# STREAM ECOSYSTEM FUNCTIONING UNDER REDUCED FLOW CONDITIONS

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Abstract. Assessments of flow reduction in streams often focus on changes to biological communities and in-stream physical characteristics, with little consideration for changes in ecosystem functioning. It is unclear whether functional indicators of ecosystem condition may be useful for assessing the impacts of reduced discharge on small streams. Using weirs and diversions to reduce stream discharge during summer baseflow conditions, we tested the response of leaf breakdown, coarse particulate organic matter (CPOM) retention, and primary production to one month of water abstraction in before-after, control-impact (BACI) designed experiments. Discharge at impact (downstream) reaches decreased by over 85% in each of three small New Zealand streams compared to controls (upstream). There also were decreases in velocity, depth, and wetted width. Sediment cover increased at impact reaches, but there were only small changes to conductivity, pH, and surface water temperature. We installed mesh bags filled with willow leaves in-stream for one month to measure leaf breakdown. Reduced discharge had little influence on leaf breakdown rate in these streams. Travel distances and retention structures for CPOM were evaluated using releases of paper strips and wooden dowelling over a range of discharges. The distance traveled by released CPOM increased with increasing discharge, and the importance of riffles as retention structures increased at lower discharges. We measured the accumulation of chlorophyll a after one month on artificial substrates as an estimate of the relative primary production of control and impact reaches. The differences in chlorophyll a concentrations between control and impact reaches were inconsistent among streams. These ecosystem functions have responded inconsistently to water removal in these streams. However, the strong response of CPOM retention to reduced discharge could complement measures of biological community structure when the influence of reduced discharge is assessed. We recommend further investigation in a wide range of streams to assess the utility of these processes as functional indicators of reduced discharge.

Key words: coarse particulate organic matter; CPOM; functional indicators; leaf breakdown; New Zealand; primary production; reduced flow; stream ecosystem; water abstraction; water diversion.

### INTRODUCTION

Escalating global demands for limited freshwater resources are making it increasingly difficult to balance in- and out-of-stream requirements for water. An increased understanding of the impacts of reduced flows on stream ecosystems might assist in finding this balance. Therefore, it is necessary to identify efficient and effective methods of monitoring the impacts of water abstraction from streams. Gessner and Chauvet (2002) stress the importance of including functional measures when undertaking bioassessments, but warn that considerably more attention should focus on identifying useful indicators of functional integrity for specific kinds of anthropogenic stress. We previously have assessed the effects of experimentally reduced discharge on benthic invertebrates (Dewson et al. 2007), levels of invertebrate drift, and hyporheic usage

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by invertebrates (A. James, *unpublished data*). To complement these community structural measures, we have investigated the impacts of reduced discharge on three functional attributes of stream ecosystems: leaf breakdown, the retention of coarse particulate organic matter (CPOM), and primary production.

Studies of the importance of leaf litter as an energy source in streams and of the dynamics of leaf breakdown have been conducted over many years (see Webster and Benfield 1986, Royer and Minshall 2003). The promotion of leaf breakdown as a potential functional bioassessment tool (Webster and Benfield 1986, Gessner and Chauvet 2002) may have prompted many recent studies to test this in relation to human-induced stressors such as agricultural development, organic pollution, and stream acidification (e.g., Young et al. 1994, Niyogi et al. 2001, Pascoal et al. 2001, Dangles et al. 2004, Hagen et al. 2006).

Factors such as nutrients, water velocity, sedimentation, water temperature, and dissolved oxygen can influence breakdown rates (Webster and Benfield 1986, Royer and Minshall 2003). Webster and Benfield (1986) proposed leaf breakdown as a useful measure of impact on freshwater ecosystems, because a combination of physical, chemical, and biological processes control its rate. Results to date suggest that the usefulness of leaf breakdown rates as an indicator of ecosystem impairment may depend on the consequences of the stressor investigated. For example, when a stress alters multiple factors, such as sedimentation, nutrient levels, water temperature, and invertebrates, there can be simultaneous positive and negative effects on leaf breakdown rate; thus the usage of leaf breakdown as an indicator of ecosystem integrity might be limited (e.g., Woodcock and Huryn 2005, Hagen et al. 2006, Young 2006).

Several of the abiotic and biotic factors that are potentially altered by water abstraction can influence leaf breakdown rates. For example, water abstraction commonly decreases water velocity (e.g., Wright and Berrie 1987, McIntosh et al. 2002), alters temperature regimes (e.g., Mosley 1983, Rader and Belish 1999), increases sedimentation (e.g., Wright and Berrie 1987, Castella et al. 1995), changes pH (e.g., McIntosh et al. 2002, Woodward et al. 2002), and decreases invertebrate diversity and abundance (e.g., Cazaubon and Giudicelli 1999, Wood et al. 2000). Unfortunately, this diversity of potential changes makes it difficult to predict how leaf breakdown will respond to discharge reduction.

Coarse particulate organic matter (CPOM, >1 mm diameter) is an allochthonous source of energy for stream ecosystems (Petersen and Cummins 1974, Allan 1995). Allocthonous material that reaches the stream is either broken down or transported downstream (Webster et al. 1999). Consequently, the study of CPOM movement, breakdown, and retention in streams has received considerable attention over the years. It has been shown that CPOM generally travels only short distances in streams (e.g., Snaddon et al. 1992, Webster et al. 1994, Wallace et al. 1995). However, a number of studies have described the positive relationship between discharge and CPOM travel distance (e.g., Jones and Smock 1991, Webster et al. 1999, Brookshire and Dwire 2003). Webster et al. (1994) also showed that retention was greater in shallower streams, emphasizing the importance of water depth to CPOM retention. The changing prominence of different retention structures with water level probably underlies the importance of water depth.

Discharge-retention relationships suggest that water abstraction will enhance CPOM retention, potentially increasing energy supply or creating anoxic conditions among decomposing leaves. Such a change could have implications for higher trophic levels (such as invertebrates and fish). Reduced CPOM retention can have strong bottom-up effects on stream ecosystems, decreasing the abundance and biomass of all invertebrates over time (Wallace et al. 1997). We might expect the reverse to occur with increased CPOM retention.

Primary producers are the first trophic level in the food web (Molles 1999). As such, this autochthonous

source of energy for the stream ecosystem might provide another useful measure of the impact of reduced discharge, because any alteration to primary production can also have flow on effects to higher trophic levels. A relationship between water velocity and periphyton accrual might exist, because velocity can affect colonization, production, and loss of the periphyton community (Biggs and Close 1989, Jowett and Biggs 1997). Examinations of this relationship in a variety of natural and experimental situations have produced both positive and negative relationships (e.g., McIntire 1966, Poff et al. 1990, Biggs and Hickey 1994, Jowett and Biggs 1997), but tend to indicate that there is some relationship between velocity and primary production.

Using weirs and diversions to create considerable reductions in discharge, our aim was to investigate the influence of decreased discharge on three functional attributes of stream ecosystems: leaf breakdown, CPOM retention, and primary production. These ecosystem processes control the energy supply for stream ecosystems and, thus, have important consequences for higher trophic levels. We conducted our experiments during the Austral summer (between November 2004 and March 2005) because this is a time of peak irrigation, as well as naturally low flows. At this time, we expected that any water removal would have the greatest impact on the stream ecosystem.

Our hypotheses for each of the ecosystem functions were: (1) that reduced discharges would decrease leaf breakdown; (2) that reduced discharge, velocity, and depth would increase CPOM retention by increasing the efficiency of riffles as retention structures; and (3) that decreased velocities would enhance primary production.

#### Methods

#### Study streams

This discharge reduction experiment was conducted on three small streams in the Wairarapa Region of the lower North Island, New Zealand: Booths Creek and unnamed tributaries of Kiriwhakapapa Stream and Reef Creek. The three perennial, runoff-fed streams ranged in mean discharge from 52 to 80 L/s during the study period, November 2004 to March 2005 (Table 1). The streams are all <4 m wide (Table 2) and represent different levels of water quality. The stream with the lowest water quality is Booths Creek (41°04'40.29" S, 175°31'58.53" E). It is a small (80 L/s), low-gradient, meandering stream, with pool-riffle morphology and gravel-cobble substrate of hardened mud-sandstone (greywacke). This stream receives some inflow from stock-watering channels. Cropping land surrounds the Booths Creek study reaches, on Quaternary sediment, with patches of willow (Salix spp.) in the riparian zone. The Kiriwhakapapa Stream tributary is a small (54 L/s), moderately modified stream in the foothills of the Tararua Ranges (40°49'07.10" S, 175°34'21.04" E). This meandering stream also has a pool-riffle morphology and gravel-cobble greywacke substrate, with fine

TABLE 1.	Discharge (mean	$\pm$ SE) at control	I and impact	reaches of	f Booths C	Creek,	Kiriwhakapapa	Stream,	and	Reef	Creek,
Wairara	apa, North Island,	New Zealand, af	er discharge	reductions	began (Jar	nuary	to March 2005).				

Stream	Booths Creek	Kiriwhakapapa Stream	Reef Creek		
Discharge control (L/s) Discharge impact (L/s) Change in discharge (%)	$\begin{array}{r} 84.43  \pm  0.56 \\ 4.24  \pm  0.02 \\ -95.0\% \end{array}$	$\begin{array}{r} 28.17 \pm 0.24 \\ 3.88 \pm 0.02 \\ -86.2\% \end{array}$	$\begin{array}{c} 10.85 \pm 0.59 \\ 1.02 \pm 0.02 \\ -90.6\% \end{array}$		

Note: Percentage changes are from control to impact reaches.

sediments contributed by erosion of the mud-sandstone stream banks. The study reaches on the Kiriwhakapapa Stream tributary are within an extensive sheep and beef farm where stock has access to the stream and the channel has little shading. Pasture grass and native reeds are the dominant streamside vegetation. The Reef Creek tributary is a relatively pristine headwater stream (52 L/s) within a second-growth, native, conifer-broadleaf forest catchment (40°48 34.46' S, 175°32 21.84' E). The high gradient channel of this stream is characterized by pool, step, and riffle sequences and gravel-boulder greywacke substrate with outcropping greywacke bedrock. Of the three study streams, the Reef Creek tributary is the most prone to flash floods. The study reaches on the Reef Creek tributary are in a V-shaped valley, with the forest canopy providing almost complete shade to the channel. We will subsequently refer to unnamed tributaries by the names of the streams that they feed.

## Experimental design

We constructed weirs and diversions on three streams to reduce stream discharge for a distance of  $\sim 100$  m. This distance provided enough area for sampling and was not long enough for flow to be restored by groundwater inflow. Weirs extended across the entire stream, with no overflow during the period of the study. The wooden board weirs were not completely sealed so that a proportion of the flow and invertebrates could move through, under, and around these weirs, while the majority of the flow was diverted out of the experimental reaches through open diversion channels (Booths Creek and Kiriwhakapapa Stream) or diversion pipes (Reef Creek). By removing a high proportion of the discharge in this way, we have created a barrier to invertebrate drift into downstream reaches. However, this approach is consistent with the type of water abstraction that occurs from streams of this size. Study reaches (100 m) were identified immediately upstream (control) and downstream (impact) of weirs on each stream and we measured leaf breakdown, CPOM retention, and primary production within these reaches both before (between November 2004 and January 2005) and during discharge reduction (between January and March 2005). Therefore, our experiment has a BACI (before–after, control–impact) design (Downes et al. 2002).

## Flow-related and physicochemical characteristics

Throughout the experiment, we recorded water height in control and impact reaches on each stream at intervals of 20 minutes using TruTrack WT-HR 1000 Water Height Data Loggers (TruTrack, Christchurch, New Zealand) with an accuracy of  $\pm 1\%$ . Water height recorders were located in stable control sections in each reach so that the relationship between water depth and discharge remained constant (Gordon et al. 2004). We calculated discharge on seven occasions during the study by measuring depth and velocity at  $0.4 \times$  depth from the bed for at least 10 equidistant intervals across the stream using a Marsh McBirney Model 2000 Portable Flowmeter (Marsh McBirney, Frederick, Maryland, USA) to an accuracy of 0.01 m/s. The relationship between water height and discharge was described using a power function ( $y = cx^b$ , where c and b are constants) so that discharge could be calculated from the water height records (Gordon et al. 2004). In each reach, five additional depths and velocities were measured within riffles, to characterize the habitat used for the installation of leaf bags, primary production artificial substrates, and sediment traps, and for the release of CPOM. Average measurements of conductivity, dissolved oxygen, and pH were recorded twice before and twice during discharge reduction, at installation and collection of leaf bags, from approximately one hour of

TABLE 2. Physicochemical variables (mean ± SE) in control and impact reaches after discharge reduction (January to March 2005) in Booths Creek, Kiriwhakapapa Stream, and Reef Creek.

Stream and reach	Wetted width (m)	Depth (cm)	Velocity (m/s)	Conductivity (µS/cm)	pН	Dissolved oxygen (%)
Booths control Booths impact Kiriwhakapapa control Kiriwhakapapa impact Reef control Reef impact	$\begin{array}{c} 3.6 \pm 0.2 \\ 2.6 \pm 0.1 \\ 2.2 \pm 0.1 \\ 1.5 \pm 0.1 \\ 1.8 \pm 0.2 \\ 1.2 \pm 0.0 \end{array}$	$\begin{array}{c} 17.2 \pm 4.8 \\ 6.8 \pm 0.1 \\ 10.0 \pm 1.8 \\ 5.7 \pm 0.4 \\ 6.4 \pm 1.2 \\ 6.6 \pm 0.5 \end{array}$	$\begin{array}{c} 0.49 \pm 0.06 \\ 0.14 \pm 0.04 \\ 0.58 \pm 0.07 \\ 0.08 \pm 0.01 \\ 0.18 \pm 0.10 \\ 0.03 \pm 0.00 \end{array}$	$\begin{array}{c} 160.5 \pm 1.5 \\ 157.5 \pm 2.5 \\ 81.5 \pm 1.5 \\ 87.0 \pm 2.0 \\ 59.0 \pm 2.0 \\ 63.0 \pm 2.0 \end{array}$	$\begin{array}{c} 7.4 \pm 0.1 \\ 7.3 \pm 0.0 \\ 8.1 \pm 0.6 \\ 7.0 \pm 0.1 \\ 7.1 \pm 0.2 \\ 7.1 \pm 0.2 \end{array}$	$78.2 \pm 8.1 73.0 \pm 11.0 106.5 \pm 10.6 94.4 \pm 7.8 88.8 \pm 1.7 79.8 \pm 0.9$

data logging at intervals of one minute using a YSI multi-probe system instrument (YSI 556 MPS, YSI, Yellow Springs, Ohio, USA). Temperature was also recorded every 30 minutes throughout the study using Onset Hobo H8 temperature loggers (Onset Computer Corporation, Bourne, Massachusetts, USA). We measured the wetted width of the channel at 14 fixed locations at 5-m intervals within each 100-m reach.

We installed sediment traps in both control and impact reaches to assess how reduced discharge affected the rate of sediment deposition. Our sediment traps were similar to those described by Bond (2002), although we used small plastic buckets as the collection container (depth 200 mm, radius 82.5 mm), providing a settlement area of 0.0213 m<sup>2</sup>. Once installed, traps were flush with the streambed and were covered with a layer of coarse substrate material, supported by wire mesh over the trap to minimize the alteration of hydraulic conditions (Bond 2002). Sediment was trapped for 24 hours at control and impact reaches on two occasions before (between November 2004 and January 2005), and on three occasions during, discharge reduction (between January and March 2005). We also collected 300-mL water samples at midstream to measure the quantity of suspended sediment in the water column. The stream was at base flow during these collections. We analyzed ash-free dry mass (AFDM) of suspended and trapped sediment samples by vacuum filtration, using pre-ashed Whatman glass fibre filters (GF/C). Sample filtration was followed by drying at 50°C for 24 hours. Then filters were weighed, ashed for four hours at 450°C, and reweighed.

The coverage of fine sediment on the substrate was visually estimated by one person at 15 cross sections of the stream at each study reach on three occasions while diversions were operating (between January and March 2005). From a randomly selected starting point, cross sections were located at 5-m intervals along the study reach. At each cross section, we estimated the percentage of substrate covered by fine sediment within a 300 mm wide strip across the width of the stream. From these measurements, we calculated an average percentage cover of fine sediment for each reach and time.

## Leaf breakdown

We used leaf samples contained in mesh bags as a measure of leaf breakdown rates in these streams. Abscised leaves were not available at the time of this experiment, because it was conducted in the Austral summer, rather than at a time of natural leaf fall. To ensure that the initial condition of leaves did not vary between samples, we collected fresh willow leaves (*Salix* spp.) from a single tree seven days before installation and immediately weighed the leaves into ~10-g bundles. We recorded exact leaf mass before sealing leaves into  $150 \times 150$  mm mesh bags and air-drying for one week. We also weighed five additional 10-g samples of fresh willow leaves to calculate the average percentage of mass

lost between the fresh and air-dried leaves. We used three mesh sizes to exclude progressively larger invertebrates. We included coarse (5-mm) and fine (1-mm) mesh leaf bags and 100 mm lengths of PVC tube (40 mm diameter) with ends covered in 0.25-mm mesh. Tubes contained only  $\sim$ 3 g fresh mass of leaves.

Five replicates of each mesh type were attached to the substrate within riffles at control and impact reaches before (35 days, December 2004–January 2005) flow reduction. The installation of leaves was repeated (31 days, February–March 2005) after the flow reduction had been operating for one month at each of the three study streams.

Upon removal from the stream, leaf bags were transported to the laboratory on ice and were stored at  $-20^{\circ}$ C until analysis. The contents of each bag were rinsed through a 250-µm sieve and invertebrates and detritus were removed by hand. Samples were dried at 50°C for 24 hours, weighed, ashed at 600°C for two hours, and then reweighed.

We calculated both the percentage of mass lost during the experiment and the rate of leaf breakdown. The rate of leaf breakdown was calculated using an exponential decay model as described by Petersen and Cummins (1974). By using degree-days for this calculation, we factored out the effects of temperature differences between the before and after periods, as suggested by Minshall et al. (1983).

#### Coarse particulate organic matter (CPOM) retention

We used paper strips and wooden dowelling as analogues for natural CPOM (leaves and sticks; see Plate 1). Artificial leaves were cut as rectangles  $(100 \times 15 \text{ mm})$  from heavy red paper  $(200 \text{ g/m}^2)$  and artificial sticks were cut as 100 mm lengths of 8 mm diameter wooden dowelling, following the methods of James and Henderson (2005).

We released 30 of each CPOM type from marked points within riffle habitat in impact reaches of the three streams before and after flow reduction began in order to cover a wide range of stream discharges (0.5-180 L/s). In total, there were 15 CPOM releases over the three streams. We recorded the distance traveled downstream for each item after one hour and the mechanism of retention (riffles/rocks, instream or bank vegetation, eddies, debris dams, and undercut banks). Items not found within 150 m were identified as missing.

#### Primary production

We assessed periphyton growth on artificial substrates to provide relative comparisons of primary production between control and impact reaches. Arrays of six artificial substrates (unglazed terracotta tiles,  $100 \times 100$ mm) were attached to modular floor grating tiles ( $400 \times$ 400 mm) with dowelling pegs (10 mm diameter). The purpose of the dowel pegs was to elevate the tiles slightly and to minimize colonization by invertebrate grazers. Before flow reduction, floor gratings were attached to

TABLE 3.	Results of	of AN	OVAs	testing	for	differenc	es in	phy	sicoch	emical	measures	between	before-after,	control-i	mpact
treatmer	nts in Boo	ths Cre	eek, Ki	riwhaka	papa	Stream,	and	Reef	Creek	during	installatio	n of leaf	bags between	December	2004
and Ma	rch 2005.														

	Before-A	After (BA)	Control-I	mpact (CI)	Stream	(blocks)	$BA \times CI$	
Variable	F	Р	F	Р	F	Р	F	Р
Wetted width (m)	24.47	< 0.01	3.77	0.07	37.09	< 0.01	14.65	< 0.01
Depth (cm)	14.13	< 0.01	2.35	0.14	1.85	0.19	4.68	0.04
Velocity (m/s)	33.78	< 0.01	11.60	< 0.01	10.75	< 0.01	9.90	< 0.01
Conductivity (uS/cm)	13.44	< 0.01	0.52	0.48	817.79	< 0.01	0.07	0.79
рН	0.11	0.75	1.60	0.22	4.85	0.02	1.65	0.21
Dissolved oxygen (%)	3.74	0.07	1.68	0.21	1.36	0.28	0.26	0.62

*Notes:* For all factors except Stream (blocks) (with df = 2, 18), df values are 1, 18. A significant BA  $\times$  CI interaction term indicates that discharge reduction affected that factor. Values significant at P < 0.05 are indicated in boldface.

the streambed with tent pegs so that tiles were 50-100 mm below the water surface, in velocities of 0.3-0.7 m/s. We ensured that depths and velocities were as consistent as possible between control and impact reaches on each stream. Tiles remained in the same location after the diversions began; hence, depths and velocities were lower at impact reaches.

After one month in the stream, both before and during (one month after discharge reduction started) discharge reduction, we sampled the tiles for chlorophyll *a* by scouring three circular samples (7.06 cm<sup>2</sup> each) from the surface of each tile (Davies and Gee 1993). Samples were transported on ice in the dark and were stored at  $-20^{\circ}$ C. We extracted photosynthetic pigments from scourers by submerging them in 50 mL of 90% acetone for 24 hours at 5°C. Absorbency was read at 750, 665, and 664 nm on a Varian Cary 50 Conc. UV-Visible spectrophotometer (Varian Australia, Mulgrave, Australia) before and after 0.1 mol/L HCl was added. We calculated the amount of chlorophyll *a* (µg/cm<sup>2</sup>) for each sample as described by Steinman and Lamberti (1996).

#### Data analysis

Our decomposition and primary production experiments had BACI designs, in which measurements were made at control and impact reaches once before and once after the impact (Downes et al. 2002). In this case, the impact was discharge reduction. Therefore, all physicochemical, leaf breakdown, and primary production data were analyzed with a two-factor ANOVA (SAS Institute 2004). Factors were before-after (BA) and control-impact (CI). Streams were treated as blocks in the analysis of physicochemical data, but each stream was analyzed separately for leaf breakdown and primary production, because opposite responses were observed among the streams. The term of interest was the interaction between BA and CI. A significant  $BA \times CI$ interaction would indicate that the relationship between control and impact was different before than after the impact, suggesting that the discharge reduction might have had some effect. To test the differences in sediment cover between control and impact sites, we used a oneway ANOVA to test the  $H_0$ : mean percentage sediment cover at control = mean percentage sediment cover at impact, because sediment cover was not recorded at control and impact sites before flow reductions began. Leaf breakdown rates and chlorophyll *a* concentrations were  $\log_{10}$ -transformed, and stream depths and widths were square-root transformed to meet assumptions of normality and equality of variances.

#### RESULTS

## *Effects of discharge reduction on flow and physicochemical characteristics*

Weirs and diversions decreased the discharge at impact reaches by an average of 95%, 86%, and 91% in Booths Creek, Kiriwhakapapa Stream, and Reef Creek, respectively (Table 1). Maximum discharge reductions were greater than 97% for each of the streams at some time during this period (based on water heights recorded at intervals of 20 minutes). There were significant decreases in wetted width, depth, and water velocity at impact reaches compared to controls, but conductivity, pH, and dissolved oxygen were unaltered by discharge reduction in these streams (Table 3). Mean surface water temperatures in control reaches of Booths Creek, Kiriwhakapapa Stream, and Reef Creek were 19°C, 18°C, and 13°C, respectively. Mean daily surface water temperatures were lower in impact reaches after discharge reduction for Booths Creek ( $F_{1, 127} = 162.3$ , P < 0.01), Kiriwhakapapa Stream ( $F_{1,130} = 107.5, P <$ 0.01), and Reef Creek  $(F_{1,131} = 3.2, P = 0.08)$ . However, the differences in means were, on average, less than 1°C. Consequently, control and impact leaf bags in each stream were relatively equal in terms of the number of degree-days of exposure that they received, although there were differences between streams and the before and after periods.

Discharge reduction did not change the quantity of suspended sediments in the water column ( $F_{1,24} = 1.03$ , P = 0.32). Furthermore, when corrected for the discharge over each sediment trap (calculated as width × depth × velocity over the trap), there was no more sediment deposited in sediment traps at impact reaches than at controls after flow reduction ( $F_{1,14} = 0.62$ , P = 0.45). However, after flow reduction, fine sediments covered a significantly greater percentage of the substrate at



FIG. 1. Percent cover (mean + SE) of substrate by fine sediments for control (solid) and impact (open) reaches on Booths Creek, Kiriwhakapapa Stream, and Reef Creek.

impact reaches on Booths Creek (control = 9.2%, impact = 46.4%) ( $F_{1,88} = 74.1$ , P < 0.01) and Kiriwhakapapa Stream (control = 43.0%, impact = 81.2%) ( $F_{1,88} = 66.5$ , P < 0.01). There was no difference in sediment cover between control and impact reaches on Reef Creek ( $F_{1,88} = 0.3$ , P = 0.58) (Fig. 1).

### Effects of discharge reduction on leaf breakdown

Leaf breakdown occurred faster in warmer streams in both coarse- (linear,  $F_{1,10} = 40.65$ , P < 0.01) and finemesh bags (second-order polynomial,  $F_{2,9} = 5.34$ , P =0.03) at both control and impact reaches (Fig. 2). We allowed for this in all subsequent analyses by using breakdown rate per degree-day. There was no apparent relationship between leaf breakdown and degree days in the leaf tubes (linear,  $F_{1,9} = 1.78$ , P = 0.22).

Breakdown rates were often higher in the before than the after period (Fig. 3). Leaf breakdown was also faster in coarse-mesh bags than in fine-mesh bags and leaf tubes (Fig. 3). In two instances, breakdown at impact reaches changed relative to controls between before and after the discharge reduction. However, in both cases, breakdown rates were more similar at control and impact reaches after flow reduction (Fig. 3). In Reef Creek, breakdown in coarse-mesh bags decreased at impact reaches relative to controls ( $F_{1,16} = 6.67$ , P =0.02). Conversely, breakdown at the impact reach on Kiriwhakapapa Stream increased relative to control in fine-mesh bags ( $F_{1,16} = 5.7$ , P = 0.03).

### *Effects of discharge reduction on coarse particulate organic matter (CPOM) retention*

There was a linear increase in the distance traveled by released artificial leaves ( $F_{1,13} = 22.06$ , P < 0.001) and wooden dowelling ( $F_{1,13} = 13.70$ , P = 0.003) with increasing discharge (Fig. 4). Therefore, the average distance traveled by CPOM until retention was lower after flow reduction. In this study, the average distance traveled was 0.5–51 m for leaves, whereas the range was

0.4–37 m for sticks (Fig. 4). The maximum travel distances observed in this study were 125 m for leaves and 75 m for sticks. Changes in discharge also affected the type of structure that retained CPOM (Fig. 5). At higher discharges before flow reduction, the range of retention structures included riffles, edge, and in-stream vegetation, eddies, snags, and undercut banks. After flow reduction, riffles were the dominant retention structure, retaining, on average, 91% of artificial leaves and 85% of dowels.

#### Effects of discharge reduction on primary production

The chlorophyll *a* concentration on artificial substrates was higher over one month at the impact reach on Booths Creek both before and after discharge reduction, but chlorophyll *a* concentration was relatively unchanged by flow reduction ( $F_{1,20} = 0.33$ , P = 0.57). There was less algal accumulation at the impact reach on Kiriwhakapapa Stream after discharge reduction ( $F_{1,20} = 27.3$ , P < 0.01). Algal accumulation was greater at the



FIG. 2. Relationship between percentage of leaf mass remaining (mean  $\pm$  SE) and number of degree-days exposed in (A) coarse-mesh bags and (B) fine-mesh bags for normal flow (solid symbols are before control, before impact, and after control) and reduced flow (open symbols are after impact) treatments on Booths Creek (triangles), Kiriwhakapapa Stream (squares), and Reef Creek (circles).



FIG. 3. Leaf breakdown rate (mg/degree-day, mean  $\pm$  SE) for control (solid symbols) and impact (open symbols) treatments in (A) coarse 5-mm mesh, (B) fine 1-mm mesh, and (C) 0.25-mm mesh (leaf tubes) installed in Booths Creek, Kiriwhakapapa Stream, and Reef Creek for one month before and one month after discharge reduction between December 2004 and March 2005. Results of ANOVA for Before–After Control–Impact (BA × CI) treatments are given.

impact reach on Reef Creek relative to the control reach before reduction ( $F_{1,20} = 4.5$ , P = 0.05). However, after flow reduction, chlorophyll *a* concentrations were very similar at control and impact reaches (Fig. 6).

#### DISCUSSION

### Effects of discharge reduction on leaf breakdown

Reduced discharge had little influence on leaf breakdown rate in these streams. Leaf breakdown rate was always fastest in the coarse-mesh bags and slowest in the leaf tubes. We anticipated this response because leaves in large-mesh bags are more likely to lose particles through physical abrasion than those in fine-mesh bags (Webster and Benfield 1986). Leaves in coarse-mesh bags had the greatest exposure to physical abrasion, as well as being the most accessible to invertebrate shredders, suggesting that these factors might have an important role in leaf breakdown in these streams.

The only apparent change in leaf breakdown rate following flow reduction was a decrease in breakdown in the coarse-mesh bags at Reef Creek. There was decreased breakdown at the impact reach relative to the control, but the difference in breakdown between control and impact reaches was small. However, reduced physical abrasion could explain this pattern, because we would expect more physical abrasion and faster leaf breakdown at the higher velocity control reaches. However, despite low velocities in the reduced flow reaches of the other two streams, there were no decreases in leaf breakdown rates, making the physical abrasion explanation less plausible. Comparable findings are reported in the literature. Although physical abrasion controlled leaf breakdown during short-term peaks in flow, reduced flows did not decrease leaf breakdown rates downstream of a headwater dam (Casas et al. 2000). Similarly, Rader et al. (1994) found no difference in breakdown rates between fast and slow water and concluded that flow-related fragmentation was not an important determinant of leaf breakdown.

Macroinvertebrates may also play an important role in leaf breakdown (Wallace and Webster 1996), and faster leaf breakdown rates in larger mesh bags are often



FIG. 4. Relationship between mean CPOM (coarse particulate organic matter) travel distance and stream discharge for (A) artificial leaves and (B) 10-cm wooden dowels in impact reaches at Booths Creek, Kiriwhakapapa Stream, and Reef Creek before (solid circles) and after (open circles) flow reduction began.

attributed to invertebrates (Webster and Benfield 1986). However, specialized leaf-shredding taxa are rare in New Zealand streams (Winterbourn 2000). We did not assess leaf-pack invertebrate communities in this study, but discharge reduction did decrease invertebrate densities and the proportion of EPT individuals present in the riffle habitat where leaf packs were installed in Reef Creek (Z. Dewson, *unpublished data*). This potentially reduced the density of shredding invertebrates for the impact reach and could be responsible for the decrease in leaf breakdown at this reach. In contrast, invertebrate densities did not decrease significantly in the other streams in our study (Z. Dewson, *unpublished data*), with correspondingly no change in leaf breakdown rate.

Leaf breakdown was very similar at control and impact reaches in the fine-mesh bags. Although breakdown rate increased at the impact reach on Kiriwhakapapa Stream relative to the control reach, control and impact breakdown rates were the same during flow reduction. Large invertebrates were excluded from these bags, so any changes were thought to be attributable to changes in microbial decomposition. In addition, breakdown rates were similar in coarse- and fine-mesh bags at Reef Creek, suggesting that microbes were controlling decomposition in that stream. Temperature primarily controls microbial processing (Minshall et al. 1983), so the absence of temperature differences between control and impact reaches probably explains this lack of response to flow reduction. Increased sedimentation can decrease microbial decomposition (Rader et al. 1994, Niyogi et al. 2003), but there was no evidence that sedimentation at impact reaches was reducing leaf breakdown rates. Sediment cover of the substrate was greater for impact reaches on Booths Creek and Kiriwhakapapa Stream, but the low sediment supply from the forested catchment of Reef Creek was probably responsible for the unchanged sediment cover between control and impact reaches in that stream. Previous studies generally agree that sedimentation increases with reductions in discharge (e.g., Kraft 1972, Castella et al. 1995, Wood and Armitage 1999, Wood and Petts 1999).



FIG. 5. Percentage of (A) artificial leaves and (B) 10-cm wooden dowels captured by each type of retention structure before (n = 6 CPOM release occasions) and after (n = 9 CPOM release occasions) discharge reduction in impact reaches at Booths Creek, Kiriwhakapapa Stream, and Reef Creek.

## Effects of discharge reduction on coarse particulate organic matter (CPOM) retention

Discharge strongly influences the retention of CPOM in streams. In this short-term study, CPOM traveled farther before retention at higher discharges and impact reaches accumulated noticeably more organic material (particularly leaf litter) than controls. Many previous studies have related higher discharges to higher CPOM transport distances (Raikow et al. 1995, Larned 2000). Snaddon et al. (1992) also found that at any discharge, slow-flowing reaches generally retained more CPOM than medium- or fast-flowing reaches. Therefore, over time, reduced discharge would tend to enhance the accumulation of CPOM. The distance traveled by released CPOM increased linearly with discharge over the range of discharges tested in these streams. The natural variability of the flow regime is essential to ecosystem functioning (Poff et al. 1997). In the longer term, flow variability might be equally as important as discharge when considering the implications of water abstraction on CPOM retention. The relationship between discharge and CPOM transport depends on the temporal scale of CPOM measurement. Longer term studies have demonstrated the importance of storms and the size of storm discharges as determinants of CPOM export (Cuffney and Wallace 1989, Cuffney et al. 1990, Wallace et al. 1995). Similarly, Jones and Smock (1991) found that the mean travel distance of leaves was significantly greater at winter base discharges than at summer base discharges, and was higher again during winter spates.

Riffles retained a much higher proportion of released CPOM at low discharges in our study. In shallower water, rocks were closer to, or protruding from, the water surface, making riffles more effective retention structures. Similarly, Snaddon et al. (1992) reported that the trapping efficiency of riffles decreased with increasing discharge because the proportions of retention features alter with discharge. Webster et al. (1994) found greater retention in shallower streams, with rocks, boulders, and woody debris as the most important retention structures.

#### Effects of discharge reduction on primary production

Sampling of artificial substrates showed that relatively less algal biomass accumulated at the impact reach on Kiriwhakapapa Stream after discharge reduction, while there was relatively more accumulation at the impact reach on Reef Creek. The impact reach on Booths Creek was unchanged relative to the control. These inconsistencies between the study streams are consistent with the varying responses presented in the literature. Studies of water velocity and algae generally report that there are relationships between water velocity and periphyton (e.g., McIntire 1966, Poff et al. 1990, Biggs and Hickey 1994). However, relationships between water velocity and algae can vary depending on the growth form of the algae (Biggs et al. 1998), levels of light and nutrients,



FIG. 6. Chlorophyll *a* concentration ( $\mu$ g/cm<sup>2</sup>; mean ± SE) for control (solid symbols) and impact (open symbols) treatments installed in (A) Booths Creek, (B) Kiriwhakapapa Stream, and (C) Reef Creek for one month before and one month after discharge reduction between December 2004 and March 2005.

and the influence of velocity on the distribution of grazing invertebrates (Stevenson 1996). By reviewing the findings of numerous studies investigating the effects of water velocity on algae, Stevenson (1996) concluded that intermediate current velocities (10–50 cm/s) tend to promote the highest algal biomasses in most habitats. Increased velocities increase algal metabolism up to a point, after which the drag caused by the faster water velocities increases algal export and decreases algal biomass (Stevenson 1996).

The relative increase in algal biomass at the impact reach on Reef Creek corresponded with a significant



PLATE 1. Artificial coarse particulate organic matter (CPOM) trapped by rocks in a tributary of Kiriwhakapapa Stream, North Island, New Zealand. Photo credit: Z. Dewson.

decrease in the abundance of *Deleatidium* sp., the most common mayfly grazer at Reef Creek (Z. Dewson, unpublished data). This decrease in density of an important grazer might be responsible for the response of algae to reduced flow in this stream. In Booths Creek, we observed no change in invertebrate densities (Z. Dewson, unpublished data), and periphyton growth was unchanged by the discharge reduction. Grazer densities cannot explain decreased algal biomass at the impact reach on Kiriwhakapapa Stream, although increased sediment cover in this stream could have inhibited periphyton growth. In Kiriwhakapapa Stream, densities of Potamopyrgus antipodarum, the dominant grazer, decreased at the impact reach following discharge reduction, as did densities of Deleatidium sp. (Z. Dewson, unpublished data).

## The application of stream ecosystem functions to assess the effects of water abstraction

In this study, short-term evaluations of stream ecosystem functioning in response to water abstraction generally provided small or inconsistent responses that were not easily explained by changes in physicochemical characteristics and the macroinvertebrate community with reduced discharge. Leaf breakdown was relatively insensitive to marked decreases in discharge, although differences might have developed if the experiment had continued for a longer period. The relative importance of factors such as sedimentation, physical abrasion, and invertebrate processing on leaf breakdown were unclear. The responses of periphyton production to severely reduced discharges in these streams were inconsistent. Of the three ecosystem functions investigated in this study, CPOM retention was the most responsive to reduced discharge. The negative relationship between CPOM retention and discharge has been documented in numerous previous studies (e.g., Jones and Smock 1991, Raikow et al. 1995, Larned 2000) and was evident in the streams that we studied. There may be threshold discharges below which CPOM retention increases greatly (Raikow et al. 1995), but we did not detect this pattern over the range of discharges observed in our streams. Increases in CPOM accumulation were not matched by increases in decomposition, and invertebrate densities were lower at reduced flow reaches. Therefore, increases in CPOM retention could alter food web dynamics, habitat types, and flow characteristics, having wider implications for the invertebrate community in the longer term than a change in hydrology alone.

If the responses of leaf decomposition, CPOM retention, and primary production to flow reduction were tested over a wider range of streams, predictable responses might emerge (e.g., consistent responses within stream types, land uses, or levels of water abstraction). If so, measures of ecosystem function could enhance assessments of water abstraction impacts, and might help in interpreting the longer term implications of reduced discharge on stream ecosystems by enhancing our understanding of changes to energy supply and habitat.

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