

# Density reductions by predatory trout increase adult size and fecundity of surviving caddisfly larvae in a detritus-based stream food web

HAMISH S. GREIG AND ANGUS R. McINTOSH

School of Biological Sciences, University of Canterbury, Christchurch, New Zealand.

## SUMMARY

1. In some situations, individuals surviving in environments where predation is intense can grow faster because the benefits of release from intraspecific competition outweigh costs associated with anti-predator responses. Whether these 'thinning' effects of predation occur in detritus-based food webs where resource renewal occurs independently of consumption by consumers was studied. We investigated how effects of predatory brown trout (*Salmo trutta*) on the larvae of the detritivorous stream caddisfly, *Zelandopsycha ingens*, influenced the size and fecundity of the caddisfly adults.

2. Trout substantially reduced the abundance of *Z. ingens* larvae, but adult male and female *Z. ingens* were significantly larger in trout streams compared to fishless streams. Females in trout streams had 33% more eggs than fishless stream females, and egg sizes were not significantly different. In mesocosms, *Z. ingens* larvae in low density treatments reflecting trout stream abundances grew significantly faster than larvae in high density treatments that were characteristic of fishless stream abundances. Non-lethal trout presence did not influence case building behaviour, feeding rates or growth of *Z. ingens* larvae, indicating non-lethal effects of predators were negligible.

3. Increased adult size and fecundity associated with trout stream individuals were probably a result of predator thinning of larval density indirectly releasing surviving *Z. ingens* from intraspecific competition. Thus, predator thinning did influence interactions between larvae in this detritus-based food web as larval growth was strongly density-dependent. However, extrapolating the total number of eggs potentially produced indicates the increased fecundity of females in trout streams would not compensate for losses of larvae to trout predation.

*Keywords:* complex life cycles, indirect effects, intraspecific competition, non-lethal costs, thinning

## Introduction

Predators can mediate the influence of intraspecific competition by increasing resource availability for surviving individuals (Begon, Townsend & Harper, 2006). This can occur through both trait-mediated effects of predators that reduce prey foraging rates (e.g. Diehl *et al.*, 2000; Peacor, 2002), and lethal effects

of predators that thin prey density (e.g. Van Buskirk & Yurewicz, 1998; Brodin & Johansson, 2002; Relyea, 2002). Consequently predators may increase the growth and/or fecundity of prey if the growth benefits of predators exceed their non-lethal costs (Resetarits, Rieger & Binckley, 2004; Relyea, 2007). However, the release of resources associated with these interactions depends on resource supply (Oedekoven & Joern, 2000), so detrital-based food webs may present a special case. We investigated the effects of predation on the size and fecundity of surviving prey in a detritus-based food web.

---

Correspondence: Hamish Greig, School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand. E-mail: hsg12@student.canterbury.ac.nz

If detrital-based food webs are essentially 'donor-controlled' through resources being constantly renewed independent of consumer abundance (Polis & Strong, 1996), the potential for tightly coupled dynamics between consumers and resources may be affected. Detritus is sometimes regarded as a super abundant resource (Reice, 1991), so competitive interactions involving detritus food sources may be less likely. Indeed, most examples of reduced intraspecific competition associated with predator thinning come from predominantly autotrophic systems (Oedekoven & Joern, 2000). However, indirect effects involving consumer-resource interactions in detritus-based food webs are poorly understood (Rosemond *et al.*, 2001).

Intraspecific interactions could still be important if high quality detrital food is actually in short supply. This is likely since microbial processing improves the food value of detritus and the extent of decomposition and microbial colonization within leaf packs are variable (Webster & Benfield, 1986; Cummins *et al.*, 1989). Negative effects of experimental reductions of detritus on detritivore populations, and reduced growth of detritivores associated with declines in detritus quality support this view (Wallace *et al.*, 1997, 1999). Moreover, if access to detritus is limited by negative behavioural interactions between consumers, then competition may still be important, regardless of resource abundance. Thus, reduced prey competition resulting from predator thinning could have important impacts in detritus-based food webs.

As mentioned above, the net effect of predators on individual fitness will also depend on the balance between the non-lethal effects of predators on individuals, and their lethal effects that potentially indirectly increase resource availability. Many organisms alter phenotype when exposed to the threat of predation (Dill, 1987; Lima, 1998a; Tollrian & Harvell, 1999; Benard, 2004; Relyea, 2007). Energy invested in behavioural or morphological defences to avoid predation, or lost through forgoing foraging, is not available for growth and reproduction. Thus, a trade-off exists between anti-predator defence and growth (Werner & Anholt, 1993) that often results in the non-lethal reductions to prey fitness (Lima, 1998b). If detritivores are still vulnerable to predators despite the usually dense cover provided by detrital layers, then any benefits from reduced intraspecific competition because of predation could be offset by non-lethal costs associated with predator avoidance. Thus,

the lethal and non-lethal effects of predators need to be considered together (Werner & Peacor, 2003).

Considerations of the effects of predators on prey fitness also need to take into account the prey's life history. For organisms with complex life cycles (Moran, 1994), interactions occurring in one life stage may also have a disproportionately large influence on fitness in other stages (Pechenik, 2006). Adult fitness correlates are likely to be most strongly coupled with larval interactions in species that do not feed as adults, as all resource acquisition occurs pre-metamorphosis (Peckarsky & Cowan, 1991; McPeck & Peckarsky, 1998; Wissinger *et al.*, 2004).

To investigate these issues, our study considered the effects of predation by brown trout (*Salmo trutta* L.) to the larval stages on the adult size and fecundity of the detritivorous stream caddisfly, *Zelandopsyche ingens* Tillyard (Oeconesidae). These caddisflies are found in significantly lower densities in trout streams than fishless streams (McIntosh *et al.*, 2005) and trout reduce densities of *Z. ingens* in experimental tanks through direct predation (Greig & McIntosh, 2006). Furthermore, *Z. ingens* appears to exhibit anti-predator behaviour by building heavier, more robust cases in trout streams (McIntosh *et al.*, 2005), consistent with the anti-predator responses of other caddisflies despite the potential energetic costs (Otto, 1987; Stevens *et al.*, 1999). Consequently, the costs of anti-predator behaviour could reduce larval growth rates and size at emergence. As well as being under top-down control, *Z. ingens* populations appear to be limited by detritus resources in both trout and fishless streams (McIntosh *et al.*, 2005) and may compete for food and space as seen in some other detritivorous stream insects (e.g. Richardson, 1991; Jonsson & Malmqvist, 2003). Trout-induced reductions in density may therefore increase resource acquisition and growth rates of survivors released from intraspecific competition. We examined *Z. ingens* adult size and fitness correlates in trout and fishless streams to investigate whether surviving larvae in trout streams produced larger, more fecund adults in comparison to those in fishless streams. We also manipulated trout presence/absence and *Z. ingens* larval density in experimental tanks to investigate whether potential changes in larval growth rate associated with reduced intraspecific competition might contribute to patterns in adult size observed in the field. Finally by extrapolating to adult fecundities and densities, we

considered the potential for interactions occurring in the larval phase to influence subsequent generations.

## Methods

### *Survey of Z. ingens adult size*

The larvae of *Z. ingens*, an obligate detritivore, inhabit small headwater streams flowing through southern beech forest [*Nothofagus solandri* var. *cliffortioides* (Hook f.) Poole] in Canterbury, New Zealand. Previous stable isotope analysis in these densely forested streams indicates the vast majority of secondary production is derived from allochthonous detritus (Rounick, Winterbourn & Lyon, 1982; Rounick & Winterbourn, 1986). Many of these streams have waterfalls or dry lower reaches that block access to fish including introduced brown trout (*S. trutta*) and are fishless. We know of only four streams containing both trout and *Z. ingens* in the Cass basin (McIntosh *et al.*, 2005), one of which is not accessible at night when *Z. ingens* adults are active. Therefore, we were limited to sampling three trout streams (Pylon Gully, Peacock and Binser Saddle) and three fishless streams (Sugarloaf Bush, Middle Bush and Poverty). The fish faunas and general characteristics of these streams have been described previously (McIntosh, 2000; Nyström, McIntosh & Winterbourn, 2003; McIntosh *et al.*, 2005). Adult *Z. ingens* were collected by hand by two workers scanning opposite banks of each stream between dusk and 03:00 hours on the nights of 1 and 2 April 2003. Female *Z. ingens* were more difficult to find than males, and sampling continued until at least 10 males and five females had been collected from each stream. Adults were frozen separately prior to processing. The behaviour of the caddisflies makes emergence traps largely ineffective, but the sizes of emerging individuals caught (H.S. Greig & A.R. McIntosh, unpubl. data) is consistent with the patterns reported here. Moreover, the isolation of the streams used in this study in individual forest fragments, and the flight behaviour of the adults (Winterbourn & Crowe, 2001) indicate the adults used in the analysis were almost certain to have emerged from the streams where they were caught.

In the laboratory, mass of abdomen and thorax, wing length and fecundity were measured on all adults collected. For both males and females, the right forewing was measured to the nearest 0.05 mm with

vernier callipers. Thorax (with legs removed at the coxa) was separated from the abdomen and head, dried for 48 h at 50° C and weighed on a microbalance to the nearest 0.0001 mg. Abdomen dry weight (DW, exclusive of eggs) and egg masses dissected from female abdomens were weighed using the same procedure. A subsample of 40 eggs was removed from each female and weighed separately to enable calculation of mass per egg. Total egg number was calculated by dividing the weight of the total egg mass (dissected mass + mass of subsample) by the mass per individual egg. All eggs were mature and in the same state of development. Some females had deposited all their eggs prior to collection and were excluded from all analyses.

We measured a number of physicochemical characteristics of each stream to test for confounding variables between trout and fishless streams. Stream width and three depths were measured every 5 m along a 50 m study reach in each stream. Water velocity was measured by monitoring the rate of travel of fluorescein dye over 20 m. Discharge was measured using the velocity–area integration method (Gordon, McMahon & Finlayson, 1992) with a Flo-mate model 201 (Marsh-McBirney, Frederick, MD, U.S.A.) velocity meter. Substrate composition was assessed by measuring the longest axis of 100 randomly selected particles in each stream and was expressed as the substrate index of Jowett *et al.* (1991). Water temperature was recorded with Hobo (Onset, Bourne, MA, U.S.A.) data loggers and pH and specific conductance were measured with calibrated handheld meters (Oakton 10 series; Oakton Instruments, Vernon Hills, IL, U.S.A.).

We also quantified leaf standing stock by measuring the length and width of all leaf packs (accumulations of beech detritus with surface area >0.01 m<sup>2</sup>) within the 50 m study reach of each stream. We collected 10 leaf packs from each reach to dry and weigh to enable calculations of leaf mass per unit area. Every 5 m along the reach a leaf pack was measured, washed into a 1 mm mesh net and transferred into a plastic bag for transport. Leaf packs >0.1 m<sup>2</sup> were subsampled with a 0.06 m<sup>2</sup> quadrat. In the laboratory, large stick and bark fragments were removed and leaves were washed in a 1 mm sieve to remove fine particles, dried for 72 h at 50° C and weighed to the nearest 1 mg. The total DW of leaf in each 50 m reach was extrapolated from the mean DW per unit area of

the 10 leaf packs collected from the corresponding stream.

Body size attributes of male and female *Z. ingens* adults were analysed separately. We used principle components analysis (PCA) as a variable reduction technique to assess intercorrelated response variables as replication of streams was insufficient for MANOVA. Abdomen DW, thorax DW and wing length were included for both male and female PCA, with egg mass DW included in female PCA. Variables were  $\log_e$ -transformed to meet assumptions of normality. PCA produced one component explaining 98.3% and 99.4% of total variation in body size and other fitness correlates for females and males respectively. *T*-tests were used to test for significant differences in this component between trout and fishless stream populations, followed by *t*-tests on individual variables using stream means as replicates. The potential for differences in stream physicochemical attributes was assessed via multivariate comparisons. We reduced physicochemical data into independent factors with PCA of  $\log_e$ -transformed mean depth, discharge and DW of leaf per m<sup>2</sup> stream, and untransformed mean width, velocity, discharge, substrate index, DW of leaf per m<sup>2</sup> stream (g m<sup>-2</sup>), DW of leaf per m<sup>2</sup> leaf pack, pH, specific conductance and mean water temperature. Differences in environmental conditions between trout and fishless streams were assessed by performing MANOVA on PCA components with eigenvalues >1.

#### *Experimental examination of Z. ingens larval growth*

To assess mechanisms behind the effects of trout on the size and fecundity of adult *Z. ingens*, we manipulated trout presence/absence and the density of late instar *Z. ingens* in 16 oval black polythene tanks (surface area: 0.8 m<sup>2</sup>), similar to those illustrated by McIntosh & Peckarsky (1996), at the University of Canterbury's Cass Field Station. We were particularly interested in both the effects of reduced *Z. ingens* larval density and the non-lethal costs of anti-predator behaviour in the presence of trout on the growth rates of *Z. ingens* larvae. Thus, we manipulated the density of larvae to reflect the mean *Z. ingens* density in trout and fishless streams respectively. As trout cause large *Z. ingens* density reductions (Greig & McIntosh, 2006) which are evident in natural populations after the third instar (McIntosh *et al.*, 2005) and the majority of *Z. ingens* larval mass is gained in the fourth and fifth

instars, this density manipulation represents a direct test of the consequences of thinning by trout on *Z. ingens* larval growth.

We also manipulated the non-lethal presence and absence of trout by separating trout from the benthos with a 1 mm mesh screen installed 6 cm above the gravel substratum in each tank. This prevented the strong consumptive effects seen in previous experiments (Greig & McIntosh, 2006) while enabling the transmission of chemical, visual and hydrodynamic cues. Cover for trout was provided by six cobbles and a 12 cm long section of PVC pipe placed on the mesh screen. Each of the four treatment combinations was replicated four times in a randomized block design.

Tanks were fitted with a central standpipe with openings covered with 1 mm mesh to regulate water depth at 21 cm, and were gravity-fed by well water free of fish chemical cues (pH 7.7, conductivity 114  $\mu\text{S}_{25} \text{ cm}^{-1}$ , temperature 10° C) through two water jets that created circular flow. Water temperature in tanks ranged from 9.2 to 15.6° C (mean = 11.8° C) over the course of the experiment. Tank bottoms were covered with washed 0.5–3 cm gravel particles from a dry river bed. Beech leaves (*N. solandri*), in various states of decomposition from a fishless stream, were added to provide a realistic, patchy food resource in each tank. 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 30 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 (after Winterbourn & Davis, 1976). After 7 days, leaves were removed, rinsed again over a 1 mm sieve, and added to each tank to create two leaf packs (*c.* 10 × 10 cm) in the low velocity zones behind each water jet.

On 27 February 2004, *Z. ingens* collected from a nearby fishless stream (80% fourth instar, 20% early fifth instar) were evenly distributed within the leaf packs of each tank below the mesh screen. Eight tanks received 15 larvae each and eight received five larvae each, reflecting densities commonly found in natural trout and fishless streams, respectively (McIntosh *et al.*, 2005; Greig & McIntosh, 2006). Brown trout (mean fork length  $\pm$  SE: 109  $\pm$  2 mm, range: 102–123 mm) were placed in eight randomly selected tanks later the same day. Trout were fed 20 *Deleatidium* spp. (Ephemeroptera, Leptophlebiidae) larvae added twice

weekly, plus an additional two fifth instar *Z. ingens* per week to ensure the full range of chemical cues elicited by the consumption of *Z. ingens* larvae by trout were present. A similar density of *Deleatidium* was also maintained above mesh screens in the fishless tanks. The experiment ran for 43 days, after which trout were removed, measured and released, and *Z. ingens* larvae were recovered from tanks by carefully picking through the substrate and frozen. The head capsule width (HCW) of *Z. ingens* larvae was measured with an ocular micrometer to the nearest 0.03 mm and individuals were dried for 48 h at 50° C and weighed to the nearest 0.0001 mg. During the fifth instar, *Z. ingens* larvae alter their cases from a mosaic of leaf segments to a 'log cabin' design of interlocked segments of leaf petiole and sticks (see pictures in Winterbourn & Davis, 1976; McIntosh *et al.*, 2005). As no larvae introduced to the tanks at the start of the experiment had reached this stage, we were able to identify and isolate cylindrical additions made to cases during the experiment. The length and internal diameter of case additions were measured to calculate surface area, and cases were dried for 48 h at 50° C and weighed to the nearest 0.01 mg. We also collected fine particulate organic matter (FPOM) produced by *Z. ingens* feeding from the tanks to assess whether *Z. ingens* feeding rates were influenced by larval density or the presence of trout. FPOM was decanted from gravel into a 125 µm sieve, dried for 72 h at 50° C, weighed to the nearest 0.01 mg, ashed in a muffle furnace at 450° C for 2 h and reweighed to calculate ash-free dry mass.

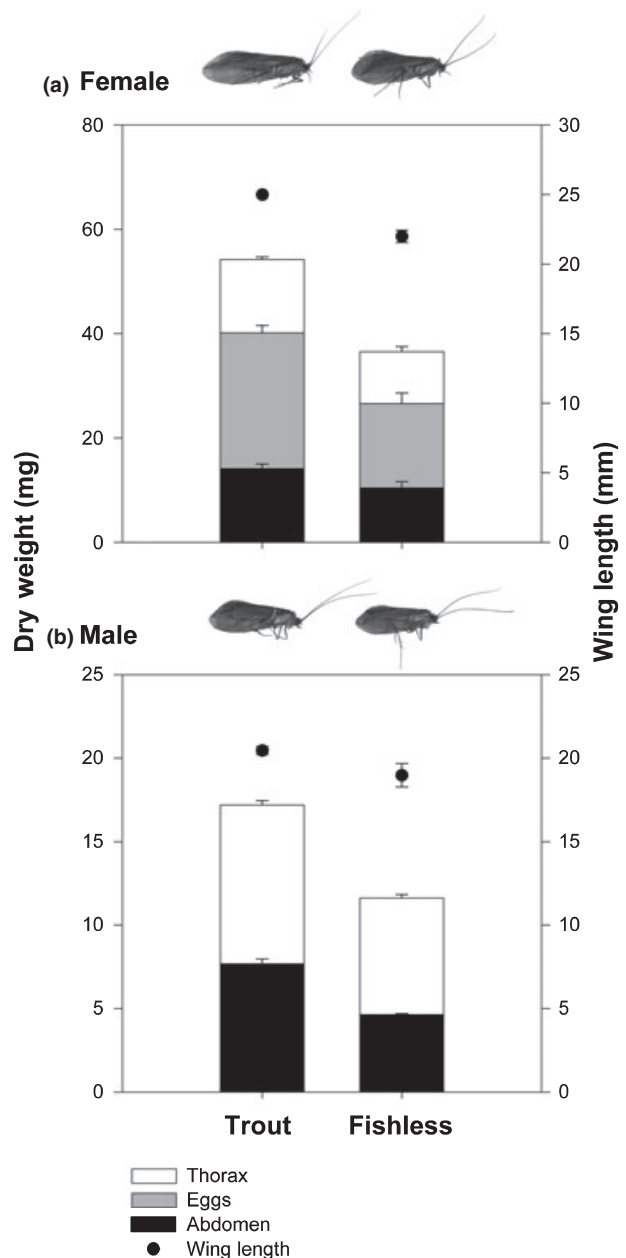
We analysed responses from the tank experiment using randomized block ANOVA, with trout and initial *Z. ingens* density as treatment factors and tank means as replicates. Mean individual DW, HCW and the weight per unit area of case additions were analysed with MANOVA followed by univariate ANOVAs. Individual DW and case weight required log<sub>e</sub>-transformation. FPOM produced per tank was converted into per capita FPOM (square-root transformed) production prior to analysis by dividing total FPOM by the final density of *Z. ingens* in the respective tank.

## Results

### Survey of *Z. ingens* adult size

Adult male and female *Z. ingens* caught at trout streams were significantly larger and more fecund

than those from fishless streams (Fig. 1, Table 1). PCA produced one component for males and females which was strongly and positively correlated



**Fig. 1** Mean and SE for dry weight of abdomen, thorax and eggs, and mean wing length of female and male *Zelandopsyche ingens* adults collected from three trout and three fishless streams at Cass, South Island, New Zealand. Replicates were stream means. Representative *Z. ingens* adults, photographed at the same scale, are shown from one trout (Pylon Gully) and one fishless (Sugarloaf) stream. The largest adult caddisfly is 28 mm long (head to wing tip).

**Table 1** T-tests on a principle component summarizing size and fecundity variables, and each variable individually, for adult female and male *Zelandopsyche ingens* from three trout and three fishless streams in the Cass region, South Island, New Zealand

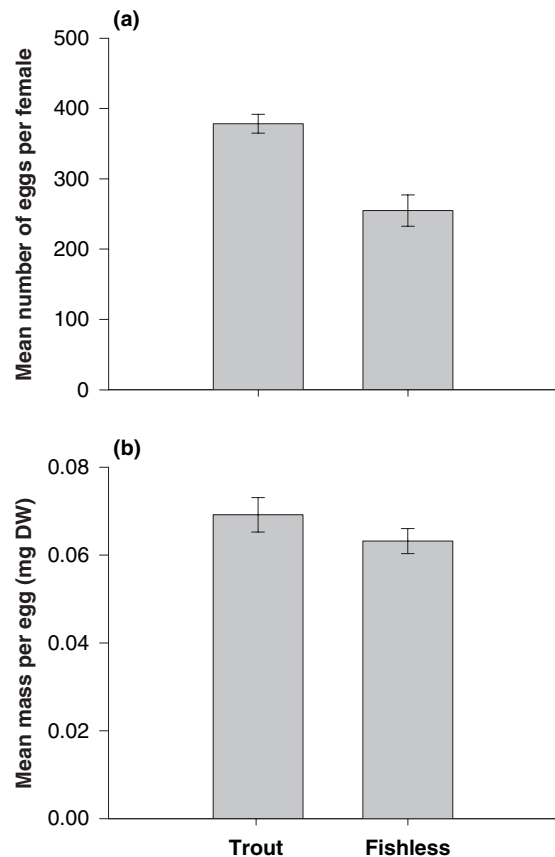
	Response	d.f.	<i>t</i>	<i>P</i> -value
Female	PC 1	4	3.97	0.017
	Abdomen mass	4	3.31	0.030
	Egg mass	4	3.55	0.024
	Thorax mass	4	3.38	0.028
	Wing length	4	6.43	0.003
Male	PC 1	4	10.50	<0.001
	Abdomen mass	4	12.68	<0.001
	Thorax mass	4	7.43	0.002
	Wing length	4	10.92	0.001

( $r > 0.98$ ) with all variables. Abdomen DW, thorax DW and wing length of both males and females and the total DW of eggs of females, were all significantly greater in adults from trout than fishless streams. The increase in total egg mass in trout stream females corresponded to 33% more, rather than larger eggs, than fishless stream females (Fig. 2).

Physicochemical and resource variables were reduced to three PCA factors that explained 87.4% of the variation in physicochemical conditions and resources. MANOVA followed by univariate ANOVAS on the individual factors showed there were no significant differences between trout and fishless streams (Pillai trace = 0.629,  $F = 1.13$ ,  $P = 0.501$ ; Univariate ANOVAS,  $P > 0.09$ ). However, individual assessment of variables indicated trout streams were significantly deeper than fishless streams, and there was a general trend towards trout streams being larger than fishless streams (see Supplementary material).

#### Experimental examination of *Z. ingens* growth

*Zelandopsyche ingens* larvae from low density tanks were significantly heavier after 43 days (Fig. 3a, Table 2) than larvae from high-density tanks, indicating that larvae grew faster at low (mean  $\pm$  SE:  $0.33 \pm 0.03$  mg DW day<sup>-1</sup>) compared to high densities ( $0.21 \pm 0.01$  mg DW day<sup>-1</sup>). However, we found no effect of trout, or a trout  $\times$  density interaction on larval growth (Fig. 3a, Table 2), suggesting that non-lethal costs of trout presence were negligible. Also there was no evidence of trout-induced robust cases in *Z. ingens*, as mass per unit area of case added



**Fig. 2** Mean ( $\pm$ SE) number of eggs per female (a) and mean mass per egg (b) for *Zelandopsyche ingens* adults collected from three trout and three fishless streams. Females from trout streams contained significantly more eggs than fishless stream females ( $t_4 = 4.75$ ,  $P = 0.009$ ); however, there was no difference in the size of individual eggs ( $t_4 = 1.24$ ,  $P = 0.284$ ).

during the experiment did not differ significantly between treatments (Fig. 3b, Table 2). Moreover, trout presence had no effect on the feeding rates of individual *Z. ingens*, because per capita FPOM production was not significantly different between trout and fishless tanks ( $F_{1,9} = 0.408$ ,  $P = 0.539$ ) and there was no interaction between trout and density ( $F_{1,9} = 0.217$ ,  $P = 0.652$ ; Fig. 4). However, density had a significant effect on feeding rates, as per capita FPOM production was less in high density compared to low density tanks ( $F_{1,9} = 7.398$ ,  $P = 0.024$ ; Fig. 4). Although larval density had a strong effect on *Z. ingens* growth, we found no difference in HCW between treatments after 43 days (Table 2); 93% of *Z. ingens* larvae had reached the fifth and final instar regardless of density or trout treatment. Background mortality of larvae averaged ( $\pm$ SE)  $12.9 \pm 1.9\%$  and

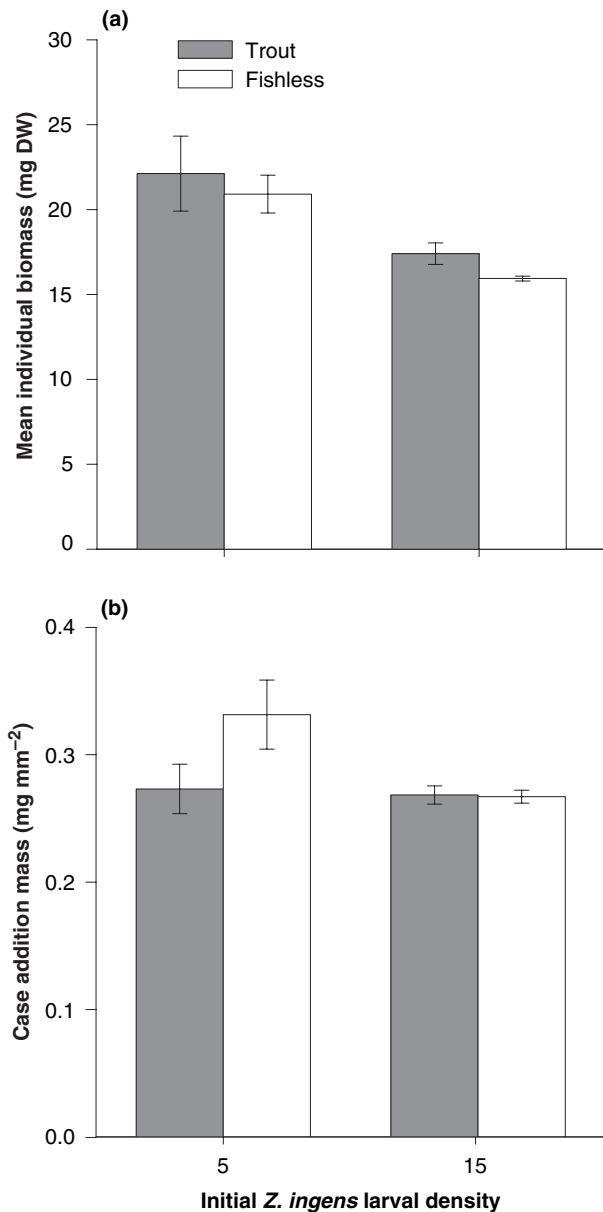


Fig. 3 Mean ( $\pm$ SE) individual biomass (a) and mass of case additions per mm<sup>2</sup> (b) of *Zelandopsycha ingens* larvae after 43 days in a tank experiment in which the non-lethal presence of trout and larval density were manipulated. Bars shown are treatment means with tanks as replicates. Mean initial dry mass of larvae was 7.5 mg.

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:  $F_{1,9} = 0.288$ ,  $P = 0.66$ ), indicating density manipulations remained in place for the duration of the experiment, and reduced growth rates at high-larval densities did not increase mortality.

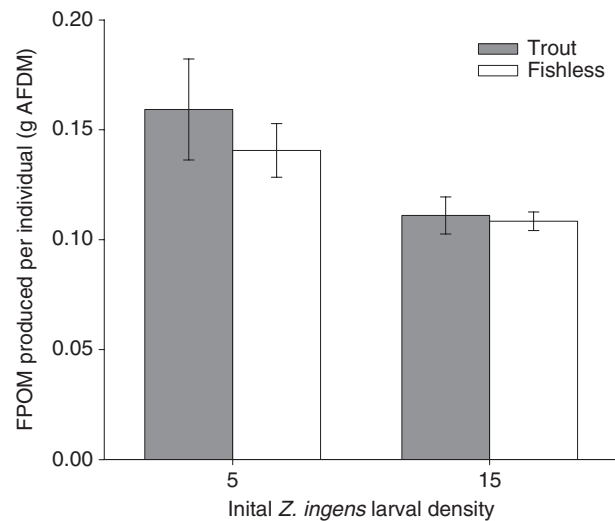


Fig. 4 Mean ( $\pm$ SE) fine particulate organic matter (FPOM) produced per individual *Zelandopsycha ingens* larvae (g AFDM) in a tank experiment with and without the non-lethal presence of trout at two initial densities (5 and 15 larvae per tank).

## Discussion

We observed significantly larger, more fecund adult *Z. ingens* at trout streams compared to fishless streams, which when combined with experimental evidence of higher larval growth rates at trout stream densities suggests that thinning of *Z. ingens* larval densities by predatory trout leads to an increase in the adult size and fitness of survivors. Thus, even in this detritus-based food web, individuals surviving the intense predation probably grew larger because of release from intraspecific competition, that overwhelmed any costs of anti-predator behaviour (Van Buskirk & Yurewicz, 1998; Brodin & Johansson, 2002). This is an intriguing result because trout show positive selection for large invertebrate prey and their predatory impacts have been linked to reductions in the size of stream invertebrates that remain (Huryn, 1998; Meissner & Muotka, 2006). Below we explain the rationale for these conclusions and describe their implications.

Adult *Z. ingens* do not have a digestive tract, so interactions in the larval phase that influence resource acquisition were responsible for the large size of adults in trout compared to fishless streams. Larger size is likely to result in considerable fitness benefits; Trout stream females had 33% higher fecundity than those in fishless stream, and greater male size may

**Table 2** MANOVA and univariate ANOVAs testing responses of late instar *Zelandopsyche ingens* larvae to manipulations of the non-lethal presence/absence of trout and *Z. ingens* density (5 or 15 larvae per tank) in flow-through polythene tanks at the Cass field station, South Island, New Zealand.

Response variable	Source	d.f.	Pillai trace	Mean square	F	P-value
MANOVA	Trout	3,7	0.293		0.967	0.460
	Density	3,7	0.685		5.066	<b>0.036</b>
	Trout × density	3,7	0.292		0.962	0.462
	Block	9,17	0.592		0.738	0.671
Larval dry weight	Trout	1		0.0174	1.071	0.328
	Density	1		0.224	15.03	<b>0.004</b>
	Trout × density	1		0.00169	0.104	0.754
	Block	3		0.0107	0.623	0.618
	Error	9		0.0162		
Head capsule width	Trout	1		0.00005	0.009	0.928
	Density	1		0.00024	0.038	0.850
	Trout × density	1		0.0110	1.716	0.223
	Block	3		0.00813	1.269	0.342
	Error	9		0.00641		
Case weight	Trout	1		0.00189	2.391	0.156
	Density	1		0.00275	3.484	0.095
	Trout × density	1		0.00207	2.630	0.139
	Block	3		0.00040	0.505	0.689
	Error	9		0.00079		

Significant *P*-values are shown in bold.

provide fitness benefits in the form of female attraction, male–male competition and longevity (Choe & Crespi, 1997 and examples in Peckarsky *et al.*, 2002). However, the nature of the male size–fitness relationship is dependent the mating system, which is poorly understood in *Z. ingens*, and aquatic insects in general (Peckarsky *et al.*, 2002; Wissinger *et al.*, 2004).

Two hypotheses could explain larger adult size in trout streams: first, trout may have positive indirect effects on *Z. ingens* growth through thinning prey densities, thereby releasing surviving individuals from intraspecific competition for resources. Alternatively, if the costs of antipredator responses to trout are high, growth rates may be reduced such that larvae may not be able to complete development necessary to emerge in summer; *Z. ingens* adults have not been observed later than April at Cass (Winterburn, 1978) probably because low air temperature would constrain adult flight in this montane habitat. In this case, final instar larvae would be forced to overwinter until the next summer, potentially increasing the net gain of resources by larvae.

Results from our tank experiment support the first explanation, a positive indirect effect of trout on *Z. ingens* larval growth. *Z. ingens* larvae grew faster in treatments that reflected the low densities observed in

trout streams compared to the higher densities characteristic of fishless streams, and this is likely to result in greater net resource accumulation over the larval period. Moreover, the reduction in per capita production of FPOM observed in the high density treatment suggests that reduced *Z. ingens* feeding rates at high densities were responsible for reduced growth rates. As we found no evidence of anti-predator behaviour by *Z. ingens* larvae in trout tanks through either case construction or feeding rates, there was no evidence for potential non-lethal costs of trout presence on *Z. ingens* at either density.

The lack of antipredator responses of *Z. ingens* to trout was unexpected given our previous work and the prevalence of these responses in other species. The non-lethal presence of trout in our experiment did not induce the heavier, more robust cases seen multiple surveys of trout stream *Z. ingens* (McIntosh *et al.*, 2005), possibly because the behaviour is either induced earlier in *Z. ingens* life history than the fourth instars used in this experiment, or generally inflexible in the populations examined. Furthermore, we saw no change in larval feeding activity in the presence of trout as measured by fine particle production. This was surprising as reductions in foraging activity are consistent responses of prey to predation threats in a

wide variety of taxa (Lima, 1998a), including some mobile stream detritivores (Short & Holomuzki, 1992; Åbjörnsson *et al.*, 2000). However, these foraging tradeoffs are most likely in species where the fitness costs of active foraging are high (Dill, 1987; Peckarsky, 1996). Large-bodied detritivores such as *Z. ingens*, may be able to utilize leaf packs as refugia while feeding (Reice, 1991; Rosenfeld, 2000) and therefore be less likely to reduce foraging rates in response to predation threat than mayflies foraging on the exposed surface of rocks for example.

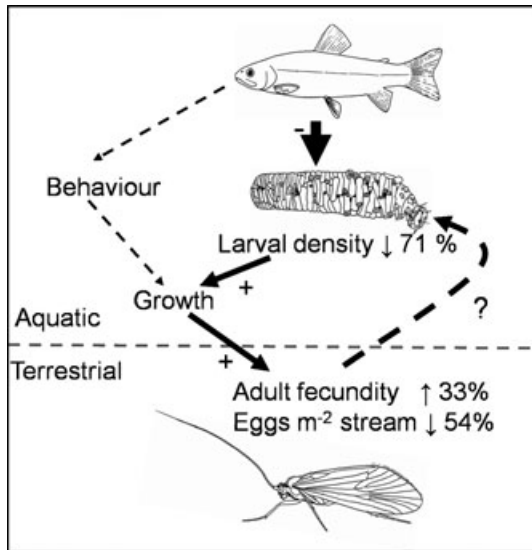
As we did not observe altered case building behaviour of *Z. ingens* in our experiment, we were unable to quantify any cost of building the robust cases observed in trout populations, and thus not completely rule out their potential role in extending *Z. ingens* larval development. Nevertheless, costs associated with building heavier cases in trout streams are likely to be overwhelmed by the strong positive effects of thinning observed in our experiment. We observed a 29% increase in growth of *Z. ingens* in only 43 days when larvae were reared at trout stream densities compared to fishless stream densities. The fifth instar of *Z. ingens* lasts 7–8 months (Winterbourn & Davis, 1976) during which approximately 70% of larval mass is added. Thus, an increase in growth rate over this long period should have considerable benefits to adult size and fecundity, and overwhelm any potential increase in the costs of case construction in trout streams. Moreover, while building new cases is costly (Stevens *et al.*, 1999), all *Z. ingens* in trout and fishless streams rebuild their cases through the fifth instar and additional costs associated with adding thicker sticks in trout stream populations than those in fishless streams are uncertain.

Several factors could conceivably confound the thinning effects of trout on *Z. ingens* growth. First, trout may have released *Z. ingens* from interspecific interactions by affecting predatory invertebrates and/or other detritivores. However, while trout reduce predator biomass in cobble substrates in these streams (Nyström *et al.*, 2003), there is no evidence of trout influencing the biomass of predators or other detritivores in leaf packs to which *Z. ingens* are restricted (Greig & McIntosh, 2006). Secondly, trout may have fertilized the microbial community within leaf packs resulting in higher quality food for *Z. ingens* compared to fishless streams. While we

did not specifically measure microbial biomass, we observed no difference in leaf breakdown rates between trout and fishless streams within invertebrate exclusion cages in a previous experiment (Greig & McIntosh, 2006) suggesting microbial activity is similar between trout and fishless streams. Finally, as the trout streams used in this study were deeper than fishless streams we cannot rule out confounding effect of stream size on *Z. ingens* adult size. However, this is unlikely as our experiment and previous work (McIntosh *et al.*, 2005) suggests *Z. ingens* larvae are limited by resource abundance, which did not differ between trout and fishless streams in this study. Similarly, mean water temperature, a major determinant of growth of larval caddisflies (e.g. Wagner, 2002; Spanhoff, 2005), also did not differ between trout and fishless streams.

That we observed strong density-dependent growth of a detritivore in a forested stream demonstrates that strong competitive interactions between consumers in detritus-based food webs are possible. However, whether differential growth rates were a result of exploitation of resources or interference by conspecifics is difficult to determine based on knowledge of resource abundance alone (Anholt, 1990). There was a considerable amount of leaf remaining in tanks at the conclusion of the experiment (c. 74% of initial dry mass), so the raw quantity of food resources did not appear to have been limiting. However, feeding trials suggest that *Z. ingens* larvae preferentially select older, softer leaves, presumably because of their higher microbial content (Winterbourn & Davis, 1976; Rounick & Winterbourn, 1983), and these 'high quality' resources may have become limiting over the course of the experiment. Thus, the high abundance and independent renewal of detritus do not necessarily preclude competitive interactions for this resource, and the mosaic of detritus patches in the stream and/or their variable food value probably set the scene for the interactions observed.

How the individual fitness costs or benefits of interactions during larval stages influence population dynamics of animals with complex life cycles is poorly understood (Lima, 1998a; but see McPeck & Peckarsky, 1998). Although we have considerable knowledge of the non-lethal effects of predators on prey, and are beginning to understand the balance of these with indirect positive effects of predators on prey fitness (Peacor & Werner, 2004), their



**Fig. 5** Summary of interactions between brown trout (*Salmo trutta*) and larval *Zelandopsyche ingens* in beech forest streams and the subsequent influence on adult *Z. ingens* in the Cass region, South Island, New Zealand. Arrows represent hypothesized effect strengths, with + or - indicating positive and negative effects, respectively, and dashed arrows indicating inferred or unknown effects. Larval density was calculated from McIntosh *et al.* (2005). The effects on local production of eggs and larval settlement parts of the recruitment process are unknown (indicated by '?'). Numbers of eggs per female were calculated from mean trout and fishless stream values, where eggs per m<sup>2</sup> stream were calculated as mean no. per female × late instar density m<sup>-2</sup> × 0.5, assuming 50% of late instar larvae are female.

consequences for prey populations are less clear. Certainly, the non-lethal effects of predators can outweigh their lethal effects on prey larval density within generations (e.g. Peckarsky *et al.*, 2001), but the effect of altered adult fitness on the following generations is uncertain. In our study, females from trout streams had 33% more eggs than those from fishless streams. However, high mortality during larval stages means on average 71% fewer late-instar larvae in trout streams compared to fishless streams (McIntosh *et al.*, 2005). Assuming that mortality in the pupal and adult phase is similar in fishless and trout streams, sex ratios are 1 : 1, and there is negligible between-stream dispersal, we still predict fewer eggs would be available for oviposition in trout streams than fishless streams (Fig. 5). However, the dispersal dynamics of *Z. ingens*, and adult caddisflies in general, are not well known, and the effects of fewer eggs on the following generation depends on whether recruitment is

limiting; an aspect of aquatic insect population dynamics that is poorly understood in general (but see Hildrew *et al.*, 2004). To predict the effect of predator-related changes in adult abundance and fitness on the population dynamics of subsequent generations, detailed knowledge of dispersal and recruitment are needed. We have demonstrated that predators can have contrasting effects on prey, indirectly increasing individual prey fitness but decreasing population density. Thus, the apparent effects of predators on prey will depend on whether individuals or populations are investigated (Peckarsky, Cooper & McIntosh, 1997). The lethal effects of predation on prey populations can be strong, and can outweigh any fitness benefits of predators on surviving individuals at the population scale. However, determining how these effects on adult fecundity from interactions during larval stages influence population dynamics over multiple generations is vital to understanding of the population dynamics of organisms with complex life cycles.

### Acknowledgments

We thank Annabel Barnden, Tanya Blakely, Francis Burdon, Jon Harding, Bridget Keenan, Phillip Jellyman and Linda Morris for assistance in the field and Cora-Lynn Station and the Department of Conservation for access to streams. Comments from two anonymous reviewers, Mike Winterbourn and the University of Canterbury Freshwater Ecology Research Group greatly improved this manuscript. This study was financed by a Royal Society of New Zealand Marsden Fund grant to ARM and experiments were conducted under approval from the University of Canterbury Animal Ethics Committee.

### References

- Åbjörnsson K., Dahl J., Nyström P. & Brönmark C. (2000) Influence of predator and dietary chemical cues on the behaviour and shredding efficiency of *Gammarus pulex*. *Aquatic Ecology*, **34**, 379–387.
- Anholt B.R. (1990) An experimental separation of interference and exploitative competition in a larval damselfly. *Ecology*, **71**, 1483–1493.
- Begon M., Townsend C.R. & Harper J.L. (2006) *Ecology: From Individuals to Ecosystems*, 4th edn. Blackwell, Oxford.

- Benard M.F. (2004) Predator-induced phenotypic plasticity in organisms with complex life histories. *Annual Review of Ecology and Systematics*, **35**, 651–673.
- Brodin T. & Johansson F. (2002) Effects of predator-induced thinning and activity changes on life history in a damselfly. *Oecologia*, **132**, 316–322.
- Choe J.C. & Crespi B.J. (1997) *The Evolution of Mating Systems in Insects and Arachnids*. Cambridge University Press, Cambridge.
- Cummins K.W., Wilzbach M.A., Gates D.M., Perry J.B. & Taliferro W.B. (1989) Shredders and riparian vegetation – leaf litter that falls into streams influences communities of stream invertebrates. *BioScience*, **39**, 24–30.
- Diehl S., Cooper S.D., Kratz K.W., Nisbet R.M., Roll S.K., Wiseman S.W. & Jenkins T.M. Jr (2000) Effects of multiple, predator-induced behaviors on short-term producer-grazer dynamics in open systems. *The American Naturalist*, **156**, 293–313.
- Dill L.M. (1987) Animal decision making and its ecological consequences: the future of aquatic biology and behaviour. *Canadian Journal of Zoology*, **65**, 803–811.
- Gordon N.D., McMahon T.A. & Finlayson B.L. (1992) *Stream Hydrology*. John Wiley & Sons Ltd, Chichester.
- Greig H.S. & McIntosh A.R. (2006) Indirect effects of predatory trout on organic matter processing in detritus-based stream food webs. *Oikos*, **112**, 31–40.
- Hildrew A.G., Woodward G., Winterbottom J.H. & Orton S. (2004) Strong density dependence in a predatory insect: large-scale experiments in a stream. *Journal of Animal Ecology*, **73**, 448–458.
- Huryn A.D. (1998) Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream system. *Oecologia*, **115**, 173–183.
- Jonsson M. & Malmqvist B. (2003) Mechanisms behind positive diversity effects on ecosystem functioning: testing the facilitation and interference hypotheses. *Oecologia*, **134**, 554–559.
- Jowett I.G., Richardson J., Biggs B.J., Hickey C.W. & Quinn J.M. (1991) Microhabitat preferences of benthic invertebrates and the development of generalised *Deleatidium* spp. habitat suitability curves, applied to four New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, **25**, 187–199.
- Lima S.L. (1998a) Stress and decision making under the risk of predation: recent development from behavioural, reproductive, and ecological perspectives. *Advances in the Study of Animal Behaviour*, **27**, 215–290.
- Lima S.L. (1998b) Nonlethal effects in the ecology of predator–prey interactions: what are the ecological effects of anti-predator decision-making? *BioScience*, **48**, 25.
- McIntosh A.R. (2000) Habitat- and size-related variations in exotic trout impacts on native galaxiid fishes in New Zealand streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 2140–2151.
- McIntosh A.R. & Peckarsky B.L. (1996) Differential responses of mayflies from Rocky Mountain streams with and without fish to trout odour. *Freshwater Biology*, **35**, 141–148.
- McIntosh A.R., Greig H.S., McMurtrie S.A., Nyström P. & Winterbourn M.J. (2005) Top-down and bottom-up influences on populations of a stream detritivore. *Freshwater Biology*, **50**, 1206–1218.
- McPeck M.A. & Peckarsky B.L. (1998) Life histories and the strengths of species interactions: combining mortality, growth and fecundity effects. *Ecology*, **79**, 867–879.
- Meissner K. & Muotka T. (2006) The role of trout in stream food webs: integrating evidence from field surveys and experiments. *Journal of Animal Ecology*, **75**, 421–433.
- Moran N.A. (1994) Adaptation and constraint in the complex life-cycles of animals. *Annual Review of Ecology and Systematics*, **25**, 573–600.
- Nyström P., McIntosh A.R. & Winterbourn M.J. (2003) Top-down and bottom-up processes in grassland and forested streams. *Oecologia*, **136**, 596–608.
- Oedekoven M.A. & Joern A. (2000) Plant quality and spider predation affects grasshoppers (Acrididae): food-quality-dependent compensatory mortality. *Ecology*, **81**, 66–77.
- Otto C. (1987) Behavioral adaptations by *Agrypnia pagetana* (Trichoptera) larvae to cases of different value. *Oikos*, **50**, 191–196.
- Peacor S.D. (2002) Positive effect of predators on prey growth rate through induced modifications of prey behaviour. *Ecology Letters*, **5**, 77–85.
- Peacor S.D. & Werner E.E. (2004) Context dependence of nonlethal effects of a predator on prey growth. *Israel Journal of Zoology*, **50**, 139–167.
- Pechenik J.A. (2006) Larval experience and latent effects – metamorphosis is not a new beginning. *Integrative and Comparative Biology*, **46**, 323–333.
- Peckarsky B.L. (1996) Alternative predator avoidance syndromes of stream-dwelling mayfly larvae. *Ecology*, **77**, 1888–1905.
- Peckarsky B.L. & Cowan C.A. (1991) Consequences of larval intraspecific competition to stonefly growth and fecundity. *Oecologia*, **88**, 277–288.
- Peckarsky B.L., Cooper S.D. & McIntosh A.R. (1997) Extrapolating from individual behavior to populations and communities in streams. *Journal of the North American Benthological Society*, **16**, 375–390.
- Peckarsky B.L., Taylor B.W., McIntosh A.R., McPeck M.A. & Lytle D.A. (2001) Variation in mayfly size at

- metamorphosis as a developmental response to risk of predation. *Ecology*, **82**, 740–757.
- Peckarsky B.L., McIntosh A.R., Caudill C.C. & Dahl J. (2002) Swarming and mating behavior of a mayfly *Baetis bicaudatus* suggest stabilizing selection for male body size. *Behavioral Ecology and Sociobiology*, **51**, 530–537.
- Polis G.A. & Strong D.R. (1996) Food web complexity and community dynamics. *American Naturalist*, **147**, 813–846.
- Reice S.R. (1991) Effects of detritus loading and fish predation on leafpack breakdown and benthic macroinvertebrates in a woodland stream. *Journal of the North American Benthological Society*, **10**, 42–56.
- Relyea R.A. (2002) The many faces of predation: how induction, selection, and thinning combine to alter prey phenotypes. *Ecology*, **83**, 1953–1964.
- Relyea R.A. (2007) Getting out alive: how predators affect the decision to metamorphose. *Oecologia*, **152**, 389–400.
- Resetarits W.J., Rieger J.F. & Binckley C.A. (2004) Threat of predation negates density effects in larval gray treefrogs. *Oecologia*, **138**, 532–538.
- 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. & Paul M.J. (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. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 1369.
- Rounick J.S. & Winterbourn M.J. (1983) Leaf processing in two contrasting beech forest streams: effects of physical and biotic factors on litter breakdown. *Archiv fur Hydrobiologie*, **96**, 448–474.
- Rounick J.S. & Winterbourn M.J. (1986) Stable carbon isotopes and carbon flow in ecosystems. *BioScience*, **36**, 171–177.
- Rounick J.S., Winterbourn M.J. & Lyon G.L. (1982) Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New Zealand streams: a stable carbon isotope study. *Oikos*, **39**, 191–198.
- Short T.M. & Holomuzki J.R. (1992) Indirect effects of fish on foraging behavior and leaf processing by the isopod *Lirceus fontinalis*. *Freshwater Biology*, **27**, 91–97.
- Spanhoff B. (2005) Effect of permanent shading on adult size and biomass of the caddisfly *Lype phaeopa* (Stephens, 1836) (Psychomyiidae). *Hydrobiologia*, **549**, 179–186.
- Stevens D.J., Hansell M.H., Freel J.A. & Monaghan P. (1999) Developmental trade-offs in caddisflies: increased investment in larval defence alters adult resource allocation. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 1049–1054.
- Tollrian R. & Harvell C.D. (1999) *The Ecology and Evolution of Inducible Defenses*. Princeton University Press, Princeton, NJ.
- Van Buskirk J. & Yurewicz K.L. (1998) Effects of predators on prey growth rate: relative contributions of thinning and reduced activity. *Oikos*, **82**, 20–28.
- Wagner R. (2002) The influence of temperature and food on size and weight of adult *Chaetopteryx villosa* (FABRICIUS) (Insecta : Trichoptera) along a stream gradient. *Archiv fur Hydrobiologie*, **154**, 393–411.
- Wallace J.B., Eggert S.L., Meyer J.L. & Webster J.R. (1997) Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science*, **277**, 102–104.
- Wallace J.B., Eggert S.L., Meyer J.L. & Webster J.R. (1999) Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs*, **69**, 409–442.
- Webster J.R. & Benfield E.F. (1986) Vascular plant breakdown in fresh-water ecosystems. *Annual Review of Ecology and Systematics*, **17**, 567–594.
- Werner E.E. & Anholt B.A. (1993) Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist*, **142**, 242–272.
- Werner E.E. & Peacor S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**, 1083–1100.
- Winterbourn M.J. (1978) The macroinvertebrate fauna of a New Zealand forest stream. *New Zealand Journal of Zoology*, **5**, 157–169.
- Winterbourn M.J. & Crowe A.L.M. (2001) Flight activity of insects along a mountain stream: is directional flight adaptive? *Freshwater Biology*, **46**, 1479–1489.
- Winterbourn M.J. & Davis S.F. (1976) Ecological role of *Zelandopsycha ingens* (Trichoptera: Oeconesidae) in a beech forest stream ecosystem. *Australian Journal of Marine and Freshwater Research*, **27**, 197–215.
- Wissinger S.A., Steinmetz J., Alexander J.S. & Brown W. (2004) Larval cannibalism, time constraints, and adult fitness in caddisflies that inhabit temporary wetlands. *Oecologia*, **138**, 39–47.

(Manuscript accepted 16 February 2008)

### Supplementary material

The following supplementary material is available for this article:

**Table S1** Physicochemical parameters and resource abundance of six beech forest streams in the upper

Waimakariri catchment measured over 50 m stream reaches.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2427.2007.01881.x>

(This link will take you to the article abstract).

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.