

Per Nyström · Angus R. McIntosh

## Are impacts of an exotic predator on a stream food web influenced by disturbance history?

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**Abstract** Predatory species have been introduced to habitats spanning a wide range of environmental conditions. To better understand the consequences of predation in natural communities we need to examine how variations in abiotic factors modify the influence of predation. The effects of introduced predators may vary amongst habitats if natural disturbance affects the abundance and taxonomic composition of consumers and their resources, or the predator alters recolonisation after disturbance. We tested whether a bed-moving disturbance altered subsequent interactions involving native and introduced predatory fish, invertebrate grazers and algae in experimental channels within a New Zealand stream. Disturbance reduced the abundance of invertebrates by 84%, and induced mortality of Conoesucidae caddisflies. However, the relative abundance of taxa changed little immediately following the disturbance. Invertebrate communities recovered following disturbance in fishless channels and those with native galaxiids (*Galaxias vulgaris*), and were almost indistinguishable from undisturbed fishless controls after 2 weeks. Invertebrate abundance declined and algal abundance increased in channels with exotic brown trout (*Salmo trutta*) and their effect was strongest in previously disturbed channels. However, predators and disturbance only had interactive effects on grazer emigration rates. Trout affected grazers through direct consumption (e.g. Conoesucidae caddisflies), and induced higher emigration rates of grazers from channels via drift (e.g. the mayfly *Deleatidium*). The effects of predatory trout and galaxiids combined differed in disturbed and stable channels. The observed combined effects of

predatory trout and galaxiids on invertebrate grazers were lower than expected in stable channels partly due to low emigration rates of Conoesucidae, whereas emigration of grazers was higher than expected in the disturbed channels. The biomass of algae was higher than expected in disturbed channels with both predators. Collectively, our results indicate that predator substitutability and the non-lethal effects of introduced predators varied depending on disturbance history, but their effects on the biomass of grazers and algae did not.

**Keywords** Multiple predators · Trophic cascade · Fish · Invertebrates · Algae

### Introduction

Ecological communities are typically complex and may contain many native and exotic predators that interact in a varying environment. However, few experimental studies have tested how environmental factors interact with biotic interactions in complex food webs. Such studies are needed if a predictive theoretical framework of community structure is to be developed for managing the effects of exotic species (Townsend 1991). Habitat disturbance affects whether habitats can be invaded (e.g. Moyle and Light 1996; Dukes and Mooney 1999; Byers 2002), but effects of introduced predators, once established, will also vary according to environmental conditions. In particular, disturbance to physical habitat could alter the influence of a predator on the community.

Disturbances affect animals, plants and micro-organisms (Pickett and White 1985), may alter the impact of predators (Connell 1975; Thomson et al. 2002) and herbivores (Poff and Ward 1995; Nystrand and Granström 2000) on lower trophic levels, and may alter food web structure (Townsend et al. 1998). Conceptual models predict that the influence of biotic factors on community structure will be affected by the strength of abiotic factors, spatial and temporal scale, and how well predators and prey are adapted to changes in local environ-

P. Nyström (✉) · A. R. McIntosh  
Department of Zoology,  
University of Canterbury,  
Private Bag 4800, Christchurch, New Zealand  
e-mail: per.nystrom@limnol.lu.se  
Fax: +46-46-2224003

#### Present address:

P. Nyström, Department of Ecology, Ecology Building,  
Lund University,  
223 62 Lund, Sweden

mental conditions (Connell 1975; Peckarsky 1983; Menge and Sutherland 1987; Menge and Olson 1990; Wellborn et al. 1996).

Whether physical factors or biotic interactions predominate in determining the structure of stream and river communities has been the subject of debate (cf. Allan 1995). It is well known that floods can reduce the abundance of stream invertebrates directly (Matthaei and Townsend 2000), and that populations can recover rapidly if predation pressure and competition are reduced (Scrimgeour et al. 1988; Zhang et al. 1998). Thus, biological interactions may be particularly important in structuring many stream communities during more stable periods (Power 1990; Marks et al. 2000). However, recent studies indicate that biotic interactions may be just as important in disturbed environments (Wootton et al. 1996; Thompson et al. 2002).

Predatory fish are often the most important predators in streams, but their impact on benthic communities varies greatly (see review in Wooster et al. 1997). It can be expected that trophic interactions involving predatory fish in streams will be affected by disturbances caused by floods. For example, after a flood, predatory fish may prevent the recolonisation of substrate patches by invertebrates and changes in composition of the invertebrate community caused by flooding may also alter the susceptibility of invertebrates to predators (Wootton et al. 1996).

Floods and predatory fish both influence the community structure of New Zealand streams (e.g. Flecker and Townsend 1994; Death and Winterbourn 1995; Death 1996; McIntosh and Townsend 1996; Townsend et al. 1997), but the relative importance of the two factors and how they interact is unknown. Introduced trout have replaced native galaxiid fishes in many New Zealand streams (Cowl et al. 1992) and in Canterbury high country streams either exotic brown trout (*Salmo trutta*) or native Canterbury galaxiids (*Galaxias vulgaris*) are usually present (McIntosh 2000a). Canterbury galaxiids are nocturnal benthic foragers, whereas trout are predominantly diurnal drift feeders (Cadwallader 1975; McIntosh and Townsend 1995). Thus, prey may be better adapted to avoid predation by galaxiids, and trout are more likely to consume prey that drift in the water column (McIntosh 2000b).

We were interested primarily in whether disturbance history influenced the effects of these two predatory fish on a stream food web. However, some streams contain both trout and galaxiids, whereas others contain either trout or galaxiids. Thus, it was of interest to know whether the effects of galaxiids and trout were substitutable (i.e. whether the two fish species had equivalent effects when together or alone). Furthermore, it is difficult to predict the influence of predatory fish on a stream community because spatial scale and prey movement have a large influence on the outcome of interactions (Cooper et al. 1990; Englund 1997). Therefore, we were also interested in what mechanisms were responsible for any differences in community structure associated with predatory fish or

their interaction with the disturbance regime. We subsequently determined the amount of prey consumed by fish and estimated the relative importance of direct predation and prey emigration.

## Materials and methods

A field experiment was undertaken using 24 in-stream channels from 1 to 15 March 2001 in Grasmere stream, Cass, South Island, New Zealand. Grasmere stream is a stable lake-fed stream of circumneutral pH that rarely experiences bed-moving spates. It is nutrient poor, contains abundant macrophytes (e.g. *Nasturtium* sp., *Myriophyllum* sp., and *Ranunculus* sp.) and flows through tussock grassland. The fish fauna comprises two exotic salmonids (*Salmo trutta*, *Oncorhynchus tshawytscha*) and the native longfin eel (*Anguilla dieffenbachii*) (McIntosh 2000a). Galaxiids were not present in Grasmere stream because they are often excluded by large trout (McIntosh 2000a). The invertebrate fauna of Grasmere stream is typical of stable South Island trout streams, i.e. grazers with cases and shells are abundant and predatory invertebrates are less common (Nyström et al. 2003). It was necessary to undertake the experiment in a stable stream because the "control" situation of a stream fauna characteristic of a stable stream would be impossible to achieve in a frequently flooded stream, as would be erecting stream channels. Although experience of trout can influence the behaviour of some stream invertebrates (McIntosh and Townsend 1994), and may influence the outcome of an experiment such as this, the behaviours of the most important grazers change according to the local presence/absence of predatory trout and galaxiids (McIntosh and Townsend 1996).

Stream channels were constructed from 1.5-m lengths of PVC pipe (25 cm inner diameter,  $\approx 0.4 \text{ m}^2$ ) cut longitudinally in half (see Flecker and Townsend 1994) and were located in a 200-m-long reach (mean width=2.15 m, mean velocity=0.71 m/s, mean depth=29 cm, mean $\pm$ SE temperature measured by an Onset datalogger during the experiment =15.1 $\pm$ 0.03°C). Each channel had a set of removable stainless steel screens (6 mm mesh) at each end to allow free immigration and emigration of invertebrates but prevent the passage of fish. The top of each channel was covered with 3-mm-diameter mesh netting to prevent fish from escaping. The bottom of each channel was covered with a layer of gravel and 16 similar-sized rocks (mean $\pm$ SE=88 $\pm$ 3.5 cm<sup>2</sup>) collected from a dry riverbed. The channels, were set up on 22 and 23 February 2001, positioned at the water surface, approximately 20 cm above the streambed, and left for a week to enable algae to colonise.

We used a randomised block design to investigate the effects of bed movement and predators. A block consisted of two groups (approximately 25 m apart) of four channels. The four channels in a group were located side by side in the stream. Blocks were separated by 40 m. The two disturbance treatments (simulated bed movement and undisturbed channels) and four predator treatments: (1) two Canterbury galaxiids (galaxiids), (2) two brown trout (trout), (3) one galaxiid+one brown trout (both), (4) no fish (fishless) were replicated 3 times. The predator treatments were assigned randomly to channels within a group, and disturbance treatments were assigned randomly to one of the groups of channels within a block.

The biomass of fish used in the experimental channels (29.8 g/m<sup>2</sup> $\pm$ 2.0 SE) represented values from the higher end of the natural range in the Cass area (McIntosh 2000a; unpublished data). Fish were obtained from local streams and were of similar sizes (means $\pm$ SD fork length: trout, 8.9 $\pm$ 0.7 mm; galaxiids, 7.9 $\pm$ 0.9 mm). Individual trout (7.3 $\pm$ 1.4 g,  $n=18$ ) were heavier than similar sized galaxiids (3.9 $\pm$ 1.4 g) and consequently the fish biomass in channels with trout or both trout and galaxiids was significantly higher than in the channels with galaxiids only (one-way ANOVA,  $F_{2,15}=23.56$ ,  $P<0.001$ , Tukey's post hoc test,  $P<0.01$  in both cases). This situation reflects the higher fish biomass per unit area normally

found in trout streams compared to galaxiid streams (McIntosh 2000a).

When an algal biofilm had started to grow on the rocks in the channels, invertebrates were collected from riffles downstream of the study reach using a Surber sampler (5×0.0625 m<sup>2</sup> samples per channel, 250- $\mu$ m mesh) and added to the channels on 1 March. The next morning the invertebrates had settled because grazers were observed grazing on rocks and net spinners had built nets. Subsequently, 12 channels were disturbed by hand tumbling of the substrates for 2 min to simulate a bed-moving flood. Invertebrates dislodged during the bed-movement were caught in a net at the downstream end of the channels to prevent drift into downstream channels. Immediately after the disturbance, one Surber sample (0.0225 m<sup>2</sup>, 250  $\mu$ m mesh) was taken from the middle of each channel and preserved with ethanol. At 1630 hours on the same day, fish were introduced to the experimental channels. Although it would have been ideal to subject fish to the same disturbance as the invertebrates, human-induced frightening of the fish during the rock tumbling would have confounded this. Moreover, in reality fish probably seek refuge or reduce foraging during flood disturbances and may take some time to resume normal feeding activity (Scrimgeour and Winterbourn 1987; Al Shaw and Richardson 2001). It is likely that the time taken for fish to resume normal feeding in the channels after handling [normally around 24 h (McIntosh and Townsend 1995)] mimicked the recovery time from a natural, bed-moving disturbance. Fish survival was checked each day at the time the stainless steel screens were cleaned.

To obtain an estimate of invertebrate emigration from the channels, all invertebrates were collected in drift nets attached to the downstream screen on each channel. Collections of drift were made over 2 h in the middle of the day on 14 March and for 1 h starting at 2300 hours the same day with a rectangular net (width=11 cm, depth=6 cm, mesh=250  $\mu$ m). All drifting invertebrates were preserved in 80% ethanol, counted, and identified to the lowest possible taxonomic level using keys in Winterbourn et al. (2000). Drift dispersal into the channels could not be measured without disturbing the channels and we therefore assumed immigration rates were unaffected by the presence of fish (e.g. Forrester 1994; Forrester et al. 1999).

The experiment was terminated on 15 March when all fish were netted, killed with an overdose of anaesthetic (2-phenoxyethanol), weighed to the nearest 0.1 g, and then frozen for later examination of foreguts. All invertebrates were washed into a fine-mesh net (250  $\mu$ m) at the downstream end of each channel and preserved in 80% ethanol. After enumeration and identification, invertebrates were dried for 24 h at 65°C, weighed to the nearest 10  $\mu$ g, ashed in a muffle furnace at 450°C for 1 h, and reweighed to enable calculation of ash-free dry mass per metre square. Lastly, four rocks from the centre of each channel were frozen for algal biomass determination. After thawing, an 18.6-cm<sup>2</sup> circle of periphyton was removed with a toothbrush from the top surface of each rock. The algal sample was filtered onto a glass fibre filter (Whatman GF/C) and chlorophyll *a* content was measured spectrophotometrically after extraction with ethanol.

Most invertebrates in the channels were collector-browsers (mean±SE of total invertebrate end biomass=86.6±6.9%, *n* =24), predominantly conoesucid caddisflies (*Pycnocentria* sp. and *Olinga feredayi*, 50.5±1.4% and 4.0±0.7%, respectively), the snail *Potamopyrgus antipodarum* (7.7±1.2%), and the mayfly *Deleatidium* (14.0±1.6%). The filter-feeding mayfly *Coloburiscus humeralis* (8.4±1.3%) was also common. Predatory invertebrates, mostly small Hydrobiosidae larvae (2.9±0.3%) and *Archichauliodes diversus* (Megaloptera), were not abundant.

## Statistics

In most cases our analysis was two-way factorial with disturbance regime and predators as main effects. We used a blocked design because water velocity in channels differed between blocks (two-way ANOVA, block effect;  $F_{2,14}=7.26$ ,  $P=0.0069$ ), but did not

differ between stable and disturbed channels, or between predator channels within blocks ( $P>0.3$  in all cases). Our analysis focused primarily on the direct effects of predatory fish and disturbance on grazing invertebrates (total grazers, Conoesucidae and *Deleatidium*) and their indirect effect on algal biomass. Conoesucidae and *Deleatidium* are abundant collector-browsers in many New Zealand streams (Winterbourn 2000). First we tested the general effect of disturbance, predators and their interactions on invertebrate grazers (i.e. total grazer biomass, total grazer abundance, and the biomass and abundance of Conoesucidae and *Deleatidium*) using a two-way MANOVA with blocks. We were particularly interested in the effects of trout and galaxiids in comparison to patterns in control channels and this was tested by contrasts (i.e. trout vs. control and galaxiid vs. control). Then, univariate ANOVAs were performed for each of the dependent variables to clarify interpretation of the MANOVA. The effects of disturbance and predatory fish on per capita drift rates for total grazers, Conoesucidae and *Deleatidium* were tested using separate two-way MANOVAs with drift rates during day and night as the dependent variables in each analysis.

Our design allowed us to test if predators had identical but independent effects because predator density was kept constant (Sih et al. 1998; Sokol-Hessner and Schmitz 2002). Thus, in our case, the expected values in channels with one trout and one galaxiid (i.e. the “both” treatment) were the means from the values obtained in channels with two galaxiids and channels with two trout (e.g. Sih et al. 1998). Moreover, in order to be able to test whether predator substitutability was affected by disturbance regime we compared the expected and observed values (the actual measurement from “both” channels) in disturbed and stable channels in an additional analysis. This was done by using multiple one-way ANOVAs that included blocks and predators as main effects. A contrast then tested the values in channels with two galaxiids and two trout (expected) versus the values in channels with one trout plus one galaxiid (observed) (e.g. Sokol-Hessner and Schmitz 2002).

Due to the low abundance of prey in foreguts of galaxiids during the day we only tested whether direct predation or avoidance behaviour by prey was most important in producing observed patterns of grazers in channels with trout only. We calculated the daily consumption rate by trout and emigration of prey per day, using data on gut contents, drift rates and prey densities. Predation rate (an estimate of the percentage of prey consumed per day in a channel with two trout) was calculated for Conoesucidae and *Deleatidium* because they were the most common grazers and were easily identified in the guts. Predation rate was estimated using a simple model that uses the abundance of prey in the foregut and the gut evacuation rate in trout (e.g. Elliott and Persson 1978; Forrester et al. 1999). To estimate daily emigration rate of grazers we calculated a per capita emigration index for Conoesucidae and *Deleatidium*. We assumed that the 2 h day drift samples and the 1 h night drift samples were representative of day and night drift rates, respectively, and estimated the number of drifting invertebrates in 24 h (using 14:8 h, light:dark regime). This 24-h rate was divided by the benthic abundance at the time to estimate the percentage of the population emigrating in 24 h (Forrester et al. 1999). The daily consumption rate of two trout and the daily emigration rate of prey was compared with a paired *t*-test (results from stable and disturbed channels were pooled in the analyses since disturbance did not affect or interact with trout effects,  $P>0.09$  in all cases). To be able to assess the overall relationship between predator impact and emigration rate of grazers we calculated the predator impact index (PI) of Cooper et al. (1990) and related this to the daily emigration index for all grazers combined (covariate) in an analysis of covariance. The PI for galaxiids, trout and trout+galaxiid was calculated as the natural logarithm of the ratio of prey biomass in the absence and presence of predators using data for groups of channels that were located side by side in the stream. PI has a large positive value if prey biomass is significantly reduced by a predator, and is negative when prey biomass has been enhanced by the presence of a predator. To normalise data in all the above analyses, percentages were arc sin transformed; other data were  $\log_e$  transformed.

## Results

### Fish growth and diet

All fish appeared to behave normally during the experiment, except for one trout that died midway through the experiment and was replaced. Over the 15 days of the experiment the change in the wet weight of trout varied between  $-0.8$  g to  $+0.6$  g and the corresponding values for galaxiids were  $-0.5$  g to  $+0.2$  g. Stomach content analyses showed that trout had consumed a diverse range of prey items (14 taxa), mainly aquatic insect grazers, but also including terrestrial flies, ants and spiders (Fig. 1). All 18 trout sampled contained prey; the mayfly *Deleatidium*, *Pycnocentria* (Conoesucidae) and *Oxyethira* (Hydroptilidae) caddisflies were found in all trout guts, but although present in the channels, snails and the large filter-feeding mayfly *Coloburiscus*, were never found in trout stomachs. The 18 galaxiid stomachs were less full than those of trout and two were empty. Eight aquatic prey taxa were identified from their guts, *Deleatidium* (75%) and *Oxyethira* (75%) occurring most frequently (Fig. 1). Conoesucid caddisfly larvae were found in only 10% of galaxiid stomachs. Using these data we tested whether per capita consumption rates of conoesucid caddisflies and *Deleatidium* by trout were affected by disturbance and the presence of galaxiids (Table 1), and found that consumption rates by trout did not differ between treatments and the interactions were not significant (two-way ANOVA with block,  $P > 0.47$  in all cases for conoesucid caddisflies, and  $P > 0.11$  in all cases for mayflies). Because galaxiids feed predominantly at night, they subsequently had few prey in their foreguts when the experiment was

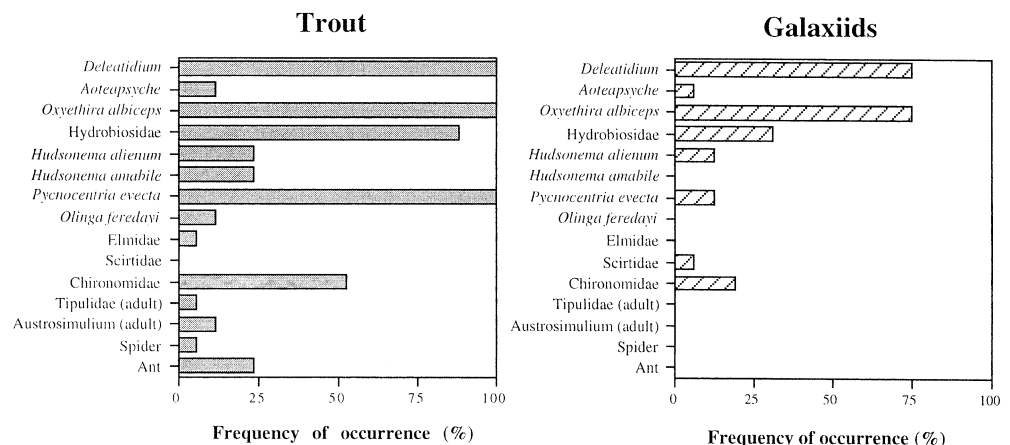
terminated (Table 1). Therefore we did not test for differences in galaxiid prey consumption between treatments.

### Invertebrates

The abundance of grazers in channels that were kept as undisturbed and fishless did not change during the experiment (initial,  $2356 \pm 68$  SE,  $n=3$ ; final,  $2668 \pm 358$  SE,  $n=3$ , abundance of grazers, paired  $t$ -test,  $t = -0.61$ ,  $P > 0.60$ ,  $df = 2$ ). Before the fish introductions and the simulated disturbance, the invertebrate community in channels that were going to be kept as undisturbed (mean  $\pm$  SE =  $2240 \text{ m}^{-2} \pm 400$ ,  $n = 12$ ) was dominated by grazers, particularly conoesucid caddisflies (67%), *Deleatidium* (10%) and *Oxyethira* (3%). Although the simulated disturbance reduced the abundance of grazers by 84% (one-way ANOVA,  $F_{1,22} = 30.67$ ,  $P < 0.001$ ), the relative abundance of different taxa changed little immediately following the disturbance (Conoesucidae, 67%; *Deleatidium*, 3%; *Oxyethira*, 1%). Moreover, few invertebrates were found in samples from the disturbed channels immediately after the disturbance and it was only possible to assess disturbance-induced mortality for conoesucid caddisflies. On average ( $\pm$  SE)  $67 \pm 4\%$  of conoesucid cases sampled were crushed in the disturbed channels compared to only  $7 \pm 1\%$  in the stable channels ( $F_{1,22} = 208.59$ ,  $P < 0.001$ ).

Overall, disturbance had a significant effect on invertebrate community structure by reducing the final biomass and abundance of grazers (two-way MANOVA with blocks, disturbance effect:  $F_{6,9} = 5.39$ ,  $P = 0.0127$ , Tables 2,

**Fig. 1** Frequency of occurrence (%) of prey taxa identified in the guts of trout ( $n=18$ ) and galaxiids ( $n=16$ ) at the end of the experiment



**Table 1** Average number ( $\pm$  SE) of caddisflies (Conoesucidae) and mayflies (*Deleatidium*) in the foreguts of predators from undisturbed and disturbed channels at the end of the experiment

Predator treatment	Stable		Disturbed	
	Conoesucidae	<i>Deleatidium</i>	Conoesucidae	<i>Deleatidium</i>
Trout only	9.83 ( $\pm 4.87$ )	1.33 ( $\pm 0.33$ )	9.50 ( $\pm 2.84$ )	0.83 ( $\pm 0.17$ )
Trout (with one Galaxiid)	5.67 ( $\pm 1.20$ )	0.67 ( $\pm 0.67$ )	10.67 ( $\pm 5.49$ )	1.67 ( $\pm 0.33$ )
Galaxiid only	0.50 ( $\pm 0.50$ )	0.17 ( $\pm 0.17$ )	0.67 ( $\pm 0.67$ )	0
Galaxiid (with one trout)	0	0.33 ( $\pm 0.33$ )	0	0.33 ( $\pm 0.33$ )

**Table 2** Two-way ANOVAs with blocks and contrasts comparing the effects of disturbance and predators on final grazer biomass, final biomass of Conoesucidae and final biomass of *Deleatidium* in experimental channels (MANOVA results in text)

Source	df	MS	F	P
<b>Grazer biomass</b>				
Block	2	0.16	1.63	0.2301
Disturbance	1	1.51	15.23	0.0016
Predator	3	0.49	4.97	0.0148
Galaxid vs. control	1	0.53	5.36	0.0363
Trout vs. control	1	1.38	13.90	0.0022
Disturbance×predator	3	0.28	2.79	0.0794
Error	14	0.10		
<b>Conoesucidae biomass</b>				
Block	2	0.52	3.16	0.0734
Disturbance	1	0.51	3.07	0.1015
Predator	3	0.55	3.30	0.0518
Galaxid vs. control	1	0.63	3.80	0.0717
Trout vs. control	1	1.51	9.13	0.0091
Disturbance×predator	3	0.39	2.35	0.1168
Error	14	0.16		
<b><i>Deleatidium</i> biomass</b>				
Block	2	0.10	0.27	0.7696
Disturbance	1	10.70	27.54	0.0001
Predator	3	0.93	2.40	0.1109
Galaxid vs. control	1	0.83	2.14	0.1653
Trout vs. control	1	2.01	5.18	0.0391
Disturbance×predator	3	0.34	0.88	0.4728
Error	14	0.39		

3) although most invertebrates showed an almost complete recovery in channels without fish (Fig. 2a, b). Grazers were significantly reduced in predator channels (two-way MANOVA with blocks, predator effect:  $F_{18,25}=2.12$ ,  $P=0.0393$ , Tables 2, 3). The biomass of both Conoesucidae and *Deleatidium* was lower in trout channels than in controls (two-way MANOVA with blocks, trout vs. control:  $F_{6,9}=12.30$ ,  $P=0.0007$ , Table 2, Fig. 2a). Although the biomass of grazers was lowest in the disturbed channels with trout (disturbance by predator interaction,  $P=0.0794$ , Table 2), there was no overall significant disturbance by predator interaction (two-way MANOVA with blocks, disturbance by predator interaction:  $F_{18,25}=0.90$ ,  $P>0.57$ ).

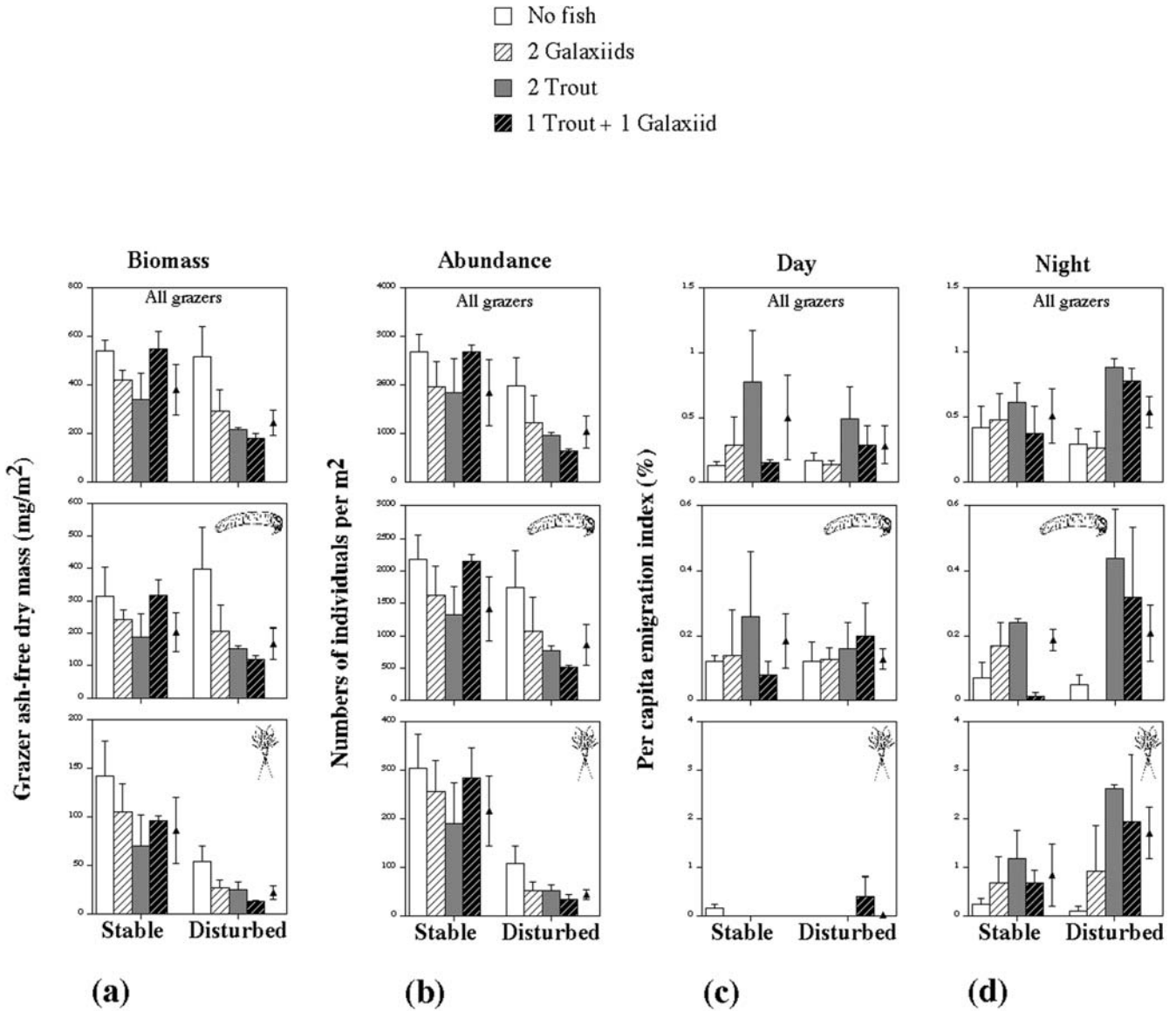
Trout increased total grazer drift rate (Fig. 2c, d); however, their overall effect on drift rate was influenced by the disturbance regime, indicated by a significant disturbance by predator interaction (Table 4). This significant interaction occurred because drift rates were typically low in stable channels during the day, but increased in disturbed channels at night. Moreover, the overall effect of trout on drift rates was due mainly to increased night drift of mayflies and taxa other than Conoesucidae because the latter had generally low drift rates (Fig. 2c, d). In contrast to trout, galaxiids had no significant overall effect on invertebrate biomass or abundance (two-way MANOVA with blocks, galaxiid vs. control:  $F_{6,9}=1.46$ ,  $P>0.29$ , Tables 2, 3) or on drift rates (Table 4). However, the total biomass of grazers was reduced in channels with galaxiids compared to controls

**Table 3** Two-way ANOVAs with blocks and contrasts comparing the effects of disturbance and predators on final grazer abundance, final abundance of Conoesucidae and final abundance of *Deleatidium* in experimental channels (MANOVA results in text)

Source	df	MS	F	P
<b>Grazer abundance</b>				
Block	2	0.55	3.06	0.0791
Disturbance	1	3.14	17.51	0.0009
Predator	3	0.42	2.35	0.1167
Galaxid vs. control	1	0.68	3.80	0.0715
Trout vs. control	1	0.98	5.48	0.0346
Disturbance×predator	3	0.31	1.74	0.2054
Error	14	0.18		
<b>Conoesucidae abundance</b>				
Block	2	0.74	3.79	0.0485
Disturbance	1	2.62	13.50	0.0025
Predator	3	0.51	2.61	0.0928
Galaxid vs. control	1	0.71	3.66	0.0765
Trout vs. control	1	1.23	6.33	0.0247
Disturbance×predator	3	0.34	1.76	0.2010
Error	14	0.19		
<b><i>Deleatidium</i> abundance</b>				
Block	2	0.03	0.07	0.9323
Disturbance	1	14.03	29.06	<0.0001
Predator	3	0.57	1.18	0.3514
Galaxid vs. control	1	0.67	1.38	0.2593
Trout vs. control	1	1.35	2.79	0.1170
Disturbance×predator	3	0.46	0.9466	0.4447
Error	14	0.48		

**Table 4** Two-way MANOVAs with blocks and contrasts comparing the effects of disturbance and predators on total grazer emigration rate, emigration of Conoesucidae and emigration of *Deleatidium* in experimental channels. Emigration rate during the day and night are the two dependent variables in the analyses

Source	df	Wilks' lambda	F	P
<b>Grazer emigration</b>				
Block	4, 26	0.36	4.34	0.0080
Disturbance	2, 13	0.80	1.64	0.2319
Predator	6, 26	0.29	3.65	0.0092
Galaxid vs. control	2, 13	0.99	0.06	0.9397
Trout vs. control	2, 13	0.42	9.09	0.0034
Disturbance×predator	6, 26	0.36	2.92	0.0258
<b>Conoesucidae emigration</b>				
Block	4, 26	0.94	0.22	0.9269
Disturbance	2, 13	0.99	0.08	0.9229
Predator	6, 26	0.54	1.55	0.2025
Galaxid vs. control	2, 13	0.99	0.02	0.9810
Trout vs. control	2, 13	0.62	4.00	0.0441
Disturbance×predator	6, 26	0.55	1.50	0.2159
<b><i>Deleatidium</i> emigration</b>				
Block	4, 26	0.81	0.70	0.5981
Disturbance	2, 13	0.97	0.19	0.8309
Predator	6, 26	0.50	1.77	0.1444
Galaxid vs. control	2, 13	0.89	0.78	0.4789
Trout vs. control	2, 13	0.60	4.30	0.0367
Disturbance×predator	6, 26	0.64	1.08	0.4024



**Fig. 2** Mean ( $\pm 1$  SE) biomass (a), abundance (b) and per capita emigration rates (drift), during the day (c) and at night (d) of total grazers (top row), Conoesucidae caddisflies (middle row) and *Deleatidium* mayflies (bottom row) in stable and disturbed channels at the end of the experiment. Drift rates are the number of

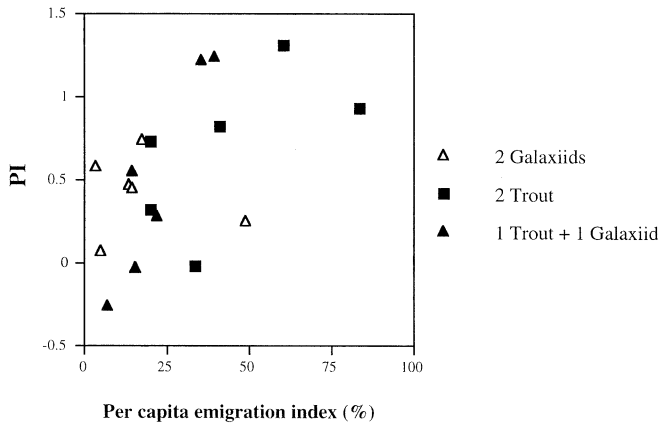
individuals leaving the channels per hour as a percentage of the number of individuals found in the channels.  $\blacktriangle$  Expected values in channels with one trout+one galaxiid. Note the different scales on the y-axes

(Table 2, Fig. 2a). Moreover, the overall effect on invertebrate biomass and abundance was significantly lower for galaxiids compared to trout (two-way MANOVA with blocks: galaxiid vs. trout,  $F_{6,9}=5.84$ ,  $P=0.0098$ ).

**Direct predation versus avoidance behaviour**

The relative importance of direct predation and avoidance behaviour of Conoesucidae and *Deleatidium* was examined in channels with two trout. We estimated that 12% of Conoesucidae were consumed per 24 h and 16% avoided trout via drift (paired  $t$ -test:  $t=-0.77$ ,  $P>0.47$ ,  $df=5$ ). For *Deleatidium*, we estimated that 16% were consumed per

24 h and 44% were lost via drift (paired  $t$ -test:  $t=-4.52$ ,  $P=0.0063$ ,  $df=5$ ). The PI was calculated for the three predator regimes. An ANCOVA with daily per capita emigration index as the covariate indicated a significant effect of per capita emigration on PI ( $F_{1,12}=12.36$ ,  $P=0.0043$ ) but also a significant predation regime by emigration index interaction ( $F_{2,12}=5.79$ ,  $P=0.0174$ ). The significant interaction occurred because PI was positively related to emigration index in channels with trout present (i.e. the “trout only” and “both” treatments), but not in channels lacking trout (Fig. 3).



**Fig. 3** The relationship between predator impact ( $PI$ ) and per capita emigration index of all invertebrate grazers (percentage of grazers emigrating out of channels in 24 h) in experimental channels

### Algae

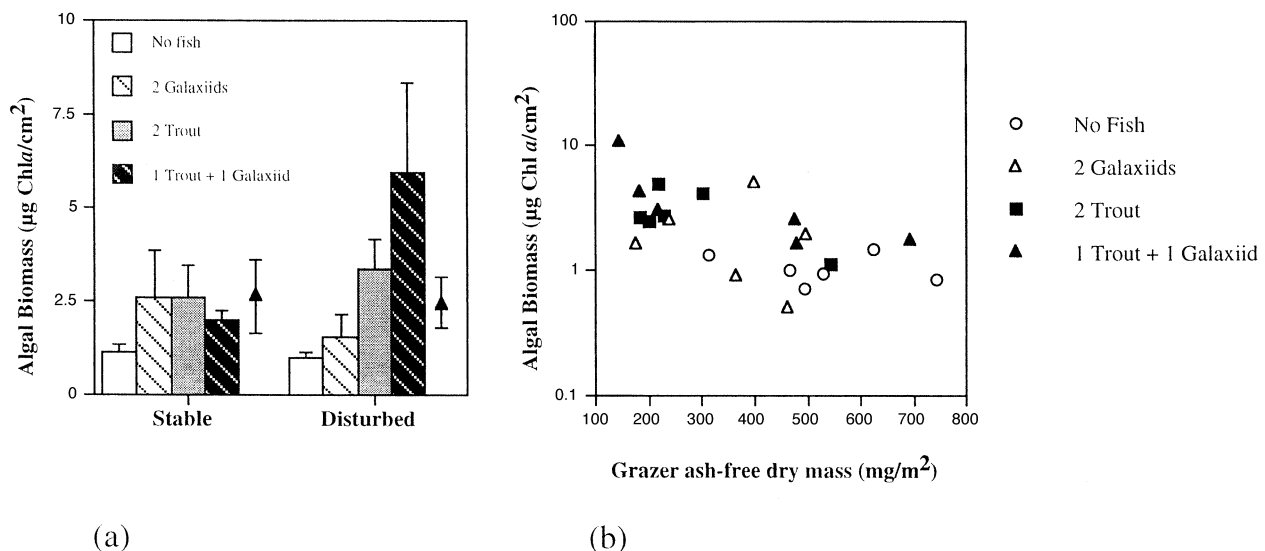
The biomass of algae on rocks was not affected by the disturbance regime (two-way ANOVA with blocks, disturbance effect:  $F_{1,14}=0.44$ ,  $P > 0.51$ ), but differed between predator treatments (two-way ANOVA with blocks, predator effect:  $F_{3,14}=4.25$ ,  $P = 0.0248$ ). Algal biomass was significantly higher in trout channels than controls (two-way ANOVA with blocks, trout vs. control:  $F_{1,14}=7.65$ ,  $P = 0.0152$ ) and was highest in disturbed channels with both predators, but the disturbance by predator interaction was not significant (two-way ANOVA with blocks, disturbance by predator interaction:  $F_{3,14}=1.65$ ,  $P > 0.22$ , Fig. 4a). In contrast to trout channels, algal biomass in galaxiid channels was indistinguishable

from that in the controls (two-way ANOVA with blocks, galaxiid vs. control:  $F_{1,14}=1.74$ ,  $P > 0.20$ , Fig. 4a).

To assess the relationship between grazer biomass and algal biomass, and at the same time compare algal biomass at the same grazer biomass in channels with trout and galaxiids, respectively, we used two-way ANCOVA. The initial analysis included final biomass of grazers as the covariate, effects of trout, galaxiids and their interactions, but since all interactions were non-significant these were omitted from subsequent analyses. This ANCOVA indicated that algal biomass was negatively correlated with grazer biomass ( $F_{1,20}=8.00$ ,  $P = 0.01$ , Fig. 4b), and that trout channels had significantly higher algal biomass at the same grazer biomass than control channels ( $F_{1,20}=6.92$ ,  $P = 0.016$ , Fig. 4b). However, algal biomass in galaxiid channels did not differ from that in controls ( $F_{1,20}=1.16$ ,  $P = 0.29$ , Fig. 4b).

### Predator substitutability

Although observed and expected values were not statistically different in many cases, disturbance regime influenced predator substitutability so that the observed final abundance and biomass of grazers was higher than expected in stable channels (Fig. 2a, b; Table 5). This pattern was associated with higher than expected values of Conoesucidae in stable channels with both predators (Table 5). Additionally, per capita emigration rate of Conoesucidae at night was lower than expected in stable channels (Table 5). Both the per capita emigration at night of total grazers and the final algal biomass was higher than expected in disturbed channels (Table 5, Fig. 2d, Fig. 4a).



**Fig. 4 a** Mean ( $\pm 1$  SE) algal biomass on rocks in stable and disturbed channels at the end of the experiment.  $\blacktriangle$  Expected values in channels with one trout+one galaxiid. **b** The relationship

between algal biomass on rocks (log scale) and total grazer biomass per channel

**Table 5** Contrast results from one-way ANOVAs with blocks (predator treatments as the independent variable) comparing invertebrate biomass, invertebrate abundance, prey emigration rate and algal biomass in stable and disturbed channels, respectively. The contrasts test the values in channels with two galaxiids and two trout (expected) versus the values in channels with one trout plus one galaxid (observed)

Source	Stable <i>P</i>	Disturbed <i>P</i>
Invertebrate biomass		
Total grazers	0.0483	0.1846
Conoesucidae	0.1035	0.2676
<i>Deleatidium</i>	0.4516	0.2336
Invertebrate abundance		
Total grazers	0.0403	0.1716
Conoesucidae	0.0192	0.1779
<i>Deleatidium</i>	0.3549	0.3564
Day emigration		
Total grazers	0.1760	0.8223
Conoesucidae	0.7541	0.8240
<i>Deleatidium</i>	– <sup>a</sup>	0.1536
Night emigration		
Total grazers	0.2177	0.0233
Conoesucidae	0.0139	0.5391
<i>Deleatidium</i>	0.9022	0.9937
Algal biomass	0.7120	0.0284

<sup>a</sup> Observed values were zero

## Discussion

In most cases disturbance and predators had largely independent effects on primary consumers and their resources in this study. However, disturbance regime influenced the effect of the exotic predator on grazer emigration rates, but did not influence the emigration rates in channels with native galaxiids. Disturbance also influenced whether exotic and native predators had substitutable effects on lower trophic levels. The finding that exotic trout had strong effects on stream community structure, whereas galaxiids effects were weak, is in general agreement with previous studies of these predators in New Zealand streams (e.g. Flecker and Townsend 1994; McIntosh and Townsend 1996). We acknowledge that our experimental disturbance did not mimic a natural disturbance in several potentially important ways (e.g. there were no changes in water clarity). Nevertheless, our intention was to compare the influence of predators on the recolonisation process and others have shown that recolonisation from experimental disturbance can mimic recovery from natural floods (Matthaei et al. 1997).

Even though trout effects on grazer biomass and algae were particularly strong in previously disturbed channels, it is noteworthy that the overall trout effects on grazers were not significantly influenced by disturbance history. We obtained no evidence for major changes in the species composition of invertebrates caused by the disturbance regime or predation regime. In particular, there was no change towards species more vulnerable to predation (e.g. mayflies and chironomids) but less vulnerable to distur-

bance as expected from theoretical and empirical work (Wootton et al. 1996). Our study stream was dominated by cased caddisflies (>50% of the invertebrate biomass), and even though predatory fish consume Conoesucidae, the dominant cased caddisfly in this study, they are less vulnerable to predatory fish than *Deleatidium* mayflies (A.R. McIntosh and P. Nyström, unpublished data). However, cased caddisflies are vulnerable to bed-movements as shown in this study. Furthermore, in other less stable streams in the Cass area, mayflies like *Deleatidium* dominate (Winterbourn 1997), and cased consumers typically make up <5% of the total invertebrate biomass in streams without trout and <16% in streams with trout (Nyström et al. 2003). We suggest that the lack of a disturbance effect on species composition in this study may have been because our study was conducted in a stable stream that provided an abundant source of colonists belonging to taxa usually vulnerable to disturbance such as cased caddisflies. This result is similar to other experimental disturbances in stable streams where communities have recovered quickly (e.g. Death 1996). The variability in the relative tolerances of taxa to different disturbance events makes general predictions about the interactive effects of disturbance and predation difficult (Thomson 2002). Nevertheless, following a disturbance event it seems like changes in invertebrate species composition towards taxa more vulnerable to predation may be the key factor mediating the strength of predator impacts.

Introduced trout and native galaxiids present prey with contrasting predation risks. Canterbury galaxiids are nocturnal benthic foragers, whereas trout are predominantly diurnal drift feeders (Cadwallader 1975; McIntosh and Townsend 1995). Previous studies involving drift-feeding and benthic-feeding fish suggest that benthic-feeding predators (e.g. sculpins) have a significantly larger impact on benthic prey than drift-feeding predators (e.g. trout). The weaker effect on benthic prey of trout is expected when the amount of drifting terrestrial prey is large enough to subsidise the drift feeder (Dahl and Greenberg 1996; Dahl 1998; Nakano et al. 1999). It is remarkable that our results indicate that rates of predation by drift-feeding trout were much higher than by benthic-feeding galaxiids and that trout stimulated emigration from the channels, whereas galaxiids did not. The mechanisms underlying the strong effects of trout on grazers could thus potentially be related to differences in prey abundance and prey emigration since we observed no major differences in invertebrate species composition. The most likely cause of reductions in prey biomass in trout channels in our experiment was that trout affected some prey mainly through direct consumption (e.g. caddisflies) and other prey by inducing emigration (e.g. mayflies) out of the channels. Our results support the hypothesis that predator impacts on local prey density in open systems are influenced by prey dispersal responses to predators (Wooster et al. 1997; Forrester et al. 1999; Diehl et al. 2000). Hence, following a disturbance in an open population, predator consumption of prey and prey

dispersal from patches containing dangerous predators (i.e. trout in this study) may influence local recolonisation. This may even provide a mechanism to explain the persistence of the effects of streambed movement on invertebrate communities in substratum patches for long periods after a disturbance event (Matthaei and Townsend 2000).

The particularly strong effect of trout on grazer emigration rates in disturbed channels is notable but the mechanism behind this effect is less obvious. Previous studies involving trout and grazers suggest that emigration rates increase with the density of trout (e.g. Diehl et al. 2000). The density of trout in our experimental channels was greater than in Grasmere stream, which has a comparatively low trout density (McIntosh 2000a). Drift patterns among grazers may be explained by differences in resource levels and predation risk (e.g. Forrester et al. 1999). In the disturbed channels with trout, grazer density was low and algal biomass was high. Grazers drifting into these channels would therefore experience a higher predation risk than outside the channels but also higher resource levels. We speculate that prey drifting into trout channels experienced higher predation risks and subsequently emigrated from these channels at a higher rate. Thus predation risk was more important than resource levels in determining emigration responses in trout channels. In contrast, the opposite would be the case for grazers entering channels without fish or in channels with native galaxiids, where predation risk is much lower.

The trophic cascade observed in the presence of trout is consistent with the findings of other studies involving trout in New Zealand streams (e.g. Flecker and Townsend 1994). The high algal biomass observed in channels with trout was likely due to reductions in grazer density and a behaviourally induced trophic cascade (e.g. McIntosh and Townsend 1996) since algal biomass in the trout channels was higher than that in channels without fish at the same grazer biomass. Algal biomass in streams often varies temporally and spatially, depending on disturbance associated with bed movement (Biggs 1996). Our study indicates that because disturbance also affects prey density it can increase the indirect effects of predators on algae in periods between bed movements.

Most food webs contain multiple predators, but predation studies typically examine the effects of only one predator at a time. However, multiple predator effects frequently cannot be predicted from studies of single predators because of risk reduction or risk enhancement associated with the presence of additional predators (summarized in Sih et al. 1998). By keeping total predator density constant we were able to assess whether interspecific and intraspecific interactions are of similar magnitude. This study shows that predator effects on the abundance of some taxa (e.g. *Deleatidium*) can be predicted by using the average of the individual predator effects, corroborating recent work on predatory spiders and their grasshopper prey (Sokol-Hessner and Schmitz 2002). However, our results also indicate that the magnitude of the interactions between multiple predators

and lower trophic levels can vary depending on environmental conditions. For example, the observed effects of combined predators (i.e. both trout and galaxiids) on components of the stream communities (total grazer biomass, total grazer drift rates at night, and algal biomass) differed in the stable and disturbed channels. The reason for this discrepancy seems to be that the combined impact of galaxiids and trout on the dominant invertebrate grazer (Conoesucidae) was low in stable channels, likely due to reduced emigration by Conoesucidae at night. In contrast, galaxiids alone had weak effects on grazer drift rates and algal biomass in both stable and disturbed channels, whereas effects of trout alone were particularly strong in the disturbed channels. Because the combined fish treatment more reflected the drift and algal patterns of trout only channels, predator effects were not substitutable.

We hypothesize that the structure of food webs will be determined by interactions between predation and disturbance when foraging of prey or predators is affected by the disturbance history, and when predators and prey have the potential to control their resources, either directly or indirectly. It is, however, possible that predators and disturbance have interactive effects on primary consumers and their resources only when the species composition of primary consumers is altered towards more vulnerable prey types. This means the relative importance of disturbance and predation in regulating community structure will vary not only with spatial and temporal scale (Menge and Olson 1990), but also with the magnitude of lethal and non-lethal effects posed by predators during recovery periods.

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