REPORT

Disturbance, resource supply, and food-web architecture in streams

Colin R. Townsend,[1] Ross M.
Thompson,[1] Angus R. McIntosh,[1,2]
Cathy Kilroy,[3] Eric Edwards,[1,4]
and Mike R. Scarsbrook[1,5]

[1]*Department of Zoology,
University of Otago, P.O. Box 56,
Dunedin, New Zealand. E-mail:
colin.townsend
@stonebow.otago.ac.nz*
[2]*Department of Zoology,
University of Canterbury,
Christchurch, New Zealand.*
[3]*National Institute of Water and
Atmospheric Research,
Christchurch, New Zealand.*
[4]*Department of Conservation,
Southland Conservancy, P.O.Box
783, Invercargill, New Zealand.*
[5]*National Institute of Water and
Atmospheric Research,
Hamilton, New Zealand.*

Abstract

We studied food webs comprising fish, macroinvertebrates, and algae (identified to species or morphospecies) in small streams using a consistent methodology at the same spatial and temporal scales. Our aim was to test *a priori* hypotheses derived from dynamic-demographic and energetics models concerning the effects of disturbance and resource availability on food-web attributes. The regime of bed disturbance affecting the organisms in the webs was measured in 10 streams. We also derived measures of the supply of resources for animals in the webs in terms of algal primary productivity and detritus standing crop. Both web size and number of links per species were significantly negatively related to mean intensity of bed disturbance. Mean chain length had a significant positive relationship with algal primary productivity but not disturbance. No food-web attribute was related to detritus standing crop.

Keywords

INTRODUCTION

Connectivity food webs provide a qualitative picture of who eats whom. They have been used as a basis for extracting statistics that describe regularities among communities and to test conclusions drawn from theoretical models about community structure (e.g. Pimm *et al.* 1991). However, generalizations drawn from meta-analyses of catalogues of published food webs have been strongly criticised because of the idiosyncratic and variable effort applied to the gathering of data (Lawton 1989; Hall & Raffaelli 1993; Polis 1994; Begon *et al.* 1996). For example, taxonomic resolution has been highly variable (Lawton 1989; Martinez 1991; Polis 1991) and webs are inevitably incomplete in terms of species richness and the feeding interactions sampled (Polis 1991, 1994). The problem of defining appropriate spatial and temporal scales makes meaningful comparisons between webs derived from different habitats particularly difficult (Closs & Lake 1994).

This study involves the description of a new catalogue of food webs in small streams using consistent methods at the same spatial and temporal scales. The webs, which are time specific rather than cumulative (i.e. we did not amass

information on species composition and diet from more than one occasion) and highly resolved taxonomically rather than aggregated (i.e. we did not combine information on taxonomically or trophically related species), were described from 10 habitats that were as similar as possible to each other but which differed in fundamental ways. Our focus is on the extent to which measures of habitat disturbance and resource availability can account for variation in food-web attributes.

Dynamic models of food webs are the basis for conflicting predictions regarding the influence of disturbance on food-web architecture. In models based on locally stable equilibrium points, longer food chains reduce the rate at which population densities recover from a perturbation (Pimm 1982), making the persistence of species in long chains unlikely and invasion more difficult in disturbed environments (Pimm *et al.* 1991). In addition, the presence of more species or higher connectivity reduce food-web stability (May 1972; Cohen *et al.* 1990). On the other hand, in their alternative approach involving analysis of community permanence, Law & Blackford (1992) have shown that four-level food chains become more likely to persist (and to reassemble after species loss) when feeding links across more than one

trophic level are added. These results indicate that increased connectance can promote food-web persistence, running counter to the earlier results of Pimm & Lawton (1978) who modelled the exact same food webs but focused on local stability. Moreover, Pimm & Lawton (1978) themselves found that of the more complex four-level food chains, those that were locally stable had shorter return times after a perturbation than the corresponding linear food chains. This also argues in favour of higher connectance promoting food-web persistence in disturbed environments. A further twist in this complex theoretical tale is the finding that increases in species richness or connectance only reduce local stability in models based on Lotka–Volterra dynamics; donor-controlled models, where food supply is not affected by consumer populations, show either no effect or an increase in local stability (Pimm 1982). We evaluate the alternative predictions of these models by comparing species richness, connectance, number of links per species, and food-chain length in food webs in streams subject to contrasting disturbance regimes.

We also consider an alternative hypothesis that proposes that chain length is limited by the efficiency with which energy is transmitted through feeding links (Hutchinson 1959; Slobodkin 1961) and thus predicts that food chains will be longer in more productive environments. In connection with food-web models, environments are formally considered to be more productive either where there is a greater carrying capacity of primary producers "in the absence of consumers" or, in the case of donor-controlled situations, where the rate of supply of organic matter is greater (Oksanen *et al.* 1981; Pimm 1982). As a first approximation to this elusive concept of environmental productivity we use spot measures of algal primary productivity and of the standing crop of detritus in each of our streams.

Both web size and number of links per species proved to be significantly negatively related to mean intensity of bed disturbance. Mean chain length had a significant positive relationship with algal primary productivity but not disturbance, whereas no food-web attribute was related to detritus standing crop.

MATERIALS AND METHODS

Study sites

The 10 study sites (Fig. 1), each of which was 30 m long and included at least one pool and one riffle, were in separate third- or fourth-order tributaries of the Taieri River in New Zealand. The study sites all occurred in grassland catchments, but they varied in the extent to which the land has been developed for pasture (Table 1;

Townsend *et al.* 1997a). Each site was sampled for food-web data once during the austral summer between 5 and 16 January 1995.

Water samples, taken in January 1995, were analysed for pH, alkalinity, conductivity, total phosphorus (TP), dissolved reactive phosphorus (DRP), total nitrogen (TN), nitrate (NO_3), nitrite (NO_2), and organic and inorganic seston (see Jaarsma *et al.* 1998).

Particulate organic matter was collected from the benthos in Surber samplers (area 0.06 m^2 and mesh size 250 microns) and fractionated by wet sieving into fine particulate organic matter (FPOM; < 1 mm) and coarse particulate organic matter (CPOM; > 1 mm) before ashing and weighing. Two 1 litre water samples were taken from the water column on arrival at the head of each site to estimate organic seston; samples were filtered (4.7 cm Whatman GF/C), oven dried (60°C for 24 h), weighed, ashed (550°C for 1 h), and reweighed.

Measurement of disturbance regime

Particles corresponding to the 50th, 75th and 90th percentiles of the substratum size distribution at each site were painted and arranged on the surface of the stream bed (five rows of three particles in each of the three size classes randomly assigned to transects placed 1 m apart). The movement of these particles was monitored on five occasions from September 1993 to June 1994. Mean intensity of bed disturbance at a site was calculated as the average of the percentage of the painted tracer particles of all size classes combined that moved between consecutive sampling occasions (see Townsend *et al.* 1997b). This measure of intensity of disturbance was chosen to be appropriate for streams of similar dimensions as a comparative index of the proportion of the stream bed that moves during discharge events. Average intensity of bed disturbance is a consequence both of discharge patterns and physical aspects of bed composition (particularly size class composition). Our index, which integrates these two aspects, has been shown to be superior to alternative measures related to discharge variation (Townsend *et al.* 1997c). Note that intensity and frequency of disturbance (the proportion of occasions when more than a given percentage of the bed moved) are highly correlated (Townsend *et al.* 1997c). None of the 10 streams suffered a notable disturbance in the 2 months prior to our assessment of their food webs.

Estimates of resource availability–algal primary productivity and detritus standing crop

Primary productivity was estimated at each site between 12.00 and 14.00 hours on a date in January 1995 using a
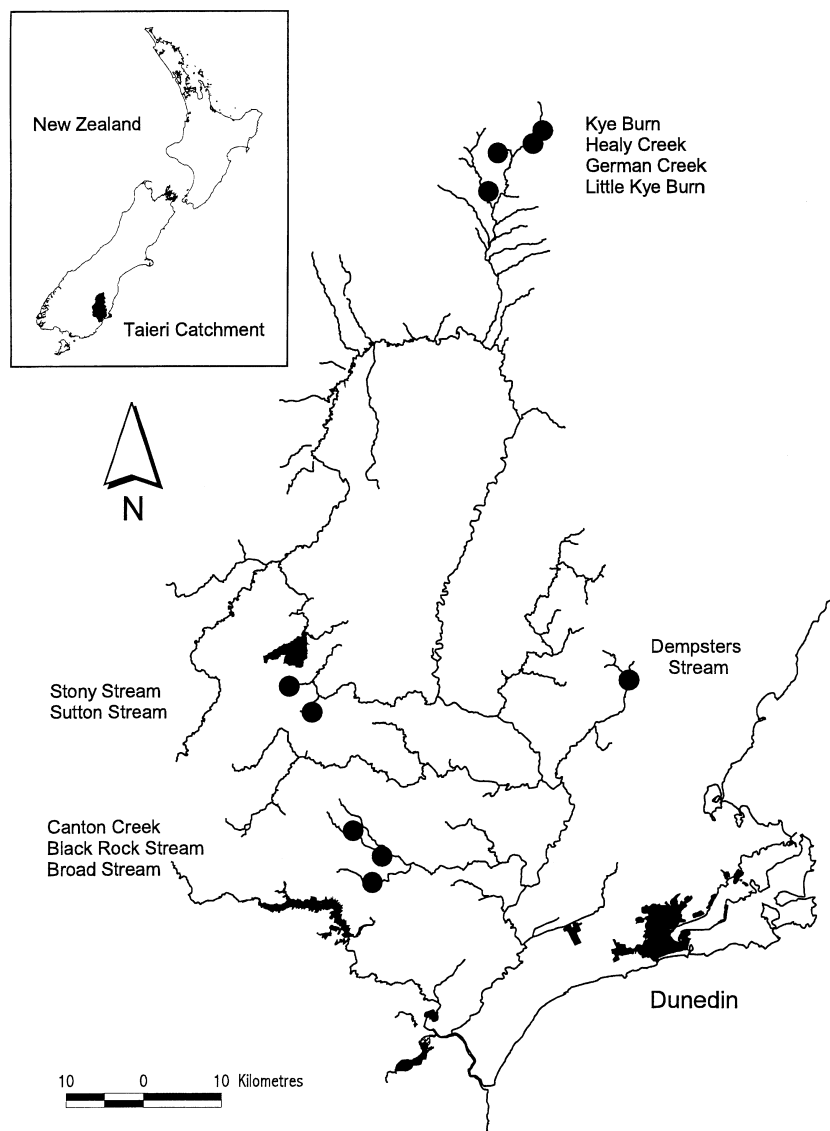
Figure 1 Map of the Taieri River in the South Island of New Zealand, showing the location of the 10 study streams.

radioactive carbon isotope ($^{14}CO_2$ in the form of $NaHCO_3$) in two portable, recirculating chambers (Fuller & Bucher 1991). Ten 3×3 cm sections of substrate were collected from random locations along the study reach and placed in each chamber. The surface area of the rocks was calculated by foil wrapping and using a weight/area regression. Our estimate of primary productivity has the limitation that it is a spot measure. However, a seasonal study of two of our streams has revealed differences in absolute values and relative rankings both in rates of primary productivity and in food-web attributes (Thompson 1996), providing some justification for our decision to analyse spot estimates of each. Measures of photon flux density indicated that in all cases we were assessing the production of epilithic algae operating at full photosynthetic capacity (Young & Huryn 1996). Thus, the values

were not standardized for light intensity and comparisons between streams are valid.

The amount of organic seston available instantaneously over each square metre of streambed was calculated by multiplying a seston measure (grams organic matter being transported in the water column per cubic metre) by the mean depth of the stream. This was added to the amount of fine and coarse particulate organic matter found per square metre of streambed. This measure of detritus availability is not ideal because, rather than measuring the rate of supply of the various components of dead organic matter, we have produced an index that combines the standing crops of particulate organic matter with an instantaneous measure of the rate of supply of organic seston. Because some detritivores feed on seston (collector-filterers), some on fine (collector-gatherers), and some

Table 1 Habitat variables in the 10 study streams

Site	Land use	Trout	Altitude (m)	Catchment area (km²)	Average width (m)	Average depth (m)	NO₃ + NO₂	Total N	DRP	Total P	AFDW biofilm (g/m²)	MID	APP	ADA
Blackrock	P	−	440	8.8	1.20	0.14	15.7	197.3	8.2	18.1	1.5	46.6	20.7	11.3
Broad	P	+	460	6.0	1.18	0.16	8.8	159.1	7.5	13.6	1.2	43.5	27.4	4.9
Canton	P	−	520	5.7	1.25	0.20	16.8	199.1	7.9	21.4	2.0	26.3	23.0	11.5
Dempsters	T	+	300	24.5	3.72	0.14	21.2	219.1	13.0	38.9	1.3	28.6	85.4	3.4
German	T	+	600	11.1	3.28	0.07	4.1	88.2	2.1	8.4	2.3	62.2	88.3	0.8
Healy	T	+	660	5.9	3.03	0.16	7.3	75.4	4.6	9.1	3.6	39.8	61.8	2.6
Kye Burn	T	+	740	1.6	1.97	0.07	5.1	157.3	14.9	20.1	1.2	42.2	15.6	0.6
Little Kye Burn	T	+	500	78.9	6.65	0.22	5.3	190.0	11.1	16.8	2.1	84.6	11.1	13.3
Stony	T	−	800	15.9	2.85	0.14	4.5	146.3	2.1	9.1	12.0	28.4	22.5	1.1
Sutton	T	+	520	15.2	2.40	0.12	1.5	219.1	13.0	16.2	1.0	45.9	9.3	4.1

Land use is native tussock (T) or pasture (P). Brown trout (*Salmo trutta* L.) are present (+) or absent (−). Nutrient concentrations are recorded in µg/L. DRP, dissolved reactive phosphorus. Mean intensity of disturbance (MID) is recorded as the average percentage of marked particles that moved during several sampling periods (see text). Average primary production (APP) is displayed in mg of ^{14}C that is taken up per m² of rock surface per hour. Average detritus availability (ADA) is in AFDW of organic matter per m² of streambed.

on coarse particulate organic matter (shredders), we have produced an integrated measure that should reflect, in comparative terms, the relative availability of dead organic material to detritivores in the streams.

Ideally, our estimates of primary productivity and detritus availability would have had identical units (rate of supply of fixed carbon), making it possible to combine them into a single environmental productivity measure. This could not be accomplished for logistic reasons.

Algae, macroinvertebrates, crayfish, and fish

Ten rocks (maximum diameter 12 cm) were either picked up or chiselled off (in the case of bedrock) from random locations in each site and their epilithic algae were scrubbed into individual containers and stored on ice in the dark. The samples from each site were pooled and blended for 1 minute in a commercial food blender (Biggs 1987). A 500 ml subsample was frozen for later identification of algae (Jaarsma *et al.* 1998).

Macroinvertebrate samples were taken from 10 random locations using a Surber sampler (area 0.06 m², mesh size 250 microns, taking the top 5 cm of substratum). Samples were preserved in 5% formalin for return to the laboratory where the 10 samples were pooled into two groups of five, which were searched for invertebrates. Both sets of samples were picked until 1500 individuals were taken, or until all individuals were removed, before pooling into a single set for food-web analysis. Invertebrate identification was carried out at 10–40 × magnification, using the keys listed in Jaarsma *et al.* (1998). In some cases, such as for chironomids and oligochaetes, keys to the New Zealand fauna are incomplete and the individuals were described according to morphospecies within major familial groupings. Morphospecies groupings were based on simple external characters such as number and shape of chaetae, head capsule shape and colouration, and body shape. Subsequent microscopic taxonomy (by Peter Cranston, CSIRO, Australia) revealed that the chironomid morphospecies represented either a single taxonomic species or a group of very closely related species. More than 90% of individuals were ascribed to either a species or a morphospecies.

Fish and crayfish were sampled by electric fishing after isolating the study site with weighted 1 cm mesh nets.

Dietary analysis

Invertebrate and fish diet analysis was carried out on gut contents mounted on microscope slides. Ten individuals of each species (or as many as were present if fewer than 10) were chosen to represent all size classes present. Taxonomy of algae in invertebrate guts (and from field

samples) was determined as described in Jaarsma *et al.* (1998). Terrestrial invertebrates identified in gut contents were grouped as a single diet category. Unidentifiable material in invertebrate guts was classified as a basal "detritus" category.

Compilation of food webs and calculation of food-web attributes

A food web was compiled for each site as a symmetrical matrix by forming a list of dead organic matter (two categories–detritus, terrestrial invertebrates), algae, invertebrates, and fish identified from the field samples (column headings) and from dietary analysis (row headings). Some guts contained prey species that were not recorded in the stream itself. In these cases the prey species was added to the matrix, where it was attributed its own feeding links according to those of the most closely taxonomically and trophically related species. Known suctorial species (such as Empididae) were omitted from analyses.

Food-web attributes were calculated by entering the food-web matrix into a Microsoft Excel macro. This used recursive programming to trace and record each food chain present in the matrix, calculating mean and maximum chain length, number of links and number of species. These primary attributes were then used to calculate linkage density and connectance statistics. We calculated linkage density as the mean number of links down (number of prey species per consumer species). Connectance (C) was calculated using a slightly modified version of the formula of Warren (1994):

$$C = L/(S^2 - \{[(pp + ba) \times S] + [S - (pp + ba)] + [pr \times (pp + ba)]\})$$

where L is the number of links, S is the number of trophic elements, pp is the number of primary producers, ba is the number of non-algal basal elements, and pr is the number of predators. S^2 represents the number of links in a web if all possible links were present. The first subtracted term multiplies primary producers and basal categories (such as detritus) by the number of web elements to allow for the fact that these categories are nonfeeding. The second term removes all cannibalistic links not removed by the first term. The final term removes the possible links of predators eating primary producers or basal categories.

Statistical analyses

Independent variables We used least squares linear regression to determine whether differences in disturbance regime or resource availability (algal productivity and standing crop of detritus) were associated with significant

changes in food-web structure. Because our hypotheses were formulated *a priori* and involved different, independent variables, we conducted separate statistical tests for the effects of disturbance and resources.

Dependent variables Many aspects of food-web structure were measured. To avoid analysing a large number of food-web attributes, thereby increasing the chances of a type 1 statistical error, we conducted statistical tests on only four key attributes, namely web size (species richness), connectance, average number of links down, and mean chain length. Web size, connectance, and average number of links down are not independent because all incorporate in their calculation measures of total number of species. Thus, we first conducted a multivariate ANOVA to test the regressions for these three attributes. If the multivariate test statistics were significant (alpha = 0.05) we performed univariate tests to evaluate the regressions for each attribute separately. Because mean chain length can be considered independent of species richness, only univariate ANOVA was used to test the regression models in this case. The distributions and patterns of residuals for all attributes were checked to ensure that assumptions of ANOVA were satisfied.

To determine whether differences in species richness were confounding the influence of disturbance on the composite web variables that incorporated species richness in their calculation (connectance, links down per species), we analysed residuals from regressions between log transformed species richness and the log transformed composite variables, as suggested by Bengtsson (1994).

To determine the potential importance of variables other than those selected *a priori* (disturbance and resource supply) we conducted stepwise multiple regression analyses (Table 1 shows predictor variables). Multiple regression models for each of the four food-web attributes were built and tested using randomization techniques. For each attribute the initial predictor was randomly selected from the data base and tested for predictive power. Another predictor was then randomly selected and the power of the combined model was tested. This was continued until each model included 10 variables. The process was repeated 5000 times until the best model for both probability and predictive power was found.

RESULTS

Food-web attributes in the 10 webs

There was moderate variation in species richness across the sites (78–113; Table 2). Invertebrate densities and biomasses were also variable; Kye Burn supported very low densities and biomass, whereas the agricultural Broad Stream site had notably high values. The variation in

Table 2 Food-web attributes of the 10 study streams

Site	No. sp.	No. algal sp.	No. fish sp.	No. invert. sp.	No. inverts /m²	AFDW inverts. (g/m²)	C	Avg. no. links down/sp.	Mean chain length	No. top sp.	No. int. sp.	No. basal sp.	cg	ff	gr	om	pr	sh
Blackrock	87	45	1	37	11887	4.7	0.13	9.87	2.24	15	22	49	9	2	9	6	8	4
Broad	95	49	1	41	20020	5.4	0.17	13.45	2.25	22	19	53	15	2	9	5	9	2
Canton	109	52	1	52	10160	3.9	0.14	13.35	2.45	31	21	56	15	4	11	6	14	3
Dempsters	107	46	4	64	14463	4.0	0.18	16.66	4.42	13	44	50	17	4	14	4	18	1
German	86	46	2	35	13673	2.5	0.13	9.54	2.40	12	24	48	16	2	6	5	8	0
Healy	96	43	2	48	10407	3.4	0.15	11.78	2.99	20	29	47	20	4	11	3	11	1
Kye Burn	98	53	1	40	5990	1.1	0.18	15.34	2.35	16	24	58	17	2	10	4	7	1
Little Kye Burn	78	37	3	35	10420	3.0	0.15	9.87	2.39	14	22	42	12	3	3	5	14	1
Stony	113	59	1	49	9827	1.7	0.17	16.64	2.38	20	29	63	16	3	13	5	11	2
Sutton	92	55	1	33	8347	2.9	0.17	12.44	1.79	10	13	63	10	3	10	2	8	1

Connectance (C) is indicated as a proportion of the total number of links possible. Top species are those species that are found at the top of all food chains in which they occur, basal species are those that occur only at the base of food chains. All other species are considered intermediate (int.). The number of species in each of the functional feeding groups are abbreviated as follows: cg, collector-gatherer; ff, filter feeder; gr, grazer; om, omnivore; pr, predator; sh, shredder.

connectance, in contrast, was relatively small, with most sites realising about 15% of all conceivable links. However, the distribution of these realized links, as reflected in mean chain length and the average number of links down per species, varied considerably.

The shape of the food webs ranged from "square" at Canton Creek, with comparatively similar numbers of basal, intermediate, and top species, to a strongly "pyramidal" structure at Little Kye Burn, where the number of species approximately halved between each class. The functional organization of the invertebrate communities was also variable, ranging from dominance by collector-gatherers in Healy Creek to approximately equal representation of the functional feeding categories, as in Blackrock Creek.

Disturbance

Multivariate analysis of variance indicated significant effects of disturbance on the food-web variables incorporating species richness in their calculation (Wilk's lambda = 0.148, $F_{3,\ 6} = 11.54$, $P = 0.007$). Univariate ANOVAs for these variables and for chain length showed that intensity of disturbance had significant negative relationships with species richness ($F_{1,\ 8} = 42.4$, $P < 0.001$, $R^2 = 0.84$) and with mean number of links down per species ($F_{1,\ 8} = 9.65$, $P < 0.015$, $R^2 = 0.55$), but not with connectance ($F_{1,\ 8} = 1.38$, $P = 0.27$, $R^2 = 0.14$) or mean chain length ($F_{1,8} = 0.97$, $P = 0.35$, $R^2 = 0.11$) (Fig. 2).

Of the groups of organisms that contribute to species richness, the numbers of algal species (Pearson correlation coefficient $r = -0.67$), basal species (algae plus dead organic matter categories; –0.64), primary consumers (of algae and/or dead organic matter; –0.86), and carnivorous invertebrate species (–0.65) were negatively correlated with disturbance intensity. There were also negative correlations between disturbance intensity and the mean number of links down from omnivores (–0.71) and primary consumers (–0.75), but not from predators (0.05).

Regression analysis indicated that the number of links down per species had a positive relationship with species richness ($F_{1,8} = 24.8$; $P = 0.001$, $R^2 = 0.75$). When the residual values from this regression were used as the dependent variable in a regression with disturbance intensity, there was no significant relationship ($F_{1,8} = 0.10$; $P = 0.75$, $R^2 = 0.013$).

Primary productivity

The rate of production of algal resources was not significantly related to any of the attributes incorporating species richness (Wilk's lambda = 0.889, $F_{3,6} = 0.25$, $P = 0.86$). However, there was a significant positive
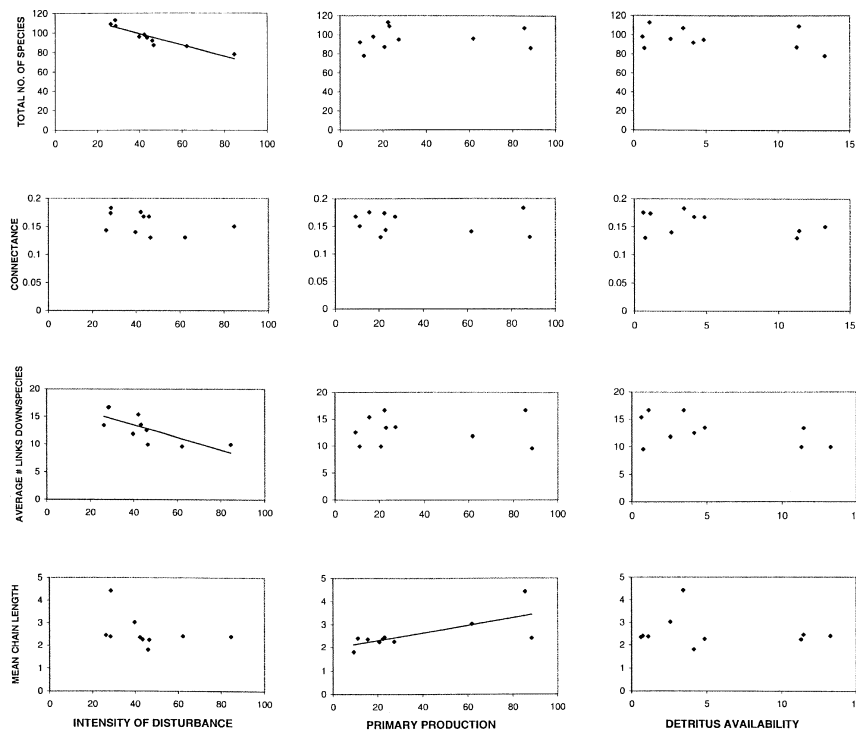
Figure 2 Relationships between four food-web attributes (total number of species, connectance, average number of links down per species, and mean chain length) and disturbance intensity, primary productivity, and detritus availability. Regression lines are included where the relationship is significant ($P < 0.05$).

relationship between primary productivity and mean chain length ($F_{1,8} = 7.58$, $P = 0.025$, $R^2 = 0.49$) (Fig. 2).

Detritus

The standing crop of detritus was not significantly related to any food-web attribute (Fig. 2). The MANOVA for regressions between detrital standing crop and variables incorporating species richness was not significant (Wilk's lambda = 0.745, $F_{3,6} = 0.68$, $P = 0.59$). Likewise, the regression between detrital standing crop and mean chain length was not significant ($F_{1,8} = 0.23$, $P = 0.65$, $R^2 = 0.03$).

Regression models incorporating other variables

None of the other variables we measured was able to explain more than 26% of the variance in connectance or 34% of the variance in species richness or mean number of links down. The combination of primary productivity with two variables expected to be closely related to algal production, total phosphorus, and mean stream depth, was able to increase the proportion of the variance in mean chain length explained from 49% to 91%. The introduction of land use (pasture *versus* tussock) or fish predation regime (brown trout *versus* nontrout) as covariates did not significantly improve the predictive power of the models.

DISCUSSION

Both the number of species present and the number of species fed on by each animal species declined as the intensity of disturbance increased, whereas connectance and the length of chains in the webs were unaffected. These results provide partial support for dynamic models involving local stability (e.g. May 1972), which predict negative relationships between all four attributes and disturbance intensity. There is no support for the model based on community permanence (Law & Blackford 1992), which indicates that increased connectance can promote food-web persistence.

It is important to bear in mind that none of the streams had suffered a notable disturbance in the 2 months prior to our assessment of their food webs. Previous studies indicate that the relationship between disturbance and invertebrate taxon richness is not affected by the timing of the most recent disturbance event (Townsend *et al.* 1997d), but the proportional representation of "resilience" and "resistance" species traits is greater after a recent event (Townsend *et al.* 1997b). Thus, it seems that disturbances may immediately reset the pattern of relative abundance of species, with those possessing appropriate traits becoming relatively more common, while species richness and some of the food-web attributes we measured depend on the medium to long-term disturbance regime. Note that the resistance and resilience traits of species

living in disturbed habitats (e.g. clinging life-styles, streamlining, effective recolonization mechanisms; Townsend *et al.* 1997b) are independent of any characteristics of food-web architecture that may confer stability.

The average number of links down was negatively related to intensity of disturbance. This pattern was due primarily to a reduction in links down from primary consumers (algivores and detritivores) and omnivores in more disturbed streams. When variance in links down per species due to changes in species richness was removed, by analysing residuals of a regression between species richness and links down, no significant effect of disturbance was detected. This means that alterations in the number of links down per species was due to the reduction in the number of species. Furthermore, because the number of links down was scaled according to the number of species present (i.e. it was calculated as links down per species) but was still positively correlated with species richness, we can conclude that the primary effect of disturbance on the number of predatory links was due to a reduction in the number of potential prey species available.

We found that the total number of species (algae, invertebrates, and fish) was smaller in more intensely disturbed environments. In our earlier analysis of macroinvertebrate communities in 54 stream sites (Townsend *et al.* 1997d) we did not resolve many of the taxa to species or morphospecies. Nevertheless, taxon richness was lower in the more disturbed sites, as recorded here in our more detailed community analysis. In the 54-site study we also found that richness was low in the least disturbed sites, conforming with the prediction of Connell's (1978) intermediate disturbance hypothesis that competitive exclusion will reduce richness in the most stable habitats. This does not conflict with the present results because none of the 10 streams in this study was among the least disturbed of the 54 sites.

It is important to recognize that there are alternative explanations for significant patterns in species richness and number of links down per species. Species richness may decline with disturbance simply because fewer species are capable of coping with intense and/or frequent disturbances to the streambed. Links down per species may decline with disturbance because of a reduction in the likelihood of encounters between a predator and potential prey. Mean abundance of invertebrates per unit area of habitat was not significantly correlated with intensity of disturbance ($r = 0.01$), so the pattern is not a simple consequence of fewer encounters per unit time leading to fewer links detectable via the gut contents. Perhaps the more disturbed streams possess a more patchy distribution of prey (particularly algae) and/or predators, leading to a reduction in the range of prey encountered per unit time. This deserves further investigation.

Food chains were on average longer in streams with higher levels of algal productivity, whereas none of the food-web attributes was significantly related to the availability of detrital resources. This suggests that algal productivity is more influential than detrital input in determining stream food-web structure. It is tempting to conclude that higher rates of input of dead organic matter will be reflected strongly in microorganism activity, whereas greater rates of production of algal biomass, a higher quality food for invertebrates, are reflected more strongly in animal activity and longer food chains (Townsend & Riley, in press). Perhaps the microbial loop described by lake ecologists (Pomeroy & Wiebe 1988), in which much of the available energy is utilized by microscopic elements of the community and fails to find its way to macroinvertebrates and fish, will also prove to be an important feature of stream communities.

Because of inefficiencies in energy-conversion processes, at each feeding link at most 30% and sometimes as little as 1% of energy consumed is available to the next trophic level (Begon *et al.* 1996). In theory, therefore, the generally observed pattern of just three or four trophic levels in communities could be due to energetic considerations; a further level just could not be supported by the available energy. This important prediction has been subject to surprisingly few tests. In a meta-analysis of published webs, Briand & Cohen (1987) found no difference in length of food chains when a variety of high and low productivity webs from terrestrial and aquatic habitats were compared. Similarly, Schoenly *et al.* (1991) surveyed 95 insect-dominated webs and found that food chains from tropical habitats (presumed to be more productive) were no longer that those in temperate and desert situations. Moreover, food chains composed of insects were no longer than those involving vertebrates, despite the higher energy transfer efficiencies associated with the former (Schoenly *et al.* 1991). In contrast, Yodzis (1984) reanalysed the webs of Briand & Cohen and found a trend towards longer food chains when these were built above energetically efficient groups, such as invertebrates. These analyses are based on webs from diverse habitats described using different methods and their results cannot be considered definitive. A more sensible approach was taken by Jenkins *et al.* (1992), who experimentally manipulated resource supply to communities in water-filled containers, designed to mimic tree holes; a 10-fold or 100-fold reduction in leaf litter input reduced maximum food chains by one link, because the principal predator, a fly larva, was usually absent from less productive habitats. This parallels the results of Persson *et al.* (1992), who found that pelagic piscivorous fish tended to be absent in lakes of low productivity. In a similar vein, Spencer & Warren (1996) manipulated

aquatic microcosm communities of bacteria, protozoans, rotifers, microcrustaceans, and *Hydra*. They found no strong effects of energy supply on food-web structure, although they reported nonsignificant trends towards longer food chains in high-energy systems.

Our support for the prediction relating productivity to food chain length is the first involving detailed descriptions of food webs in natural communities. It seems unlikely that a simple energy constraint explanation holds for this result, given Pimm's (1982) suggestion that an order of magnitude increase in energy supply at the base of a food web might be needed to support an extra trophic level. Streams with longer food chains contained more carnivorous invertebrate species and fish, and it is not uncommon in more productive streams to find food chains with up to nine or 10 links, featuring a sequence of up to seven or eight carnivorous invertebrate species, although never more than one fish. The positive relationship between food chain length and algal productivity could be due to the predicted energetic considerations or to a joint correlation with a third, unmeasured factor.

There are no significant intercorrelations among the three habitat variables of interest. We might have expected that more disturbed beds would have been less conducive to high levels of primary productivity (Biggs & Close 1989) and less retentive of organic matter (Scarsbrook & Townsend 1993). The lack of any relationships makes interpretation of results more straightforward and allows us to conclude, for example, that our results for food-chain length provide support for an energetic hypothesis but not for the competing dynamical stability hypothesis (Briand & Cohen 1987). Multiple regression models indicate that no other measured stream habitat variable is significantly affecting food-web structure, apart from disturbance and algal resource production. This suggests that the 10 streams can properly be considered "replicates" that differed significantly in disturbance and productivity but not in other physicochemical factors.

Finally, we believe that further re-working of the old catalogue of food webs is unlikely to be profitable. Progress is much more likely to be made by comparing the attributes of new food webs, described using consistent methodology by the same scientists (Pimm *et al.* 1991) in habitats that differ in terms of specified fundamental features (Begon *et al.* 1996), as we have done here.

ACKNOWLEDGEMENTS

REFERENCES

Begon, M.B., Harper, J.L. & Townsend, C.R. (1996). *Ecology: Individuals, Populations and Communities*, 3rd edn. Oxford: Blackwell Science.

Bengtsson, J. (1994). Confounding variables and independent observations in comparative analyses of food webs. *Ecol.*, 75, 1282–1288.

Biggs, B.J.F. (1987). The effect of storage and blending on the quantitative analysis of periphyton samples. *Freshwater Biol.*, 18, 197–203.

Biggs, B.J.F. & Close, M.E. (1989). Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biol.*, 22, 209–231.

Briand, F. & Cohen, J.E. (1987). Environmental correlations of food chain length. *Sci.*, 238, 956–960.

Closs, G.P. & Lake, P.S. (1994). Spatial and temporal variation in the structure of an intermittent-stream food web. *Ecol. Monographs*, 64, 1–21.

Cohen, J.E., Luczak, T., Newman, C.M. & Zhou, Z.M. (1990). Stochastic structure and nonlinear dynamics of food webs: qualitative stability in a Lotka–Volterra cascade model. *Proc. Royal Soc., London B*, 240, 607–627.

Connell, J.H. (1978). Diversity in tropical rainforests and coral reefs. *Sci.*, 199, 1302–1310.

Fuller, R.L. & Bucher, J.B. (1991). A portable chamber for measuring algal primary production in streams. *Hydrobiologia*, 209, 155–159.

Hall, S.J. & Raffaelli, D.G. (1993). Food webs: theory and reality. *Adv. Ecol. Res.*, 24, 187–239.

Hutchinson, G.E. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Naturalist*, 93, 145–159.

Jaarsma, N.G., de Boer, S.M., Townsend, C.R., Thompson, R.M. & Edwards, E.D. (1998). Characterising food webs in two New Zealand streams. *NZ J. Mar. Freshwater Res.*, 32, 271–286.

Jenkins, B., Kitching, R.L. & Pimm, S.L. (1992). Productivity, disturbance and food web structure at a local spatial scale in experimental container habitats. *Oikos*, 65, 249–255.

Law, R. & Blackford, J.C. (1992). Self-assembling food webs: a global viewpoint of coexistence of species in Lotka–Volterra communities. *Ecol.*, 73, 567–578.

Lawton, J.H. (1989). Food webs. In *Food Webs*, ed. Cherret, J.M. Oxford: Oxford University Press, pp. 43–78.

Martinez, N.D. (1991). Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecol. Monographs*, 61, 367–392.

May, R.M. (1972). Will a large complex system be stable? *Nature*, 238, 413–414.

Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *Am. Naturalist*, 118, 240–261.

Persson, L., Diehl, S., Johansson, L., Andersson, G. & Hamrin, S.F. (1992). Trophic interactions in temperate lake ecosystems: a test of food chain theory. *Am. Naturalist*, 140, 59–84.

Pimm, S.L. (1982). *Food Webs*. London: Chapman & Hall.

Pimm, S.L. & Lawton, J.L. (1978). On feeding on more than one trophic level. *Nature*, 275, 542–544.

Pimm, S.L., Lawton, J.L. & Cohen, J.E. (1991). Food web patterns and their consequences. *Nature*, 350, 669–674.

Polis, G.A. (1991). Complex trophic interactions in deserts: an

empirical critique of food web theory. *Am. Naturalist*, 138, 123–155.

Polis, G.A. (1994). Food webs, trophic cascades and community structure. *Aust. J. Ecol.*, 19, 121–136.

Pomeroy, L.R. & Wiebe, W.J. (1988). Energetics of microbial food webs. *Hydrobiologia*, 159, 7–18.

Scarsbrook, M.R. & Townsend, C.R. (1993). Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. *Freshwater Biol.*, 29, 395–410.

Schoenly, K., Beaver, R.A. & Heumier, T.A. (1991). On the trophic relations of insects: a food web approach. *Am. Naturalist*, 137, 597–632.

Slobodkin, L.B. (1961). *Growth and Regulation of Animal Populations*. New York: Holt, Rinehart and Winston.

Spencer, M. & Warren, P.H. (1996). The effects of energy input, immigration and habitat size on food web structure: a microcosm experiment. *Oecologia*, 108, 764–770.

Thompson, R. (1996). Food web studies in stony streams: the implications of resolution and seasonal variation. Unpublished Thesis, University of Otago, Dunedin, New Zealand.

Townsend, C.R. & Riley, R. (in press). Assessment of river health: accounting for perturbation pathways in physical and ecological space. *Freshwater Biol.*, in press.

Townsend, C.R., Crowl, T.A., Arbuckle, C.J. & Scarsbrook, M.R. (1997a). The relationship between land use and physicochemistry, food resources and macroinvertebrate communities in tributaries of the Taieri River, New Zealand: a hierarchically scaled approach. *Freshwater Biol.*, 37, 177–192.

Townsend, C.R., Dolédec, S. & Scarsbrook, M.R. (1997b). Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. *Freshwater Biol.*, 37, 367–388.

Townsend, C.R., Scarsbrook, M.R. & Dolédec, S. (1997c). Quantifying disturbance in streams: an analysis of alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *J. North Am. Benthol Soc.*, 16, 531–544.

Townsend, C.R., Scarsbrook, M.R. & Dolédec, S. (1997d). The intermediate disturbance hypothesis, refugia and biodiversity in streams. *Limnol. Oceanogr.*, 42, 938–949.

Warren, P.H. (1994). Making connections in food webs. *Trends Ecol. Evol.*, 9, 136–141.

Yodzis, P. (1984). Energy flow and the vertical structure of real ecosystems. *Oecologia*, 65, 86–88.

Young, R.G. & Huryn, A.D. (1996). Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. *Can. J. Fish Aquat Sci.*, 53, 2199–2211.

BIOSKETCH

Colin Townsend, joint author of the widely used text *Ecology: Individuals, Populations and Communities* (Begon, Harper & Townsend) and joint editor of the journal *Freshwater Biology*, researches the impacts on stream communities of land use, introduced species, and disturbances.