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## Top-down and bottom-up processes in grassland and forested streams

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**Abstract** The influence of predatory fish on the structure of stream food webs may be altered by the presence of forest canopy cover, and consequent differences in allochthonous inputs and primary production. Eight sites containing introduced brown trout (*Salmo trutta*) and eight sites that did not were sampled in the Cass region, South Island, New Zealand. For each predator category, half the sites were located in southern beech (*Nothofagus*) forest patches (range of canopy cover, 65–90%) and the other half were in tussock grassland. Food resources used by two dominant herbivores-detritivores were assessed using stable isotopes.  $^{13}\text{C}/^{12}\text{C}$  ratios were obtained for coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM), algal dominated biofilm from rocks, and larvae of *Deleatidium* (Ephemeroptera) and *Olinga* (Trichoptera). Total abundance and biomass of macroinvertebrates did not differ between streams with and without trout, but were significantly higher at grassland sites than forested sites. However, taxon richness and species composition differed substantially between trout and no-trout sites, irrespective of whether streams were located in forest or not. Trout streams typically contained more taxa, had low biomass of predatory invertebrates and large shredders, but a high proportion of consumers with cases or shells. The standing stock of CPOM was higher at forested sites, but there was less FPOM and more algae at sites with trout, regardless of the presence or absence of forest cover. The stable carbon isotope range for biofilm on rocks was broad and encompassed the narrow CPOM and FPOM ranges. At trout sites, carbon isotope ratios of *Deleatidium*, the most abundant invertebrate primary consumer, were closely related to biofilm values, but no

relationship was found at no-trout sites where algal biomass was much lower. These results support a role for both bottom-up and top-down processes in controlling the structure of the stream communities studied, but indicate that predatory fish and forest cover had largely independent effects.

**Keywords** Stable isotopes · New Zealand · Detritus processing · Trophic cascade · Invertebrates

### Introduction

Understanding the relative importance of predators and resource supply on food webs is an important issue in community ecology (e.g., Hunter and Price 1992; Power 1992). Many theoretical and empirical studies of closed systems suggest that both resource availability (bottom-up) and predation (top-down) affect the dynamics of communities (e.g., Oksanen et al. 1981; Polis and Winemiller 1996; McQueen et al. 1989). Most models of food chains have been developed for closed systems, but many systems are open to immigration and emigration of organisms, which can significantly affect predator impact (e.g., Cooper et al. 1990). Few population models have investigated the simultaneous effects of predators and resource supply on the dynamics of open systems (Wootton and Power 1993; Nisbet et al. 1997; Diehl et al. 2000). In contrast to traditional food-chain theory, some models of open systems predict that densities at all trophic levels will increase with enrichment (Nisbet et al. 1997). This is because immigration into a system is independent of the systems internal state, whereas emigration and behaviour of organisms in open systems may be influenced by predator presence as well as resource supply (Forrester et al. 1999; Diehl et al. 2000).

Theoretical models of trophic and behavioural dynamics of open systems usually assume time scales and spatial scales typically employed in short-term field experiments. Since feedback between predator and prey populations occurs, short term responses may be different from those

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observed when predators have time to respond numerically to changes in prey density (e.g. Holt and Lawton 1994). Moreover, the influence of prey movements on prey densities decreases with increasing spatial scale and we would expect predator-induced mortality to be more important at larger scales (Englund 1997). At larger scales, prey populations are in effect closed systems, and although experimental and theoretical studies of open systems have provided mechanistic explanations for many patterns at local scales, we still know little about the effects of predation on prey populations in open systems (Englund 1997; Wooster et al. 1997). In this work we examined whether patterns of invertebrates in natural streams could best be predicted by traditional food chain theory where the presence of a top predator would significantly affect lower trophic levels through direct and indirect means (e.g. Wootton and Power 1993), or whether the presence of canopy cover and associated variations in algal biomass and detritus inputs would be more important (e.g. Richardson 1991; Hill et al. 1995; Wallace et al. 1997).

Fish are among the most important predators in streams and potentially consume a very large proportion of invertebrate production (e.g., Huryn 1996, 1998). Nevertheless, the impact of predatory fish on invertebrate abundance is highly variable (Cooper et al. 1990; Allan 1995; Wooster et al. 1997). In some cases predatory fish have substantial impacts on communities through direct and indirect trophic effects, thereby supporting traditional food chain models (Bowly and Roff 1986; Power 1990; Wootton and Power 1993). In other locations predatory fish can have comparatively little influence on stream community structure (see reviews by Allan 1983; Thorp 1986; Dahl and Greenberg 1996; Wooster et al. 1997).

Factors such as omnivory, excretion by consumers, and prey vulnerability all influence the relative importance of resource availability and predation in structuring closed communities (e.g. Hansson et al. 1998). Other factors such as the availability and quality of alternative food sources for predators and prey, and risks of predation-associated feeding may also influence the relative strengths of top-down and bottom-up forces. Models of closed systems suggest that predator-resistant species may benefit from the presence of predators, particularly in more productive habitats (Holt et al. 1994; Leibold 1996). It has also been shown that open stream systems contain consumers that are "vulnerable" (e.g., mayflies) and "less vulnerable" (consumers with cases or shells) to top predators and that "less vulnerable species" tend not to respond as strongly to predators (Kohler and McPeck 1989; Power 1992; Kuhara et al. 1999). Experiments and theoretical models involving drift-feeding fish have shown that changes in the behaviour of mayflies induced by a predator may affect algal biomass, indirectly (e.g., Flecker and Townsend 1994; McIntosh and Townsend 1996; Diehl et al. 2000). The species composition of a prey community therefore may significantly affect the impact of predators on lower trophic levels. If "less vulnerable species" are abundant they may inhibit the

development of a predator-induced trophic cascade (e.g., Power 1992; Brönmark and Weisner 1996). A behavioural response by one group of consumers may also affect energy flow and resources available to other consumers in the food web (Werner and Anholt 1996; Peacor and Werner 2000). Thus, if vulnerable species are abundant, one might expect heavy predator impacts (through direct consumptive effects and indirectly through effects on prey behaviour), whereas if predator-resistant species are abundant, consumers might be expected to be resource limited (e.g., Osenberg and Mittelbach 1996).

The resource base for many food webs is derived directly from primary producers, but most food webs, notably those of streams, are also subsidised by allochthonous inputs (Polis and Strong 1996; Jefferies 2000; Murakami and Nakano 2002; Sabo and Power 2002). Inputs of terrestrial plant matter to open systems can have complex effects on the interactions between prey and predators. Nisbet et al. (1997) predicted that the abundance at all trophic levels would increase with inputs of detritus because of low consumer emigration rates. Indeed, patterns and responses of stream invertebrate populations in natural streams have supported this prediction (Richardson 1991; Wallace et al. 1997). Inputs of terrestrial invertebrates derived from surrounding forest may also reduce the impact of drift-feeding fish on the abundance of benthic prey (Dahl and Greenberg 1996; Nakano et al. 1999). In the long term, however, large inputs of allochthonous subsidies may sustain consumers at such high levels that focal prey may be reduced (e.g. Holt and Lawton 1994). The presence of riparian forest provides a source of allochthonous inputs to streams, but its shading effect may simultaneously limit primary production and therefore food sources for herbivores and their subsequent abundance and growth (Rounick et al. 1982; Wallace and Gurtz 1986; Hill et al. 1995; Friberg et al. 1997).

Our research was conducted in multiple streams that exhibited little variation in abiotic variables, but differed with respect to the presence of brown trout (*Salmo trutta*) and forest cover. Three main hypotheses were tested. We suspected the presence of forest cover and the subsequent reduction in algal biomass would be offset by an allochthonous subsidy from forest detritus resulting in little difference in total invertebrate abundance in forested and grassland streams, but substantial change in primary consumer composition. Predatory trout were expected to influence the abundance of organisms at lower trophic levels because of the presence of "vulnerable consumers" like mayflies. However, we predicted that the utilisation of detritus by "vulnerable consumers" in forested streams would decrease the potential for trait-mediated and/or density mediated indirect effects of predatory trout in forested streams.

## Materials and methods

The study was conducted at 16 sites (Table 1) on 11 tributaries of the upper Waimakariri River, on the eastern slopes of the Southern Alps in Canterbury, New Zealand. Eight of the study sites were located in patches of *Nothofagus* (evergreen southern beech) forest (hereafter forested sites) and eight sites were located in open tussock grassland (hereafter open sites). Six of the grassland sites were on streams with forested headwaters. Eight sites were known to contain trout (e.g., McIntosh 2000b), and eight sites were either fishless or contained only small native fish because the passage of trout was prevented by waterfalls or culverts. Thus, the categories of streams used in this study were forest with and without trout, and grassland with and without trout. Each category was replicated four times.

All stream faunas were dominated numerically by the mayfly *Deleatidium*, a grazer that feeds on algae and small detritus particles (Collier and Winterbourn 1990). Experimental studies have shown that it reduces the time spent foraging on the tops of stones during daytime in trout streams, although trout do not necessarily affect its density (McIntosh and Townsend 1995, 1996). All streams also contained the cased caddisfly *Olinga*, which feeds on biofilm growing on the tops of stones and is also a shredder (Lester et al. 1994; Winterbourn 2000). In contrast to mayflies, cased caddisflies occur less frequently in trout stomachs in New Zealand streams (Glova et al. 1992; McIntosh 2000a) and are often found on the tops of rocks during daytime in trout streams (authors' unpublished data).

Biological and physico-chemical characteristics of the study sites were investigated between 29 November and 14 December 2000. Temperature was recorded every 15 min between 29 November and 14 December with Onset data-loggers, and one measurement was taken of current velocity, average depth, width, substratum size and bed stability [Pfankuch bottom score: a subjective index of stream bed stability (Death and Winterbourn 1994)] as described in McIntosh (2000b). Altitude was obtained from topographical maps, and canopy cover was estimated by determining the proportion of the stream in a 30 m reach covered by beech canopy. A water sample was taken at each site for analysis of pH, conductivity, soluble inorganic nitrogen (SIN) and soluble reactive phosphorus (SRP). SIN and SRP were analysed by Environment Canterbury on an autoanalyser according to the APHA method (20th edn).

All sites were electrofished to determine whether fish were present (McIntosh 2000b). Reaches (20–35 m) were delineated with stop nets (5 mm mesh) and electrofished with three downstream runs. Captured fish were anaesthetised, identified to species, measured to the nearest millimetre (fork length), weighed to the nearest milligram, and released. Fish densities were calculated using the maximum likelihood equations for three-pass depletion sampling (Cowx 1983). This method was used at all eight sites containing trout and at site 2 (containing *Galaxias vulgaris*), but not at a single site where a longfin eel (*Anguilla dieffenbachii*) was captured during the first run only. Eel density at this site was estimated from the absolute number of fish captured.

Invertebrates were collected from riffles with a Surber sampler (5×0.0625 m<sup>2</sup> samples per site, 250 µm mesh) and preserved in 80% ethanol. After enumeration and identification (mostly to genus or family using the keys in Winterbourn et al. 2000), invertebrates were dried (genera from the same family grouped together) for 24 h at 65°C, weighed to the nearest 0.1 mg, ashed in a muffle furnace at 450°C for 1 h and reweighed to enable calculation of ash-free dry mass.

Algal biomass at each site was estimated by collecting periphyton samples from five unglazed paving stones (11.5×11.5×3.5 cm) that had been placed in multiple riffles at each site 6 weeks, previously. A 13.8 cm<sup>2</sup> circle of periphyton was removed with a toothbrush from the top surface of each paving stone. The algal sample was transferred to a glass fibre filter (Whatman GF/C), stored on dry ice and frozen within 8 h. After thawing, chlorophyll *a* content was measured spectrophotometrically using 95% ethanol as the solvent (Friberg et al. 1997).

**Table 1** Locations and physico-chemical characteristics of study sites. Sites 9–16 contain trout

Site	Altitude (m)	Current velocity (m s <sup>-1</sup> )	Mean depth (cm)	Mean width (m)	Pfankuch bottom score	Canopy cover (%)	Median substrate size (cm)	Mean temperature (°C)	Conductivity at 25° C (µS cm <sup>-1</sup> )	pH	SIN (mg l <sup>-1</sup> )	SRP (mg l <sup>-1</sup> )
1. Middle Bush Stream (lower)	600	0.38	11	0.7	24	0	6	8.8	109	7.9	0.07	0.014
2. Ski Field Stream <sup>a</sup>	900	0.43	11	1.8	24	0	6	8.7	50	7.0	0.07	0.007
3. Fan Stream	550	0.41	8	1.3	31	0	6	8.8	138	7.1	0.11	0.009
4. Mt. White Hut Stream <sup>a</sup>	605	0.50	15	2.0	34	0	10	10.3	73	7.2	0.08	0.007
5. Middle Bush Stream (upper)	640	0.41	8	1.3	30	85	6	7.8	103	7.5	0.07	0.024
6. Poverty Stream	650	0.43	10	1.9	30	80	5	8.0	81	7.5	0.21	0.029
7. Camp Stream	1000	0.47	16	2.6	29	70	6	6.2	35	7.1	0.06	0.007
8. Manson Creek (upper)	780	0.74	19	3.2	31	80	8	6.5	37	6.9	0.09	0.008
9. Pylon Gully <sup>a</sup> (lower)	700	0.57	17	1.5	30	0	8	8.2	95	6.7	0.07	0.009
10. Binsler Saddle (lower)	550	0.50	12	1.9	42	0	10	8.9	81	6.7	0.06	0.004
11. Manson Creek (lower)	680	0.98	17	2.3	32	0	8	7.9	38	7.2	0.07	0.009
12. Ray Ban Stream <sup>a</sup>	775	1.25	18	1.8	23	0	7	8.4	56	7.2	0.15	0.007
13. Pylon Gully <sup>a</sup> (upper)	740	0.52	18	1.9	29	90	8	8.2	95	7.0	0.07	0.007
14. Binsler Saddle (upper)	600	0.66	18	2.0	31	80	9	8.2	58	6.7	0.08	0.006
15. Manson Creek (middle)	750	0.86	18	1.8	31	65	11	7.4	38	6.9	0.07	0.008
16. Peacock Stream <sup>a</sup>	550	0.46	11	1.7	19	80	8	8.5	64	7.0	0.07	0.007

<sup>a</sup> Unofficial name

Coarse and fine detritus (coarse particulate organic matter, CPOM, and fine particulate organic matter, FPOM, respectively) were collected from riffles with a small Surber sampler ( $5 \times 0.0225 \text{ m}^2$  samples per site;  $64 \mu\text{m}$  mesh) and frozen. After thawing, invertebrates, macrophytes and bryophyte fragments, twigs and pieces of wood were removed. The CPOM fraction in New Zealand beech forest streams tends to be dominated by *Nothofagus* leaves (Friberg et al. 1997), which predominated at all our sites except open sites 2 and 12 where beech forest was absent upstream and CPOM biomass was very low and predominantly grass and macrophytes. Leaves were dried for 24 h at  $65^\circ\text{C}$ , weighed to the nearest 0.1 mg, ashed in a muffle furnace at  $450^\circ\text{C}$  for 1 h and reweighed to enable calculation of ash-free dry mass. FPOM ingested by non-shredding detritivores in New Zealand streams is typically less than  $<500 \mu\text{m}$  (Winterbourn 2000), and the ash-free dry mass of this fraction was also determined.

Food (carbon) resources used by two dominant herbivore-detritivores in our streams were assessed using stable carbon isotope analysis.  $^{13}\text{C}/^{12}\text{C}$  ratios were obtained for CPOM (beech leaves at all sites except sites 2 and 12 where grass and macrophytes, respectively, were sampled), FPOM, algal dominated biofilm from rocks, and larvae of *Deleatidium* (Ephemeroptera) and *Olinga* (Trichoptera). *Deleatidium* dominated grazer biomass in our survey streams ( $51 \pm 3\%$  SE of total grazer biomass) and *Olinga* was the most widespread cased consumer ( $8.5 \pm 2\%$  SE). Samples for stable isotope analysis were collected from the 16 stream sites during the December survey. Coarse detritus was dead, but not strongly decomposed leaf material, whereas fine detritus was organic matter that had passed through a 0.5-mm mesh sieve and included no invertebrates.

Samples for isotope analyses were frozen in the field and later dried at  $65^\circ\text{C}$ . Before drying, guts were dissected from 20 medium-large larvae of each insect species from each site to eliminate potentially contaminating food material. Each lot of 20 larvae was combined as a single sample. All samples were homogenised to a fine ( $<0.2 \text{ mm}$ ) powder prior to analysis with a Europa Scientific 20/20 isotope analyser spectrophotometer (University of Waikato Stable Isotope Unit). Isotope ratios ( $^{13}\text{C}/^{12}\text{C}$ ) are reported in the standard delta ( $\delta$ ) notation (Peterson and Fry 1987). Analytical precision of measurements was  $\pm 0.5\%$  for  $\delta^{13}\text{C}$ .

We tested the general effect of canopy cover (open or forest) and predation regime (trout or no trout) on response variables using multiple two-way ANOVAs. However, the biomass of shredders was not normally distributed. Therefore we first tested the general effect of canopy cover using a Mann-Whitney *U*-test and since shredders were only present at two open sites we compared the biomass of shredders at the forested sites with and without trout using a *t*-test. Species composition of invertebrate assemblages at the 16 sites was compared using abundance data for the 58 identified taxa by means of cluster analysis (PC-ORD, version 4, McCune and Mefford 1999) using the Sorensen (Bray-Curtis) distance measure and group average linkage.

To test whether any of the 11 measured physico-chemical variables differed between sites with and without trout, variables were subjected to principal component analysis (PCA), using the correlation matrix to extract factors that described the sites in terms of a limited number of independent variables. We retained axes having eigenvalues greater than 1 (Dillon and Goldstein 1984). To test for differences in physico-chemical characteristics between stream categories we derived the principal component scores for each site first. Differences in scores between stream categories were then compared using a two-way MANOVA with the factor scores as independent variables. To normalise data in all the above analyses, percentages were arcsin transformed; other data were log<sub>e</sub> transformed.

## Results

Eight sites contained brown trout and eight sites did not. The density of trout at the former ranged from 0.2 to 10.1

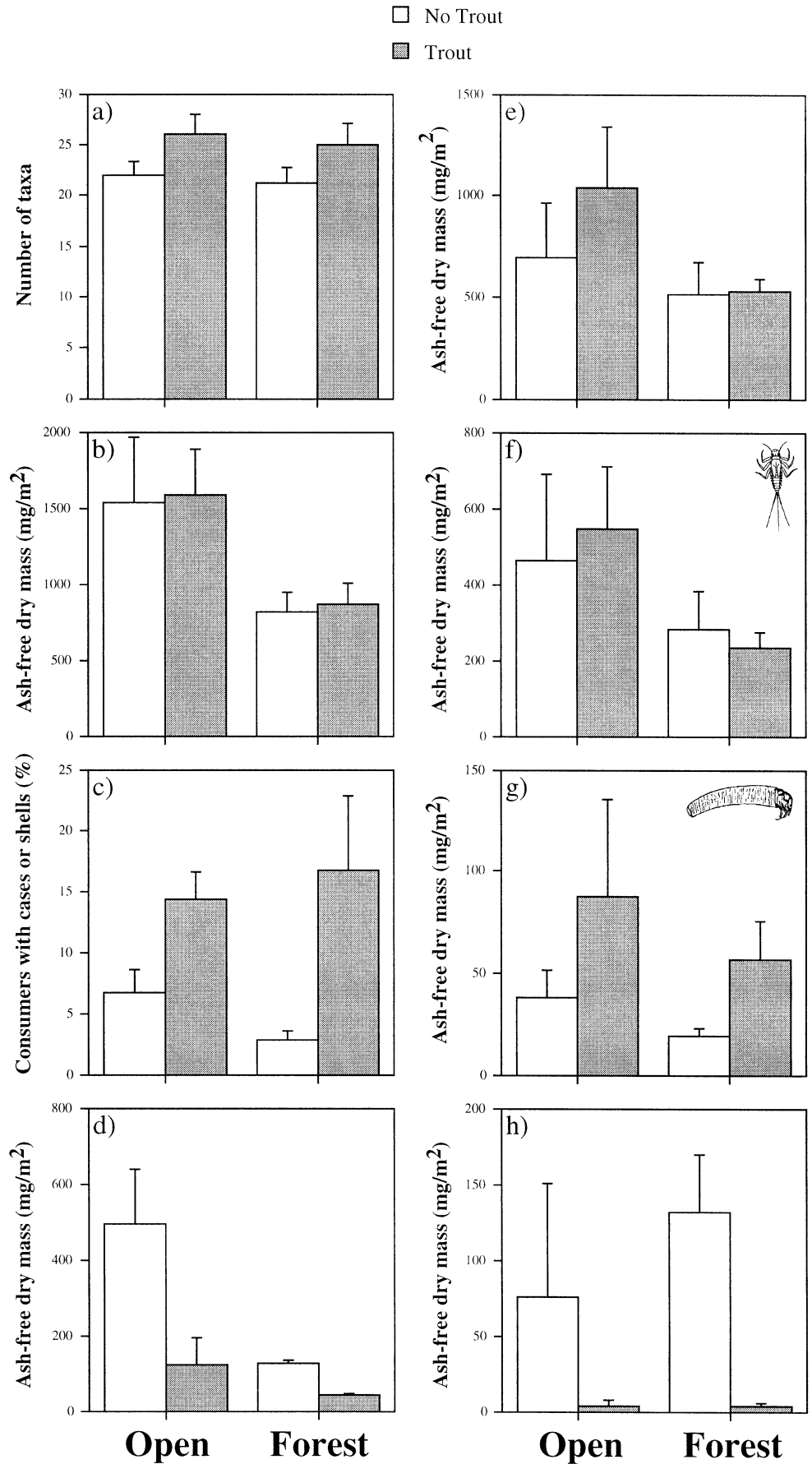
with an average of 4.7 trout per  $10 \text{ m}^2$  ( $\pm 0.1 \text{ SE}$ ,  $n=8$ ). The density and biomass of trout at open and forested sites did not differ significantly (*t*-test,  $P>0.22$ ,  $n=4$ , in both cases). All sites contained trout larger than 15 cm (fork length). Length of trout varied between 6.8 and 23.5 cm with an average of 9.5 cm ( $\pm 1.4 \text{ SE}$ ,  $n=8$ ). Three of the trout sites also contained longfin eels (*Anguilla dieffenbachii*) or the benthic galaxiid, *Galaxias brevipinnis*. Of the sites without trout, six were fishless. Site 2 contained another benthic galaxiid *G. vulgaris* (1.8 per  $10 \text{ m}^2$ ) and a longfin eel was captured at site 3 (0.3 per  $10 \text{ m}^2$ ).

All sites had circum-neutral pH, low nutrient concentrations and low Pfrank bottom scores, indicating that their beds were not prone to severe disturbance (Table 1). Four PCA axes with eigenvalues greater than one, collectively explained 81.5% of the variation in 11 physico-chemical variables from each study site. A two-way MANOVA using the four PCA factor scores as dependent variables indicated no significant difference in measured physico-chemical characteristics between streams with and without canopy ( $F_{4,9}=0.48$ ,  $P>0.75$ ), or with and without trout ( $F_{4,9}=1.48$ ,  $P>0.28$ ) and the interaction was not significant ( $F_{4,9}=0.83$ ,  $P>0.53$ ).

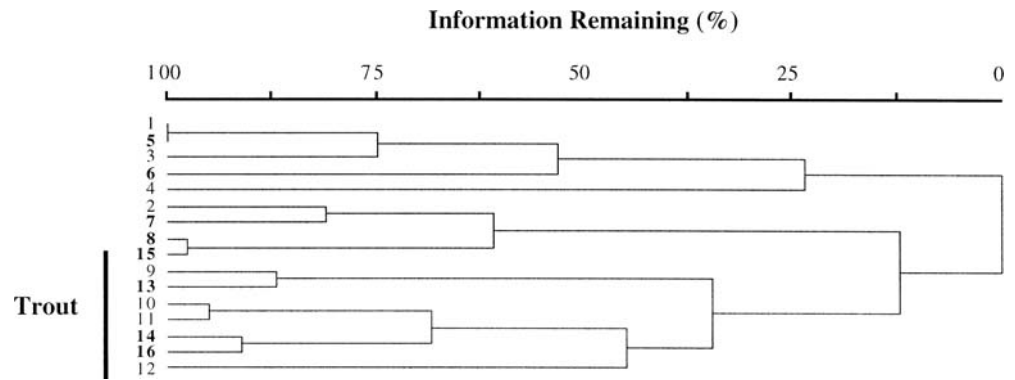
Forested sites had lower total biomass of invertebrates than open sites, but trout had no significant effect on total invertebrate biomass (Table 2, Fig. 1b). Patterns of total invertebrate abundance were similar to biomass patterns. Invertebrates were more abundant at the open sites ( $1596 \pm 171 \text{ SE}$ ,  $n=8$ ) compared to the forested sites ( $2878 \pm 442 \text{ SE}$ ,  $n=8$ , two-way ANOVA canopy effect:  $F_{1,12}=4.97$ ,  $P=0.0457$ ), and invertebrate density was not altered in the presence of trout (trout effect:  $F_{1,12}=1.98$ ,  $P>0.18$ ). Unsurprisingly, forested sites had significantly higher biomass of shredders (dominated by a large caddisfly *Zelandopsycha ingens* and a stonefly *Austroperla cyrene*) than open sites (Mann-Whitney  $U=12$ ,  $df=1$ ,  $P=0.031$ , Appendix). Shredders were found at only two of the eight open sites (1 and 9), both with forested headwaters upstream.

Although trout did not affect the total biomass or numbers of invertebrates, community composition and taxonomic richness differed between trout- and no-trout sites. Significantly more taxa were recorded from sites containing trout (Table 2, Fig. 1a) and cluster analysis separated almost all trout from no-trout sites, indicating that the invertebrate communities at trout-sites were more similar to each other than to no-trout communities (Fig. 2). In terms of biomass, trout sites typically had a higher percentage of consumers with cases or shells ( $15.6 \pm 3.0\% \text{ SE}$ ,  $n=8$ ) than no-trout sites ( $4.8 \pm 1.2\% \text{ SE}$ ,  $n=8$ , Table 2, Fig. 1c). Dominant predatory invertebrates at all sites were *Neppia* (Turbellaria), *Stenoperla* (Plecoptera) and *Archichauliodes* (Megaloptera). Grazers were predominantly mayflies (*Deleatidium*) and to a lesser extent the cased caddisfly *Olinga* and the snail *Potamopyrgus* (Appendix). Trout sites had a low biomass of predatory invertebrates (Fig. 1d), whereas the total biomass of grazers did not differ significantly between

**Fig. 1** Mean number of taxa (a), biomass of all taxa (b), percentage of consumers with cases or shells (c), biomass of predators (d), biomass of all grazers (e), biomass of nymphs of the mayfly *Deleatidium* and (f), the cased caddisfly *Olinga* (g) and biomass of shredders (h) of macroinvertebrates collected in stream riffles at open and forested sites and at sites with and without trout. Vertical bars denote 1 SE. Note the different scales on the y-axes



**Fig. 2** Cluster analysis of macroinvertebrate communities (using density data for 58 taxa collected in riffles listed in Appendix). No-trout sites 1–8, trout 9–16. Study sites in bold face are forested sites and numbers correspond to those in Table 1



**Table 2** Results of two-way ANOVAs, for effects of canopy cover (open or forest) and predation regime (no trout or trout) on taxon richness, total biomass of invertebrates, percentage of consumers with cases or shells, biomass of predatory invertebrates, total biomass of invertebrate grazers, biomass of *Deleatidium* and biomass of *Olinga*

Source	df	MS	F	P
<b>Taxon richness</b>				
Canopy	1	0.0058	0.2867	0.6021
Trout	1	0.1050	5.1590	0.0423
Canopy × Trout	1	0.0001	0.0004	0.9851
Error	12	0.0204		
<b>Total biomass</b>				
Canopy	1	1.2555	6.3204	0.0272
Trout	1	0.0364	0.1830	0.6764
Canopy × Trout	1	0.0007	0.0035	0.9538
Error	12	0.1986		
<b>Consumers with cases or shells</b>				
Canopy	1	0.0050	0.5223	0.4837
Trout	1	0.1375	14.2798	0.0026
Canopy × Trout	1	0.0112	1.1597	0.3027
Error	12	0.0096		
<b>Predatory invertebrates</b>				
Canopy	1	2.2787	2.8786	0.1155
Trout	1	9.8094	12.3916	0.0042
Canopy × Trout	1	0.6559	0.8285	0.3806
Error	12	0.7916		
<b>Total grazers</b>				
Canopy	1	0.9588	1.8561	0.1981
Trout	1	0.6858	1.3276	0.2717
Canopy × Trout	1	0.0402	0.0778	0.7850
Error	12	0.5165		
<b><i>Deleatidium</i></b>				
Canopy	1	1.6264	2.0966	0.1732
Trout	1	0.3269	0.4214	0.8643
Canopy × Trout	1	0.0502	0.0647	0.8035
Error	12	0.7757		
<b><i>Olinga</i></b>				
Canopy	1	0.6402	1.2568	0.2842
Trout	1	2.6731	5.2472	0.0409
Canopy × Trout	1	0.2220	0.4357	0.5217
Error	12	0.5094		

sites with and without trout (Table 2, Fig. 1e). Biomass of the dominant mayfly, *Deleatidium*, did not differ between sites (Fig. 1f), but trout sites had significantly higher

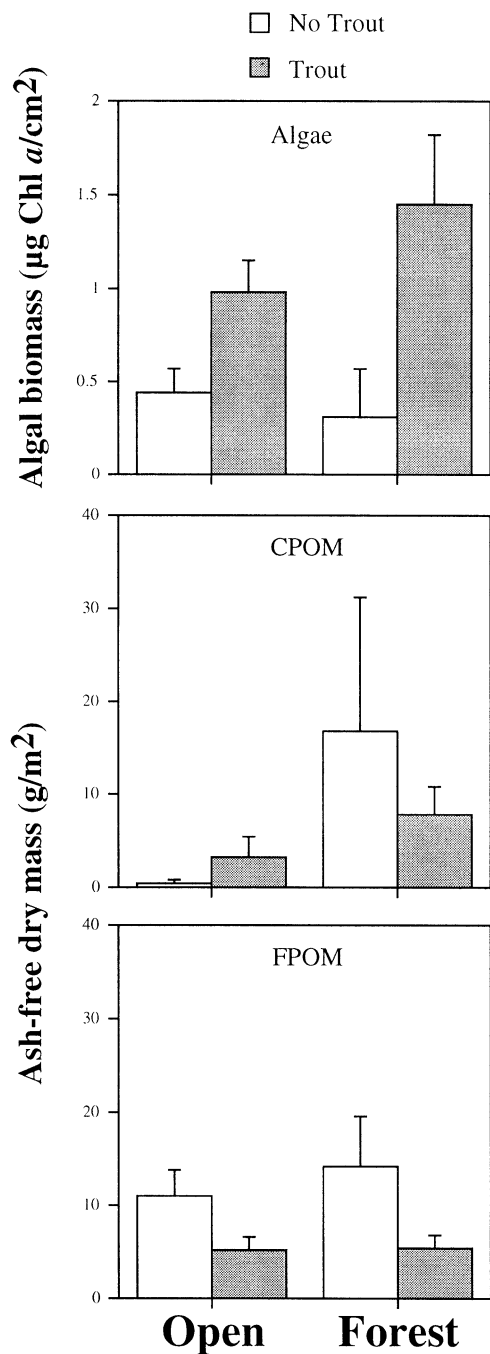
**Table 3** Univariate two-way ANOVAs, testing for differences in algal biomass, CPOM (as beech leaves) and FPOM in streams with and without canopy cover and with and without trout

Source	df	MS	F	P
<b>Algal biomass</b>				
Canopy	1	0.1265	0.2127	0.6529
Trout	1	9.0218	15.1673	0.0021
Canopy × Trout	1	0.1343	0.2258	0.6432
Error	12	0.5948		
<b>CPOM</b>				
Canopy	1	7.0902	7.8401	0.0160
Trout	1	0.6594	0.7291	0.4099
Canopy × Trout	1	0.4744	0.5245	0.4828
Error	12	0.9044		
<b>FPOM</b>				
Canopy	1	0.0352	0.0758	0.7878
Trout	1	2.2646	4.8776	0.0474
Canopy × Trout	1	0.6559	0.000	0.9954
Error	12	0.4643		

biomass of the cased caddisfly *Olinga* compared to sites without trout (Table 2, Fig. 1g). When only forested streams were considered, trout sites were found to contain a significantly lower biomass of shredders (Fig. 1h) than no-trout sites [trout and no-trout means ( $\pm$  SE) were  $131.4 \text{ mg/m}^2 \pm 37.9$  and  $3.84 \pm 1.64$ , respectively;  $t=7.43$ ,  $df=6$ ,  $P=0.0003$ ].

Algal biomass was highest at sites with trout, a pattern that persisted even at forested sites, as indicated by the non-significant trout by canopy interaction (Table 3, Fig. 3). Biomass of beech leaves (CPOM) was significantly greater at forested sites than open sites (Fig. 3), but did not differ between trout sites and no-trout sites (Table 3). In contrast, biomass of FPOM did not differ between open and forested sites, but was significantly lower at sites with trout than sites without trout (Table 3, Fig. 3).

Because the carbon isotope ratios of biofilm and terrestrial detritus at many of our sites were overlapping or fell outside the limits of the insects isotope signatures (even when adjusted for trophic fractionation of 0.8‰) we were unable to use mixing models to estimate their relative contributions to diet. Instead of using mixing models the  $\delta^{13}\text{C}$  values for *Deleatidium* and *Olinga* were



**Fig. 3** Mean algal biomass (as chlorophyll *a*) on paving stones after 6 weeks (top) and biomass of coarse organic matter (beech leaves, middle) and fine particulate organic matter (<500 µm, bottom) in stream riffles at open and forested sites and at sites with and without trout. Vertical bars denote 1 SE

related to values of biofilm and CPOM, graphically and by regression analysis.  $\delta^{13}\text{C}$  varied little among samples of CPOM and FPOM in the full sample set (ranges 4.6 and 3.7‰, and by only 1.6 and 1.4‰ when the two open sites 2 and 12, with non-beech detritus were excluded). In contrast, the ranges of  $\delta^{13}\text{C}$  values for biofilm (16.8‰), *Deleatidium* (11.8‰) and *Olinga* (15.6‰), were much

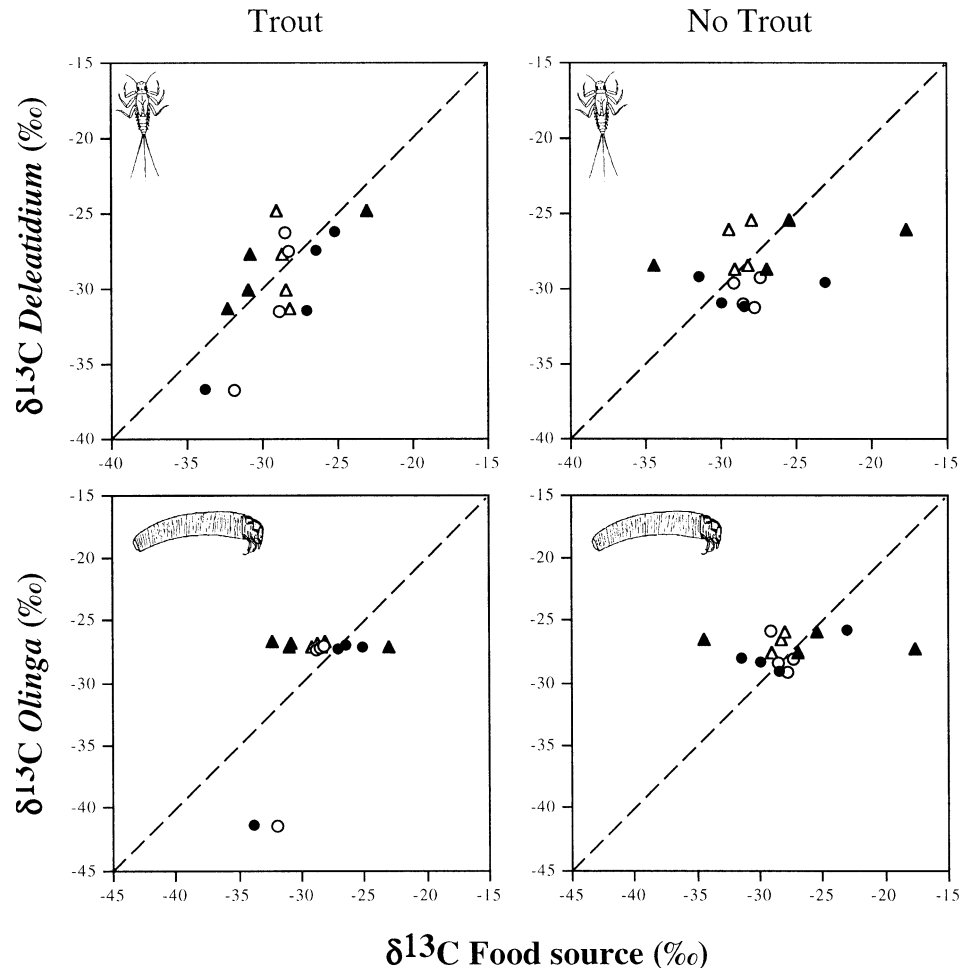
broader and encompassed the narrow detrital range. No significant differences in stable carbon isotope values of potential foods and insect consumers were found among stream categories (two-way ANOVAs,  $P > 0.05$  in all cases). However, in all streams, greater variance around terrestrial CPOM values was shown by *Deleatidium* than *Olinga* (Fig. 4). The importance of biofilm as a carbon source for *Deleatidium*, especially in the trout streams, was supported by the significant positive relationship between  $\delta^{13}\text{C}$  of biofilm and  $\delta^{13}\text{C}$  of *Deleatidium* in those streams ( $P = 0.017$ ,  $r^2 = 0.64$ ,  $n = 8$ , Fig. 4) but not in no-trout streams ( $P > 0.22$ ,  $r^2 < 0.3$ , Fig. 4).

## Discussion

We found that the structure of invertebrate communities differed between New Zealand mountain streams with and without trout, but except for CPOM, anticipated differences in algal and FPOM standing crops associated with forest canopy cover were not found. Forest cover did not reduce the standing stocks of algal resources, consistently, or alter the composition of invertebrate communities. Instead, predatory trout appeared to regulate the standing crop of both algae and detrital resources and affected the composition of macroinvertebrate communities. In contrast, macroinvertebrates were generally more abundant at open sites than forested sites, regardless of the presence or absence of trout. Collectively, these patterns imply that predatory fish and variations in resource supply associated with the presence or absence of a forest canopy had significant but largely independent effects on community structure.

The consistently lower abundance of invertebrates at forested sites compared to grassland sites implies that the presence of a forest canopy constrained the size of the benthic community. It seems likely that this was brought about by differing levels of resources at the two kinds of sites. Canopy cover of our forested study streams ranged from 65% to 90% and could be expected to reduce the availability of light energy to epilithic algae (Rounick et al. 1982; Wallace and Gurtz 1986; Hill et al. 1995; Friberg et al. 1997). However, algal biomass in spring-early summer did not reflect expected differences in light energy in open and forested streams, but instead differences in algal biomass were more likely associated with differences in grazing pressure caused indirectly by trout (discussed below). We did not measure primary production of biofilms directly, but since primary production is a product of both algal standing crop and the availability of light energy (Lamberti and Resh 1983), it is likely that biofilms in shaded locations were less productive per unit biomass than those at open locations (i.e., they had lower P:B ratios). Acclimation to low light levels by periphyton in forested streams may result in increased photosynthetic efficiency (up to twice that of periphyton at open sites), but daily photosynthesis per unit biomass is much higher at open sites (summarised in Hill 1996). Because light-enhanced primary production may contribute to an

**Fig. 4** Stable isotope values ( $\delta^{13}\text{C}$ ) for the mayfly *Deleatidium* (top) and the caddisfly *Olinga* (bottom) in relation to two potential food sources, biofilm from rocks (solid symbols) and coarse particulate organic matter (open symbols) from stream riffles with trout (left) and without trout (right). Triangles are samples from forested sites and circles are samples from open sites. Identical values on the  $x$  and  $y$  axes would lie on the dashed diagonal line (assuming no fractionation). The relationship between isotope values of biofilm and *Deleatidium* in trout streams is significant ( $P=0.017$ ,  $r^2=0.64$ ,  $n=8$ )



increase in grazer growth or density in streams (Hill et al. 1995), lower productivity of biofilms at forested locations may have contributed to the overall lower invertebrate biomass at those sites. Moreover, models of open systems dominated by mobile consumers (e.g., *Deleatidium*) that decrease emigration as resource abundance increases predict that abundance will increase at all trophic levels with an increase in resource availability (Nisbet et al. 1997). In our case, difference in the productivity of biofilms is unlikely to be the only factor involved in determining consumer abundance because substantial differences in primary production at open sites would be required to overshadow the large differences in standing crop associated with trout. Further work is required to determine the exact mechanism causing the patterns observed in total invertebrate biomass among open and forested streams, but the consistency of the pattern is remarkable considering the changes in composition of invertebrate communities associated with trout.

Several studies of interactions between predatory fish and stream invertebrates indicate that visually hunting fish such as trout are selective consumers that prefer large active prey (e.g., predatory invertebrates and mayflies), and feed less on small prey, or prey protected by cases or shells (Cooper 1988; Power 1990, 1992; Bechara et al.

1992; Dahl 1998; McIntosh 2000a). Although native, predatory fish were present at a few of our no-trout sites they are nocturnal benthic-foragers, and likely to present much lower predation risk to invertebrates than diurnal drift-feeders such as trout (see review by McIntosh 2000a). In contrast, the selection pressure associated with introduced trout appears to have a large influence on the composition of prey communities of streams. Our results indicate that the proportion and abundance of consumers potentially less vulnerable to trout (i.e., consumers with mineral cases like the conoesucid caddisflies *Pycnocentroides*, *Pycnocentria*, *Bareoptera* and *Olinga*, Appendix), was higher in trout streams. The greater relative biomass of cased consumers in our trout streams and the absolute biomass of *Olinga* indicates cased consumers may have an advantage over less protected taxa (e.g., mayflies) when trout are present. This could be due to several factors acting in concert such as increased biomass of algal sources, lower predation pressure from trout, and also from predatory invertebrates, which were less abundant where trout were present. Theoretical models predict that defended grazers may benefit from the presence of predators in more productive environments (Holt et al. 1994; Leibold 1996), consistent with our findings.

Taxa with particularly low population biomass in our trout streams were predatory invertebrates and large shredders. Their small numbers in trout streams compared with no-trout streams may be associated with their high vulnerability to predatory trout because of their large size (e.g., Bowlby and Roff 1986). Moreover, the life-cycles of predatory invertebrates and shredders typically are longer than those of smaller primary consumers, e.g., *Deleatidium* and *Olinga* (Scarsbrook 2000), and their levels of production have been found to be comparatively low in some other upland New Zealand streams (Hurn 1998). Because studies of secondary production indicate that most invertebrate production in New Zealand trout streams is likely to be consumed (Hurn 1996, 1998) we hypothesise that low production rate and low larval and adult dispersal, together with direct predation by trout, could explain the low biomass of predatory invertebrates and large shredders in our trout streams.

In contrast to the effect of trout on large predatory invertebrates and shredders, abundance of the dominant mayfly grazer, *Deleatidium*, did not differ between stream types. This mayfly is one of the most important foods of trout in New Zealand streams (McIntosh 2000a), so the lack of an effect is remarkable. *Deleatidium* is also a major food of predatory invertebrates (Winterbourn et al. 1984; Winterbourn 2000), so there is potential for trout to have a positive indirect effect on mayfly abundance by decreasing the abundance of predatory invertebrates. This has been demonstrated in other studies of large omnivorous invertebrate predators and their prey (reviewed in Diehl 1993). It is also possible that the same biomass of *Deleatidium* could be sustained in comparable streams with and without trout. In the absence of trout, *Deleatidium* could overexploit their algal resources and larval growth of mayflies may be low. In the presence of trout, grazing activity is likely to be reduced and algal biomass will increase. Mayfly larvae are then able to consume more algal food despite their foraging time being reduced and as a consequence production of *Deleatidium* may be higher than in streams without trout. Thus, even if individual foraging rates are reduced in the presence of predators, the combined effect of reduced foraging by an entire group of abundant prey species may free up resources and result in increased individual growth rates (Diehl et al. 2000; Peacor 2002).

Multiple factors, including substratum stability, irradiance, grazers and nutrients affect periphyton biomass in streams (Biggs 1996), but in the streams we studied, predatory trout appeared to have a major influence on algal standing crop. This was despite the total biomass of grazers, including that of the dominant mayfly grazer, *Deleatidium*, not differing between streams with and without trout, and a lack of significant differences among streams in measured nutrient levels and bed stability. Our field results support findings from previous theoretical and experimental work on mayflies, that changes in grazer behaviour (such as those that force *Deleatidium* from the substrate surface during the day when trout are

present) can result in increased epilithic algal biomass (McIntosh and Townsend 1996; Diehl et al. 2000).

We also found lower biomass of FPOM in trout streams than no-trout streams, but no effect of canopy cover on its abundance. Manipulations of detrital inputs to streams have indicated strong bottom-up control of shredders and their predators (Dobson et al. 1985; Wallace et al. 1997) but shredder biomass was substantially lower in our trout streams, indicating that top-down forces appear to influence shredder populations. The large shredding caddisfly, *Zelandopsycha ingens*, is common in retentive mountain beech forest streams in our study area where they can process significant amount of beech leaves and produce large amounts of FPOM (Winterbourn and Davis 1976). All our forested sites contained *Z. ingens* and a detailed study by McMurtrie (2000) showed that it is usually less abundant in trout streams than fishless streams, and that its foraging activity is restricted when trout are present. Thus, the lower biomass of FPOM in the trout streams in our survey could be associated with lower shredder abundance as found by Ruetz et al. (2002).

Even though biomass of *Deleatidium*, the most abundant primary consumer, did not differ in streams with and without trout, trout influenced their foraging. Thus, our stable isotope data indicate that *Deleatidium* at trout sites assimilated greater proportions of algal carbon than at no-trout sites, even though *Deleatidium* larvae in trout streams avoid the upper surfaces of stones during the day, resulting in lower individual algal consumption rates (McIntosh and Townsend 1995). Mayflies including *Deleatidium* grow better on algae than detritus (Gupta et al. 1993; Ledger and Winterbourn 2000), and it is likely that *Deleatidium* derives most of its energy from epilithic algae when they are abundant. In streams without trout, our data indicate that algal biomass was low and by inference, invertebrate grazing pressure was high. Biggs et al. (2000) also observed that grazing pressure was likely to be particularly high in New Zealand streams lacking trout. Therefore, many consumers including *Deleatidium* may have to rely more on allochthonous energy sources in no-trout streams. In contrast to *Deleatidium*, the stable isotope data indicated that at most sites *Olinga* had an isotope signature close to that of terrestrial leaves. *Olinga* is primarily a detritivore although it also ingests epilithic and filamentous algae (Quinn et al. 2000; Ledger et al. 2000). Quinn et al. (2000) found that larval growth was fastest when conditioned leaf material was a major component of the diet, consistent with the preference for allochthonous detritus indicated by our study.

Our results support a role for both habitat effects and top-down processes in controlling the structure of the stream communities in the upper Waimakariri catchment. In no-trout streams, primary consumer populations appeared to be affected simultaneously by bottom-up and top-down controls, with their abundance being at least partially limited by the rarity of algal resources (a bottom-up effect), and the scarcity of the algal resource being limited by their own grazing activities (a top-down effect). In contrast, top-down control of invertebrate

community composition, algal standing crop and by inference grazing, was observed in trout streams, although no reduction in total invertebrate biomass was found. These patterns are similar to those observed by Huryn (1998) in two adjacent southern New Zealand streams, one with and one without trout. The lack of strong top-down effects on invertebrate abundance is of particular note and likely to be related to the dominance of taxa such as *Deleatidium* that show strong antipredator responses to trout, but also the presence of relatively invulnerable species (e.g., conoesucid caddisflies). Theoretical and empirical work suggests that heterogeneity within trophic levels (i.e., the presence of invulnerable species) can lead to patterns of abundance and dynamics of food webs not predicted by traditional food chain theory (Holt et al. 1994; Leibold 1996). However, our finding of a strong indirect effect on algal standing crop despite no change in grazer numbers adds weight to the bulk of accumulating empirical and theoretical evidence that trait-mediated indirect effects (e.g., changes in grazing behaviour), can be just as important as density-mediated indirect effects (McIntosh and Townsend 1996; Peacor and Werner 1997; Schmitz et al. 1997; Diehl et al. 2000; Trussel et al. 2002).

The results of our study also partially support Hildrew's (1996) conceptual food web model of trout streams, whereby in relatively stable streams with limited

flow disturbance trout depress large, vulnerable invertebrates (e.g., many predatory species). However, the patterns of primary consumer biomass observed in our study streams provide equivocal support for the prediction of strong links between primary consumers (both detritivores and herbivores) and invertebrate predators (see Bowlby and Roff 1986 for another empirical example). Despite large differences in the composition of benthic invertebrate communities in the presence and absence of trout, total invertebrate biomass and abundance in trout- and no-trout streams reflected whether sites were forested or open. Thus, forested streams and open streams maintained contrasting levels of total invertebrate biomass, despite substantial differences in community composition associated with predatory fish. The maintenance of a fundamental ecosystem property (invertebrate biomass) in the face of biotic perturbation and species change appears to represent a good example of "ecosystem homeostasis" (Ernest and Brown 2001).

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## Appendix

### Abundance

Mean invertebrate abundance (individuals per m<sup>2</sup> ± 1 SE, *n*=4) of 58 aquatic taxa found at open and forested sites with and without trout (*P* predator, *G* grazer, *F* filter feeder, *S* shredder, *N* non-feeder of aquatic food sources).

Taxa	Functional Group	No trout		Trout	
		Open	Forest	Open	Forest
<b>Megaloptera</b>					
<i>Archichauliodes</i>	P	42±25	1±1	6±4	9±5
<b>Ephemeroptera</b>					
<i>Austroclima</i>	G	38±27	19±19	14±10	36±27
<i>Coloburiscus</i>	F	140±140	1±1	98±72	127±76
<i>Deleatidium</i>	G	1,107±264	646±177	1,358±261	650±77
<i>Neozephlebia</i>	G	0	1±1	0	1±1
<i>Nesameletus</i>	G	22±9	151±114	7.2±6.2	9±5
<i>Oniscigaster</i>	G	2±2	0	1±1	0
<b>Plecoptera</b>					
<i>Austroperla</i>	S	5±5	15±13	0	5±5
<i>Cristaperla</i>	G	1±1	0	0	1±1
<i>Halticoperla</i>	G	0	0	0	1±1
<i>Spaniocerca</i>	G	51±50	56±32	7±6	20±6
<i>Stenoperla</i>	P	3±3	22±7	10±7	8±5
<i>Taraperla</i>	G	0	6±6	0	0
<i>Zelandobius</i>	G	13±5	27±16	6±2	9±3
<i>Zelandoperla</i>	G	1±1	5±2	0	1±1
<b>Trichoptera</b>					
<i>Aoteapsyche</i>	F	10±7	1±1	50±26	17±7
<i>Beraeoptera</i>	G	15±10	0	385±136	113±60
<i>Costachorema</i>	P	24±20	2±2	10±2	0

Taxa	Functional Group	No trout		Trout	
		Open	Forest	Open	Forest
<i>Edpercivalia</i>	P	2±2	2±2	0	0
<i>Helicopsyche</i>	G	170±170	0	0	0
<i>Hudsonema</i>	G	1±1	0	0	0
<i>Hydrobiosella</i>	F	8±5	0	32±31	47±29
<i>Hydrobiosis</i>	P	3±3	11±6	8±5	8±3
<i>Hydrochorema</i>	P	1±1	0	2±1	4±2
<i>Neurochorema</i>	P	0	42±42	0	26±24
<i>Oeconesus</i>	S	2±2	0	0	1±1
<i>Olinga</i>	G	70±31	35±8	138±61	106±16
<i>Philorheithrus</i>	P	5±4	6±3	5±3	6±5
<i>Polyplectropus</i>	P	0	0	2±2	0
<i>Psilochorema</i>	P	3±3	0	7±5	5±4
<i>Pycnocentria</i>	G	0	1±1	45±43	0
<i>Pycnocentrodus</i>	G	0	1±1	26±13	46±28
<i>Triplectides</i>	S	0	0	2±2	0
<i>Zelandopsyche</i>	S	3±3	6±3	6±6	3±0
<i>Zelolessica</i>	G	1±1	0	43±21	17±7
Coleoptera					
Elmidae	G	1±1	44±41	40±21	238±67
Hydraenidae	G	3±1	5±2	6±5	6±3
Hydrophilidae	G	2±2	17±7	10±7	10±4
Ptilodactylidae	G	6±6	0	0	0
Scirtidae	G	96±72	10±6	2±2	1±1
Diptera					
<i>Aphrophila</i>	G	10±6	0	86±47	10±6
<i>Austrosimulium</i>	F	18±12	134±127	250±85	60±35
Chironomidae	G	172±93	34±5	377±295	73±16
Empididae	G	2±2	2±1	1±1	1±1
Eriopterini	G	2±1	2±2	3±2	4±2
Hexatomini	G	3±1	1±1	2±1	0
Muscidae	P	13±13	0	5±5	0
<i>Nothodixa</i>	G	0	1±1	0	0
Pelecorhynchidae	P	0	2±2	0	3±3
Tanyderidae	G	0	0	1±1	0
Mollusca					
<i>Potamopyrgus</i>	G	146±81	10±10	64±41	55±38
<i>Sphaerium</i>	F	0	0	1±1	0
Platyhelminthes					
<i>Neppia</i>	P	314±161	41±16	13±5	50±42
Nematoda	P	0	0	1±1	0
Nematomorpha	N	1±1	0	1	0
Annelida					
Oligochaeta	G	46±26	38±22	58±42	29±22
Amphipoda					
<i>Paraleptamphopus</i>	G	0	0	1±1	5±5
Acari	P	0	0	1±1	0

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