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Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour?

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Abstract Experiments in laboratory stream channels compared the behaviour of *Deleatidium* mayfly nymphs in the absence of fish with that in the presence of either native common river galaxias (*Galaxias vulgaris* Stokell) or introduced brown trout (*Salmo trutta* L.). Galaxias present similar predation risks to prey during day and night but are more active at night. Whereas, trout present a higher predation risk during the day. *Deleatidium* maintained a fixed nocturnal drift periodicity that is characteristic of streams containing visually feeding fish regardless of the nature of the predation regime presented in the laboratory. However, the number on the substratum surface, and therefore able to graze algae, was lower when fish were present than when they were absent. The number was lower during the day in the presence of trout, when they present the highest predation risk, and lower during the night compared to the day in trials with galaxias when galaxias activity disturbs *Deleatidium* from the substratum. Increases in the probability of *Deleatidium* leaving a patch, reductions in the proportion of mayflies on high quality patches and reductions in the distance travelled from refuge also reflected variations in the predation regime. Similar differences in positioning were observed under the same predation regimes in *in situ* channels in the Shag River and these were associated with differences in algal biomass. Algal ash-free dry mass (AFDM) and chlorophyll *a* (chl *a*) were higher on the tops of cobbles when fish were present. Fish also affected the biomass and the distribution of algae on cobbles as AFDM and chl *a* were higher on the sides of cobbles from channels with trout compared to those with galaxias. Changes in grazing behaviour, caused by

predator avoidance, are likely to have been responsible for differences in algal biomass because no significant differences were detected between treatments in the biomass of *Deleatidium* or of total invertebrates.

Key words Grazing · Indirect effects · Predator-prey interactions · Streams · Trophic cascade

Introduction

Predators have often been reported to influence prey behaviour in aquatic systems (for summaries see Zaret 1980; Dill 1987; Kerfoot and Sih 1987; Lima and Dill 1990; Wooster and Sih 1995) but few studies have attempted to relate such behavioural effects to processes that are important in shaping communities (Abrams 1991; Werner 1992; Werner and Anholt 1993). The consequences of behavioural avoidance of predators by prey (as opposed to predator consumption of prey) that result in reductions in grazing, for example, remain unexplored in streams. Indirect effects (*sensu* Miller and Kerfoot 1987) mediated by behavioural changes may take on special significance in streams where the direct effects of fish predation appear to have modest effects on community structure (see reviews by Allan 1983; Thorp 1986; Wooster 1994) yet a large amount of evidence indicates that fish predators affect prey behaviour (Flecker 1992; Douglas et al. 1994; Forrester 1994; McIntosh and Townsend 1994; Wooster and Sih 1995). We consider the potential of insectivorous fish to affect algal biomass in a New Zealand stream by examining the grazing of mayfly nymphs in the presence of either introduced brown trout (*Salmo trutta* L.), native common river galaxias (*Galaxias vulgaris* Stokell) or no fish predators.

Brown trout have replaced common river galaxias as the main predatory fish in many streams in the Otago province of the South Island of New Zealand (Townsend and Crowl 1991), resulting in a significant change in the predation regime (McIntosh and

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Townsend 1995a). Brown trout forage from positions in the water column, rely principally on vision to capture prey and have higher reaction distances and rates of consumption during the day compared with the night (McIntosh and Townsend 1995a). Common river galaxias, which move around more at night, forage from benthic positions, probably use mechanical cues to capture prey and consume similar numbers of prey and have similar reaction distances during day and night (McIntosh and Townsend 1995a).

Using experiments in *in situ* channels Flecker and Townsend (1994) have shown differential effects of brown trout and common river galaxias on insect abundance and algal standing crop in the Shag River, a location that is unusual because of the occurrence of both brown trout and common river galaxias. Grazing scars on the channel sides indicated that insects grazed furthest from refugia when no fish were present, intermediate distances when galaxias were present and smallest distances when trout were present (Flecker and Townsend 1994). These data indicate that the effects of predatory fish on prey behaviour are important in determining the abundance and distribution of algal biomass in this stream.

In this study, we consider the possibility that a fish-induced trophic cascade may arise exclusively because of changes in grazer behaviour rather than grazer abundance. Our experimental animal, the leptophlebiid mayfly *Deleatidium* spp., is a ubiquitous component of New Zealand streams (Winterbourn et al. 1981). It is a grazing mayfly which consumes algae and detritus (Rounick et al. 1982; Winterbourn et al. 1984; Collier and Winterbourn 1990) and in the Shag River study contributed up to 73% of numbers of grazing macroinvertebrates (Flecker and Townsend 1994). Here, we investigate *Deleatidium* behaviour, in the presence of brown trout, common river galaxias or no fish, in laboratory stream channels, in order to interpret the behavioural patterns and effects observed on algal biomass under the same three predation regimes in a second experiment using *in situ* channels in the Shag River.

Methods

Laboratory experiments

In laboratory stream channels we compared the movement, positioning and foraging of *Deleatidium* from the Shag River under the three predation regimes (trout only, galaxias only and no fish present). Experiments were carried out during both day and night as we expected diel differences in behaviour to be important.

Mayflies and fish were captured from the Shag River (Grid reference NZMS 260 142 054557) using electrofishing techniques and transferred to holding facilities at the University of Otago. Fish used in the experiments were adult *G. vulgaris*, 75–85 mm fork length (FL), and juvenile *S. trutta*, 90–120 mm FL. Mayflies were late-instar *Deleatidium* spp. nymphs without black wing pads (i.e. not immediately about to emerge) ranging in size from 4 mm to 11 mm in length (excluding cerci). It is not possible to accurately identify individual *Deleatidium* species from nymphs although two informal groups are recognised (Winterbourn and Gregson 1989). Both

groups were represented in the animals used in these experiments so more than one species was present. Animals were allocated at random to treatments to reduce the likelihood of between treatment differences in species composition. Mayfly and fish populations were housed and fed in separate aerated aquaria (as described in McIntosh and Townsend 1994) under a 10D:14L light regime. We advanced the laboratory light regime by 1 h (compared to the environmental light regime) for our convenience and all animals were held under this light regime for at least 3 days before being used in the experiments.

Four 6-m-long channels were constructed from sections of PVC pipe cut longitudinally in half (see McIntosh and Townsend 1994 for a more detailed description). Dechlorinated tap water (at 14 °C) was pumped through the channels, producing a maximum depth of 15 cm and a mean (\pm SE) current velocity of $18 (\pm 0.6) \text{ cm} \cdot \text{s}^{-1}$ (max $20 \text{ cm} \cdot \text{s}^{-1}$, min $15 \text{ cm} \cdot \text{s}^{-1}$) in the channels. A 2.6-m-long experimental section in each channel was defined by a fine mesh grill (2.5 mm aperture) that stopped fish and mayflies from swimming upstream and a coarse mesh grill (7 mm aperture) that kept fish in but allowed mayflies to move out to be caught in a net suspended at the downstream end.

In the experimental section of each channel, we placed gravel covered by a layer of 48 unglazed ceramic tiles (10 cm \times 10 cm). Of nine tiles provisioned with green algae (as described in McIntosh and Townsend 1994), eight were distributed in a consistent pattern throughout the channel to act as food patches and one was randomly selected for algal quantification (using ash free dry mass according to the method of Flecker and Townsend 1994) to assess food availability between trials. Short pieces of PVC pipe, each associated with a small cobble, provided cover for the fish.

We ran four replicate trials during the day and another four at night for each predator treatment: either three trout, three galaxias or no fish. These densities are in the high end of the natural range found in streams in the Otago province (C. R. Townsend, unpublished work). Trials were run in random order and treatments were rotated among channels. However, the same predator treatment was always run at the same time in both channels of each pair to avoid mixing predator chemicals since channels were connected in pairs to the water tanks. After each trial the channels were washed, the gravel and tiles were changed and the water replaced.

The experiments took place during January and February 1993 (the austral summer), with 'day' experiments starting at 1000 hours and 'night' experiments starting at 2030 hours (1 h after the lights went out). Fish were introduced without food 24 h before the start of trials to acclimatise. We started each trial by lowering the current velocity to less than $5 \text{ cm} \cdot \text{s}^{-1}$ and gently poured 100 mayflies (creating a density in the low range of that found in the Shag River – Flecker and Townsend 1994) into the central region of the experimental section. The velocity was then slowly increased to $18 \text{ cm} \cdot \text{s}^{-1}$ over a 5-min period; any mayflies drifting out during the following 10 min were returned to the channel by the above process or replaced if they drifted out more than once. Experiments were ended after 3 h by removing the fish and recovering mayflies from the channels.

The behaviour of fish and mayflies was recorded on video tape using an infrared light sensitive camera (JVC model TK 5310EG) mounted above the experimental section. With the aid of infrared light, which mayflies and fish are unlikely to detect (Lythgoe 1988; Heise 1992), we were able to follow fish and mayfly movements during day and night in the middle portion (48-cm-long) of the experimental section of each channel. Behaviour was described from the last two hours of video tape by scoring movements and position in relation to the grid formed by the tiles on the bottom of the channel. We measured fish activity in terms of the number of times a fish passed through the field of view and the number of attempted and successful captures of *Deleatidium* in the field of view. The mean number of mayflies visible on the tops of tiles was recorded every 10 min together with the distance of each mayfly from the edge of the tile. All inter-patch (between tile) mayfly movements were recorded in terms of the starting patch, destination and any associated intra- or

inter-specific interactions. At the end of trials we classified mayflies as drifted out, remaining in the channel or missing. Only two mayflies went missing from control trials (no fish predators) so we assumed that those missing from other treatments were consumed by fish.

Patterns among fish predator and time treatments were assessed using two-factor analysis of variance. Data were checked for homogeneity of variance and normality and transformations (\ln or $\ln x + 1$) were used where necessary to satisfy the assumptions of analysis of variance. All factors were treated as fixed effects. The ash free dry mass of periphyton from food patches (mean \pm SE = $0.75 \pm 0.04 \text{ g} \cdot \text{m}^{-2}$) was initially included as a covariate in these analyses to determine whether food levels in trials were different between treatments but was later excluded because it was not significant.

Field experiments

The field experiment took place in the headwaters of the Shag River in the Kakanui Mountains of the South Island of New Zealand late in the austral summer of 1993 starting on 20 February. At this elevation (approximately 1200 m) the Shag River is a stony-bottomed stream draining tussock grassland (see Flecker and Townsend 1994 for a more detailed description).

We used 2-m-long flow-through, *in situ* channels, similar to but shorter than those used by Flecker and Townsend (1994), to establish the same three predation regimes used in the laboratory experiments (i.e. brown trout only, galaxias only or no fish present). The three treatments were replicated in three randomised complete blocks of channels (total = 9 channels) situated in approximately 500 m of stream with at least 50 m between blocks. Channels were constructed from lengths of PVC pipe cut longitudinally (internal diameter = 35 cm). Each channel was fitted with mesh screens (7 mm aperture) that allowed the free movement of invertebrates but prevented the passage of fishes. The bottom of each channel was covered with a layer of gravel overlaid with cobbles (that were scrubbed to remove attached invertebrates and periphyton).

The channels were left to colonise for 12 days before either three *G. vulgaris* or three *S. trutta* per channel were added to the appropriate treatments and all channels were covered with fine white nylon net covers (mesh = 3.5 mm). The end screens of the channels were gently scrubbed every second day to prevent clogging. Fish were the same size and collected in the same manner as for the laboratory experiments.

After a further 12 days with fish present we carried out a series of observations of *Deleatidium* positioning behaviour inside the channels over two consecutive cloudless days. At 1500 hours NZDST on each day the channel covers were removed to allow a clear view of the substratum. Starting at 1700 hours we counted the number of *Deleatidium* visible on the upper surface of eight specific cobbles in the downstream portion of each channel every hour for four hours. Trials using a video camera indicated that, with a careful approach and by standing motionless, accurate observations of the number of mayflies on the upper surface of cobbles could be achieved with visual counts during the day. Accurate counts could not be obtained during the night. Observations from the 2 days were combined to produce an average figure for each channel that was used to compare patterns among treatments in the analysis.

Two days later two randomly chosen cobbles were removed from each channel to determine algal standing crop. To assess the distribution of algae two samples were taken from each cobble. A 24.6-cm² circle from the middle of the top of each cobble was removed first (the "top" sample) and the remaining periphyton on the stone (mainly on the sides) was removed to produce a second sample (the "sides" sample). Algal samples were analysed for chlorophyll *a* (chl *a*) and ash-free dry mass (AFDM) according to the methods of Flecker and Townsend (1994).

After the above sampling we manipulated algal levels in the channels by distributing cobbles (cleared of invertebrates) from the channels with trout (which had a high algal abundance) around all

channels to create six patches with high algal abundance in each channel. All other cobbles in each channel were scrubbed to remove periphyton and create low algal abundance patches. After a further 2 days the six high-food cobbles and six randomly selected low-food cobbles were removed to assess the number of *Deleatidium* on high and low patches among treatments. A net was placed downstream of each cobble as it was lifted to catch invertebrates washed off. The AFDM from one cobble from each food-quality treatment in each channel was measured to compare the amount of food available on high and low food quality patches.

At the conclusion of this manipulation all invertebrates from each channel were washed into a net (250 μm mesh) at the downstream end and preserved in 10% formalin mixed with Rose Bengal as a colourant. These samples were washed through a 1000 μm sieve in the laboratory, which retained the vast majority of invertebrates. Subsamples (25%) of invertebrates were separated from detritus, the *Deleatidium* were identified and counted, and all animals were dried at 60 °C for 24 h to estimate *Deleatidium* abundance and biomass and total invertebrate biomass in the channels.

Differences between predator treatments were analysed using ANOVA (randomised complete block) and data were transformed using \ln (or $\ln x + 1$) transformations as necessary to satisfy the assumptions of ANOVA. Since we were interested in both the general effect of fish and the specific differential effects of galaxias and trout, two a priori orthogonal contrasts (Wilkinson 1989) were used to test for a fish effect (no fish vs. galaxias plus trout) and for a species effect (galaxias vs. trout). Contrasts were planned and orthogonal so we used a contrast (rather than a experimentwise) alpha value of 0.05 to determine significance.

Results

Laboratory experiments

The consumption of mayflies by both galaxias and trout (number consumed per trial, mean \pm SE: galaxias day = 0.5 ± 0.5 , galaxias night = 2.0 ± 1.41 , trout day = 2.25 ± 1.31 and trout night = 1.25 ± 0.48) was small and variable and ANOVA indicated no significant differences. Our experiments were not designed as feeding trials (their short duration and the disturbance to fish caused when adding prey limited feeding) so no conclusions should be drawn from consumption data. The behaviours of trout and galaxias were, however, very different; trout foraged from positions in the water column but galaxias foraged from benthic positions and only entered the water column to attack prey. Brown trout and galaxias also had significantly different (two-factor ANOVA: time \times predator interaction $F_{1,12} = 27.7$, $P < 0.001$) patterns of activity in the channels. Brown trout were active during the day and night (mean \pm SE number of passes per trial through the video field of view: day, 116 ± 29 ; night, 78 ± 35) but galaxias were only active during the night (day, 0; night, 46 ± 17).

The pattern of *Deleatidium* drift out of the channels was similar in all treatments (Fig. 1a), being consistently low during the day but high at night in all trials, as indicated by a significant time effect (two-factor ANOVA: $F_{1,18} = 60.4$, $P < 0.001$) but no significant predator effect ($F_{2,18} = 1.04$, $P = 0.38$) or interaction between time and predator treatment ($F_{2,18} = 0.79$, $P = 0.47$).

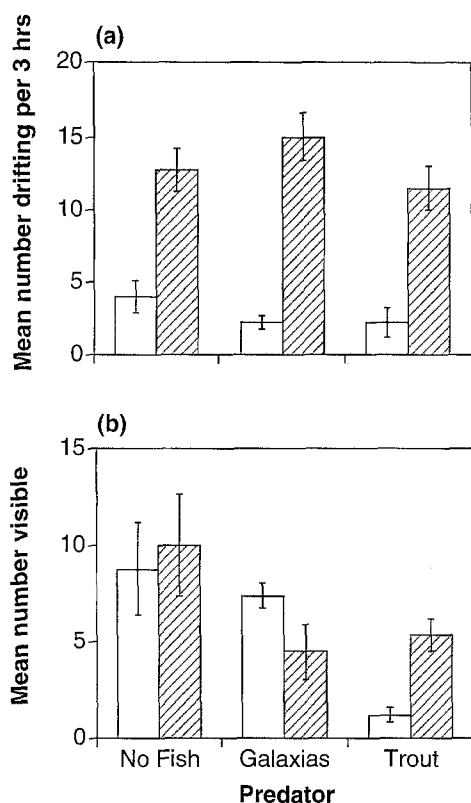


Fig. 1 **a** The mean number (\pm SE) of mayflies drifting out of the channels; and **b** the mean number of mayflies visible (\pm SE) in the camera's field of view during trials with different fish predators during the day (unhatched bars) and night (hatched bars)

Predation risk affected the number of *Deleatidium* visible on tile tops (Fig. 1b); there was a significant predator effect (two-factor ANOVA: $F_{2,18} = 12.94$, $P < 0.001$) and a significant interaction between predator treatment and time ($F_{2,18} = 9.87$, $P = 0.001$). The number visible was higher when fish were absent and, in this case, there was no diel pattern (Fig. 1b). When trout were present, very few mayflies were observed on the tops of tiles during the day. In contrast, the number visible was lower during the night when galaxias were present (Fig. 1b).

Emigration rates from patches were high at night when galaxias were present, high in the day when trout were present and higher during the day than the night when there were no fish present (Fig. 2a); significant predator (two-factor ANOVA: $F_{2,18} = 5.42$, $P = 0.014$) and interaction effects were detected ($F_{2,18} = 3.60$, $P = 0.048$).

The proportion of mayflies on patches with food (Fig. 2b) also varied according to predation regime and time of day, demonstrated by a significant effect of predator treatment (two-factor ANOVA: $F_{2,18} = 4.32$, $P = 0.029$) and a significant interaction effect ($F_{2,18} = 4.84$, $P < 0.021$). In the galaxias treatment the proportion of *Deleatidium* on food patches was lower at night while in the trout treatment the proportion was lower during the day (Fig. 2b).

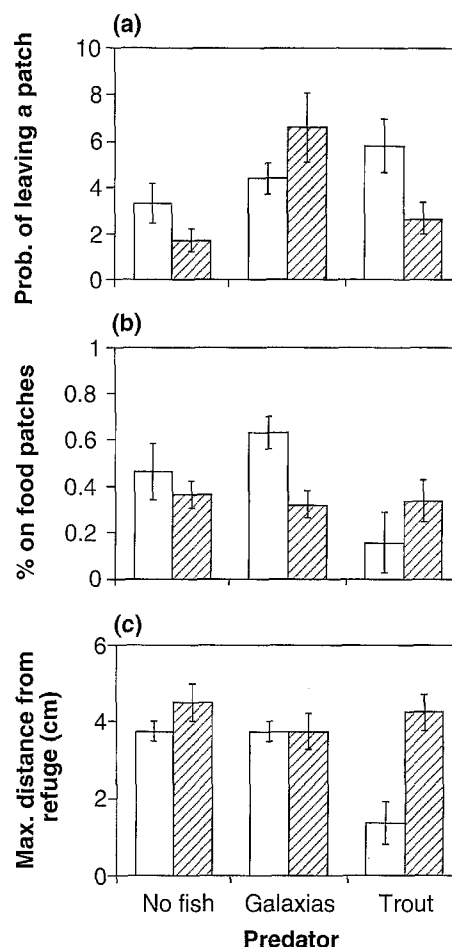


Fig. 2 **a** The mean (\pm SE) emigration rates from patch calculated as the total number leaving patches during the trial divided by the mean number present in patches during the trial; **b** the mean proportion of mayflies on patches with food in the camera's field of view; and **c** the maximum distance mayflies in the camera's field of view travelled from the edge of tiles, during trials with different fish predators during the day (unhatched bars) and the night (hatched bars)

The maximum distance that *Deleatidium* travelled from the edge of a tile (the only available refuge) was reduced during the day when trout were present (Fig. 2c), as revealed by significant predator (two-factor ANOVA: $F_{2,18} = 7.28$, $P = 0.005$), time ($F_{1,18} = 11.23$, $P = 0.004$) and interaction ($F_{2,18} = 8.18$, $P = 0.003$) effects in the analysis.

Field experiments

The number of *Deleatidium* visible on the surface of cobbles during the afternoon in our *in situ* channels was strongly influenced by the fish predation regime (randomised block ANOVA: $F_{2,4} = 35.28$, $P = 0.003$ – Fig. 3), being higher in channels without fish compared to those with fish (no fish vs. fish contrast, $P = 0.002$).

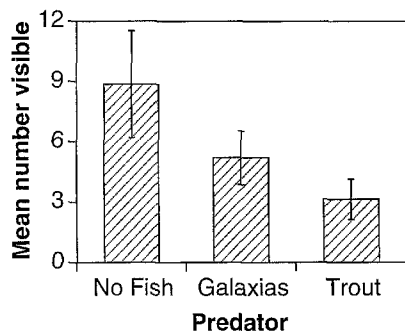


Fig. 3 The mean number (\pm SE) of *Deleatidium* mayfly nymphs observed on the upper surfaces of eight cobbles during the late afternoon in *in situ* channels with different predatory fish

and lower in channels with trout compared to those with galaxias (trout vs. galaxias contrast, $P = 0.01$).

The amounts of algal AFDM and chl *a* on the top and on the sides of cobbles (Fig. 4) were affected by predator treatment (randomised block ANOVAs, top AFDM: $F_{2,4} = 7.32$, $P = 0.046$; top chl *a*: $F_{2,4} = 4.91$, $P = 0.08$; sides AFDM: $F_{2,4} = 13.55$, $P = 0.017$; sides chl *a*: $F_{2,4} = 104.33$, $P < 0.001$). There was significantly more algal biomass on all surfaces of cobbles when fish were present than when they were absent (no fish vs. fish contrast, top AFDM: $P = 0.019$, top chl *a*: $P = 0.035$, sides AFDM: $P = 0.01$, sides chl *a*: $P = 0.01$ – Fig. 4). There was no difference between the trout and galaxias treatments in algal standing crop on the tops of tiles (galaxias vs. trout contrast, AFDM: $P = 0.9$, chl *a*: $P = 0.9$) but there was a significant difference between trout and galaxias treatments for chl *a* (galaxias vs. trout contrast, chl *a*: $P = 0.008$) on the sides of cobbles. The AFDM for the sides of cobbles followed the same trend but was not significantly different between trout and galaxias treatments (AFDM: $P = 0.057$).

The predation regime had some effect on the ability of mayflies to colonise high quality food patches in the *in situ* channels (Fig. 5). The ratio of the number of *Deleatidium* on high quality food patches (mean \pm SE = 0.73 ± 0.06 mg·cm⁻² AFDM) to the number on low quality food patches (0.073 ± 0.01 mg·cm⁻² AFDM), although not significantly different between treatments in the main ANOVA (randomised block ANOVA: $F_{2,4} = 4.68$, $P = 0.09$), was significantly different between trout and galaxias treatments (galaxias vs. trout contrast: $P = 0.04$).

There was little potential for behavioural effects on grazing to be confounded by differences in abundance because *Deleatidium* densities were not significantly different between treatments (randomised block ANOVA, *Deleatidium* density: $F_{2,4} = 0.87$, $P = 0.48$; *Deleatidium* biomass: $F_{2,4} = 0.38$, $P = 0.71$; Fig. 6a). Furthermore, there were no significant differences in the biomass of the other dominant grazer in the system, the caddisfly *Olinga*, or in total invertebrate

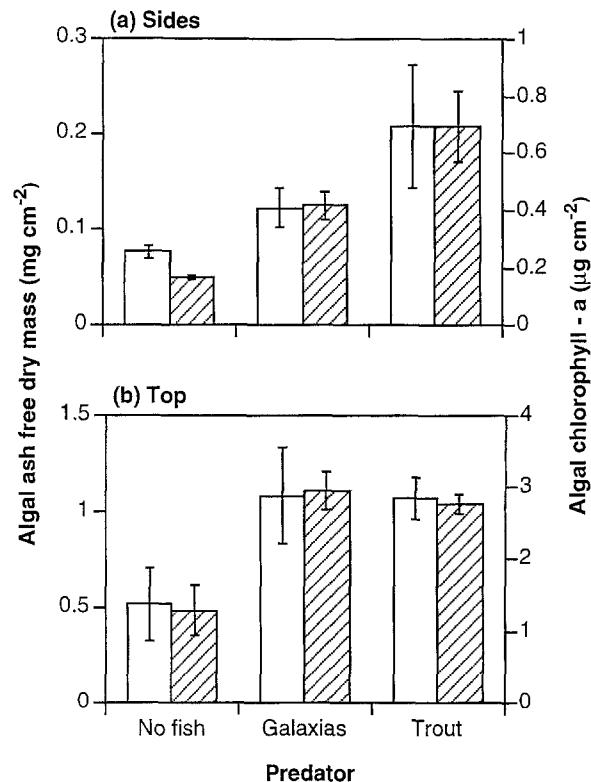


Fig. 4 The mean (\pm SE) algal ash free dry mass (unhatched bars) and chlorophyll *a* (hatched bars) on **a** the sides and **b** the top of cobbles in *in situ* channels with different predatory fish

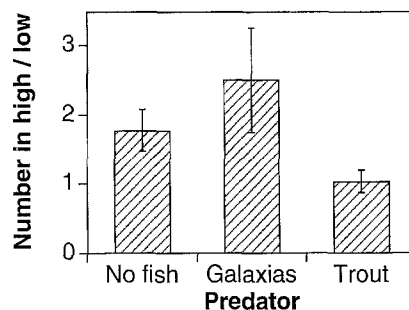


Fig. 5 The mean ratio (\pm SE) of the number of mayflies in high-quality food patches divided by the number in low-quality food patches in *in situ* channels with different predatory fish

biomass from the channels (randomised block ANOVA, *Olinga* biomass: $F_{2,4} = 0.15$, $P = 0.86$; total biomass: $F_{2,4} = 1.57$, $P = 0.31$; Fig. 6b).

Discussion

Our results provide good evidence for a behaviourally driven trophic cascade. Knowledge of the effects of fish on *Deleatidium* behaviour, derived mainly from laboratory experiments, allows us to interpret the consequences of the predation regime for algal abundance and distribution in the *in situ* channels.

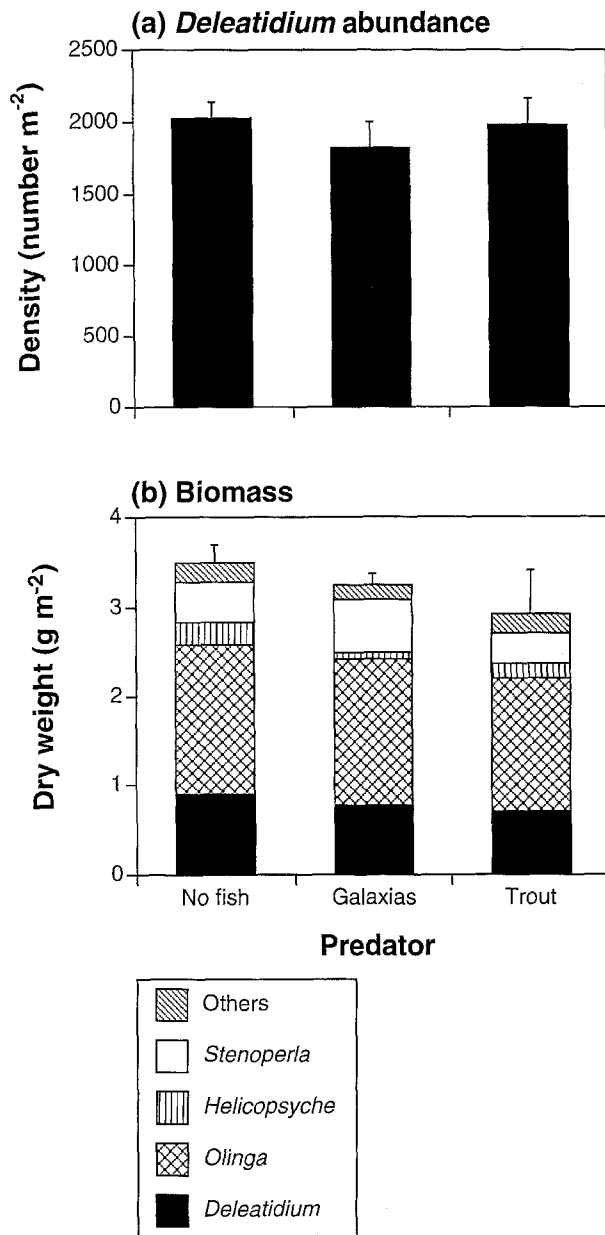


Fig. 6 The mean (\pm SE) abundance of **a** *Deleatidium* nymphs and **b** the mean biomass of invertebrates in channels with different predatory fish. The error bars for biomass indicate the standard error for mean total biomass. Common invertebrates in the channels were the caddisflies *Olinga feredayi* and *Helicopsyche albescens* and the predatory stonefly *Stenoperla prasina*

Deleatidium maintained a nocturnal drift periodicity in the laboratory throughout, regardless of the predation regime. Diel drift periodicities that appear fixed or inflexible to changes in the predation regime are often associated with the presence of visually feeding fishes. Visually feeding fish present a higher predation risk during the day (Ringler 1979; Walsh et al. 1988; Angradi and Griffith 1990; McIntosh and Townsend 1995a); by reducing daytime activity in the water column, where the chances of predation are par-

ticularly high (McIntosh and Townsend 1995a), the risk of predation is reduced.

Both concordance and nonconcordance between drift and positioning on the substrate surface have been reported (e.g. Allan et al. 1986, 1991; Casey 1987; Wilzbach 1990). Many of the conflicts in these studies might be resolved by taking into account the location of fish in the study streams. Thus, in our study, concordance between drift and positioning existed when a trout was close by (as in our trout treatment) but not when fish were absent from the immediate vicinity (as in our fishless treatment).

In both the field and laboratory studies during the day more *Deleatidium* were observed grazing in channels with no fish compared to those with fish and more in channels with galaxias compared to those with trout. Furthermore, as no significant differences in the density of *Deleatidium* or total invertebrates were detected in the *in situ* channels, the impacts on algal abundance and distribution in the *in situ* channels can be largely attributed to the behavioural effects of our manipulation of the predation regime on grazing invertebrates.

Flecker and Townsend (1994) found reduced invertebrate abundances in the presence of fish in their experiments in the Shag River. The only methodological difference between this study and theirs is the size of the channel used (they used a 6-m-long channel, we used a 2-m-long channel), something that may account for the differences observed. Prey exchange rates have a large influence on the detected impact of predation in streams (Cooper et al. 1990); thus when a shorter channel is used the potential is increased for emigration to swamp any effects of consumption.

Our manipulation of algal abundance on cobbles in the channels before the invertebrate sampling is unlikely to have affected invertebrate abundance because the majority of invertebrates were found in the gravel and would not have been disturbed. Furthermore, since the change in algal abundance would have been greatest in channels with trout (because they had greatest algal abundance) we would have expected the manipulation to accentuate any differences between treatments in invertebrate abundance. This makes our conclusions about invertebrate abundance conservative.

Another experiment where constant numbers of grazers are maintained experimentally would be the only way to test for certain that the changes in algal abundance were derived purely from differences in prey behaviour. However, it seems unlikely that the magnitude of differences observed in algal abundance here were due to the small trends for decreased invertebrate biomass in channels with fish that were not statistically significant. Thus, our field experiment indicates that introduced trout can produce a trophic cascade that is driven principally by changes in behaviour of the primary consumers.

Our observations of the behaviour of *Deleatidium*, the dominant mayfly grazer in the system, allow us to interpret these differences. Since there were no between-

treatment differences in *Deleatidium* drift in the laboratory it is likely that changes in positioning are responsible for effects observed in the *in situ* channels. The amount of time *Deleatidium* spent on the substratum surface in the laboratory was reduced when fish were present, and more so in the trout than the galaxias treatment. Thus, the effect of our manipulation of the predation regime on algal biomass can be explained by a reduction in the amount of time spent grazing.

The pattern of algal distribution on stones in the field suggests that fish were restricting *Deleatidium*'s access to certain surfaces of stones and the two fish species were having differential effects. Both fish predators were restricting access to the top surfaces but *Deleatidium* were grazing further up the sides of stones when galaxias were present compared to when trout were present. This accords with results from the laboratory showing that only the presence of trout during the day restricted the distance *Deleatidium* was prepared to venture from the refuge of gaps between tiles.

The differences in *Deleatidium* behaviour in the different treatments reflect the variations in predator behaviour. The number visible was lower and the probability of leaving a patch higher in laboratory channels with trout during the day when brown trout present a higher predation risk (McIntosh and Townsend 1995a). *G. vulgaris* present similar predation risks during day and night, but are more active at night when their benthic feeding often disturbs prey on the substrate surface (McIntosh and Townsend 1994, 1995a). Thus, the reduction in the number of *Deleatidium* on the substrate at night and a higher probability of leaving in the galaxias treatment is likely to be associated with this nocturnal increase in galaxias activity. It is important to remember that trout still present a considerable predation risk at night, and that galaxias have the potential to consume prey during the day (McIntosh and Townsend 1995a). Thus, the lower number of *Deleatidium* visible at all times in channels with fish, compared to fishless channels also reflects the risk of predation.

An extensive study of 198 stream sites in the Taieri River of Otago province has shown that brown trout and *G. vulgaris* rarely coexist. In most cases, galaxias were only found above waterfalls that were large enough to inhibit trout migration (Townsend and Crowl 1991). It is of considerable interest to know whether the introduction of brown trout has caused cascading effects in communities where it has replaced the native fish. A potentially profound effect has been revealed (Flecker and Townsend 1994) and the present study indicates that this may be mainly mediated through changes to the behaviour of grazers rather than their abundance. The challenge now is to assess whether these sort of effects are apparent at a larger scale. That is, has the presence of trout resulted in an increase in algal standing crops in streams where they have been introduced compared to streams where

they are not present? The distribution of fish is patchy in streams so that their effects will also be patchy and perhaps difficult to detect. The spatial and temporal variations in the threat of predation will determine to what extent such interactions are likely to be important. If predation pressure is persistent then changes in grazer abundances through sublethal reductions in their fitness (*sensu* Peckarsky et al. 1993) are to be expected. There is some evidence that the behavioural interactions we have described are widespread. Using measurements of gut photosynthetic pigment by fluorescence we have found that *Deleatidium* consume more algae during the night than the day in streams with trout, but consume similar amounts during day and night in streams with galaxias (McIntosh and Townsend 1995b).

Indirect effects are common (Wootton 1994) but higher-order interactions, a subset of indirect effects, where a third species qualitatively affects the nature of the interaction between two others by changing per capita effects have received little attention (Werner 1992). This is despite good theoretical evidence that the magnitude of effects on a consumer's resources caused by behavioural interactions between the consumer and a predator can be greater than the impacts due to consumption of the prey by the predator (Abrams 1991).

Most indirect effects described from aquatic communities are related to or confounded by density changes in the intermediate species (e.g. Power et al. 1985; Carpenter et al. 1987; Power 1990). However, Turner and Mittelbach (1990) found that the impacts of largemouth bass on the habitat use of bluegill sunfish caused changes in a zooplankton community (abundance and composition) and were separate from density changes since the largemouth bass ate few bluegill. Our results are important because they also indicate a link between adaptive behavioural changes and population dynamics.

Behaviourally driven trophic cascades are likely to be highly scale dependent because they are short term responses that do not require changes in population density of intermediate species. The ease with which behaviour can be modified means that such interactions are likely to be widespread (Werner 1992). It now remains for ecologists to determine how important they are in shaping ecological communities.

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