

Indirect effects of predatory trout on organic matter processing in detritus-based stream food webs

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Indirect effects of predators on basal resources in allochthonous-based food webs are poorly understood. We investigated indirect effects of predatory brown trout (*Salmo trutta*) on detritus dynamics in southern beech (*Nothofagus* spp.) forest streams in New Zealand through predation on the obligate detritivore, *Zelandopsyche ingens* (Trichoptera, Oeconesidae). Trout presence/absence and *Z. ingens* density were manipulated in flow-through tanks to investigate the lethal and sub-lethal effects of trout on litter processing by *Z. ingens*. An experiment that allowed trout access to *Z. ingens* showed trout predation reduced densities of *Z. ingens* resulting in slower breakdown of coarse particulate organic matter (CPOM) and reduced production of fine particulate organic matter (FPOM). A second experiment that prevented trout access to *Z. ingens*, but allowed the transmission of trout cues, resulted in no change in litter processing rates in the presence of trout. Litter processing rates were higher in high *Z. ingens* density treatments compared to low density treatments. Thus, trout effects on litter processing were due to reduced *Z. ingens* densities, not trout-induced modifications to *Z. ingens* feeding behaviour. Field assays of litter processing rates using artificial leaf packs in natural streams showed significant reductions in CPOM loss in trout streams compared to fishless streams. *Z. ingens* dominated biomass in fishless stream leaf packs, but a facultative shredder, *Olinga feredayi*, dominated trout stream leaf packs. Thus, the absence of *Z. ingens* drove differences in processing rates between trout and fishless streams and the indirect effects of trout on litter processing observed in mesocosms were evident in complex, natural food webs. Overall our study provides evidence that predators can influence resource dynamics in donor-controlled food webs through their effects on consumers.

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Indirect effects have a potentially large influence on the structure of many ecological communities (Wootton 1993, Menge 1995). They can propagate through food webs resulting in trophic cascades, whereby predators indirectly affect resource dynamics through direct effects on consumers (Paine 1980, Carpenter et al. 1985). Trophic cascades have been observed in freshwater benthic and pelagic communities, marine algal beds, and a variety of terrestrial communities (Persson 1999, Halaj and Wise 2001, Shurin et al. 2002) and occur through predator-induced changes in abundance

of consumers (density-mediated effects, Power 1990, Carpenter and Kitchell 1993), and/or through alterations in consumer behaviour (trait-mediated effects, McIntosh and Townsend 1996, Schmitz et al. 1997).

Studies of trophic cascades have focused largely on autochthonous resource-based food webs, in which basal resources are derived from in situ primary production. However many food webs receive considerable energy from allochthonous resources (i.e. they are derived from external production, Polis et al. 1997), and the role of biotic interactions in these food webs is poorly

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understood (Polis and Strong 1996, but see Rosemond et al. 2001). In allochthonous resource-based food webs, the rate of transfer and renewal of resources are extrinsic to the community (i.e. donor controlled, Polis and Strong 1996), however, the standing stock and turnover of resources may be altered by intrinsic biotic interactions (Persson et al. 1996, Ruetz et al. 2002). Moreover, because the rate of input of detritus is not linked to consumer interactions, the potential for top-down control of detrital resources may be higher than in autotrophic systems where consumer-altered renewal rates of resources can compensate for consumptive losses of resource biomass (Rosemond et al. 2001). Thus, predators can affect detrital resource dynamics indirectly if they suppress the density or foraging behaviour of detritivorous consumers (Wyman 1998, Lawrence and Wise 2000, Mancinelli et al. 2002).

Forested headwater streams are excellent examples of allochthonous resource-based food webs, where spatial subsidies of terrestrial detritus and dissolved organic carbon (DOC) derived mainly from leaves form the basis of much secondary production (Fisher and Likens 1973, Wallace et al. 1997). A combination of physical, chemical and biotic breakdown of detritus occurs in streams, with detritivorous invertebrates playing a particularly important role in fragmenting large particles and egesting fine particles enriched with microbes (Anderson and Sedell 1979, Wallace and Webster 1996). Predators may influence the breakdown of coarse detritus and production of fine particles indirectly through density-mediated effects whereby predators reduce detritivore density, or through trait-mediated effects which result from predator-induced alteration in detritivore traits such as feeding behaviour.

Indirect effects of predators on detritus dynamics through the suppression of detritivorous invertebrate density have been observed in small-scale experiments (Oberndorfer et al. 1984, Short and Holomuzki 1992, Malmqvist 1993), but tests of the importance of these interactions in more complex, natural stream food webs have been equivocal (Malmqvist 1993, Ruetz et al. 2002, but see Konishi et al. 2001). Moreover, the leaf accumulations that stream detritivores inhabit may act as refuges from predation, especially by fish (Reice 1991, Rosenfeld 2000), such that density-mediated trophic cascades may not occur. Experimental tests of trophic cascades in mesocosms are useful for isolating mechanisms, but the complexities of natural food webs can act to diffuse top-down interactions and decouple trophic cascades at larger scales (Polis 1994, Polis and Strong 1996, Persson 1999). Variation in susceptibility to predation within functional groups for example, may lead to compensatory population increases by less vulnerable species in response to predation on vulnerable species (Steiner 2001). If these competing species are functionally similar, compensatory dynamics

may alleviate indirect effects of predators on ecosystem processes such as litter breakdown (i.e. the system exhibits functional redundancy; Walker 1992, Lawton and Brown 1993).

In this study we used mesocosm experiments and field assays to investigate the effects of predatory brown trout (*Salmo trutta*) on organic matter dynamics through density- and trait-mediated effects on a stream detritivore, *Zelandopsycha ingens* (Trichoptera, Oeconesidae). *Z. ingens* is an obligate shredder that feeds primarily on mountain beech detritus (*Nothofagus solandri*). Feeding trials suggest that *Z. ingens* is an integral component of litter breakdown in beech forest streams (Winterbourn and Davis 1976). Brown trout (*Salmo trutta*) are the top predators in these streams, and streams containing trout have a significantly lower biomass of shredders (Nyström et al. 2003), including *Z. ingens*, which is found at considerably lower densities in trout streams compared to fishless streams (McIntosh et al. 2005). We predicted that trout, by reducing *Z. ingens* density (and possibly by influencing foraging behaviour), would indirectly reduce litter breakdown and production of fine particles. We tested this hypothesis by manipulating trout presence/absence and *Z. ingens* larval density in mesocosms. Other large-particle detritivores inhabit these streams, including the obligate oconesiid shredder, *Oeconesus* sp., and two facultative shredders *Olinga feredayi* (Trichoptera, Conoesucidae) and *Austroperla cyrene* (Plecoptera, Austroperlidae). Thus we also conducted field assays of litter processing rates to assess whether interactions between trout, *Z. ingens*, and detritus observed in the mesocosms were influential in the dynamics of complex natural stream food webs with multiple detritivores.

Material and methods

Lethal experiment

We investigated the effects of trout on larval density and litter processing rates of *Z. ingens* by manipulating trout presence and absence and *Z. ingens* density in a two by two factorial experiment, set up in a randomised block with four replicates using sixteen oval black polythene tanks (1.24 × 0.7 m, 0.8 m²), similar to those illustrated by McIntosh and Peckarsky (1996), at the University of Canterbury's Cass Field Station. The tanks were gravity-fed by bore water (pH, 7.7; conductivity, 114 µS₂₅ cm⁻¹; temperature, 10°C), free of fish chemical cues and fine particles. A central standpipe with openings covered with 1 mm mesh regulated water depth at 21 cm and prevented escape of insects and CPOM. Nylon stockings (150 µm mesh) attached to the standpipe outflows collected any organic matter leaving the tanks. Perspex baffles (L × W: 28 × 35 cm) attached to the standpipe directed water from two jets on opposite sides of the

tank, producing circular flow. Velocity within tanks ranged from 0.02–0.07 m s⁻¹ depending on proximity to the water jets, but was similar between tanks (mean ± SE: 0.05 m s⁻¹ ± 0.01). Tanks were aerated through air stones and covered with black 1 mm mesh for the duration of the experiment. Tank bottoms were covered with gravel particles collected from a dry river bed and trout cover was provided by 12 cm lengths of PVC pipe set into the substratum. Beech leaves (*Nothofagus solandri*) collected from fishless streams were added to each tank to provide a realistic, patchy food resource. After collection, leaves were washed in a 1 mm mesh sieve to remove fine particulates, dried for 72 h at 50°C and weighed into 35 g leaf packs. Each leaf pack was soaked in aerated bore water containing 20 ml of solution prepared from homogenized wet beech leaves freshly collected from a fishless stream as a microfloral inoculant (Winterbourn and Davis 1976). After 7 days, leaves were removed, rinsed in a 1 mm sieve, and added to each tank to create two leaf packs (approximately 10 × 10 cm) in the low velocity zone behind each water jet. Four grams of dried beech leaves enclosed in a 600 µm mesh bag (L × W: 8 × 8 cm) that prevented consumption by *Z. ingens* was tethered to the gravel substrate of each tank to compare “shredder independent” loss of CPOM between treatments.

Late instar *Z. ingens* larvae (mainly fourth instar) were collected from a fishless stream (Middle Bush Stream) on 7 February 2003, and kept in aerated bore water for one hour until the start of the experiment. Ten larvae per tank were distributed evenly between leaf packs in eight tanks, with 20 larvae per tank added to the other eight tanks. This created low *Z. ingens* density treatments similar to mean densities in fishless streams and high *Z. ingens* density treatments within the upper range observed in fishless streams (McIntosh et al. 2005). Brown trout (*Salmo trutta*) were collected by electric fishing a stream in which *Z. ingens* was also present (Peacock Stream). One trout was introduced to four of the low and four of the high density tanks (mean fork length ± SE: 125 ± 3 mm, range: 111–140 mm). Trout density in tanks (1.25 per m²) was within the range found in trout streams in the Cass area (McIntosh 2000). Supplementary food was provided by adding 30 larvae of a leptophlebiid mayfly, *Deleatidium*, to each tank (trout and troutless) at the start of the experiment, and 20 further individuals twice weekly to trout tanks only thereafter. Thus, a total of 170 mayflies were added to each trout tank over the duration of the experiment. Midway through the experiment, 20 *Deleatidium* were also added to fishless tanks to compensate losses via emergence. The experiment ran for 32 days and ended on 10 March 2003 when trout were removed, measured and weighed. *Z. ingens* and *Deleatidium*, were recovered from tanks by carefully picking through the substrate and enumerated. MANOVA and univariate ANOVAs

on temperature, pH, conductivity and velocity at the conclusion of the experiment indicated no significant difference in physico-chemical conditions between treatments.

Organic matter was collected from tanks by passing the tank water through 125 µm sieves and separated into CPOM (>1 mm) and FPOM (<1 mm). CPOM was searched for any remaining *Z. ingens*, which were removed before being dried at 50°C for 72 h and weighed to the nearest 1 mg. FPOM was dried at 50°C for 72 h, weighed to the nearest 0.1 mg, ashed at 450°C for 6 h and then reweighed to calculate ash free dry mass (AFDM). Organic matter collected in outflow stockings and remaining in invertebrate exclusion packs were processed using the same procedure.

Sub-lethal experiment

A second mesocosm experiment was conducted to investigate whether trout influence litter processing by modifying feeding behaviour of *Z. ingens*. Each tank was fitted with a 1 mm insect mesh screen supported by cobbles 6 cm above the substratum. Trout were placed above the screen and *Z. ingens* below, thus allowing the passage of trout cues but preventing trout predation on *Z. ingens*. Tanks were set up as in the lethal experiment, except that the Perspex baffles around the stand pipe were removed so the mesh screen could be fitted. On 27 February 2004, caddisflies, gravel and preconditioned leaf matter (30 g) were placed below the screen in the same arrangement as for the lethal experiment. An additional six cobbles were placed on top of the mesh along with a PVC trout hide. Caddisfly density was manipulated to reflect mean *Z. ingens* density in trout and fishless streams, with 5 or 15 *Z. ingens* per tank, respectively. Brown trout (mean fork length ± SE: 109 ± 2 mm, range: 102–123 mm) were placed in eight randomly selected tanks later the same day. In this way, both density-suppression and trait-mediated effects of trout on litter processing rates were investigated in a fully factorial design with four replicates of each treatment arranged in randomised blocks. Trout were fed 20 *Deleatidium* larvae twice weekly, and each week an additional two fifth instar *Z. ingens* were introduced into each tank above the mesh screen to ensure the full range of chemical cues elicited by the consumption of *Z. ingens* larvae by trout were present. The experiment ran for 43 d when trout, *Z. ingens*, and organic matter were removed and processed as in the lethal experiment. MANOVA and univariate ANOVAs on temperature, pH and conductivity at the conclusion of the experiment indicated no significant differences in physico-chemical conditions between treatments.

Field assay of organic matter processing

To assess the importance of the interactions observed in the mesocosms in natural food webs, artificial leaf packs were placed in four trout streams (Binser Saddle Stream, Peacock Stream, Pylon Gully Stream and Manson Creek) and four fishless streams (Sugarloaf Bush Stream, Reservoir Bush Stream, Poverty Stream and Affluent Stream) at Cass to compare leaf breakdown rates. The fish faunas and general characteristics of these streams have been described previously (McIntosh 2000, Nyström et al. 2003, McIntosh et al. 2005). Chambers made from two 7.5 cm tubes of 10.2 cm diameter opaque PVC pipe joined side by side were used to retain the small *Nothofagus* leaves (<20 mm). The ends of one chamber of each pair were closed with 5 mm nylon mesh, the others with 200 µm mesh, and will be referred to as the coarse and fine leaf packs, respectively. The 5 mm mesh allowed access to detritivorous invertebrates, including *Z. ingens*, whereas the 200 µm mesh prevented colonisation by all but the smallest invertebrates. Chambers were filled with 10 g DW of mountain beech leaves collected from a fallen branch. Six pairs of enclosures were tethered in low velocity (<15 cm s⁻¹) zones along a 50 m reach in each of the eight streams on 28 February 2003. Three pairs of leaf enclosures selected at random were removed from each stream after 31 d and frozen, with the remainder collected after 74 d. In the laboratory, the contents of enclosures were washed over a 1 mm sieve and invertebrates removed and identified using standard keys (Winterbourn et al. 2000). Shredders (according to Winterbourn 2000) in coarse mesh enclosures were enumerated and fine mesh enclosures were checked for their presence. Weight loss of leaves was determined after drying for 72 h at 50°C and weighing to the nearest 1 mg.

To evaluate alternative hypotheses accounting for differences in litter breakdown rates between trout and fishless streams, we measured physical, chemical and geographic characteristics within the 50 m study reach in each stream. Altitude was estimated from 1:50000 scale topographical maps. The quantity and distribution of beech leaf was assessed by measuring the two longest axes of every leaf pack with an area >100 cm² in each reach. From this we calculated leaf area per m² stream and mean area per leaf pack. Every five metres, stream width and three depths across the channel were recorded. Mean water velocity was estimated by monitoring the rate of travel of fluorescing dye over 20 m. Discharge was measured using the velocity–area integration method (Gordon et al. 1992) with a Marsh-McBirney model 201 meter. We measured the longest axis of 100 randomly selected substrate particles in each stream to calculate the substrate index of Jowett et al. (1991). Streambed stability was assessed with the bottom component of the Pfankuch index (Death and

Winterbourn 1994). Water temperature was recorded every 40 min from 14 March to 15 April 2003 with Hobo (Onset Corp) data loggers and this was averaged over the sample period. Conductivity and pH were measured with calibrated hand-held meters.

Statistical analysis

MANOVAs, ANOVAs and GLMs were used to test response variables in the two tank experiments, with trout presence/absence and low/high *Z. ingens* density as fixed effects, and experimental block included as a random factor. In all cases, the block effect was not significant but was retained in the final model to reflect the design of the experiments. Differences in the final density of *Z. ingens* between treatments in both tank experiments were analysed with ANOVA after log_e(x+1) transformation of counts. Other data transformations are indicated in table captions.

The 12 measured physico-chemical variables in the stream survey were reduced into independent factors by principal components analysis (PCA) using a correlation matrix. Leaf area per m² stream and mean area per leaf pack required inverse square root transformation with the remaining variables not transformed. PCA factors with standardised eigenvalues greater than one were retained (Dillon and Goldstein 1984) and analysed with MANOVA to test for differences in physico-chemical conditions between trout and fishless streams. Two leaf enclosures, one in a trout stream (Peacock Stream) and one in a fishless stream (Sugarloaf Stream), were damaged by wildlife and were not included in analyses. Shredder biomass and composition in coarse leaf packs were analysed with split-plot MANOVA and univariate ANOVAs for each shredder species. CPOM biomass remaining at the end of the field assay was analysed with split-plot ANOVA (using GLM procedures to account for the unbalanced design). MANOVA and GLM tests were performed using S-Plus 4.5 software, while SYSTAT 10 was used for other tests.

Results

Lethal experiment

Significantly fewer *Z. ingens* larvae remained in trout tanks compared to fishless tanks at the end of the experiment (Fig. 1a; ANOVA trout main effect: $F_{1,9} = 163$, $P < 0.0001$) and fewer larvae were present in the low density tanks than the high density tanks (Fig. 1a; density main effect: $F_{1,9} = 9.51$, $P = 0.013$). The lack of a significant interaction ($F_{1,9} = 0.005$, $P = 0.948$) indicated that the effect of trout on *Z. ingens* mortality was not dependent on initial density.

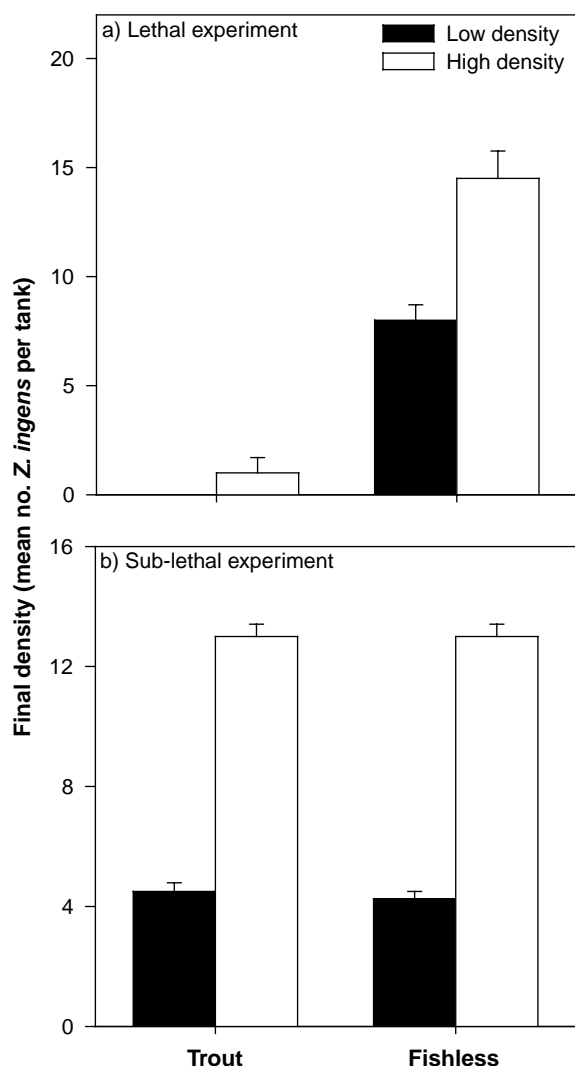


Fig. 1. Mean number (+SE) of late instar *Zelandopsycha ingens* larvae remaining in the lethal (a, where trout could prey on *Z. ingens*) and sub-lethal (b, where trout predation on *Z. ingens* was prevented) after 32 and 43 days, respectively, in trout and fishless tanks with low (10 larvae in a, 5 larvae in b) and high (20 larvae in a, 15 larvae in b) starting densities. No *Z. ingens* larvae survived in the low density trout treatment in the lethal experiment.

Trout had an indirect effect on organic matter dynamics in the mesocosms. CPOM loss over 32 d was significantly lower in trout tanks (Fig. 2a, Table 1a) although there was no significant effect of initial density on CPOM loss (Table 1a). The density \times trout interaction was marginally non significant but post-hoc analysis indicated CPOM loss was higher in high density fishless treatments compared to the other treatments (Fig. 2a). The presence of trout also resulted in reduced FPOM production, but density of *Z. ingens* larvae within trout and fishless treatments had no effect (Fig. 2b, Table 1a).

Leaf mass from invertebrate exclusion packs did not differ between trout (two-way ANOVA trout effect: $F_{1,9} = 0.839$, $P = 0.38$), and density (density effect: $F_{1,9} = 2.80$, $P = 0.13$) treatments, and there was no significant interaction (interaction: $F_{1,9} = 1.744$, $P = 0.22$) indicating leaf breakdown from microbial activity and leaching was similar between treatments.

Sub-lethal experiment

At the end of the sub-lethal experiment significantly more *Z. ingens* larvae remained in the high density treatments than low density treatments (Fig. 1b; ANOVA density effect: $F_{1,9} = 478$, $P < 0.0001$) but the presence of trout had no effect (Fig. 1b; trout effect: $F_{1,9} = 0.311$, $P = 0.59$; interaction: $F_{1,9} = 0.697$, $P = 0.59$). Background mortality of larvae averaged (\pm SE) $12.9 \pm 1.9\%$ and did not differ between treatments (binomial GLM trout effect: $F_{1,9} = 0.268$, $P = 0.62$; density effect: $F_{1,9} = 0.030$, $P = 0.87$; interaction: $F_{1,9} = 0.288$, $P = 0.66$).

Trout did not influence litter processing rates when they were prevented access to *Z. ingens* but larval density had significant effects on leaf processing rates and FPOM production (Fig. 2c, 2d, Table 1b). At the end of the experiment, treatments with high larval densities had greater CPOM loss and FPOM production than low density treatments (Fig. 2c, 2d). This supports the hypothesis that the influence of trout on litter breakdown rates is restricted to density-mediated not trait-mediated effects.

Field assay

The 12 physico-chemical variables measured in each stream were reduced to three PCA factors explaining 85.3% of the variation in physico-chemical parameters. MANOVA (Pillai trace_{3,4} = 0.570, $P = 0.292$) and all univariate ANOVAs on PCA factors indicated no significant difference ($P > 0.105$) in physico-chemical and resource conditions between trout and fishless streams.

Four shredder taxa (listed in the methods section) colonized coarse mesh artificial leaf packs, their biomass varying over time (31 and 74 d) and between trout and fishless streams (Fig. 3, Table 2a). Total shredder biomass was not consistently different between trout and fishless streams (Fig. 3; split-plot ANOVA, fish main effect: $F_{1,6} = 8.65$, $P = 0.107$), however it did increase over time in both trout and fishless streams (Fig. 3; time main effect: $F_{1,36} = 16.7$, $P = 0.0002$). MANOVA indicated significant differences between the composition of shredder assemblages in artificial leaf packs in trout streams and fishless streams and between times, but there was no significant interaction (Table 2a).

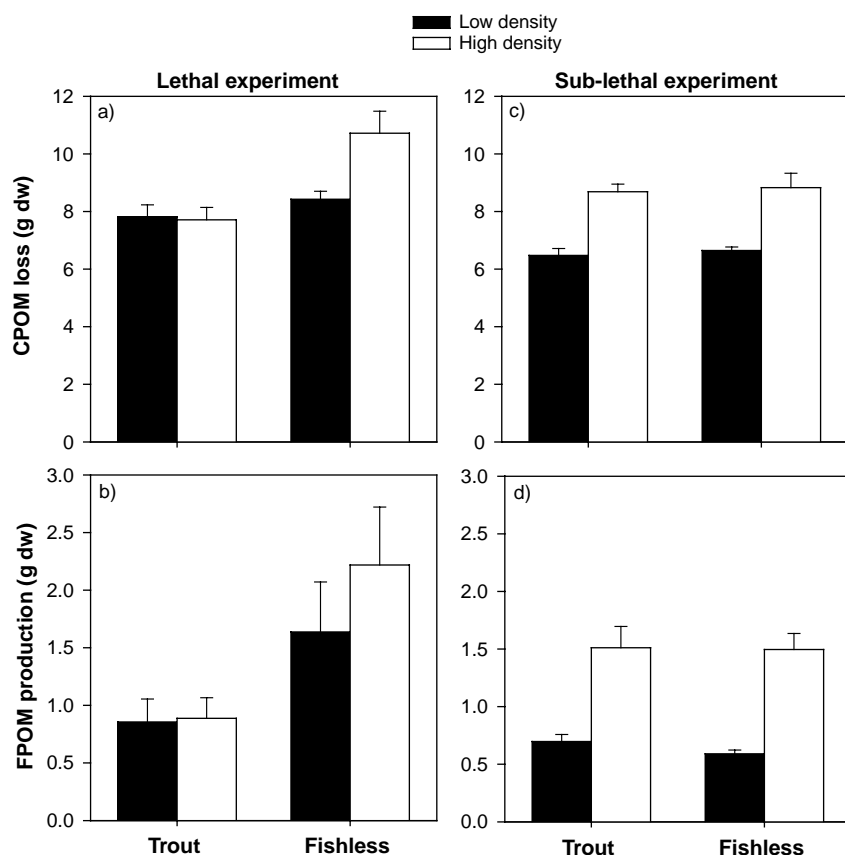


Fig. 2. Mean (+SE) loss of CPOM (a and c) and production of FPOM (b and d) in mesocosm experiments that tested the lethal (a and b) and sub-lethal (c and d) effects of trout on low (10 larvae in a and b, 5 larvae in c and d) and high (20 larvae in a and b, 15 larvae in c and d) initial densities of late instar *Zelandopsyche ingens*. CPOM loss and FPOM production for both experiments included organic matter caught in tank outflow traps.

Univariate analyses conducted for each species indicated that differences in biomass of *Z. ingens* and *O. feredayi* were responsible for the significant MANOVA effects (Table 2b). *Zelandopsyche ingens* was found only in fishless stream enclosures, and accounted for 53–63% of total biomass (Fig. 3). *Olinga feredayi*, the most abundant shredder in trout stream enclosures, increased in abundance in over time in both trout and fishless streams, but more so in trout streams as indicated by the significant trout \times time interaction (Table 2b). The abundance of *A. cyrene* and *Oeconesus* was patchy and did not vary consistently over time or between trout and fishless streams (Table 2b). Effects of trout on litter processing were evident in natural streams. The loss of CPOM from coarse mesh leaf packs, where shredders had access, was significantly lower in trout streams than fishless streams, but did not differ in fine mesh treatments that excluded shredders (Fig. 4, Table 3). As expected, CPOM loss from fine mesh leaf packs was lower than that from coarse mesh packs and increased over time for both mesh sizes (Fig. 4, Table 3). The effect of time on CPOM loss did not differ between trout and fishless streams, as indicated by the non-significant fish \times time interaction (Table 3).

Discussion

In donor controlled food webs, in which resources are derived externally, consumers may have the ability to affect resource dynamics through altering transfer rates and standing stocks of those resources (Persson et al. 1996). Our study provides evidence that predatory fish can indirectly reduce litter processing rates though effects on shredding invertebrates in stream food webs. In mesocosms, trout preyed on *Z. ingens*, significantly reducing their densities, and as a consequence, lowered rates of CPOM loss and FPOM production. These results were supported by the sub-lethal experiment, in which treatments with densities of *Z. ingens* reflecting those of trout streams had lower CPOM loss and FPOM production than treatments with *Z. ingens* densities typical of fishless streams. Furthermore, instream assays of CPOM loss rates in trout and fishless streams indicated that the strong effects of trout seen in mesocosms were present in natural stream food webs.

Previous studies have suggested that invertebrates inhabiting leaf packs are less susceptible to fish predation than those in cobble substrates (Reice 1991, Rosenfeld 2000). However the magnitude of the effect of trout on the density of *Z. ingens* seen in the lethal

Table 1. Two factor ANOVA with randomised blocks testing the influence of trout and the initial density of late instar *Zelandopsyche ingens* on FPOM production and CPOM loss in mesocosm experiments that assessed a) lethal and b) sub-lethal effects of trout. Data were log_e-transformed.

| Source | df | MS | F | P |
|--------------------------|----|--------|-------|---------|
| a) Lethal experiment | | | | |
| CPOM loss | | | | |
| Trout | 1 | 0.163 | 12.5 | 0.006 |
| Density | 1 | 0.049 | 3.71 | 0.086 |
| Density × trout | 1 | 0.062 | 4.75 | 0.057 |
| Block | 3 | 0.009 | 0.70 | 0.575 |
| Error | 9 | 0.013 | | |
| FPOM production | | | | |
| Trout | 1 | 2.48 | 61.61 | <0.0001 |
| Density | 1 | 0.111 | 2.76 | 0.131 |
| Density × trout | 1 | 0.092 | 2.29 | 0.165 |
| Block | 3 | 0.045 | 1.21 | 0.391 |
| Error | 9 | 0.040 | | |
| b) Sub-lethal experiment | | | | |
| CPOM loss | | | | |
| Trout | 1 | 0.0016 | 0.233 | 0.640 |
| Density | 1 | 0.329 | 46.9 | <0.0001 |
| Density × trout | 1 | 0.0002 | 0.031 | 0.927 |
| Block | 3 | 0.001 | 0.150 | 0.863 |
| Error | 9 | 0.007 | | |
| FPOM production | | | | |
| Trout | 1 | 0.026 | 0.604 | 0.457 |
| Density | 1 | 2.83 | 66.7 | <0.0001 |
| Density × trout | 1 | 0.025 | 0.559 | 0.459 |
| Block | 3 | 0.017 | 0.407 | 0.752 |
| Error | 9 | 0.042 | | |

experiment suggests that in some cases trout can be successful at preying on invertebrates within leaf packs. The results from the tank experiments provide evidence supporting the hypothesis that trout predation is responsible for the consistently lower *Z. ingens* densities observed in trout streams compared to fishless streams in this area (McIntosh et al. 2005).

It is not surprising that trout-induced changes in *Z. ingens* density altered rates of organic matter processing in mesocosms, as *Z. ingens* produces significant

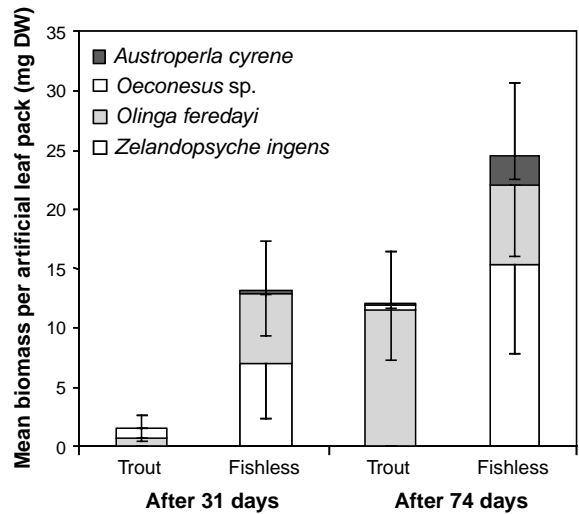


Fig. 3. Mean biomass of four shredder species colonising artificial leaf packs after 31 and 74 days in four trout and four fishless streams in the Cass region, South Island, New Zealand. Negative error bars are 1 SE of species biomass, and positive error bars are 1 SE of total shredder biomass.

quantities of FPOM in feeding (Winterbourn and Davis 1976). However, we observed different effects on CPOM and FPOM. FPOM production in the lethal experiment was influenced by moderate changes in density, but CPOM loss was elevated only in the highest density treatment. This suggests FPOM production (at least in the >125 µm category) may be more tightly coupled to shredder density than CPOM loss. CPOM breakdown is influenced by leaching and microbial activity (which in the shredder exclusion packs within the mesocosms was around 20% of the initial dry weight), and this may obscure the effects of small changes in shredder density on rates of CPOM breakdown. In comparison, it is likely that FPOM produced from microbial breakdown of

Table 2. Split plot MANOVA of the composition and biomass of shredder assemblages colonising artificial leaf chambers after 31 and 74 d in four trout and four fishless streams in the Cass region of New Zealand's South Island. Data were log_e (x+1) transformed. Univariate tests were split plot ANOVAs with streams as replicates for trout effects (error df =6) and chambers as replicates for time and interactive effects (error df =36). *P ≤ 0.05, **P < 0.01, ns not significant.

| a) Multivariate test | | | | | |
|--------------------------------|--------------|----------------|--------------|------|-------|
| Source of variation | Numerator df | Denominator df | Pillai trace | F | P |
| Fish | 4 | 24 | 0.544 | 3.17 | 0.031 |
| Time | 4 | 33 | 0.344 | 4.32 | 0.006 |
| Time × fish | 4 | 33 | 0.207 | 2.16 | 0.095 |
| b) Univariate test for species | | | | | |
| Source | Effect | | | | |
| | Trout | Time | Time × trout | | |
| <i>Zelandopsyche ingens</i> | * | ns | ns | | |
| <i>Olinga feredayi</i> | ns | ** | * | | |
| <i>Oeconesus</i> sp. | ns | ns | ns | | |
| <i>Austroperla cyrene</i> | ns | ns | ns | | |

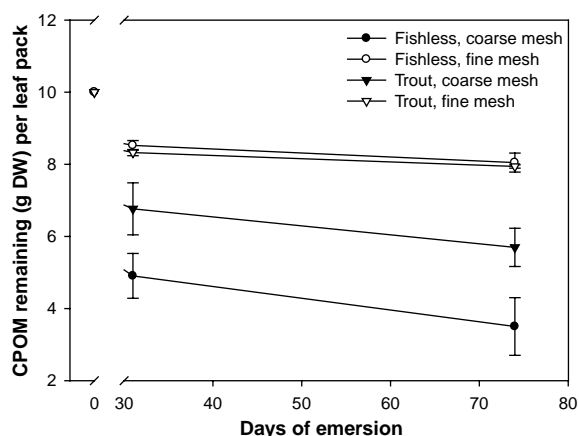


Fig. 4. CPOM remaining (\pm SE) in artificial leaf packs with coarse (C: 5 mm) and fine (F: 200 μ m) mesh after 31 and 74 days in four trout (T) and four fishless (NT) streams in the Cass region, South Island, New Zealand.

CPOM and flocculation of dissolved organic carbon is finer than 125 μ m, and would not have been detectable in this study. This, combined with assimilation of carbon by *Z. ingens* and losses during the process of extracting organic matter from tanks at the end of the experiment may also explain the apparent disparity between CPOM loss and FPOM production in both mesocosm experiments (Fig. 2).

The influence of predator-induced changes in consumer density on the strength of trophic cascades should be greater if predators do not change consumer behaviour. This is because trait-mediated effects on resource abundance (e.g. by the suppression of prey foraging behaviour) decouple the link between consumer density and resource dynamics. We did not observe any trout effect on litter processing in the sub-lethal experiment suggesting reduced litter processing was due to trout

Table 3. Three-scale split-plot ANOVA of CPOM loss from artificial leaf chambers of coarse (5 mm) and fine (200 μ m) mesh after 31 and 74 days in four trout and four fishless streams in the Cass region of New Zealand's South Island. Fish effects were tested with streams as replicates, time and time \times fish interactions were tested with pairs of leaf packs as replicates, and mesh-size effects, and interactions of other main effects with mesh, tested with individual leaf packs as replicates. Data were not transformed.

| Source | df | MS | F | P |
|-----------------------------------|----|-------|-------|---------|
| Fish | 1 | 0.944 | 3.51 | 0.110 |
| Error (stream) | 6 | 0.269 | | |
| Time | 1 | 2.44 | 11.1 | 0.002 |
| Time \times fish | 1 | 0.023 | 0.104 | 0.749 |
| Error (stream \times leaf pack) | 36 | 0.221 | | |
| Mesh | 1 | 16.9 | 106 | <0.0001 |
| Mesh \times fish | 1 | 2.37 | 15.0 | 0.001 |
| Mesh \times time | 1 | 0.087 | 0.551 | 0.463 |
| Mesh \times fish \times time | 1 | 0.118 | 0.747 | 0.392 |
| Error (residual) | 42 | 0.158 | | |

predation reducing *Z. ingens* density rather than altered feeding behaviour of larvae in the presence of trout. Inhibition of feeding through increased refuge use when exposed to predation risk, as seen in some grazing mayflies in cobble habitats (McIntosh and Townsend 1996), may be less important in detritus-based streams because detritivorous invertebrates can utilise refugia while still being able to feed (Reice 1991, Rosenfeld 2000). Predator effects on detritivore feeding behaviour have mostly been observed in small, mobile detritivores such as amphipods, (Short and Holomuzki 1992, Åbjörnsson et al. 2000).

Trophic cascades reported for detritus-based stream food webs have been in systems with predatory invertebrates (Oberndorfer et al. 1984, Malmqvist 1993), which can have significant effects on the abundance of detritivorous invertebrates (Woodward et al. 2005). However extrapolation of these effects to the field with natural predator densities has proved difficult (Malmqvist 1993, Ruetz et al. 2002). Moreover, fish-induced trophic cascades in detritus-based streams are rare. Reice (1991) and Rosenfeld (2000) found no effect of fish on the density of detritivores in leaf packs, and consequently no cascading effects on litter processing. Konishi et al. (2001) did see cascading effects of fish on litter processing rates in stream channels through reductions in the biomass of an amphipod shredder, however it was unclear if consumption by predators or increased emigration reduced shredder biomass in the channels. Ruetz et al. (2002) found differences in leaf breakdown rates between predator treatments were inconsistent, most likely from variability in species-specific vulnerability to fish predation.

Variability in predation risk is a common caveat of trophic cascade theory, where compensatory increases in less vulnerable species within high predation environments can alleviate effects of predators on resource dynamics (Hunter and Price 1992, Persson 1999, Duffy 2002). Our results indicate that the indirect effects of trout on leaf breakdown observed in mesocosms were also present in natural food webs. The large, vulnerable nature of *Z. ingens* combined with the absence of other large shredders, resistant to trout predation, resulted in the trout having substantial effects on litter processing in natural streams.

The composition of shredder assemblages present in artificial leaf packs differed significantly between trout and fishless streams. In particular, *Z. ingens* only colonised leaf packs in fishless streams, whereas *O. feredayi* biomass was higher in trout streams than fishless streams after 74 d. However, total shredder biomass did not differ significantly between trout and fishless streams. This conforms to predictions of compensatory dynamics, where species in interactive communities increase in abundance or biomass in response to declines in other species (Tilman 1996,

Ernest and Brown 2001) and suggests species compete within the shredder functional group (Richardson 1991, Jonsson and Malmqvist 2000, Ruesink and Srivastava 2001). Shredder biomass was similar between trout and fishless streams, especially in the late removal leaf packs, but we still observed differences in CPOM loss between them. This suggests there was limited functional redundancy (Walker 1992, Lawton and Brown 1993) within the shredder guilds, and indicates differences in leaf breakdown in trout and fishless streams were largely due to differences in the density of *Z. ingens* larvae. *Z. ingens* is an obligate shredder restricted to beech forest streams, whereas *O. feredayi* is a facultative shredder that inhabits a wide range of streams and feeds on a variety of resources (Winterbourn 2000). Thus it is not surprising that *Z. ingens* larvae are more efficient shredders than *O. feredayi*. This result suggests species identity and specialisation, as well as biomass or abundance, are important aspects of shredder functioning (Jonsson and Malmqvist 2000, Jonsson et al. 2001, Ruesink and Srivastava 2001) and ecosystem function in general (Power et al. 1996, Vanni et al. 2002, Jonsson and Malmqvist 2003).

Trophic cascades are common in predominately autotrophic food webs (Shurin et al. 2002), but emerging evidence indicates they are not restricted to them. The results of this and other studies (Wyman 1998, Konishi et al. 2001, Mancinelli et al. 2002) indicate that predators can influence detritivore densities and have an indirect impact on the dynamics of detritus breakdown. Our results indicate the ability of predators to induce trophic cascades in detrital systems is likely to be contingent on their ability to suppress prey populations well below carrying capacity, and on the degree of functional similarity of species within detritivore guilds.

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References

- Åbjörnsson, K., Dahl, J., Nyström, P. et al. 2000. Influence of predator and dietary chemical cues on the behaviour and shredding efficiency of *Gammarus pulex*. – *Aquat. Ecol.* 34: 379–387.
- Anderson, N. H. and Sedell, J. R. 1979. Detritus processing by macroinvertebrates in stream ecosystems. – *Annu. Rev. Entomol.* 24: 351–377.
- Carpenter, S. R. and Kitchell, J. F. 1993. The trophic cascades in lakes. – Cambridge Univ. Press.
- Carpenter, S. R., Kitchell, J. F. and Hodgson, J. R. 1985. Cascading trophic interactions and lake productivity. – *Bioscience* 35: 634–639.
- Death, R. G. and Winterbourn, M. J. 1994. Environmental stability and community persistence: a multivariate perspective. – *J. N. Am. Benthol. Soc.* 13: 125–139.
- Dillon, W. R. and Goldstein, M. 1984. Multivariate analysis methods and applications. – Wiley.
- Duffy, J. E. 2002. Biodiversity and ecosystem function: the consumer connection. – *Oikos* 99: 201–219.
- Ernest, S. K. M. and Brown, J. H. 2001. Homeostasis and compensation: the role of species and resources in ecosystem stability. – *Ecology* 82: 2118–2132.
- Fisher, S. G. and Likens, G. E. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. – *Ecol. Monogr.* 43: 421–439.
- Gordon, N. D., McMahon, T. A. and Finlayson, B. L. 1992. Stream hydrology. – John Wiley & Sons Ltd.
- Halaj, J. and Wise, D. H. 2001. Terrestrial trophic cascades: how much do they trickle? – *Am. Nat.* 157: 262–281.
- Hunter, M. D. and Price, P. W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. – *Ecology* 73: 724–732.
- Jonsson, M. and Malmqvist, B. 2000. Ecosystem process rate increases with animal species richness: evidence from leaf-eating, aquatic insects. – *Oikos* 89: 519–523.
- Jonsson, M. and Malmqvist, B. 2003. Importance of species identity and number for process rates within different stream invertebrate functional feeding groups. – *J. Anim. Ecol.* 72: 453–459.
- Jonsson, M., Malmqvist, B. and Hoffsten, P. O. 2001. Leaf litter breakdown rates in boreal streams: does shredder species richness matter? – *Freshwater Biol.* 46: 161–171.
- Jowett, I. G., Richardson, J., Biggs, B. J. et al. 1991. Microhabitat preferences of benthic invertebrates and the development of generalised *Deleatidium* spp. habitat suitability curves, applied to four New Zealand rivers. – *N. Z. J. Mar. Freshwater Res.* 25: 187–199.
- Konishi, M., Nakano, S. and Iwata, T. 2001. Trophic cascading effects of predatory fish on leaf litter processing in a Japanese stream. – *Ecol. Res.* 16: 415–422.
- Lawrence, K. L. and Wise, D. H. 2000. Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. – *Pedobiologia* 44: 33–39.
- Lawton, J. H. and Brown, V. K. 1993. Redundancy in ecosystems. – In: Schulze, E. D. and Mooney, H. A. (eds), *Biodiversity and ecosystem function*. Springer-Verlag, pp. 255–270.
- Malmqvist, B. 1993. Interactions in stream leaf packs: effects of a stonefly predator on detritivores and organic matter processing. – *Oikos* 66: 454–462.
- Mancinelli, G., Costantini, M. L. and Rossi, L. 2002. Cascading effects of predatory fish exclusion on the detritus-based food web of a lake littoral zone (Lake Vico, central Italy). – *Oecologia* 133: 402–411.
- McIntosh, A. R. 2000. Habitat- and size-related variations in exotic trout impacts on native galaxiid fishes in New Zealand streams. – *Can. J. Fish. Aquat. Sci.* 57: 2140–2150.
- McIntosh, A. R. and Peckarsky, B. L. 1996. Differential behavioral responses of mayflies from streams with and without fish to trout odor. – *Freshwater Biol.* 35: 141–148.
- McIntosh, A. R. and Townsend, C. R. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour? – *Oecologia* 108: 174–181.
- McIntosh, A. R., Greig, H. S., McMurtrie, S. A. et al. 2005. Top-down and bottom-up influences on populations of a stream detritivore. – *Freshwater Biol.* 50: 1206–1218.
- Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs-patterns and importance. – *Ecol. Monogr.* 65: 21–74.

- Nyström, P., McIntosh, A. R. and Winterbourn, M. J. 2003. Top-down and bottom-up processes in grassland and forested streams. – *Oecologia* 136: 596–608.
- Oberndorfer, R. Y., McArthur, J. V., Barnes, J. R. et al. 1984. The effect of invertebrate predators on leaf litter processing in an alpine stream. – *Ecology* 65: 1325–1331.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. – *J. Anim. Ecol.* 49: 667–685.
- Persson, L. 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. – *Oikos* 85: 385–397.
- Persson, L., Bengtsson, J., Menge, B. A. et al. 1996. Productivity and consumer regulation-concepts, patterns and mechanisms. – In: Polis, G. A. and Winemiller, K. O. (eds), *Food webs: integration of patterns and dynamics*. Chapman and Hall, pp. 396–435.
- Polis, G. A. 1994. Food webs, trophic cascades and community structure. – *Aust. J. Ecol.* 19: 121–136.
- Polis, G. A. and Strong, D. R. 1996. Food web complexity and community dynamics. – *Am. Nat.* 147: 813–846.
- Polis, G. A., Anderson, W. B. and Holt, R. D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. – *Annu. Rev. Ecol. Syst.* 28: 289–316.
- Power, M. E. 1990. Effects of fish in river food webs. – *Science* 250: 811–814.
- Power, M. E., Tilman, D., Estes, J. A. et al. 1996. Challenges in the quest for keystones. – *Bioscience* 46: 609–620.
- Reice, S. R. 1991. Effects of detritus loading and fish predation on leafpack breakdown and benthic macroinvertebrates in a woodland stream. – *J. N. Am. Benthol. Soc.* 10: 42–56.
- Richardson, J. S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. – *Ecology* 72: 873–887.
- Rosemond, A. D., Pringle, C. M., Ramirez, A. et al. 2001. A test of top-down and bottom-up control in a detritus-based food web. – *Ecology* 82: 2279–2293.
- Rosenfeld, J. 2000. Effects of fish predation in erosional and depositional habitats in a temperate stream. – *Can. J. Fish. Aquat. Sci.* 57: 1369–1379.
- Ruesink, J. L. and Srivastava, D. S. 2001. Numerical and per capita responses to species loss: mechanisms maintaining ecosystem function in a community of stream insect detritivores. – *Oikos* 93: 221–234.
- Ruetz, C. R., Newman, R. N. and Vondracek, B. 2002. Top-down control in a detritus-based food web: fish, shredders and leaf breakdown. – *Oecologia* 132: 307–315.
- Schmitz, O. J., Beckerman, A. P. and Obrien, K. M. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. – *Ecology* 78: 1388–1399.
- Short, T. M. and Holomuzki, J. R. 1992. Indirect effects of fish on foraging behaviour and leaf processing by the isopod *Lirceus fontinalis*. – *Freshwater Biol.* 27: 91–97.
- Shurin, J. B., Borer, E. T., Seabloom, E. W. et al. 2002. A cross-ecosystem comparison of the strength of trophic cascades. – *Ecol. Lett.* 5: 785–791.
- Steiner, C. F. 2001. The effects of prey heterogeneity and consumer identity on the limitation of trophic-level biomass. – *Ecology* 82: 2495–2506.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. – *Ecology* 77: 350–363.
- Vanni, M. J., Flecker, A. S., Hood, J. M. et al. 2002. Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. – *Ecol. Lett.* 5: 285–293.
- Walker, B. H. 1992. Biodiversity and ecological redundancy. – *Conserv. Biol.* 6: 18–23.
- Wallace, J. B. and Webster, J. R. 1996. The role of macroinvertebrates in stream ecosystem function. – *Annu. Rev. Entomol.* 41: 115–139.
- Wallace, J. B., Eggert, S. L., Meyer, J. L. et al. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. – *Science* 277: 102–104.
- Winterbourn, M. J. 2000. Feeding ecology. – In: Collier, K. J. and Winterbourn, M. J. (eds), *New Zealand stream invertebrates: ecology and implications for management*. N. Z. Limnol. Soc., Christchurch, pp. 100–124.
- Winterbourn, M. J. and Davis, S. F. 1976. Ecological role of *Zelandopsycha ingens* (Trichoptera: Oeconesidae) in a beech forest stream ecosystem. – *Aust. J. Mar. Freshwater Res.* 27: 197–215.
- Winterbourn, M. J., Gregson, K. L. D. and Dolphin, C. H. 2000. Guide to the aquatic insects of New Zealand. – *Bull. Entomol. Soc. N. Z.* 13: 1–102.
- Woodward, G., Spiers, D. C. and Hildrew, A. G. 2005. Quantification and resolution of a complex, size structured food web. – *Adv. Ecol. Res.* 36: 85–135.
- Wootton, J. T. 1993. Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. – *Am. Nat.* 141: 71–89.
- Wyman, R. L. 1998. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition and the carbon cycle. – *Biodivers. Conserv.* 7: 641–650.

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