

Top-down and bottom-up influences on populations of a stream detritivore

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SUMMARY

1. Knowledge of the influence of predatory fish in detritus-based stream food webs is poor. We tested whether larval abundance of the New Zealand leaf-shredding caddisfly, *Zelandopsycha ingens* (family Oeconesidae), was affected by the presence of predatory brown trout, *Salmo trutta* and the abundance of their primary detrital resource (*Nothofagus* leaves).

2. The density of *Z. ingens* and the biomass of leaves were determined in seven fishless streams and four trout streams in the Cass region, central South Island, on four occasions spanning 5 years.

3. Physicochemical conditions were similar in trout and fishless streams, but ANCOVA indicated that *Z. ingens* numbers were positively related to leaf biomass and that caddisfly numbers were significantly greater in fishless streams than trout streams for any given biomass of leaf. The cases of trout stream larvae were also heavier per unit length than those in fishless streams.

4. Our results provide evidence for both top-down and bottom-up influences on a detritus-based stream food web. Although stream detritivores may benefit from a habitat that provides both food and a degree of protection from predators, top-down effects of predators on detritivore population abundance were still important. Thus, detrital resource availability may determine maximum attainable population size, whereas predation is likely to reduce the population to a level below that.

Keywords: caddisfly, case morphology, detritus, leaf packs, predation

Introduction

Terrestrial detritus is a major energy source for consumers in many stream food webs (Cummins, 1974; Wallace *et al.*, 1999), but the influence of predatory fish in detritus-based stream food webs is not

well understood. Knowledge of the relative importance of top-down influences in stream detrital food webs is important because a large proportion of the energy supporting stream food webs enter through detrital pathways (Fisher & Likens, 1973; Webster & Meyer, 1997).

The effectiveness of predators in exploiting prey is a major determinant of the extent of top-down impacts on prey populations (Power, 1992). In streams, the heterogeneous environment can decrease the effectiveness of predators, and the extent of their impact, by providing refuges for prey (Lancaster, Hildrew & Townsend, 1991; Bechara, Moreau & Hare, 1993; Hart & Merz, 1998). Thus, strong effects of predatory fish on prey abundance, behaviour and life history have been observed in autotrophic (algal-based) stream

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food webs, in situations where prey are vulnerable to water column-feeding fish (e.g. Power, 1990; Peckarsky *et al.*, 2002). These impacts may be linked to the vulnerability of invertebrates whilst exploiting algal resources in exposed positions (McIntosh & Townsend, 1996). In detritus-based food webs predatory invertebrates can consume large proportions of detritivore production (Woodward, Spiers & Hildrew, *in press*) and influence community composition (Woodward & Hildrew, 2001). In contrast, detritus may offer detritivores more effective refuge from water column predators like fish. Less pronounced top-down effects could occur in detritus-based food webs if the cover provided by accumulated detritus and leaves makes invertebrates less vulnerable to fish (Reice, 1991; Rosenfeld, 2000). Thus, detritivores occupying detritus-filled depositional zones may benefit from a habitat that provides both food and protection from predatory fish. Although predatory fish have been found to influence detritivore populations in leaf packs in a few studies (e.g. Konishi, Nakano & Iwata, 2001; Ruetz, Newman & Vondracek, 2002), investigations of detrital food webs in depositional zones have often reported limited impacts of predatory fish (e.g. Reice, 1991; Rosenfeld, 2000) and those prey taxa affected by predatory fish have often been relatively large invertebrates occupying exposed positions (e.g. Schofield, Townsend & Hildrew, 1988). Moreover, predation by water column-feeding fish on benthic prey in forested streams may be low if terrestrial arthropods falling from trees satisfy food requirements (Nakano, Miyasaka & Kuhara, 1999). These and associated studies have led to the view that bottom-up influences have a much greater impact than predators on invertebrate populations in stream detrital food webs, particularly in depositional zones. In forested streams, for example, the supply of detritus can have profound impacts on prey population size and trophic dynamics (Wallace *et al.*, 1997; Hall, Wallace & Eggert, 2000). However, the long-term effects of variations in detrital inputs for predator and prey population dynamics in streams are less well known, and top-down influences could also be important over long time scales. For example, the cumulative effects of predation on detritivore abundance may be substantial when assessed over the entire larval life history of the detritivore. Knowledge of the extent of the role of predators in influencing prey population dynamics in detrital-based stream

food webs is also limited because many examinations of trophic dynamics have been conducted in systems lacking large top predators like fish, such as acidic streams (Woodward *et al.*, 2005).

As detrital-based food webs are 'donor-controlled', whereby the availability of energy is exogenously determined (Persson *et al.*, 1996), the relative importance of top-down and bottom-up influences may differ from those observed in autotrophic food webs (Rosemond *et al.*, 2001). Many ecosystems are influenced by allochthonous inputs, but the subsequent effects on trophic dynamics are less predictable (Polis, Hurd & Pinero, 1997; Jefferies, 2000). Direct effects can be weaker in detrital food webs if allochthonous inputs result in multiple food chains with high levels of omnivory (Polis, 1991; Woodward *et al.*, 2005). However, it is possible that where large efficient predators are present, top-down effects of detritivores may still be important. For example, Nyström, McIntosh & Winterbourn (2003) found unexpectedly that top-down influences on macroinvertebrate community composition were just as prominent in retentive forested streams as in predominantly autotrophic grassland streams. Although depositional habitats like leaf packs may provide macroinvertebrates with refuges from predation, their distribution is patchy and detritivores may still be vulnerable to predatory fish when moving among them. Moreover, if allochthonous subsidies bolster predator populations by providing additional food, predators may exert stronger top-down control on prey populations (Polis & Strong, 1996; Polis *et al.*, 1997). Consequently, we suspect that both bottom-up and top-down influences are likely to be important in determining detritivore abundance in at least some detritus-based stream food webs and could interact. In particular, bottom-up influences may determine detritivore abundance when resources are in short supply, and top-down influences may be more important at other times. Alternatively, if resource shortages force detritivorous consumers to be more mobile, predation could be relatively more important when food is in short supply (McNamara & Houston, 1987; Werner & Anholt, 1993).

Predators can also have non-lethal effects on the behaviour, morphology and life history of prey (Lima, 1998). Some of the most prominent effects of predators in autotrophic stream systems are associated with predator-induced changes in prey behaviour (e.g. McIntosh & Townsend, 1996). Consequently, if stream

detritivores in depositional habitats are similarly influenced by predators, their effect may be manifest in changes in prey behavioural traits, such as locomotor activity and leaf shredding (Otto, 1993; Åbjörnsson *et al.*, 2000) as well as case construction in caddisflies (e.g. Otto, 1982).

To test whether predators could influence the abundance and morpho-behavioural traits of detritivores in depositional habitats, larval populations of a detritivorous caddisfly were examined in fish and fishless streams over a period of 5 years. We tested whether larval populations of a leaf-shredding caddisfly, *Zelandopsycha ingens* Tillyard (Oeconesidae), were affected by the presence of predatory brown trout, *Salmo trutta* L. and the abundance of their primary detrital resource (leaves). *Zelandopsycha ingens* is a relatively large caddisfly (maximum case length approximately 28 mm) so we expected them to be vulnerable to water column-feeding fish like trout. This is one of few shredders occurring in New Zealand streams and has a distribution restricted to retentive beech forest (*Nothofagus* spp.) streams in the South Island of New Zealand. Although it does not appear to have been recorded from the guts of trout (McIntosh, 2000a), perhaps because there have been very few studies of trout feeding in New Zealand beech forest streams, brown trout eat *Z. ingens* when given the opportunity in experimental tanks (H. S. Greig & A. R. McIntosh, unpublished data). There are five instars and larval growth takes more than 1 year, so early instars are present in spring and summer and final instars all year round (Winterbourn & Davis, 1976; McMurtrie, 2000).

To differentiate between the relative importance of top-down and bottom-up forces on *Z. ingens*, a number of different scenarios were considered. We expected to find a positive relationship between the number of larvae and the amount of detritus in a stream if detrital resources are important in influencing the abundance of *Z. ingens*. The lack of such a relationship would indicate that bottom-up forces were relatively unimportant in determining *Z. ingens* abundance over the spatial and temporal scales measured, and a negative relationship would indicate that populations also become more dispersed in the detritus as resources increase. If predatory fish have a negative influence on *Z. ingens* populations, we expected larvae would be less abundant per unit detritus in streams with fish than in streams lacking

fish. Interactions between top-down and bottom-up forces would be indicated by different relationships between resource abundance and *Z. ingens* abundance in fish and fishless streams. For example, the abundance of *Z. ingens* may increase in proportion to resource abundance in fishless streams, but not in trout streams. Lastly, to assess whether predatory fish could affect *Z. ingens* through non-lethal mechanisms we investigated the relative lengths and weights of cases from fish and fishless streams.

Methods

Larval abundance

The density of *Z. ingens* larvae was determined in seven fishless streams and four trout streams on four sampling occasions between March 1998 and May 2003 (Table 1). Three trout streams and one fishless stream were sampled on all four dates and the others were sampled once, twice or three times (Table 1). This enabled us to compare the abundance of *Z. ingens* in trout and fishless streams with three or four replicate streams in each category on each occasion.

Streams were selected because they provided suitable physicochemical conditions for *Z. ingens*. They were first or second order, under a mountain beech [*Nothofagus solandri* var. *cliffortioides* (Hook f.) Poole] forest canopy and consistently contained accumulations of leaf detritus. All streams were located in the Cass-Craigieburn basin near Arthur's Pass National Park, South Island, New Zealand (Table 1; Fig. 1). Logistical constraints prevented all streams from being sampled in every year (e.g., some were difficult to access, some were being used for other studies and some were only discovered in later years of the study).

The density of brown trout (*S. trutta*), an exotic fish in New Zealand, was measured by three passes with a Kainga EFM300 (NIWA instruments, Christchurch, New Zealand) back-pack electrofishing machine with upstream and downstream stop nets in place (see McIntosh, 2000b; Nyström *et al.*, 2003). Only four trout streams containing suitable *Z. ingens* habitat have been found in the study area. They all contained relatively small brown trout (<250 mm, fork length), sometimes at high density (Table 1). Longfin eels (*Anguilla dieffenbachii* Gray) were occasionally present and a native benthic fish, koaro (*Galaxias brevipinnis* Günther), was present in the lower reaches of Manson

Table 1 Sampling dates for *Zelandopsyche ingens*, fish abundance, grid references and locations in Fig. 1 (site no.) for all streams

Stream name	Site no.	Grid reference*	Fish density (number 10 m ⁻²)			Year of <i>Zelandopsyche</i> sampling [†]
			Brown trout (<i>Salmo trutta</i>)	Longfin eel (<i>Anguilla dieffenbachii</i>)	Koaro (<i>Galaxias brevipinnis</i>)	
Poverty Stream	1	L34 153 946	0	0	0	1998, 2000, 2001, 2003
Middle Bush Stream [‡]	2	K34 094 964	0	0	0	1998, 2000, 2001
Camp Stream	3	K34 044 843	0	0	0	1998, 2000, 2001
Upper Manson Creek	4	K34 080 859	0	0	0	2000
Reservoir Bush Stream [‡]	5	L34 092 964	0	0	0	2003
Sugarloaf Bush Stream [‡]	6	L34 099 964	0	0	0	2003
Affluent Stream [‡]	7	L34 148 954	0	0	0	2003
Peacock Stream [‡]	8	L33 117 009	4.4 [§] , 7.4 [¶]	0.2 [§] , 0.3 [¶]	0	1998, 2000, 2001, 2003
Pylon Gully Stream [‡]	9	K34 061 962	5.5 [¶]	0.6 [¶]	0	1998, 2000, 2001, 2003
Binsler Saddle Stream	10	L34 132 998	3.3 [§] , 3.8 [¶]	0	0	1998, 2000, 2001, 2003
Mid Manson Creek	11	K34 091 855	3.9 [¶]	0	6.1 [¶]	1998, 2003

*Infomap 260, published by Land Information New Zealand.

[†]1998, March 1998; 2000, November 2000; 2001, November 2001; 2003, May 2003.

[‡]Unofficial name.

[§]Electrofished November and December 1999.

[¶]Electrofished December 2000.

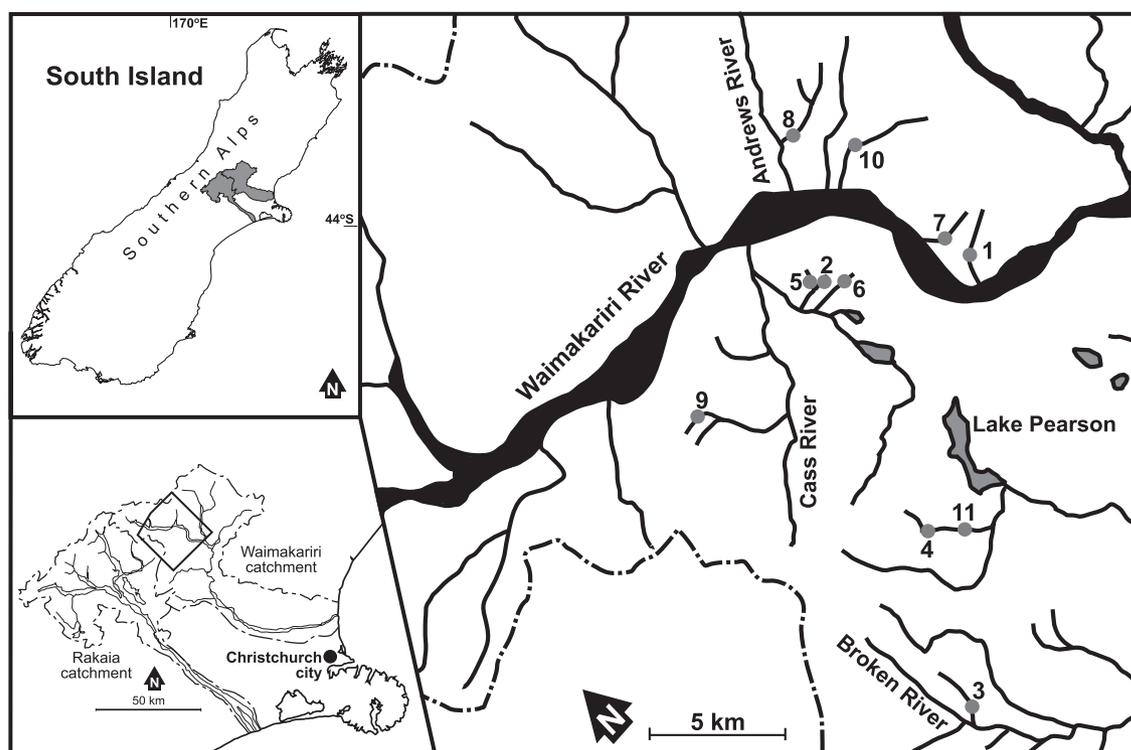


Fig. 1 The distribution of sampling sites (filled circles) among streams in the Upper Waimakariri catchment, South Island, New Zealand. Sampling site numbers correspond to those in Table 1. Only the names of major rivers are shown.

Creek in addition to brown trout (Table 1). Since quantitative fish sampling started in 1997 no fish have ever been caught by electrofishing or observed in any

of the fishless streams which are isolated by waterfalls, dry reaches or steep cascades that block fish access downstream.

Larvae of *Z. ingens* occur almost exclusively in leaf packs from the second instar onwards. Therefore, their density was estimated by counting larvae in leaf packs collected from pools and debris dams. Samples taken in gravel and cobble habitats from both trout and fishless streams during December 2000 confirmed that density was very low in non-leaf pack habitats (mean: $<5 \text{ m}^{-2}$) compared to leaf packs (mean: 329 m^{-2}). Leaf packs, defined as accumulations of leaf detritus $>0.01 \text{ m}^2$, were sampled by scooping the detritus into a D-net (600 μm mesh) held immediately downstream. On each occasion and in each stream, 10 leaf packs were sampled within a 50 m or longer reach with each leaf pack being at least 5 m upstream of any previous sampling location. Between 76 and 1378 g dry weight (DW) of leaf detritus was collected in each sample. In practise this constituted entire smaller leaf packs and a subsample of a number of leaf packs greater than about 0.1 m^2 . Subsequent work indicates that the fraction of leaf sampled as a proportion of the total leaf abundance was $<5\%$. Moreover, there is continual leaf fall to replenish resources. After frozen storage and thawing, larvae were sorted from leaf detritus in large white trays. Small size fractions of leaf detritus were searched for smaller instars in a Bogorov tray at $10\times$ magnification. Head capsule widths of larvae were measured to the nearest 0.03 mm with a linear eyepiece micrometer inserted in a binocular microscope and individuals were assigned to one of five instars, based on previous work (Winterbourn & Davis, 1976; McMurtrie, 2000). Large sticks ($>100 \text{ mm}$ length) and pieces of wood were removed from the remaining detritus (leaves and fine twigs), which was dried at $60 \text{ }^\circ\text{C}$ for at least 48 h before weighing to the nearest 0.01 g.

Case size

To evaluate whether the cases of late instar larvae in trout streams differed from those in fishless streams, case length and weight were investigated using the larvae collected in 1998 and 2003. After measuring case length to the nearest 0.5 mm with vernier callipers, cases were dried for at least 48 h and weighed to the nearest 0.01 mg. Stones and loosely attached leaves on the outsides of cases (and not incorporated into the 'log cabin' style construction of final instar cases), are not included in the weights reported here. Nevertheless, when the attachments

were included in analyses the overall patterns were essentially the same, although more variable.

Physicochemical conditions

A suite of physicochemical measurements made in November 2000 and May 2003 were analysed to determine whether habitat conditions differed in study streams with and without trout. Width and mean depth were calculated from three measurements made on at least three transects in each 50 m study reach. Velocity was estimated by determining the time taken for a slug of fluorescein dye to pass through the study reach. Median substratum particle size was assessed by measuring the longest axis of 30 (2000) or 100 (2003) randomly selected substratum particles. Mean water temperature was calculated from measurements obtained every 15 min from 20 November to 14 December 2000 and every 40 min from 14 March to 15 April 2003 with Hobo data loggers (Onset Computer Corp., Pocasset, MA, U.S.A.). Specific conductivity of the water (at $25 \text{ }^\circ\text{C}$) was measured with an Oakton 10 series meter (Oakton Instruments, Vernon Hills, IL, U.S.A.). Altitude was determined from 1 : 50 000 topographical maps (Land Information New Zealand). The stream-bed component of the Pfankuch stability index was calculated following Collier (1992). The variables measured were considered to be some of the most important physicochemical factors likely to affect the growth and abundance of stream invertebrates.

Statistical analysis

All physicochemical measurements were included as individual variables in a MANOVA followed by individual ANOVAs with trout presence as a fixed main effect to determine whether physicochemical conditions differed between trout and fishless streams.

To determine whether the relationship between the abundance of *Z. ingens* and the amount of leaf detritus was affected by the presence of trout, the data obtained from fish and fishless streams were subjected to ANCOVA, preceded by a homogeneity of slopes test. The $\ln(y + 1)$ -transformed number of late-instar *Z. ingens* (final and penultimate instars) collected from the 10 leaf packs in a stream was used as the response variable, total leaf DW sampled was used as the

covariate, and the presence of trout was a fixed main effect. Measurements from all streams on all sampling occasions were included as replicates because each year represented a separate cohort of *Z. ingens*.

MANOVA was also used to test whether the abundances of early and late instar larvae differed between fish and fishless streams, and whether there were differences between years. In the MANOVA, $\ln(y + 1)$ -transformed numbers of late and early instar *Z. ingens* per 10 g DW of leaf were used as response variables. Years, trout presence and their interaction were used as fixed main effects. Significant effects in the MANOVA were followed by univariate ANOVAs on individual variables. To determine whether population density (numbers m^{-2} of stream) differed between streams with and without trout, it was necessary to measure the total amount of leaf pack habitat available, because results indicated that population size was related to the amount of detritus present. This was carried out in 2003, and involved measuring the maximum length and corresponding width of every leaf pack in the 50 m study reach. Using these measurements the total DW of leaf in the study reach was estimated from the relationship between the DW of sampled leaf packs and their linear dimensions.

The total number of late instar *Z. ingens* larvae present per square metre of stream bed was estimated by multiplying the DW of leaf in the reach ($g m^{-2}$) by the number of caddis per gram leaf DW. These measurements (the numbers of late instar *Z. ingens* m^{-2}) were then used in a *t*-test to compare the abundance of caddis in trout and fishless streams.

To test whether case construction differed in trout and fishless streams, case mass per unit length [$\ln(\text{case DW in mg})/\ln(\text{case length in mm})$] of fourth and fifth instar larvae was compared between streams with and without trout using two factor ANOVA with uneven replication. All statistical analysis was undertaken using Systat 10 (SPSS, Chicago, IL, U.S.A.).

Results

Physicochemical conditions

Physicochemical conditions in the trout and fishless streams overlapped extensively (Fig. 2). The streams were small (0.8–3.5 m wide and <20 cm deep) with cobble-dominated substrata and cool temperatures. No significant differences between fishless and trout streams were detected by MANOVA, or any individual

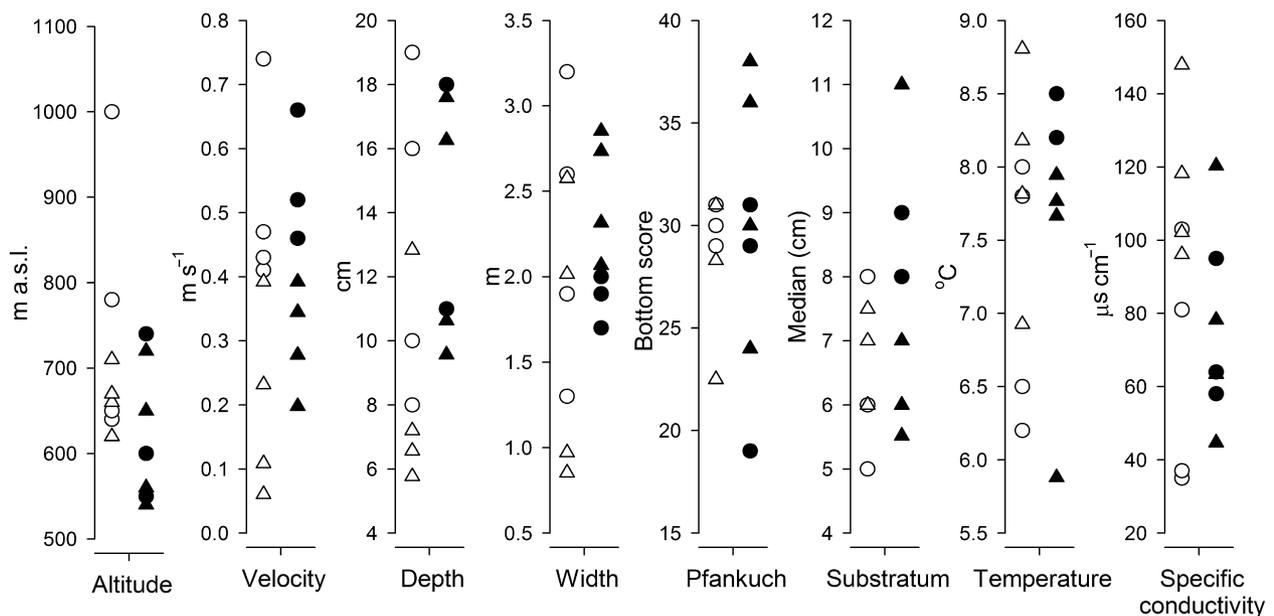


Fig. 2 Physicochemical conditions, measured in November (except for temperature) 2000 (circles) and 2003 (triangles), in fish (black symbols) and fishless (open symbols) streams sampled for *Z. ingens*. Mean water temperature was calculated from measurements made by data loggers from November to December, and from March to April in 2000 and 2003, respectively. See Methods for more information on these and other measurements.

univariate ANOVA on any variable measured. Thus, differences in caddis populations between trout and fishless streams were unlikely to be a consequence of substantial differences in the physicochemical environments of trout and fishless streams.

Larval abundance

The number of late instar *Z. ingens* in leaf packs was not affected by an interaction between the presence of trout and the biomass of leaf detritus collected (homogeneity of slopes test, fish \times leaf biomass interaction: $F_{1,25} = 1.745$, $P = 0.20$). Thus, the slope of the relationship between the biomass of leaf packs sampled and the number of late instar caddis in the sampled leaf packs was similar in trout and fishless streams (Fig. 3). ANCOVA indicated that numbers of *Z. ingens* were positively related to the amount of leaf biomass sampled and that numbers of larvae were significantly greater in fishless streams than trout streams, for any given biomass of leaf (Table 2; Fig. 3).

Table 2 ANCOVA on $\ln(y + 1)$ -transformed total number of late instar *Zelandopsyche ingens* in leaf packs collected from streams with and without trout (Fish) with the \ln -transformed total biomass of leaf sampled (g DW) as a covariate

Source	d.f.	MS	F-ratio	P-value
Ln leaf biomass	1	20.30	13.703	0.001
Fish	1	22.43	15.137	<0.001
Error	26	1.481		

Further testing of the effect of trout on caddisfly abundance using MANOVA revealed significant main effects of fish and year and a significant interaction between them (Table 3). The univariate ANOVAs showed that the significant fish effects were mainly associated with late instar larvae. Thus, there were more fourth and fifth instar *Z. ingens* per unit leaf pack in fishless streams than trout streams on all sampling occasions (Fig. 4a). Abundance data for early instar *Z. ingens* indicated no consistent fish effect (Fig. 4b), hence the significant year \times fish

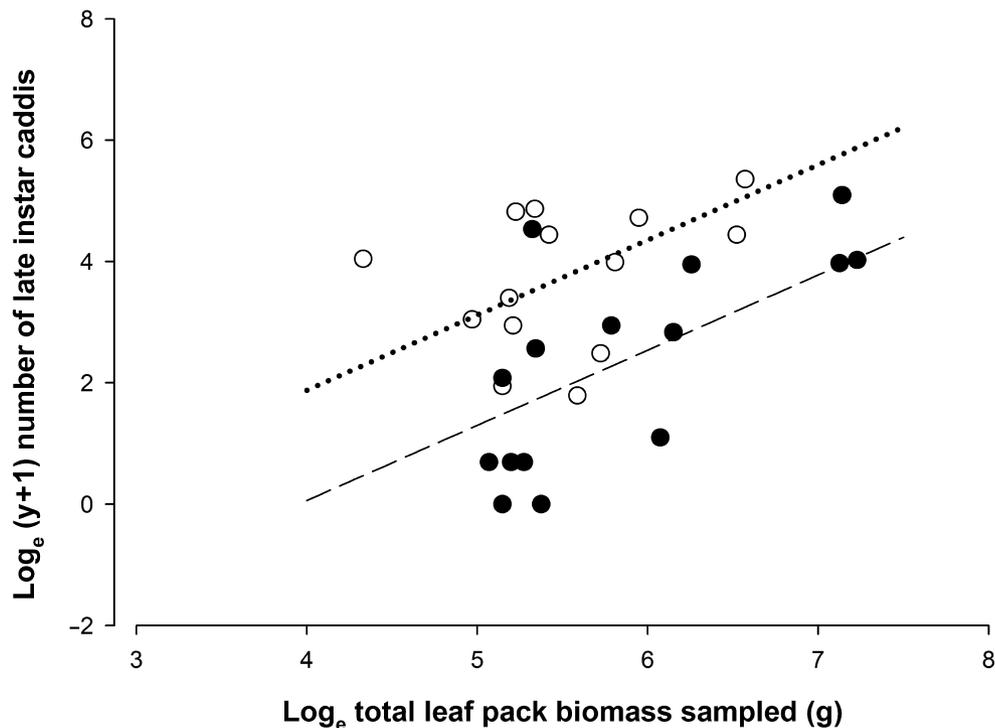


Fig. 3 Relationship between the \ln -transformed total biomass of sampled leaf packs (g dry weight, DW) and the number of late instar (fourth, penultimate; and fifth, final) *Zelandopsyche ingens* in fish (black symbols) and fishless (open symbols) streams. The ANCOVA model (Table 2) describing the relationship had $r^2 = 0.41$. Equations of the lines plotted are: fishless (dotted line), $\ln(\text{number of caddis} + 1) = 1.239 \ln(\text{leaf}) - 3.079$; and trout streams (dashed line), $\ln(\text{number of caddis} + 1) = 1.239 \ln(\text{leaf}) - 4.895$. Each point represents the measurements from one stream sampled on one occasion.

Table 3 Multivariate (MANOVA) and univariate ANOVA on the abundance of *Zelandopsycha ingens* measured as numbers per unit leaf dry weight (DW) in streams with and without fish in four sampling periods (years) for both early (one to third) and late (fourth and fifth) instars. Abundance per unit mass of leaf was calculated as $\ln(\text{number} + 1)/\ln(\text{g DW})$.

Source	d.f.	MS	F-ratio	P-value
MANOVA				
Fish	2, 20	0.363*	17.58	<0.001
Year	6, 40	0.083*	16.48	<0.001
Fish \times year	6, 40	0.371*	4.276	0.002
Early instars				
Fish	1	0.034	1.394	0.251
Year	3	0.268	11.14	<0.001
Fish \times year	3	0.203	8.456	0.001
Error	21	0.024		
Late instars				
Fish	1	0.446	32.80	<0.001
Year	3	0.347	25.47	<0.001
Fish \times year	3	0.021	1.575	0.225
Error	21	0.014		

*Wilks' Lambda.

interaction (Table 3). The density of early instar larvae was substantially greater in trout streams than fishless streams in November 2000, but density did not follow this pattern consistently (Fig. 4b).

A comparison of the density (nos. m⁻²) of late instars in May 2003 indicated that, although mean density was higher in fishless streams than trout streams (Fig. 4c,d), there was no significant difference between the two stream types when assessed per unit of stream bed ($t = 1.757$, d.f. = 6, $P = 0.13$). This was because one fish stream (Pylon Gully) contained a particularly large biomass of leaves, and therefore had a larger population of *Z. ingens* in 2003 than the other trout streams.

Case size

Cases of trout stream larvae were heavier per unit length than those in fishless streams (two-factor ANOVA, fish effect: $F_{1,13} = 14.01$, $P = 0.002$; Fig. 5). The same pattern held for both fourth and fifth instars as there was no interaction between instar and fish (interaction: $F_{1,13} = 1.504$, $P = 0.24$). There was, however, a significant effect of instar (instar: $F_{1,13} = 66.39$, $P < 0.001$) with final instars having heavier cases per unit length than penultimate instars (Fig. 5). This was because the latter use pieces of leaf to build their

cases, whereas denser twigs are used by final instars (Winterbourn & Davis, 1976).

Discussion

Many stream ecosystems, like various other types of ecosystems, are driven by energy derived from detritus (Polis & Strong, 1996; Polis *et al.*, 1997) and variations in detrital inputs to streams can affect predator-prey interactions (Hall *et al.*, 2000). However, the full extent of top-down and bottom-up influences in detrital-based food webs have not been revealed by previous studies. Many detrital food webs have consumers with comparatively long life-cycles (such as *Z. ingens*) and it is therefore possible that several generations of consumers are required to detect responses to altered detrital inputs (Richardson & Neill, 1991). Moreover, few studies have considered variations in detritivore abundance at a large enough spatial scale to assess the influence of predatory fish. Our results showed that both the quantity of resources that provide food and habitat for larvae, and the presence of predatory fish, had significant effects on the abundance of *Z. ingens*. Furthermore, fish had a significant effect on the weight of *Z. ingens* cases. The results, therefore, provide evidence for both top-down and bottom-up influences on populations of a stream detritivore.

The bottom-up influence was revealed by a positive relationship between the amount of resource sampled and the number of late instar caddisflies present in the sample. Because the amount of detritus in each stream reach was only measured in May 2003, we could test the effect of total resource availability on population size at the whole stream level once. However, because detritus provides both habitat and food for *Z. ingens* it was possible to infer the effect of resources on the abundance of *Z. ingens* from resource samples of known size. The positive relationship between *Z. ingens* abundance and leaf abundance obtained from combinations of eleven streams sampled on four occasions is good evidence for an effect of resource abundance on *Z. ingens* populations. Such a general relationship could only be generated by a consistent influence of detritus abundance on caddisfly numbers.

The finding that *Z. ingens* populations are affected by the abundance of detrital resources is in accordance with previous work on this species. Rounick &

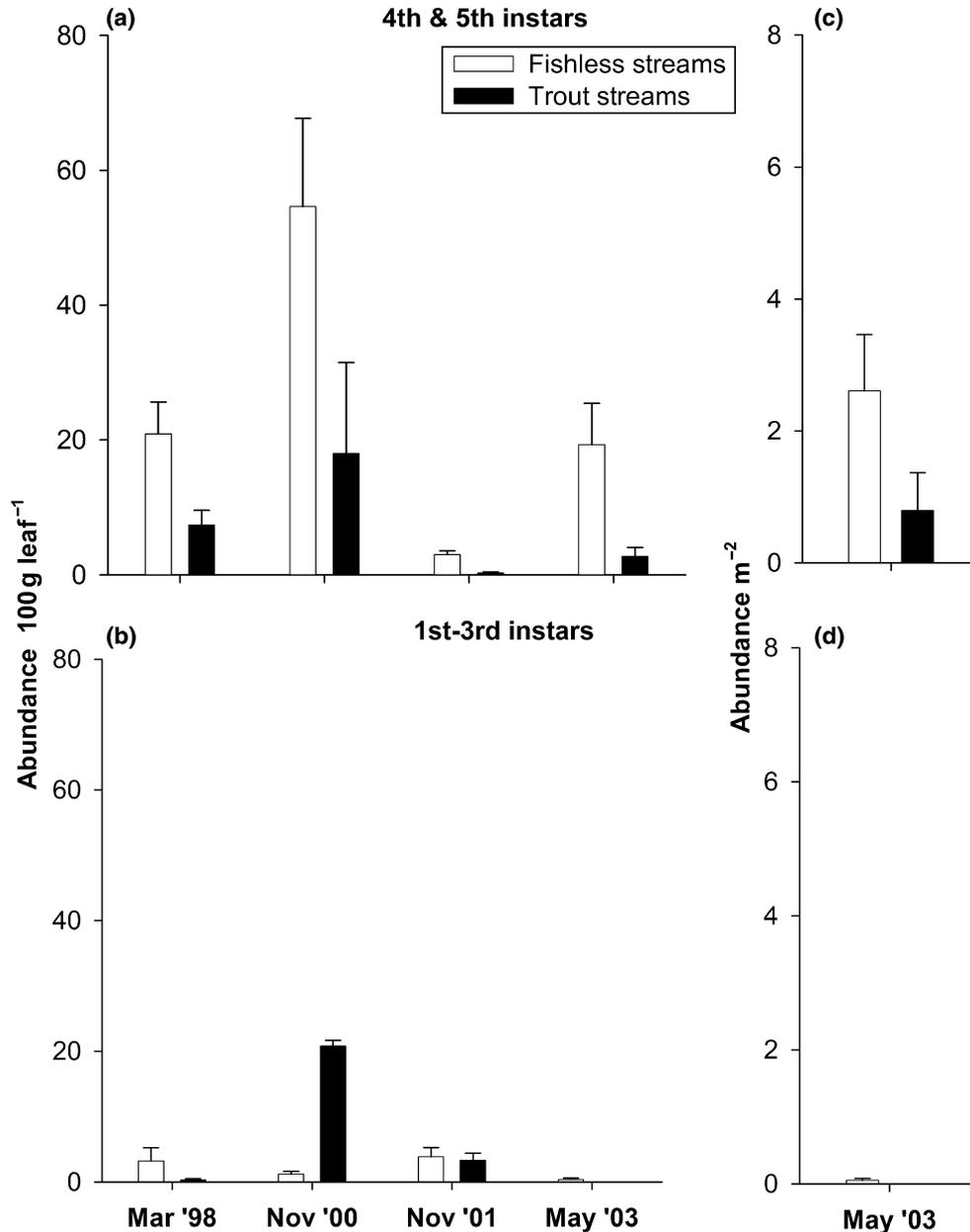


Fig. 4 Abundance of late [fourth and fifth (a & c)] and early [first to third (b & d)] instar *Zelandopsycha ingens* in streams with and without predatory fish measured on four sampling dates and expressed as numbers per 100 gram of leaf dry weight (a & b) and as numbers per square metre of stream for May 2003 only (c & d). Note the different scales on the y-axes. Three or four streams with and without fish were sampled on each date (see Table 1 for details).

Winterbourn (1983) found that, although caged *Z. ingens* grew and survived in a poorly retentive stream with normally low detritus abundance just as well as those in a retentive control stream, they were naturally absent from the former. Similarly, McMurtree (2000) found that *Z. ingens* was absent from streams that were disturbed frequently and therefore

contained low amounts of leaf detritus. Both studies concluded that retention of leaf resources was a key factor affecting shredder populations. Many other studies have concluded that the abundance of detrital resources has a substantial influence on detritivore populations (e.g. Dobson & Hildrew, 1992), and has led to the view that bottom-up forces are of primary

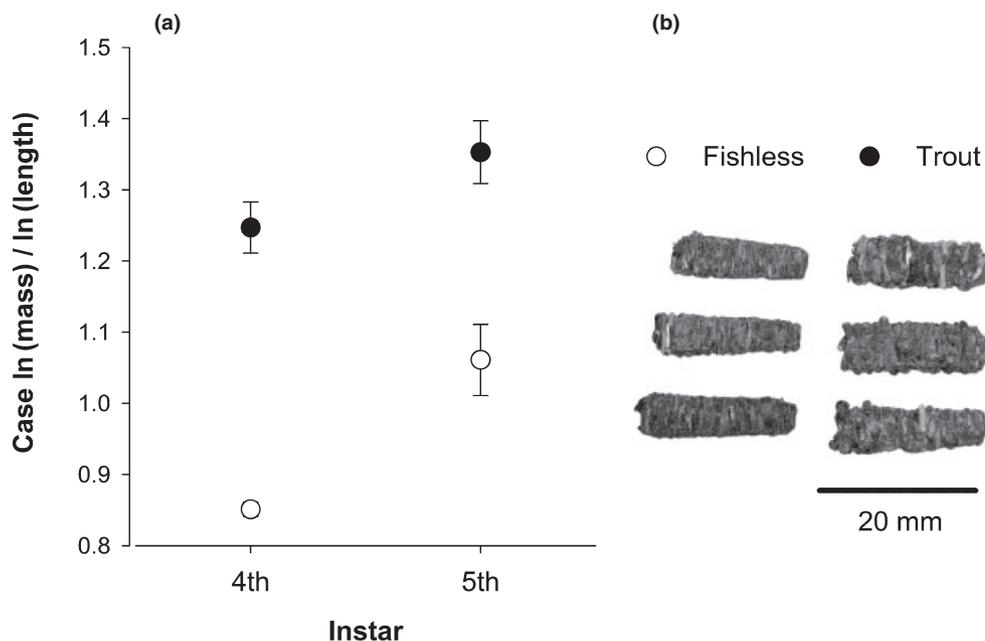


Fig. 5 The mean (\pm SE) ratio of $\ln(\text{dry weight in mg}) / \ln(\text{length in mm})$ of organic cases constructed from *Nothofagus* twigs (final instar) and leaves (penultimate instar) by *Zelandopsycha ingens* in trout (closed circles) and fishless (open circles) streams (a). Streams were used as replicates so the data used to calculate means were the averages for all individuals collected during 1998 and 2003 from a stream. For penultimate instars $n = 4$ and 3 for fish and fishless streams, respectively; and for final instars, $n = 4$ and 6 for fish and fishless streams, respectively. Examples of final instar cases from each type of stream are shown (b).

importance in detrital-based food webs (Richardson & Neill, 1991; Richardson, 1991; Wallace *et al.*, 1997; Dyer & Letourneau, 2003).

Our results like those reported by Woodward *et al.* (2005) for predatory invertebrates indicate that top-down influences also have a role to play in detrital systems. We found that the density of *Z. ingens* per unit leaf pack was consistently lower in streams containing trout than those lacking fish. Similarly, Nyström *et al.* (2003) found that forested New Zealand streams with trout contained a lower biomass of shredders than streams without fish. In the present study, the univariate ANOVAs indicated that this top-down effect was mainly associated with the larger, late-instar caddisflies, an effect that may appear surprising given that *Z. ingens* larvae occupy leaf pack habitats almost exclusively, and are not a known prey of trout (McIntosh, 2000a). However, as indicated earlier, observations made in experimental stream channels indicate that trout will prey on late instar *Z. ingens*. Therefore, large *Z. ingens*, which move on the surface of leaf packs at night, are likely to be vulnerable to trout predation. Studies of nocturnal foraging by brown trout indicate they

are capable of detecting and capturing benthic prey at night (McIntosh & Townsend, 1995; Giroux, Ovidio & Baras, 2000), and observations made by McMurtrie (2000) showed that *Z. ingens* from a trout stream spent significantly less time moving outside leaf packs than larvae from a fishless stream population. These findings support the suggestion that *Z. ingens* larvae are vulnerable to trout predation at night. Our finding that only the larger late-instars were consistently affected by fish is also in agreement with knowledge of the predatory effects of trout, which show positive size-selectivity for large prey even at night (McIntosh & Townsend, 1995; McIntosh, Peckarsky & Taylor, 2002). Because late-instar *Z. ingens* are among the largest invertebrates found in New Zealand streams, they are likely to be particularly vulnerable to a size-selective predator.

New Zealand streams containing trout can have considerably different invertebrate community structures compared to those lacking trout (Nyström *et al.*, 2003). However, indirect effects associated with the different communities are unlikely to explain the lower *Z. ingens* abundance in trout streams. No

predatory invertebrates that are large enough to present a serious threat to large *Z. ingens* larvae, occur in these streams, and we have found no difference in the biomass of predators inhabiting leaf packs in trout and fishless streams (H. S. Greig & A. R. McIntosh, unpublished data). Thus, a negative indirect effect of fish, created by facilitation of another predator by trout, is improbable. A negative indirect effect of trout on *Z. ingens* via a competitor with *Z. ingens* is also unlikely because in these streams *Z. ingens* larvae account for the great majority of shredder biomass. Moreover, the biomass of other shredders did not differ significantly between trout and fishless streams (H. S. Greig & A. R. McIntosh, unpublished data).

We found that both final and penultimate instars of *Z. ingens* from trout streams had heavier cases per unit length than those from fishless streams. An increase in case weight would strengthen the case, which could reduce predation by fish like trout. In some other caddisflies, cases are strengthened by the addition or incorporation of stones, and can make predation by trout more difficult (Otto & Svensson, 1980; Otto & Johansson, 1995); species with more rigid cases have higher survival rates after attack (Johansson, 1991). However, it is conceivable that case construction by *Z. ingens* and other caddisfly larvae from streams inhabited by fish is energetically expensive (Otto & Svensson, 1980). If this translates into fewer offspring, it may have a non-lethal effect on population size. Non-lethal effects of predators on prey population abundance are rare in streams, however (Peckarsky, Cooper & McIntosh, 1997), and we have evidence that *Z. ingens* adults from trout streams are neither smaller, nor less fecund than those in fishless streams (H. S. Greig & A. R. McIntosh, unpublished data). Our results suggest that if trout have significant non-lethal effects on *Z. ingens* populations, these are likely to be because of reduced growth and altered development rate during the larval stage rather than effects on adult fecundity.

Because there were no major physicochemical differences between fish and fishless streams, our comparison was unlikely to be confounded by other variables. Moreover, because fishless streams were rendered fishless by a variety of barriers other than stream size, they spanned a wide range of sizes that encompassed the size range of the trout streams. Hence, our study reveals that both top-down and

bottom-up forces play a role in influencing the abundance of *Z. ingens* in New Zealand forest streams. Although accumulations of detritus may provide refuges from predation and food for *Z. ingens*, we still observed that top-down forces were important. Furthermore, our findings indicate that top-down and bottom-up controls tended to operate relatively independently. Thus, over the range of resource densities sampled, fish reduced *Z. ingens* numbers by a consistent proportion despite differences in fish population size. This finding implies that resource availability determines the maximum population density attainable in these streams, whereas predation is likely to reduce the population to a level below that. Consequently, both top-down and bottom-up processes are likely to be important in detritus-based stream food webs.

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