in this river.

**Keywords** periphyton; stream ecology; invertebrate grazers; trophic levels; patch dynamics; nutrients; top-down control; bottom-up control

## INTRODUCTION

Periphyton is considered to be the primary source of energy driving higher trophic levels in unshaded streams (e.g., Minshall 1978). Where flood disturbance frequency is low, strong correlations can be found between invertebrate grazer abundance and periphyton biomass (e.g., Gregory 1983; Crowl & Schnell 1991). Studies have shown invertebrate abundance, growth rates, lipid content, and pupal size to be linked with periphyton productivity (Gregory et al. in Gregory 1983; McAuliffe 1984; Hart 1987; Lamberti et al. 1989; Hart & Robinson 1990; DeNicola & McIntire 1991; Suren & Winterbourn 1992; Hill 1992; Hill et al. 1992). However, it is now clear that in some parts of streams and/or at certain times of the year when periphyton production is low, grazer production can be food-limited (Hart & Robinson 1990; Hill 1992). Thus, periphyton productivity may be a major determinant of both the distribution (Jowett & Richardson 1990; Crowl & Schnell 1991) and production (Lamberti et al. 1989; DeNicola & McIntire 1991) of grazers in stream ecosystems.

Because of this close periphyton-invertebrate coupling, changes in primary production with factors such as nutrient enrichment may be expressed not as an accumulation of periphyton biomass, but as a change in densities/production of grazers (Gregory 1983; Lamberti et al. 1987, 1989; Hill & Harvey 1990; Hill et al. 1992). This can result in an inverted "trophic pyramid" (Gregory 1983) with grazer biomass being 10–20 times that of the associated periphyton (McIntire 1975;

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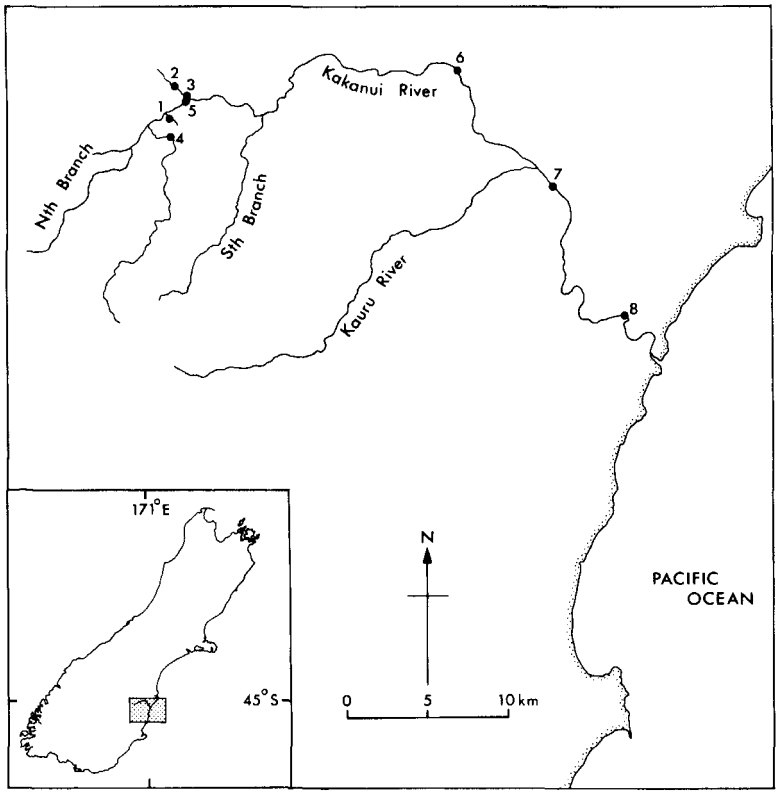


**Fig. 1** Location map of the study sites in the Kakanui River, North Otago, South Island, New Zealand.

Gregory 1983; Hill 1992; Hill et al. 1992) and with > 90% of periphyton production being consumed rather than accumulating as biomass (Lamberti et al. 1989).

In situations where stochastic physical control of ecosystem structure and function is weak, these interactions may be described in terms of "bottom-up" and "top-down" control of populations and communities. In an even-numbered trophic-level system, where there are simple links between plants and herbivores, models predict that plants will be under top-down control. In an odd-numbered system, plants may be bottom-up controlled (e.g., Fretwell 1987). However, empirical studies have shown that because nutrient saturation of plant growth rates does not always occur, primary production can be both bottom-up and top-down controlled (Hill et al. 1992). Further, some characteristics of the periphyton can be affected more strongly by nutrient additions, whereas others are more strongly affected by grazing (Rosemond et al. 1993).

The objective of our study was to investigate the interrelationship between nutrients, periphyton, and grazers at different locations down a river continuum. Through the resultant responses we wished to learn more about factors controlling spatial differences in periphyton and invertebrates in New Zealand foothills streams; and to specifically address issues of bottom-up and top-down control of periphyton development.

## KAKANUI RIVER STUDY AREA

The study was carried out in the Kakanui River, North Otago, South Island, New Zealand. The upper catchment is composed of steep hill-country reaching an altitude of 1500 m. The vegetation is largely dominated by snow-tussock which has been oversown with pastoral grasses, and fertilised, for extensive cattle and sheep grazing; the lower catchment (< 100 m) supports intensive sheep and cattle grazing on highly modified pasture. Much of the upper basin is underlain by schistose rock; however, the lower catchment is an outwash plain underlain by Tertiary sediments. Eight sites were chosen down the river, one in each of first- through fifth-order flows (Sites 1–5), and three (Sites 6–8)

in the sixth-order moving progressively down the outwash plain (Fig. 1). Sites were generally unshaded (but see below) and PAR on cloudless days was measured at 1650 μE $m^{-2}$ $s^{-1}$. Flows during this late summer period (February and March 1992) were low throughout the sampling period (i.e., there were no spates). Table 1 summarises background data on the sites during the study period.

## MATERIALS AND METHODS

### Sampling procedures

Two sets of experiments were carried out. The first, a nutrient enrichment periphyton-grazer response experiment, was conducted at all eight sites in February 1992. The second, to test the effects of enrichment on periphyton with, and without, macrograzers (i.e., snails and large caddis larvae) was conducted in February 1993 at Site 8. One set of samples, for determination of ambient nutrient concentrations and periphytic biomass, was collected at all sites with the first experiment.

*Ambient conditions*

At each site except 1 and 2 (in the first- and second-order streams) a transect was placed across the site in a typical run and it was divided into 12 equally spaced segments. Depth and velocity (at 0.4 of the depth) were measured at each point using a wading rod and Gurley cup current meter. A stone or cobble was collected beneath every point for sampling of periphyton. Periphyton were removed by scrubbing down the entire surface of the rock into a bucket using a wire brush. Replicates from each consecutive set of three points were pooled to give four samples per transect which were placed in polyethylene bottles, chilled, and returned to the laboratory for freezing until analysis. The rock dimensions of each sample were recorded with the aid of calipers and used to calculate the surface area colonised by periphyton using the equation of Biggs & Close (1989). This value was used to standardise the periphyton biomass measures and thus these results represent concentrations of periphyton per unit area of exposed substrate in the river.

At the time of periphyton sampling, a water sample was collected in a sterile 120 ml specimen container, chilled, then frozen for analysis of soluble nutrients using the methods listed in Biggs & Close (1989).

*Experiment 1: eight-site periphyton/grazer enrichment*

Sixteen nutrient-diffusing substrates (Fairchild & Lowe 1984) were deployed for 38 days at each site, representing four replicates of nitrogen, phosphorus, nitrogen plus phosphorus, and four controls. The substrates were composed of 100 mm × 100 mm unglazed ceramic tiles fixed to a 250 ml plastic reservoir of 2% agar solution, with either 0.05 molar $Na_2HPO_4$ (P), 0.5 molar $NaNO_3$ (N), or a mixture of the two at the same concentrations (N+P). Agar without nutrient addition served as a control. The tiles were soaked in distilled water for 2 days before attachment to the reservoirs.

The substrates were placed over (down and across) a 20 m reach on the bed of the river "without conscious bias" (at velocities of < 0.3 m $s^{-1}$ and depths of 0.2–0.3 m). They were placed so that there was generally a 0.2 m gap between substrates and the nearest neighbours were not of the same treatment. The exceptions were at Sites 1 and 2 in the small first- and second-order tributaries where the stream was often so narrow (< 0.5 m) that most of the substrates were deployed in a line downstream (discontinuous depending on localised bed and channel structure). They were kept in place by jamming cobbles around their bases. Small amounts of fouling debris were removed from the substrates during the 38-day accrual period.

Care was taken when retrieving the substrates to avoid dislodging the macro-invertebrates on the top surface of the substrates which were subsequently enumerated. Chironomids were abundant at Site 5, but were not enumerated. The substrates were then separated from the reservoirs and placed in zip-lock plastic bags, together with their resident invertebrates, chilled and returned to the laboratory for freezing (within 6 h). The invertebrates were removed from the substrates before periphyton processing in the laboratory.

*Experiment 2: enrichment of periphyton with, and without, macro-grazer activity*

The sampling protocol for this experiment was modified to facilitate macro-grazer exclusion. A galvanised steel box (dimensions = 0.6 m × 0.4 m × 0.2 m) was constructed and the nutrient diffusing substrates (300 ml reservoirs) placed in four lines of five replicates in an internal frame. Moist hardened-ashless filters were then placed over the tops of the reservoirs (which had been pre-filled with nutrient agar, as described above) for a

periphyton/macro-grazer colonisation surface, and held in place with push-fit plastic collars. A flat lid, with 2 cm high longitudinal partions (to maintain parallel flow and prevent diffusion onto neighbouring treatments) was then fixed to the top of the box. Holes, exactly the diameter of the reservoir necks, allowed the lid to be seated so that the filter papers were flush with the surface and exposed to the stream current.

Two of these samplers were deployed at Site 8 and incubated for 17 days. One sampler had a thick (2–4 mm) bead of petroleum jelly applied around the rim of the lid to inhibit non-drifting macro-grazers from crawling onto the substrate surfaces, and the other sampler had no petroleum jelly to allow free grazer access. On deployment, the boxes were seated in a concavity excavated in the gravel-cobble bed so that the sampling surface was approximately 10 cm above the stream-bed. The sampler lacking the petroleum jelly barrier was placed in a water velocity of 0.1–0.2 m $s^{-1}$, whereas the sampler with the macro-grazer barrier was placed in a velocity of 0.5–0.6 m $s^{-1}$ to further discourage snails from moving onto the samplers. This was found necessary since the petroleum jelly barrier does not work completely. Since velocity was used to help regulate invertebrate colonisation for the experiment, a complementary experiment was carried out at two other sites where snail grazers were largely absent to determine whether such velocity differences would influence chlorophyll *a* level independently of grazing. No significant differences (*t*-test, $P > 0.05$) occurred in comparisons of chlorophyll *a* level between run and riffle samplers for any of the treatments at both sites (a total of eight comparisons). For example, mean riffle and run chlorophyll *a* concentrations on the control substrates tested at Site 6 were 2.9 and 2.7 mg $m^{-2}$. Similarly, mean N+P treatment concentrations were 16 and 18 mg $m^{-2}$ in the riffles and runs.

On retrieval, snails and large caddis grazers were removed and counted on the substrate surfaces (none were present on the exclusion substrate). Filter papers from both treatments were then placed in 90% ethanol for the direct extraction of chlorophyll *a*.

## Laboratory procedures

Upon thawing, periphyton from the tiles in Experiment 1 was scraped into a vial of distilled water using scalpel and toothbrush. The periphyton was blended and sub-sampled for analysis of chlorophyll *a* (extracted in boiling 90% ethanol, corrected for phaeopigments using acidification, and measured on a spectrophotometer), and ash-free dry mass (AFDM) by drying at 105 °C for 24 h and ashing at 500 °C for 4 h as described by Biggs (1987). Sub-samples were also analysed for N and P as total Kjeldahl N and total P normalised to AFDM to give cellular nutrient concentrations ($\%N_c$, $\%P_c$) as described by Biggs & Close (1989). These analyses include all nutrients sorbed to inorganic particles, organic detritus, and held within bacteria/fungi. However, at all sites except Site 7 (where significant inorganic detritus accumulated), microscopic examination of the matrix revealed that the non-algal component constituted only a very small fraction of the total biomass. AFDM of grazers was determined as for periphyton.

A further subsample was analysed by light microscopy to determine the relative abundance of algal taxa present. A minimum of 200 cells were identified and counted in most sub-samples. Diatoms were identified from permanent mounts (Patrick & Reimer 1966). Soft algae were identified from wet mounts.

## Data analysis procedures

Cattle wandering through the streams resulted in loss of some Experiment 1 substrates at Site 1 (4 N, 2 N+P treatments), Site 2 (1 N, 1 P, 2 N+P, 3 Control), and Site 3 (1 N, 3 P, 3 N+P, 2 Control) which reduced the degrees of freedom. Sufficient substrates were retrieved to enable a complete set of analyses for all but Site 1. The effect of nutrient enrichment on community parameters was determined by a two-factor ANOVA and, where appropriate, with post-hoc Tukey tests using SYSTAT (Wilkinson 1990). ANOVA categories were "Site", nutrient "Treatment", and the interaction of "Site" by "Treatment".

In the second experiment (periphyton responses to enrichment with, and without, the influence of macro-grazers) the density of macro-grazers was so high on the N+P treatment (a mean of over 20 000 $m^{-2}$, almost twice that of the other treatments), and their associated feeding activity so intense, that the hardened filter paper substrates were visually bare of any periphytic algae and they also disintegrated when we attempted to retrieve them. All other substrates were intact and appeared to have some periphyton. Rather than discarding this important, obviously very low, chlorophyll *a* response we arbitrarily ascribed a chlorophyll *a*

value of 0.7 mg $m^{-2}$ to these treatments. This value was half the minimum value found in the replicates on the other treatments where algae were just visible and where grazer density was approximately half that of the N+P treatments.

## RESULTS

### Ambient conditions: physical, chemical, biological

The width of flow varied from < 1 m to 20 m over the stream orders, and the discharge varied from 0.13 l $s^{-1}$ to 812 l $s^{-1}$ (Table 1). There was a 17% reduction in flow (presumably as loss to ground water) down the sixth-order section flowing over the gravel plains (Sites 6–8). Mean section water velocities were low at all sites ( < 0.25 m $s^{-1}$) reflecting a low bed gradient in the study runs and generally coarse bed sediments.

Midday river temperatures were around 17°C and varied little with downstream distance (Table 1). Nutrient concentrations in the river were moderately low with total inorganic N (TIN) being < 60 µg $l^{-1}$ at all sites except Site 3, and dissolved reactive P (DRP) being 2 µg $l^{-1}$, or less, at all sites except Site 8 (Table 1). The TIN:DRP ratio at the time of this first survey/experiment suggested that the waters at all Sites (except Site 4 ) were more deficient in P than N for primary production. No consistent downstream pattern in any nutrients nor Cl occurred.

Periphyton chlorophyll *a* levels were moderate to low (generally < 20 mg $m^{-2}$) as were AFDM levels (generally < 8 g $m^{-2}$) (Table 1). The exception was in the first-order tributary where extensive growths of filamentous green algae occurred. The cellular N:P ratios indicated slight N deficiency in the streambed periphyton at Sites 1–3, and an appropriate balance at the other sites. Overall, there was no systematic downstream pattern in periphyton development on the river bed.

No benthic invertebrate samples were collected during this survey, but observations and subsequent sampling have identified a high biomass of macrograzers (snails and cased-caddis larvae) at most sites (pers. comm. I. G. Jowett, NIWA-Ecosystems). Only at Sites 4 and 5 were these organisms rarely seen on the surface of the cobbles.

**Table 1** Summary of physical, chemical and biological statistics at the eight Kakanui sampling sites. Values for biological parameters are geometric means and ANOVA analyses carried out on ln transformed data. ANOVA-*F* values: * $P < 0.05$, ** $P < 0.01$. Sediment size is the mean "y" axis dimension of substrates used for periphyton sampling. DRP, dissolved reactive P; TIN, total inorganic N ($NO_3$ - N + $NH_4$-N).

| | Stream Order/Site | | | | | | | | ANOVA |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 6/7 | 6/8 | *F* |
| **Physical** | | | | | | | | | |
| Width (m) | <1 | 1.5 | 3.00 | 11.4 | 15.0 | 14.2 | 18.2 | 20.0 | – |
| Hydraulic radius (m) | – | – | 0.04 | 0.11 | 0.25 | 0.26 | 0.28 | 0.41 | – |
| Flow (l $s^{-1}$) | 0.13 | 3.15 | 17.9 | 277 | 535 | 812 | 778 | 693 | – |
| Mean vel. (m $s^{-1}$) | – | – | 0.02 | 0.21 | 0.14 | 0.22 | 0.15 | 0.08 | – |
| Maximum depth (m) | 0.02 | 0.04 | 0.09 | 0.37 | 0.52 | 0.53 | 0.47 | 0.58 | – |
| Sediment size (m) | 0.110 | 0.086 | 0.073 | 0.070 | 0.086 | 0.104 | 0.086 | 0.073 | |
| Temperature (midday) | 17.0 | – | 17.0 | 17.0 | 16.0 | – | – | 17.3 | |
| **Chemical** | | | | | | | | | |
| $NO_3$–N (mg $m^{-3}$) | 43 | 29 | 154 | 10 | 20 | 11 | 52 | 29 | – |
| $NH_4$–N (mg $m^{-3}$) | 5 | 6 | 5 | 4 | 4 | 5 | 4 | 9 | – |
| DRP (mg $m^{-3}$) | 1.5 | 2.0 | 1.0 | 2.5 | 2.0 | 1.0 | <1.0 | 6 | – |
| TIN:DRP | 36 | 17 | 159 | 6 | 12 | 16 | 55 | 9 | – |
| Cell N:P | 5.8 | 4.2 | 1.7 | 3.9 | 1.6 | 3.8 | 6.0 | 7.5 | – |
| **Streambed periphyton** | | | | | | | | | |
| Chlorophyll *a* (mg $m^{-2}$) | 26 | 7 | 13 | 19 | 17 | 10 | 17 | 5 | 6.31** |
| AFDM (g $m^{-2}$) | 24 | 6 | 7 | 7 | 7 | 5 | 7 | 5 | 1.20 |
| Organic weight (%) | 20 | 14 | 10 | 20 | 19 | 20 | 25 | 16 | 3.52* |
| Cellular N:P | 7.3 | 7.5 | 4.5 | 9.8 | 9.4 | 9.9 | 11.4 | 9.0 | 5.51** |

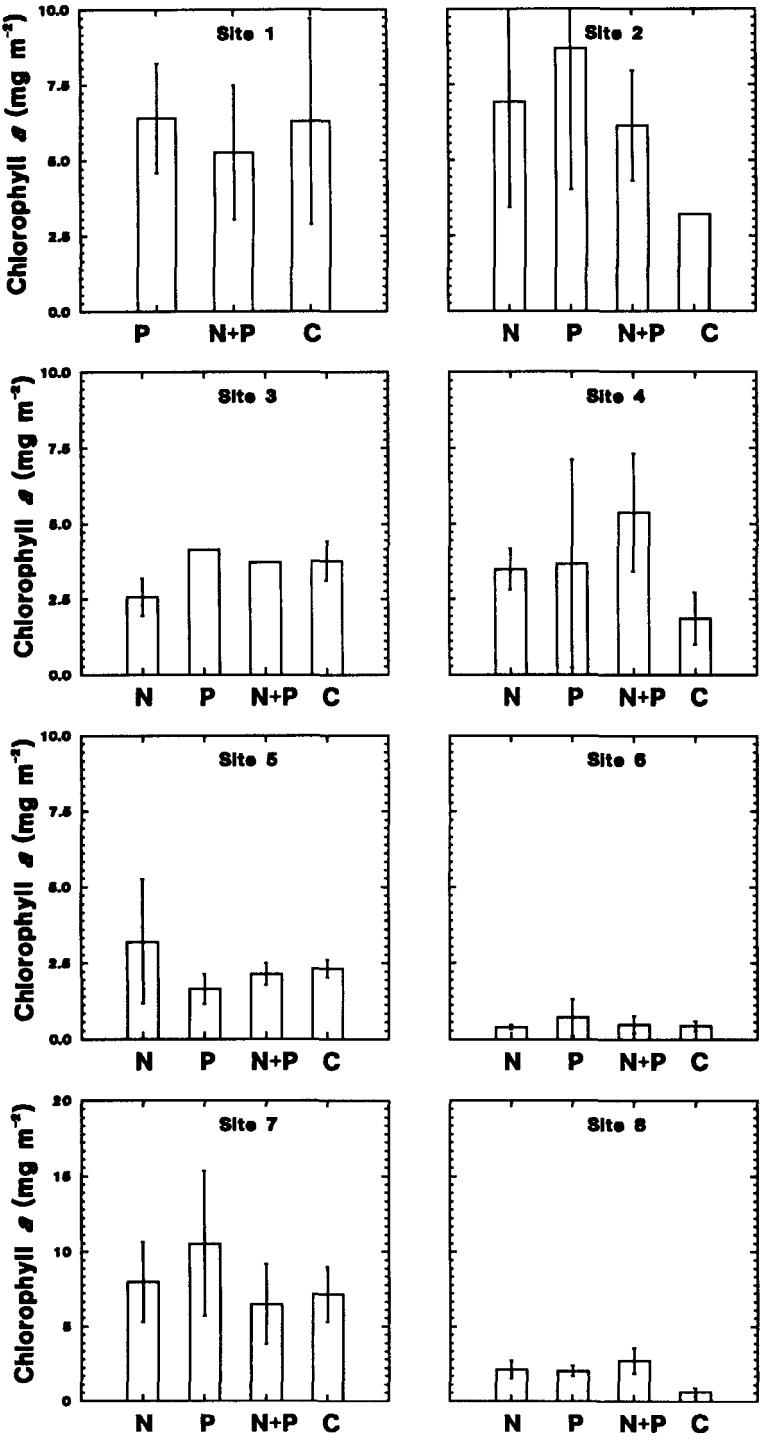


**Fig. 2** Histograms, and standard errors, of chlorophyll *a* concentrations on nutrient-diffusing substrates for control (C) and three nutrient treatments (N, P, and N + P) at eight sites in the Kakanui River.

## Trophic responses to patch enrichment

### *Periphyton*

Chlorophyll *a* concentration on the control and nutrient-enriched artificial substrates in Experiment 1 was generally < 8 mg $m^{-2}$ (i. e., low) throughout the catchment (Fig. 2). Sites 1, 2, and 3 in the upper catchment had the highest chlorophyll *a* development on the control substrates (also Site 7, but see Discussion), with Sites 6 and 8 having much lower levels. Significant variance occurred in chlorophyll *a*, AFDM, and organic weight as a function of "Site" in the catchment (Table 2). Chlorophyll *a* concentration did not show a significant nutrient "Treatment" effect across the sites (Table 2).

Mean cellular P concentrations on control substrates covered the range 0.11–0.46% P, but seven of the eight sites being < 0.4 % P (Table 3) suggested slight to moderate P deficiency, using a criterion of 0.5% P (Auer & Canale 1982). This supports the interpretation of potential P limitation of communities derived from the streamwater inorganic nutrient concentrations. The most upstream sites (Sites 1 to 4) in the low-order tributaries generally had highest cellular P concentrations on the control substrates, indicating that these sites were relatively more enriched

**Table 2** ANOVA of various parameters as a function of location in the catchment (Site) and nutrient enrichment (Treatment), Sites 2-8. (*F* and *P* value for Source.)

| | Site | | | Treatment | | | Site × Treatment | | |
|---|---|---|---|---|---|---|---|---|---|
| Parameter | DF | *F* | *P* | DF | *F* | *P* | DF | *F* | *P* |
| Periphyton | | | | | | | | | |
| Chlorophyll *a* | 6 | 27.35 | 0.000 | 3 | 2.13 | 0.105 | 18 | 1.07 | 0.397 |
| AFDM | 6 | 20.72 | 0.000 | 3 | 3.68 | 0.016 | 18 | 1.38 | 0.170 |
| Organic weight | 6 | 31.67 | 0.000 | 3 | 1.29 | 0.284 | 18 | 5.10 | 0.000 |
| Cellular P | 6 | 3.95 | 0.002 | 3 | 14.12 | 0.000 | 18 | 1.54 | 0.105 |
| Cellular N | 6 | 31.27 | 0.000 | 3 | 4.46 | 0.006 | 18 | 4.44 | 0.000 |
| *C. placentula* | 7 | 21.14 | 0.000 | 1 | 14.73 | 0.000 | 7 | 8.49 | 0.000 |
| Grazers | | | | | | | | | |
| Density | 4 | 14.27 | 0.000 | 3 | 5.75 | 0.002 | 12 | 0.91 | 0.544 |
| AFDM | 4 | 19.74 | 0.000 | 3 | 3.87 | 0.016 | 12 | 2.06 | 0.041 |
| Specific AFDM | 4 | 11.52 | 0.000 | 3 | 1.60 | 0.204 | 12 | 2.14 | 0.034 |
| Grazer inclusion/exclusion experiment at Site 8 | | | | | | | | | |
| Chlorophyll *a* | | | | | | | | | |
| Ungrazed | | – | – | 3 | 2.53 | 0.096 | – | | – |
| Grazed | | – | – | 2 | 29.25 | 0.000 | – | | – |
| Grazers | | – | – | 3 | 21.72 | 0.000 | – | | – |

**Table 3** Cellular nutrient data from periphyton on nutrient diffusing substrates at 8 sites in the Kakanui River. Each value is commonly the mean of 4 replicates. Parentheses indicate spurious values which are the mean of only 2 replicates.

| | % Cellular P Treatment | | | | % Cellular N Treatment | | | |
|---|---|---|---|---|---|---|---|---|
| Site | N | P | N+P | Ctrl | N | P | N+P | Ctrl |
| 1 | 1.13 | – | 0.38 | 0.46 | 2.10 | – | 2.04 | 3.16 |
| 2 | 0.46 | 0.34 | 0.45 | 0.25 | 4.89 | 3.00 | 2.90 | 2.88 |
| 3 | 0.30 | 1.56 | 0.43 | 0.40 | 5.55 | 5.69 | (11.8) | (7.29) |
| 4 | 0.45 | 1.16 | 0.79 | 0.39 | 4.17 | 3.99 | 4.25 | 5.12 |
| 5 | 0.31 | 0.65 | 0.55 | 0.32 | 3.79 | 3.79 | 3.66 | 3.45 |
| 6 | 0.13 | 0.84 | 0.49 | 0.11 | 2.15 | 3.97 | 3.34 | 1.67 |
| 7 | 0.29 | 0.77 | 1.06 | 0.36 | 5.12 | 5.16 | 5.88 | 5.80 |
| 8 | 0.20 | 0.37 | 0.29 | 0.28 | 4.38 | 4.24 | 4.04 | 4.28 |

(Table 3). Thus, "Site" location and nutrient "Treatment" explained significant variance in cellular P concentrations (Table 2). There was a significant correlation between ln chlorophyll *a* and cellular P concentrations ($r = 0.351$, $P < 0.001$) over the full dataset, suggesting that additional uptake of P from the nutrient treatments, and higher background cellular P concentrations in the low order tributaries, was stimulating periphyton production.

Apart from Sites 1 and 2, cellular N concentrations on control substrates were greater than 4%, suggesting that the communities were only weakly deficient in N (assuming possible limitation at N < 5%) (Table 3). However, significant "Site", "Treatment", and "Site × Treatment" effects were recorded for cellular N—indicating that some differences in N uptake were occurring among the sites and treatments. There was no downstream pattern in cellular N concentrations on the control substrates (Table 3).

At Sites 1–3, and 6 and 8, where macro-grazer densities were high (see next section) the periphyton community was dominated by the diatom *Cocconeis placentula*, and its relative abundance increased with enrichment compared with controls (Table 4). At Sites 4, 5, and 7 where *Cocconeis* was less abundant, *Achnanthes minutissima* and *Brachysira exilis* made up the balance of the non-*Cocconeis* community in approximately equal amounts (data not shown for brevity). "Site", "Treatment", and their interaction effects were significant for the relative abundance of *Cocconeis placentula* (Table 2). However, there was no clear effect attributable to either N nor P (Table 4). Relative abundances tended to be greater on both nutrient treatments compared with the controls.

**Table 4** Relative abundance of *Cocconeis placentula* (%) in periphyton communities on nutrient diffusing substrates at 8 sites in the Kakanui River. Each value is commonly the mean of 4 replicates.

| Site | N | P | N+P | Control |
|---|---|---|---|---|
| 1 | – | 61 | 86 | 53 |
| 2 | 58 | 75 | 85 | – |
| 3 | 96 | – | 61 | 82 |
| 4 | 8 | 17 | 15 | 10 |
| 5 | 17 | 34 | 28 | 27 |
| 6 | 9 | 84 | 75 | 29 |
| 7 | 0.3 | 11 | 11 | 0.6 |
| 8 | 99 | 100 | 99 | 98 |

*Macro-grazers*

In Experiment 1 the macro-grazers were dominated by the snail *Potamopyrgus antipodarum* at Sites 1, 2, 3, 6, and 7, and co-dominated by cased caddisfly larvae at Site 8. Site 4 had no visible grazers on the substrates, whereas substrates at Site 5 were heavily colonised with chironomid larvae (often > 50 tubes per substrate). These were not enumerated, because of the difficulty of establishing in the field whether each tube was inhabited. These results confirmed our visual observations during the initial benthic survey.

The densities of macro-grazers on the substrates at six of the sites were moderate to high (Fig. 3), with substrates at Sites 2 and 3 (in the second- and third-order tributaries, respectively) having densities up to 8000 $m^{-2}$. Overall, macro-grazer densities on the control substrates (excluding Site 7 because of siltation—see Discussion) averaged 1933 individuals $m^{-2}$ (367 mg $m^{-2}$ AFDM biomass).

## Bottom-up effects of nutrients and periphyton on grazers

Significant differences ($P < 0.05$) in grazer density, AFDM, and grazer-specific AFDM were explained by "Site" and "Treatment" variables, and/or their interaction (Table 2) in Experiment 1. Elevated densities of macro-grazers were found on P and/or N+P substrates at Sites 2, 3, 6, 7, and 8 when compared with the control (Fig. 3). However, only the differences at Site 8 were significant at $P = 0.05$ (post-hoc Tukey test) when treatment effects were analysed on an individual site basis.

Calculating relative macro-grazer densities on P-enriched and control substrates (i.e., the number of grazers on the P and N+P treated substrates divided by the average densities on control and N substrates for that site) and plotting these as a function of chlorophyll *a* (Fig. 4) shows that for a given value of chlorophyll *a*, much higher densities of grazers generally occurred on the P and N+P enriched substrates than the control and N-alone treatments. For low concentrations of chlorophyll *a* (i.e., < c. 3 mg $m^{-2}$), P and N+P enrichment resulted in grazer densities almost double that for a comparable chlorophyll *a* concentration on the other substrates, and when chlorophyll *a* was > c. 6 mg $m^{-2}$, enrichment increased grazer densities 3–6-fold over that of non P-enriched substrates.

Thus, while enrichment was not causing a significant increase in chloraphyll *a* levels (see previous section), it was causing an overall

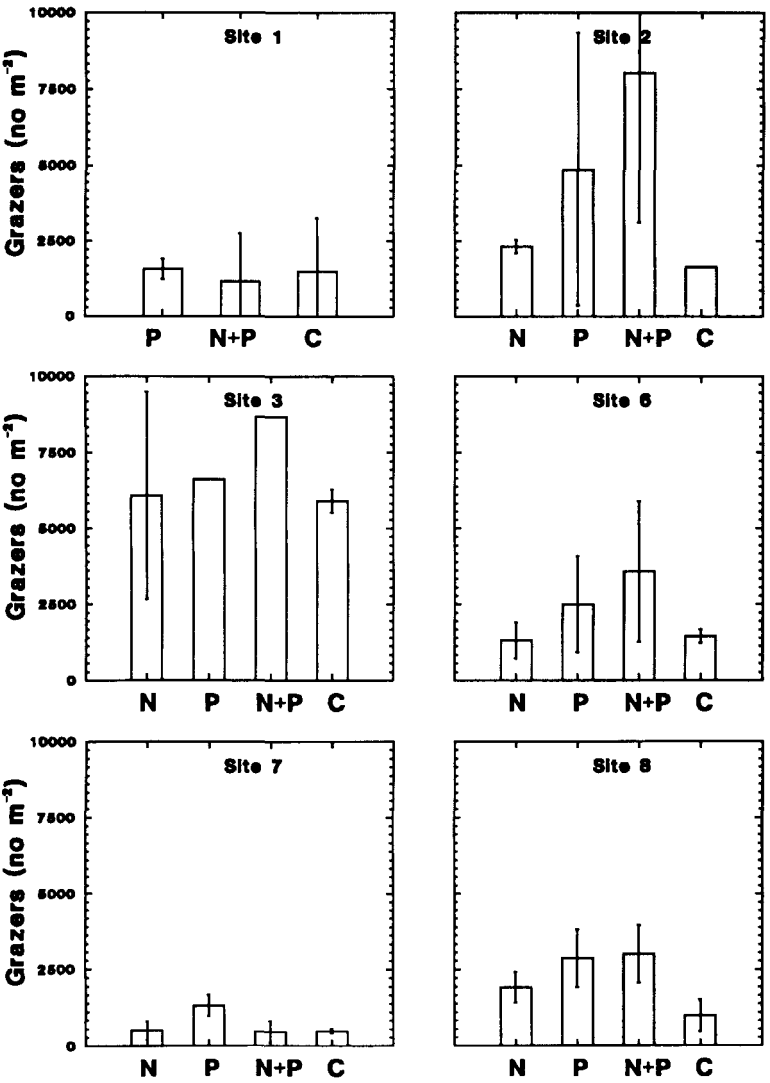


**Fig. 3** Histograms, and standard errors for the density of macro-grazers on nutrient-diffusing substrates for control (C) and three nutrient treatments (N, P, and N + P) at six sites in the Kakanui River.

stimulation of grazer densities on the substrates. This suggested that any increase in periphyton production with enrichment was being routed directly through to increased grazer activity, and that this grazing could be controlling periphyton biomass accrual. Further, where there were elevated densities of grazers, the periphyton was dominated by the grazing-resistant diatom *Cocconeis placentula* (Fig. 5), suggesting that the grazing was also altering periphyton community structure.

This enhancement of grazers with nutrient addition was investigated again in the second experiment at Site 8 (February/March 1993). There was a modest (1.1–1.2-fold) increase in mean densities of macro-grazers with N and P enrichment singularly, but a major increase in macro-grazers (2-fold) occurred with N+P enrichment (Fig. 6). This emphasised the tight coupling between grazer densities and nutrient enrichment (through changes in periphyton production) at this site as suggested in Experiment 1.

### Response of periphyton to enrichment with, and without, grazing pressure

The results of Experiment 1 suggested that, in addition to nutrients, grazers were potentially an

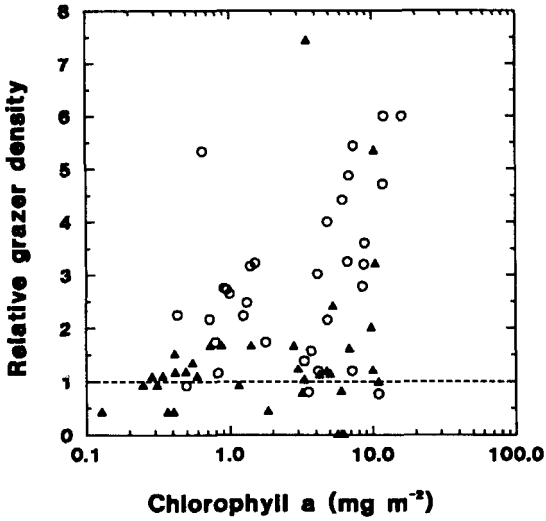


**Fig. 4** Ratio of grazers on the P-enriched (i.e., P and N+P) tiles to those on "controls" (un-amended nutrients and N treatments) according to chlorophyll *a* concentrations (triangles = controls and N enriched tiles, circles = P and N+P-enriched tiles). The horizontal line denotes the average control densities.

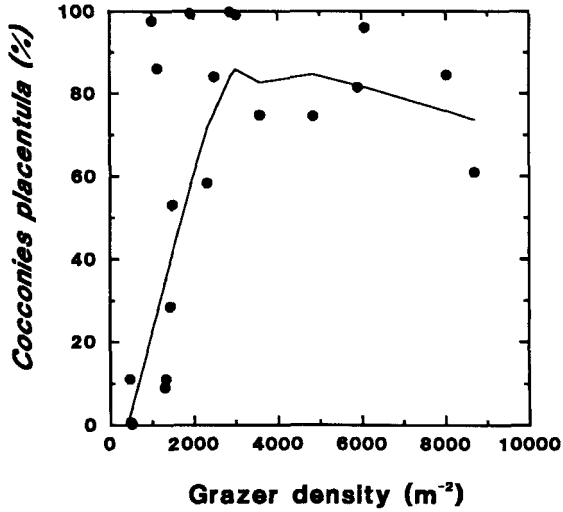


**Fig. 5** Relative abundance of *Cocconeis placentula* as a function of grazer density. Each point is the average of the replicates of a particular nutrient treatment for the different sites. The curve was generated using a locally weighted best-fit algorithm for scatter plot smoothing (Wilkinson 1990).

important factor limiting periphyton chlorophyll *a* accumulation and altering community structure in the study river. In the second experiment at Site 8, there were no significant responses to nutrient additions on the substrates without macro-grazers (Table 2, Fig. 7). However, there was a small (but significant) response across the three treatments (for which data were available: N, P, and Control) for the grazed substrates. The largest difference occurs for a comparison of the grazed vs. ungrazed substrates for any of the nutrient treatments. This clearly identifies a major influence of grazing on chlorophyll *a* concentrations (Fig. 7). For example, chlorophyll *a* was > 5-fold higher on the control substrates where macro-grazers were excluded than on the grazed substrates. Thus, Experiment 2 strongly supports the suggestion that grazers are probably a more important factor than nutrients in controlling periphyton development in the Kakanui River.

## DISCUSSION

In this study we found moderate to low periphyton chlorophyll *a* and AFDM concentrations on the stream bed in the low-velocity runs of the Kakanui River, except in the first-order tributary which had moderate development. Although benthic chlorophyll *a*, percentage organic weight, and cellular N:P ratios changed significantly among the sites, there was no downstream trend in these associated with factors such as progressive downstream enrichment with farming development.

Cellular nutrient concentrations in periphyton on the surfaces of artificial substrates placed at the sites for 38 days, and water N:P ratios, suggested that P was in short supply relative to N. In contrast to the benthic results, chlorophyll *a* accrual, and associated cellular P concentrations, in the freshly grown communities suggested that the low-order tributaries at the head of the river were more enriched than downstream reaches. Macro-grazers at six of the sites (mainly the snail *Potamopyrgus antipodarum*) actively colonised the substrates and significant between-site differences occurred in grazer densities, AFDM, and specific weight. Highest densities were recorded in the third-order tributary.

Chlorophyll *a* did not vary significantly with nutrient treatments once site differences had been accounted for. However, grazer densities/AFDM did vary significantly with treatment additions, with

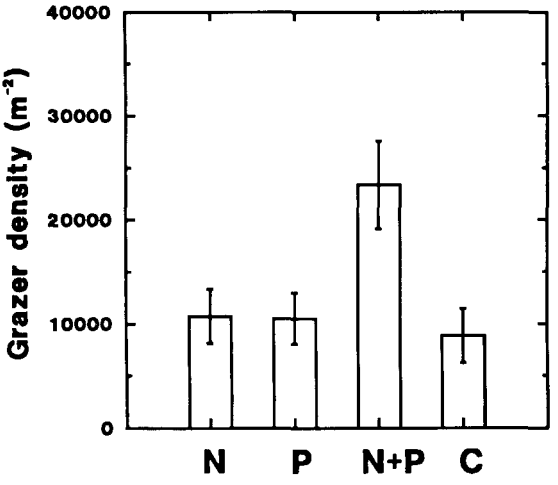


**Fig. 6** Histograms of macro-grazer densities by nutrient treatment for the grazer inclusion experiment (Experiment 2) at Site 8.

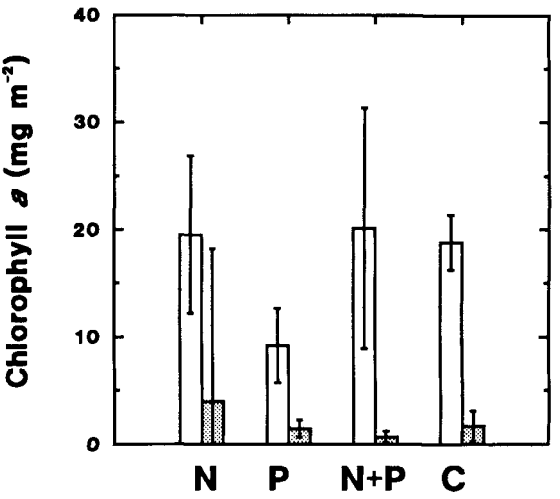


**Fig. 7** Histograms of chlorophyll *a* levels by nutrient treatment on ungrazed and grazed (hatched bars) substrates.

higher colonisation of the enriched substrates. Also, the enriched substrates supported more macro-grazers for a given chlorophyll concentration than those without amended nutrients. This suggested that this community was responding to a higher periphyton productivity under enrichment and that the grazing activity was maintaining a low level of accrued periphyton. A second experiment showed that periphyton accrual in the river could be limited by grazers and that top-down control probably predominates. The heavy grazing in our experiment also appeared to increase the relative dominance of the grazing resistant diatom *Cocconeis placentula*. Grazing has been shown to limit periphyton accrual in many other in-situ experiments (e.g., Lamberti & Resh 1983; McAuliffe 1984; Hill et al. 1992).

Similar responses of grazer growth and/or population densities to increases in production of food with enrichment have been used to imply food limitation of stream-bed fauna (Hart & Robinson 1990; Rosemond et al. 1993). Our results also suggest food limitation of grazers in the Kakanui River. If so, both primary and secondary production in the river during the study period may have been regulated by inorganic nutrient availability. Through this, it is clear that there is a tight coupling between primary and secondary production during summer low flows.

We did not assess the effect of enrichment on periphyton production rates directly, but an indication of the likely influence of added P on productivity (to determine if this can explain fully the grazer response) can be calculated from the cellular P concentrations. The link between cell division rate and cellular P is described by the Droop model (Auer & Canale 1982). From this model we estimated that cell division on the control and P and N+P-enriched substrates in the first experiment (when water and cellular nutrient concentrations suggested that P was in shorter supply relative to N) should have been about 0.57 and 0.66 divisions per day, respectively. In other words, cell division was projected to be only 16% higher on the P- and N+P-enriched substrates, even though average $\%P_c$ increased 2-fold.

Another approach to assessing potential growth differences with enrichment in P-limited communities is to calculate relative specific growth rates ($\mu:\mu_{max}$) as a function of cellular N to P ratios (Bothwell 1985: fig. 3). The cellular nutrient ratios averaged 16 on the control and 8 on the P-treated substrates. This would predict a $\mu:\mu_{max}$ of 0.88 and 0.94, respectively (which agrees well with the $\mu:\mu_{max}$ of 0.84 and 0.97 by using $\%P_c$ and the Droop model of Auer & Canale 1982). Therefore, this method predicted an increase in division rates of 8% with P enrichment.

These results indicate that, even though cellular nutrient concentrations suggested nutrient limitation, division rates under ambient nutrient levels were still quite high and thus that communities were probably only moderately P-limited. Indeed, in the second experiment at Site 8 in the following year (where macro-grazers were prevented from colonising one set of substrates), nutrient addition did not result in a significant stimulation of chlorophyll *a* accrual at all (Fig. 7). These calculations, and the 3–6-fold increases in grazer densities on P- and N+P-enrichment compared with control and N-enrichment for a given chlorophyll *a* concentration in Experiment 1 (Fig. 4), and the > 5-fold increase in grazer densities with N+P enrichment in Experiment 2, suggested that the grazers could also be responding to an improvement in food quality with enrichment. Once the animals had migrated onto the enriched tiles, many more stayed there than could be accounted for by estimated changes in production alone.

Our results suggest that macro-grazers passively tracked variations in primary production on the stream bed. This most probably occurs based on a "random walk" scenario. Hart (1981) demonstrated that a foraging caddis larva (*Dicosmoecus gilvipes*) will spend up to 97% of its time feeding and that it moves very little if there is sufficient food in the foraging area. Assuming that macro-grazers at our sites forage in a similar manner, it further suggests some degree of food shortage on the stream bed and that grazers colonising the enriched substrates stayed there to feed because cellular growth rates (and possibly food value) were higher there. Since the life cycles of the snails and caddis flies are longer than the 38-day duration of Experiment 1, reproduction is unlikely to have contributed to this patch enhancement of grazers. Several other studies have also shown increases in grazer abundance with inorganic nutrient additions (e.g., Hart & Robinson 1990; Winterbourn 1990; Hill et al. 1992). Extrapolating from this, the higher densities of macro-grazers on the control substrates at Site 3 (Fig. 3) in the upper catchment suggest that levels of natural enrichment and periphyton productivity could have been highest at that site.

Grazing influences on the biomass and taxonomic structure of periphyton (i. e., top-down effects) in North American streams have been widely reported in other studies (e.g., Feminella et al. 1989; Lamberti et al. 1989; Hill et al. 1992; Rosemond et al. 1993). Moderate to high grazer activity can reduce periphyton biomass and increase biomass-specific (but decrease areal) productivity (Steinman et al. 1991). Heavy grazing has also been shown to suppress regeneration of periphyton communities (Feminella et al. 1989). Many investigations have illustrated the ability of grazers to modify community physiognomy and taxonomic structure (e.g., Colletti et al. 1987; Jacoby 1987; Lamberti et al. 1987; Lowe & Hunter 1988; McCormick & Stevenson 1989). Several investigators have demonstrated the ability of *Cocconeis* to resist grazing (e.g., Sumner & McIntire 1982; Lowe & Hunter 1988) and the dominance of this taxon in the periphyton could be considered as an indicator of high grazing pressure.

Grazer control of periphyton biomass in New Zealand streams has become more widely recognised, particularly in unenriched habitats. Graesser (1989) found that periphyton biomass on artificial substrates was 3.6 times higher when grazers were excluded at sites in some West Coast streams, and Winterbourn & Fedgley (1989) recorded 4–13-fold increases in chlorophyll *a* level by excluding snail grazers in some spring-fed streams near Arthur's Pass. Winterbourn (1990) found that grazers only reduced periphyton biomass at sites not heavily shaded, implying that light limitation of periphyton was probably more important in forest streams. In more enriched streams, Welch et al. (1992) found that nutrient enrichment from discharges did not always promote the yield of periphyton during summer low flows and correlative evidence suggested that a high density of grazers in some streams was causing this discrepancy.

A feature of the fauna on the substrates (and on the river bed) was the dominance of *Potamopyrgus*; this invertebrate appeared to be the most agressive grazer, and predominant controller, of periphyton in the Kakanui River. Hill (1992) found in a Tennessee stream that resource depression by a similar-sized snail (*Elimia clavaeformis*) had significant ramifications for other grazers, causing reduced sizes and reductions in lipid levels in competing stone-cased caddisfly larvae. He suggested that this was because of exploitive competition and dietary overlap between the two grazers. Hawkins & Furnish (1987) also suggested that snails were the competitive dominants in stable Pacific-Northwest streams because they reduced the densities of other invertebrates through exploitive competition for food and by physical interference. Such inter-specific competition may have had a significant effect on the invertebrate

communities of the Kakanui River. Most other New Zealand foothills (gravel/cobble-bedded) rivers have a much more diverse invertebrate fauna than we observed on the artificial substrates in the Kakanui River (e.g., Quinn & Hickey 1990).

The unusual predominance of *Potamopyrgus antipodarum*, and the associated strong grazer control of periphyton, in this New Zealand foothills river is probably a result of three factors related to the habitat conditions of the catchment. First, because of their high profiles, and associated drag, these snails appear to be excluded from high-velocity areas (Jowett et al. 1991). However, in the Kakanui River, water velocities during summer baseflows are generally low by comparison with other New Zealand rivers (Biggs et al. 1990: table 2), reflecting a low catchment gradient. This will enhance the opportunities for *Potamopyrgus* to exploit this river as a habitat. Indeed, most of our results were generated in slow-flowing runs (the predominant habitat) where mean cross section velocities were < 0.25 m $s^{-1}$ (Table 1). Few of these snails were observed in the associated riffles where velocities exceeded 0.6 m $s^{-1}$ (and these conditions were used to exclude snails from one set of substrates in Experiment 2). This is also where very high periphyton biomass concentrations occurred (sometimes > 100 mg $m^{-2}$ chlorophyll *a*, authors' unpubl. data) and the occurrence of these could be a result of high velocities reducing grazing pressure by snails. Second, there is little land erosion in the catchment, and thus the riverbed sediments are generally large giving stable refugia for these organisms to escape to during spate flows. Third, this snail appears to require a moderate or high level of enrichment and associated high level of periphyton production (Quinn & Hickey 1990). Cellular nutrient concentrations indicated that moderate to high rates of cell division were present in the Kakanui River.

Concentrations of chlorophyll *a* were much higher at Site 7 than at most other sites (Fig. 2). When inorganic debris (silt) settles in the matrix it affects the biofilm quality and can interfere with the feeding of grazers (Ryan 1991). Such debris occurred at this site and is thought to have resulted in reduced grazing pressure on the periphyton and, thus, the high chlorophyll *a* values at this site. This is supported by a significant correlation ($r = 0.837$, $P < 0.001$) between % organic weight and grazer densities on replicates from Site 7. Grazer densities were low (i.e., < 1000) when organic composition was below approximately 30%. Carbon availability and cellular nutrient levels (food quality) were still high on these substrates, so there was abundant food for the grazers. The source of this silt was a gravel extraction operation 500–1000 m upstream of the site.

Although we have only addressed two trophic levels in this study, three actually exist in the Kakanui River, as fish (brown trout, native galaxids and bullies) are also present. However, extensive surveys of the river for adult trout have found that they are largely confined to the lower reaches from the estuary to just upstream of Site 8 (I. G. Jowett, NIWA-Ecosystems, pers. comm.). *Potamopyrgus antipodarum* is poor food for foraging fish (low calorific content, a hard shell that resists crushing/digestion, and an operculum: McCarter 1986). This fact may be affecting trout distribution upstream of Site 8 as *Potamopyrgus* may not be providing sufficient energy for these fish. Thus, we speculate that the second trophic level, dominated by the snail *Potamopyrgus* (reflecting the physical habitat template, as discussed above), could be controlling not only the first, but also the third trophic level in the river. This possiblity of middle-order control adds a new dimension to recent observations on "top-down" versus "bottom-up" effects on ecosystems and should be investigated further.

It is instructive to compare some of our results with those from sites in the New Zealand "100 Rivers" programme (Quinn & Hickey 1990). The mean ratio of total invertebrate to periphyton biomass (as AFDM) was 0.22 for unenriched sites in the "100 Rivers" dataset and 0.13 for enriched sites where periphyton biomass was significantly higher (7.41 vs. 18.07 g AFDW $m^{-2}$, $P < 0.001$, *t*-test). This compares with a ratio of 0.19 on the control substrates and 0.23 on the P-enriched substrates in the Kakanui. Further, cellular P concentrations at moderate and low enrichment sites (Groups 2–7 of Biggs 1990) ranged from 0.11 to 0.39% $P_c$ (cf. 0.27 for controls with grazers in this study). If grazing and assimilation rates of invertebrate communities in other New Zealand streams are comparable to those in the Kakanui River, then these similar densities of grazers per unit of periphyton, and similar cellular P concentrations, possibly indicate a wider occurrence of food limitation for grazers, and predominantly grazer control of periphyton, during late-summer low flows in New Zealand streams.

The above ratios for Experiment 1 are considerably lower than have been reported elsewhere for "inverted trophic" pyramids which

are in the range of 10–20 (Gregory 1983; Hill 1992; Hill et al. 1992). This is despite the periphyton appearing to be heavily grazer-controlled on the substrates (and confirmed at Site 8 in Experiment 2). Because of the relatively short duration of the experiment, compared with the generation time of the grazers, this could imply that the enriched substrates were still below their potential grazer carrying capacity for the given periphyton production.

Considerable research has been carried out on growth processes and spatial patterns in the distribution of periphyton in streams. Similarly, much is now known about the feeding ecology of stream grazers. Our study in the Kakanui River suggests that the production of invertebrates, and their distribution, could be both food quantity- and quality-limited at certain times of the year — which could have several important implications for invertebrate generation times and temporal dynamics. Several issues have arisen from this study which with more intensive investigation could contribute strongly to a functional ecology of New Zealand streams: first, the need to directly assess the degree of food limitation of invertebrate growth rates in a range of other New Zealand streams. From this it would be useful to ascertain the effect of food limitation on grazer density/biomass dynamics among catchments, and the frequency/temporal extent of food limitation in relation to the duration of spate-free periods (the disturbance template). Second, it would be useful to define more clearly the relative control of periphyton by grazing under spatial differences in velocity. This may help explain differences which occur in periphyton within catchments (e.g., between riffles and runs). It is commonly assumed that riffles are "physiologically richer" because of the higher velocities. However, recent studies have indicated that diatoms in such habitats may just secrete more mucilage in riffles—perhaps as a mechanism to reduce shear stress (Biggs & Hickey in press). The present study suggests also that lower grazing pressure may occur in such high-velocity areas; this could be an important factor contributing to within-stream differences in periphyton development.

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