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Fitness and community consequences of avoiding multiple predators

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Abstract We investigated the fitness and community consequences of behavioural interactions with multiple predators in a four-trophic-level system. We conducted an experiment in oval flow-through artificial-stream tanks to examine the single and interactive sublethal effects of brook trout and stoneflies on the size at emergence of *Baetis bicaudatus* (Ephemeroptera: Baetidae), and the cascading trophic effects on algal biomass, the food resource of the mayflies. No predation was allowed in the experiment, so that all effects were mediated through predator modifications of prey behaviour. We reared trout stream *Baetis* larvae from just before egg development until emergence in tanks with four treatments: (1) water from a holding tank with two brook trout (trout odour), (2) no trout odour + eight stoneflies with glued mouthparts, (3) trout odour + stoneflies and (4) no trout odour or stoneflies. We ended the experiment after 3 weeks when ten male and ten female subimagos had emerged from each tank, measured the size of ten male and ten female mature nymphs (with black wing pads), and collected algal samples from rocks at six locations in each tank. To determine the mechanism responsible for sublethal and cascading effects on lower trophic levels we made day and night observations of mayfly behaviour for the first 6 days by counting mayflies drifting in the water column and visible on natural substrata in the artificial streams. Trout odour and stoneflies similarly reduced the size of male and female *Baetis* emerging from artificial streams, with non-additive effects of both predators. While smaller females are less fecund, a fitness cost of small male size has not been determined. The mechanism causing sublethal effects on *Baetis* differed between predators. While trout stream *Baetis* retained their nocturnal periodicity in all treatments, stoneflies increased drift dispersal of mayflies at night, and trout suppressed night-time feeding and drift of mayflies. Stoneflies had less effect on *Baetis* behaviour when fish odour was present. Thus, we attribute the non-additivity of effects of fish and stoneflies on mayfly growth to an interaction modification whereby trout odour reduced the impact of stoneflies on *Baetis* behaviour. Since stonefly activity was also reduced in the presence of fish odour, this modification may be attributed to the effect of fish odour on stonefly behaviour. Only stoneflies delayed *Baetis* emergence, suggesting that stoneflies had a greater sublethal effect on *Baetis* fitness than did trout. Delayed emergence may reduce *Baetis* fitness by increasing risks of predation and parasitism on larvae, and increasing competition for mates or oviposition sites among adults. Finally, algal biomass was higher in tanks with both predators than in the other three treatments. These data implicate a behavioural trophic cascade because predators were not allowed to consume prey. Therefore, differences in algal biomass were attributed to predator-induced changes in mayfly behaviour. Our study demonstrates the importance of considering multiple predators when measuring direct sublethal effects of predators on prey fitness and indirect effects on lower trophic levels. Identification of an interaction modification illustrates the value of obtaining detailed information on behavioural mechanisms as an aid to understanding the complex interactions occurring among components of ecological communities.

Key words Behavioural trophic cascade · Interaction modification · Mayflies · Predator-prey interactions · Sublethal effects

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Introduction

Predation can have important consequences for prey populations and communities other than direct predator-induced mortality. These sublethal and indirect effects often result from changes in prey behaviour caused by predator avoidance. Predators can place behavioural constraints on prey by forcing trade-offs between predator avoidance and habitat selection, foraging, mating and movement (see reviews by Dill 1987; Sih 1987; Lima and Dill 1990). If prey individuals take fewer risks in the presence of predators, changes in microhabitat use or behaviour may reduce their rates of resource acquisition. Such risk-sensitive foraging behaviour represents a fitness trade-off between maximising survival and minimising sublethal effects of predator-mediated losses of fecundity (Gilliam and Fraser 1987; Nonacs and Dill 1990; Werner 1991; Werner and Anholt 1993). Behavioural trade-offs are common and potentially important (Dill 1987), but their actual sublethal (sensu Strauss 1991) impact on prey fitness is not well established (Werner 1992).

Predator-induced modifications of prey feeding may also have indirect effects (sensu Abrams 1995) on communities by affecting the distribution and abundance of resources for the prey (a trophic cascade).The cascading effects of predator consumption of prey on the prey resources are well known, particularly in aquatic systems (e.g. Power et al. 1985; Power 1990; Carpenter et al. 1987; Strong 1992), but also in marine (Menge 1995) and terrestrial (Spiller and Schoener 1990; Carter and Rypstra 1995; Hartvigsen et al. 1995) systems. However, we know little about how predator-induced changes in prey behaviour affect the impact of prey on their resources (Werner 1992; Billick and Case 1994; Wootton 1994a, b; Abrams 1995; Werner and Anholt 1996; Schmitz et al. 1997). Furthermore, models of community dynamics indicate that variable traits like behaviour are probably important in ecological communities (Abrams 1995). We know that area-restricted search behaviour and aggregative responses of foragers to their resources can affect resource distributions (streams: Lamberti and Resh 1983; Hart 1992; intertidal: Lubchenco and Gaines 1981; Underwood and Jernakoff 1981; terrestrial: Oksanen 1983; Schowalter et al. 1986). If predators restrict or enhance prey foraging movements, we should observe different patterns of resource distribution in predator and predator-free habitats. However, it is difficult to measure behavioural cascading effects of predators on prey resources, since predators can also change the abundance of the intermediate species.

In a Rocky Mountain stream community we investigated the sublethal fitness effects of trade-offs between predator avoidance and resource acquisition and their concurrent influence on the abundance of the resources for the prey. Mayfly nymphs are an important component of many stream communities and the most numerous primary consumers in streams around the Rocky Mountain Biological Laboratory in western Colorado (Peckarsky 1991). Visually feeding fish, such as trout, operate over large areas in these streams and present higher predation risks during the day than during the night (Ringler 1979; Allan 1981; Walsh et al. 1988; Angradi and Griffith 1990; McIntosh and Townsend 1995a). High predation risk in the presence of trout reduces the movement of mayflies in the water column of streams during the day and sometimes leads to dramatic increases in nocturnal drift (Malmqvist 1988; Flecker 1992; Douglas et al. 1994; McIntosh and Townsend 1994). Drift is also an important means by which hungry mayflies locate high food patches among heterogeneous algal resources (Kohler 1985). Visually feeding fish can also reduce prey foraging time by restricting grazers to nocturnal access to the algae-covered upper surfaces of stones (Culp and Scrimgeour 1993; Cowan and Peckarsky 1994; McIntosh and Townsend 1994, 1995b, 1996; McIntosh and Peckarsky 1996). Such predator-induced changes in prey behaviour may result in reduced prey growth rates and fecundity, and could have dramatic effects on the ability of grazers to exploit effectively patchy algal resources in streams.

In contrast to the selection pressures imposed by visually feeding fish, benthic predators are often nocturnal (Beers and Culp 1990; McIntosh and Townsend 1995a; Peckarsky and Cowan 1995), affect prey at smaller spatial scales and by a different mechanism. Benthic fish (Culp et al. 1991; McIntosh and Townsend 1994) and predatory stoneflies (Peckarsky 1980; Walton 1980; Malmqvist and Sjöström 1987; Peckarsky 1987; Williams 1987) induce mayflies to crawl away or drift at night to avoid predation. Interactions with such predators are generally tactile (Peckarsky 1987) and therefore from close range, rather than long-range responses to chemical cues associated with trout (Martinez 1987; Cowan and Peckarsky 1994; Dodson et al. 1994; Scrimgeour et al. 1994; McIntosh and Peckarsky 1996). Thus, by a different mechanism (interrupting foraging), benthic predators may likewise affect the ability of grazers to exploit efficiently the food resources in streams, and cause sublethal reductions in prey fitness (Peckarsky et al. 1993; Scrimgeour and Culp 1994a).

Both stoneflies and trout often coexist in Rocky Mountain streams so that prey encounter both predators. The interactive effects of two predators have seldom been considered when assessing the fitness consequences of trade-offs associated with predator avoidance (but see Rahel and Stein 1988; Soluk and Collins 1988; Scrimgeour and Culp 1994b; Wootton 1994a for studies of effects of prey consumption by multiple predators). In this study, we recorded the behaviour of *Baetis bicaudatus* (Ephemeroptera: Baetidae) larvae when confronted with both trout and stoneflies, separately and together. Our objective was to determine the fitness and community consequences of predator-induced changes in mayfly behaviour at larger spatial and longer temporal scales than had been studied previously. Specifically, we manipulated cues from visual

water column predators and benthic predators in stream-side cattle watering tanks modified into flow-through streams to determine the single and interactive effects of trout and stoneflies on: (1) the diel drift and positioning periodicity of *Baetis*; (2) the fitness (size and timing of emergence) of mayflies reared under the different predator regimes and (3) the indirect effects of predator-induced changes in mayfly behaviour on algal biomass.

Materials and methods

We manipulated the predation regime affecting *Baetis* in grey polyethylene plastic cattle watering tanks with length-width dimensions of 121×68 cm, providing a water surface area of 0.823 m^2. Tanks were located beside the East River, a trout stream, and received gravity-fed water from a fishless beaver pond (2950 m elevation) draining first-order streams on the east side of Gothic Mountain at the Rocky Mountain Biological Laboratory (RMBL). The water source was inspected daily for fish and electrofished to confirm its fishless state. This water was filtered through 0.5 mm mesh at the source to prevent macroinvertebrates from entering the tanks. We created circular flow with two water jets facing in opposite directions on each side of a central plexiglass baffle (Fig. 1). Mesh windows (0.5 mm) in a central standpipe regulated water depth (mean among tanks $\pm$SE = 21 ± 0.3 cm, max. = 24, min. = 17) and acted as a drain, creating a flow-through rather than recirculating unit. The mesh windows were cleaned twice daily to prevent clogging. We arranged 12 tanks in three blocks of four, in which we could regulate flow independently using gang valves. Water velocity (measured at six locations around the tanks: see cobbles in Fig. 1) was similar among tanks (31.9 ± 2.2 cm s^{-1}), but heterogeneous within tanks (range = 12–58 cm s^{-1}), depending on the vicinity to the water jets. Water temperatures in the tanks ranged from morning lows of 4°C to 11°C afternoon highs and reflected those in the East River and its tributaries, because the water source was connected to an East River tributary.

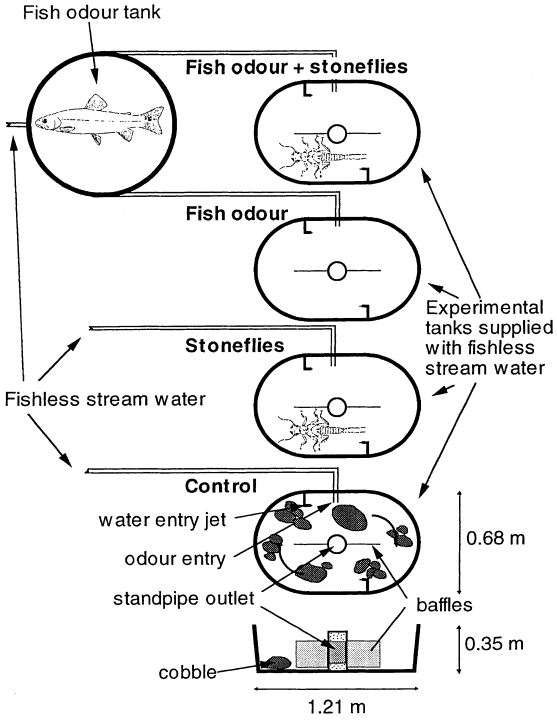

Fig. 1 The design of tanks used in the experiments (not to scale)

We covered the bottom of each tank with natural mineral substrata from fishless streams that were initially cleaned of algal resources. In each tank we arranged two large boulders (40–75 cm largest dimension), five medium cobbles (30–40 cm), and ten small cobbles (20–30 cm) in six clusters of one to four rocks with a 2-cm layer of coarse gravel between the clusters (Fig. 1). This arrangement of substrata provided a heterogenous distribution of refuges for invertebrates, characteristic of natural streams in the area. Substrata were incubated in the tanks for 2 weeks to accumulate natural periphyton communities before treatments were applied. On 5 July 1995 we collected 50 *Baetis* from the East River, measured their head capsule widths and dissected females to determine the status of egg development. Using the criteria of Delucchi and Peckarsky (1989), all mayflies were in developmental stages late II (wing pads wider than long) or early III (wing pads longer than wide). Mean $\pm$ SE head capsule widths of males and females were 1.01 ± 0.016 and 0.85 ± 0.016 mm, respectively, and there was no egg development in females (which takes place in later stage III larvae). From 6 to 11 July, we stocked 300 early-stage III *Baetis* in each chamber, to simulate the mean densities of this stage in the East River (365 m^{-2}, B.L.P., unpublished data). We added mayflies to chambers 25 at a time to maintain equal number of individuals per treatment over the extended set-up period.

On 12 July, we randomly allocated four predator treatments to each block (n = 3) as follows: (1) trout odour only, (2) non-feeding stoneflies, (3) trout odour + non-feeding stoneflies and (4) no predator cues. We placed two brook trout (*Salvelinus fontinalis* – 215 and 190 mm fork length) in a large (110 l) holding tank receiving the same fishless water as the artificial stream tanks, and water from that tank was delivered through spouts to half the stream tanks at a mean $\pm$ SE rate of 1.68 ± 0.01 l min^{-1}. Thus the same trout cue was allocated to all replicates of the fish odour treatments. Trout were fed natural assemblages of East River benthos every other day. The other stream tanks received fishless water delivered at the same rate (Fig. 1). In half the fish and half the fishless tanks we placed eight last-instar female *Megarcys signata* (Plecoptera: Perlodidae – mean head capsule width $\pm$ SE = 4.55 $\pm$ 0.04 mm) whose mouthparts had been glued with Barge Cement to prevent them from feeding on *Baetis* (as in Peckarsky et al. 1993). Densities were representative of those in the natural habitat (Peckarsky 1991). For control purposes, we put eight pebbles with Barge Cement in all stream tanks that did not receive stoneflies. We replaced 33 stoneflies that emerged during the 3 weeks of the experiment with fresh glued individuals. We fastened mesh emergence traps (white cloth, mesh diameter = 1 mm) over each stream tank to catch subimagos as they flew off the water surface. We ended the experiment after a total of 20 days, when ten male and ten female subimagoes had emerged from each stream tank. All but 3 stoneflies (of 48) were recovered, indicating that predator densities were maintained over the course of the experiment.

We measured the following response variables from each stream tank.

(1) *Behavioural responses*. At 10.00 a.m. and 10.00 p.m. daily for the first 6 days, we recorded the numbers of stoneflies visible and moving about the stream tanks, mayflies visible on the surface of substrata (including larger rocks, gravel and sides of the tanks), and mayflies drifting past a transect during a 5-min period. We made observations at night using dim red light from flashlights covered with red acetate, and during the day by staying motionless, neither of which appeared to affect *Baetis* or *Megarcys* behaviour.

(2) *Time to emergence*. We checked the emergence traps four times daily and removed all subimagos until ten males and ten females had emerged from each tank. The first individual (male) emerged on 19 July, 1 week after the start of the experiment, and the last on 1 August, after about 3 weeks of exposure to treatments. This variable estimates the onset of emergence, and was selected so that densities of mayflies remaining in the tanks would not change significantly over the course of the experiment. The onset of emergence in mayflies has been shown to be a good indication of

mean, median or mode date of emergence (Corbet 1964; Harper et al. 1983; Lauzon and Harper 1986; Peters et al. 1987).

(3) *Size at emergence*. On 2 August, after all remaining mayflies had been subjected to the predator treatments for 3 weeks, we collected ten male and ten female *Baetis* larvae in stage IV (black wing pads), which were within 24 h of emerging, and analysed the effects of treatments on their head capsule widths (HCW), a conservative linear measure of mayfly size. We used black wing pad larvae instead of subimagos because they were not confounded by different times of exposure to treatments, as were the subimagos that had emerged over a period of 2 weeks. We were also able to use these data to estimate *Baetis* growth rates (by comparison to starting sizes) and fecundity using established relationships between this linear measure and dry weights of *Baetis* in the East River. HCW of black wing pad larvae were converted to dry weights (DW) using regression equations derived for winter generation *Baetis* in the East River valley: DW males = $0.756*HCW^{3.256}$ (n = 577) and DW females = $1.446*HCW^{3.060}$ (n = 670) (B.L.P; unpublished data). Fecundity was obtained from estimated dry weights of females using the regression equation: eggs per female = $413*DW^{1.89}$ (n = 30) using data from Peckarsky et al. (1993). From these estimates of dry weights and fecundity, we compared effects of trout and stoneflies from this experiment to those obtained previously in experiments with stoneflies carried out on a smaller scale (Peckarsky et al. 1993). Since the allocation of body mass to eggs is not affected by predator treatment (Peckarsky et al. 1993), it is reasonable to apply the same regression equation across treatments.

(4) *Algal abundance*. On 3 August, we sampled the algae on six rocks (one randomly selected from each cluster – see Fig. 1) from each tank. We scraped the top and side surfaces with a toothbrush, and concentrated the algae in a known volume of stream water. We traced the surface area of each rock on an acetate sheet to standardise biomass per area sampled. We preserved samples in 5% formalin for cell counts and determination of total algal biovolume and diatom biovolume. We counted all algal cells in Palmer Cells at ×400 and identified naviculoid diatoms to species from Naphrax mounts at ×1000 (Lowe and Laliberte 1996; Lowe and Pan 1996).

We discontinued behavioural observations after 1 week to prevent loss of emerging *Baetis* while emergence traps were removed during observation periods, and to minimise the potential impact of twice daily disturbance on *Baetis* growth rates. Thus, we assumed that *Baetis* and *Megarcys* behaviour observed during the 1st week were representative of behaviours in subsequent weeks of the experiment. While we have evidence that this is a reasonable assumption for *Megarcys* with glued mouthparts (Peckarsky et al. 1993), it is possible that *Baetis* behaviour changed during development through instars and as algal resource abundance changed. However, *Baetis* behaviour did not change qualitatively in another experiment where tanks had radically different times for algal colonization (A.R. McIntosh and B.L. Peckarsky, submitted).

We analysed the effects of treatments on measured response variables using randomised complete-block 2 × 2 factorial ANOVAs with the presence or absence of fish odour and stoneflies as the two factors. We transformed variables where necessary using transformations that best satisfied the assumptions of analysis of variance. (Specific transformations are indicated in table legends.) Where multiple samples were taken from each tank (e.g. size at emergence, timing of emergence) we used tank means of equal sample sizes as replicates, because only tanks are true replicates. For behavioural response variables, we used repeated-measures ANOVAs with day vs. night observations as the repeated measure, treating separate tanks as replicates, but calculating mean behaviours over all 6 days of observation. Patterns in both total algal biovolume and diatom biovolume (the preferred food of *Baetis*; Cowan and Peckarsky 1990) were analysed using MANOVA since these two response variables were not independent. The term representing variation among blocks of tanks was included in ANOVA models when significant but was otherwise excluded. We estimated the power (or probability of detecting a false null hypothesis) of non-significant ANOVAs using Eq. 11.27 of Zar (1984).

Results

Behaviour of predatory stoneflies

During periods of activity, *Megarcys* moved around the tanks and actively pursued *Baetis* despite their glued mouthparts. Stoneflies were strongly nocturnal, making only rare appearances during the day (Fig. 2). The repeated-measures ANOVA indicated that significantly more *Megarcys* were active on the substratum surface at night, and that trout odour suppressed *Megarcys* activity (Table 1).

Drift and positioning of *Baetis* larvae

Baetis entered the water column from all locations in the tanks and often as a result of encounters with stoneflies. Drift was always nocturnal and negligible in all treatments during the day (Fig. 3a). The magnitude and

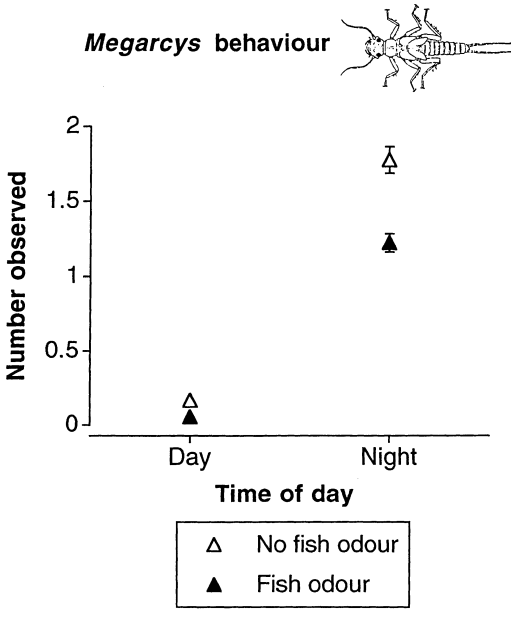

Fig. 2 The mean ± SE number of *Megarcys* visible and moving in tanks in the presence and absence of brook trout odour during the day and night

Table 1 Repeated-measures ANOVA for the number of *Megarcys* visible on the substratum surface in the presence or absence of trout odour (*Fish*) during the day and night (*Time*). Data were square root (x + 0.5) transformed

	Source	*d.f.*	Mean square	*F*	*P*
Between tanks	Fish	1	0.01087	11.39	0.028
	Error	4	0.00095		
Within tanks	Time	1	0.2787	94.94	< 0.001
	Time × Fish	1	0.0015	0.50	0.520
	Error	4	0.00294		

periodicity of drift rates in the tanks were within the range of those observed in the East River in July (Kerans et al. 1995). Fish odour generally depressed nocturnal drift, but the presence of stoneflies stimulated night-time drift. A significant fish odour by time interaction effect (Table 2) indicated that the effect of fish odour depended on the time of day. Thus, there was no effect of fish odour on daytime drift, but there was a significantly smaller increase in night-time drift when fish odour was present relative to the no-fish treatments. There was also a significant time by stonefly interaction, because *Baetis* drift rates increased in the presence of *Megarcys*, but only at night regardless of the presence of fish odour (Fig. 3a). There were no significant fish by stonefly or time by fish by stonefly interactions (Table 2).

Baetis were easily observed in the tanks. They aggregated in areas of faster current velocity and moved slowly over the surfaces of stones and the sides of the tanks where food availability was higher, often leaving conspicuous grazing trails. More mayflies were visible on the surfaces of substrata at night than during the day in all treatments (Fig. 3b), indicated by a significant time effect (Table 3). Similar to the drift data, trout odour generally reduced the number of visible *Baetis* (significant fish effect), while more mayflies were visible in the presence of stoneflies (significant stonefly effect). The effect of fish odour on mayfly positioning was only observed during the night (significant time by fish effect), and the effect of stoneflies on the number of visible mayflies was more pronounced at night (significant stonefly by time effect). Although the number of visible mayflies increased when stoneflies were present during the day and night, mayflies only appeared on the surface of substrata during the day when stoneflies were present and in the absence of trout odour. Thus, there was a significant stonefly by fish by time interaction (Table 3).

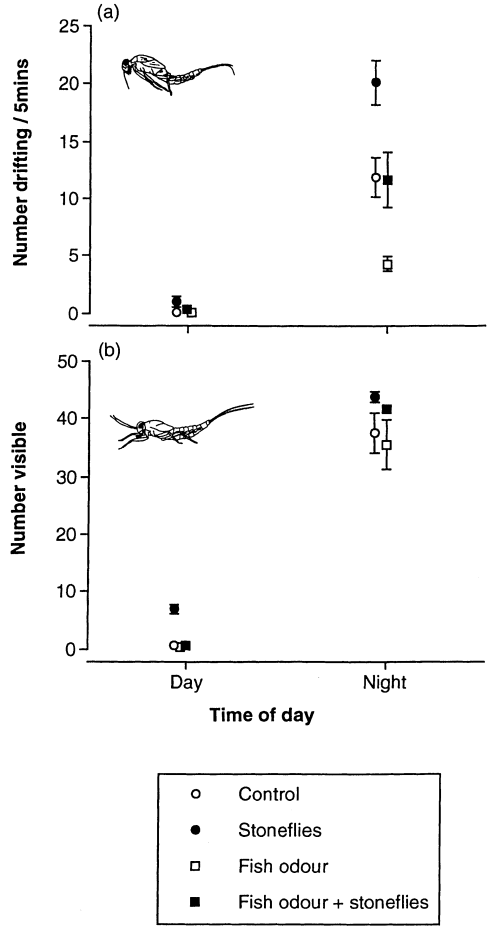

Fig. 3 The mean ± SE number of *Baetis* larvae drifting in the water column (**a**) and visible on the substratum surface (**b**) in tanks with (*closed symbols*) and without (*open symbols*) stoneflies, in the presence and absence of brook trout odour during the day and night

Size and time to emergence of *Baetis*

The presence of either trout odour, stoneflies or both was associated with reductions in growth over the 3-week period of the experiment leading to larvae that would have emerged as smaller adults. Both male and female *Baetis* matured at significantly smaller sizes in treatments with trout or stoneflies (Fig. 4) with no additive effect of both predators (Table 4). Therefore, all treatments with predator cues had biologically equivalent effects on *Baetis* growth rates. Head capsule widths of stage IV female *Baetis* were smaller than those of males because of the development of the large male eyes in late instars. When we converted mean head capsule widths to dry weights using the regression equations

Table 2 Repeated-measures ANOVA for the number of *Baetis* nymphs drifting in the water column in the presence or absence of trout odour (*Fish*) in tanks with or without predatory stoneflies (*Stonefly*) during the day and night (*Time*). Data were square root transformed

	Source	*d.f.*	Mean square	*F*	*P*
Between tanks	Stonefly	1	4.5629	58.66	< 0.001
	Fish	1	2.7466	35.31	0.001
	Block	2	0.3886	5.00	0.053
	Stonefly × Fish	1	0.0199	0.256	0.631
	Error	6	0.0778		
Within tanks	Time	1	48.79	567.11	< 0.001
	Time × Stonefly	1	0.5846	6.79	0.040
	Time × Fish	1	1.8648	21.67	0.004
	Time × Block	2	0.1826	2.123	0.201
	Time × Stonefly × Fish	1	0.2344	2.725	0.150
	Error	6	0.0860		

Table 3 Repeated-measures ANOVA for the number of *Baetis* nymphs visible on the substratum surface in the presence or absence of trout odour (*Fish*) in tanks with or without predatory stoneflies (*Stonefly*) during the day and night (*Time*). Data were square root transformed

	Source	*d.f.*	Mean square	*F*	*P*
Between tanks	Stonefly	1	3.2435	20.41	0.002
	Fish	1	2.0496	12.90	0.007
	Stonefly × Fish	1	1.222	7.69	0.024
	Error	8	0.159		
Within tanks	Time	1	154.53	2725.40	< 0.001
	Time × Stonefly	1	0.3097	5.46	0.048
	Time × Fish	1	1.0557	18.61	0.003
	Time × Stonefly × Fish	1	1.2673	22.34	0.001
	Error	8	0.0567		

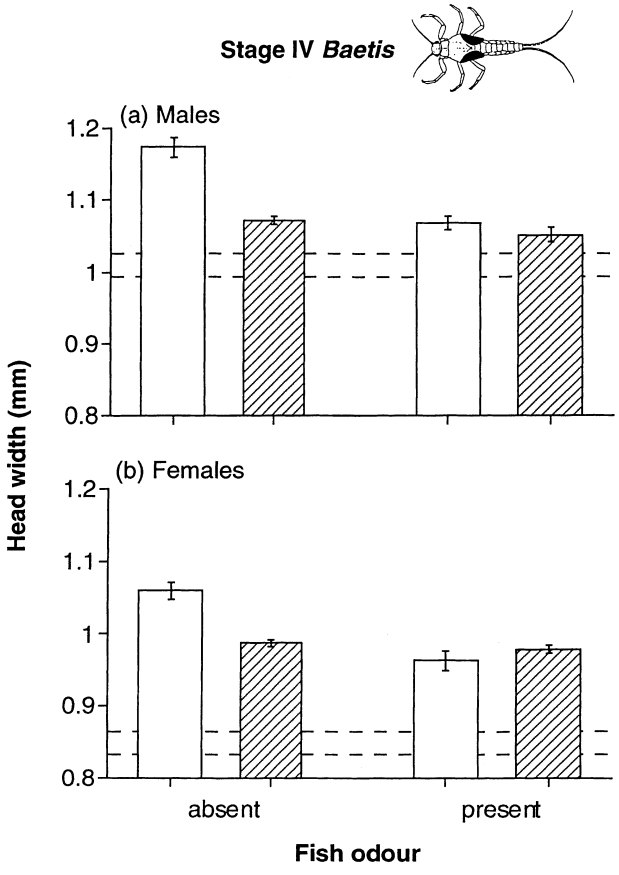

Fig. 4 The mean ± SE head capsule widths of male (**a**) and female (**b**) *Baetis* mayfly nymphs at stage IV (= mature and about to emerge) from tanks with (*hatched bars*) and without (*open bars*) stoneflies, in the presence and absence of brook trout odour. Measurements were taken from ten randomly selected individuals of each sex from each tank at the conclusion of the experiment. The *horizontal bar* near the origin indicates the mean ± SE initial size of mayflies used in the experiment

Table 4 Results of factorial ANOVA for the mean head capsule width of male and female *Baetis* nymphs with black wing pads in tanks with and without stoneflies and in the presence and absence of fish odour. Data were not transformed

	Source	*d.f.*	Mean square	*F*	*P*
Males					
	Stonefly	1	0.107	35.05	< 0.001
	Fish	1	0.0118	38.66	< 0.001
	Stonefly × Fish	1	0.0055	18.20	0.003
	Error	8	0.0003		
Females					
	Stonefly	1	0.0023	8.39	0.020
	Fish	1	0.0083	29.67	< 0.001
	Stonefly × Fish	1	0.0056	20.08	0.003
	Error	8	0.00028		

described in the Materials and methods section, we estimated that stoneflies reduced the mean dry weight of males by 25.9% and females by 19.2%. Interestingly, these values are comparable to reductions in dry weight observed in earlier experiments conducted at much smaller scales (males: 21.5%, females: 26.8%; Peckarsky et al. 1993). Estimated fecundity reductions of stoneflies (33.1%) were also comparable to those of the previous study (35%; Peckarsky et al. 1993), indicating that these sublethal effects of stoneflies were consistent over two different scales. Since the head capsule widths of *Baetis* from the three treatments with predators were not significantly different, we estimated that either predator alone or both predators together similarly reduced *Baetis* body mass by about 20–25% and fecundity by 30–35%.

Mean time to emergence was slightly slower for females compared to males (Fig. 5) suggesting developmental protandry typical of mayflies. Trout cues had no effect on time to maturity for either sex, but stoneflies significantly delayed emergence of female *Baetis* by a mean of about 1–2 days (Fig. 5, Table 5). The power of detecting a stonefly effect in the male maturation time was very low because of high variability among replicates. This resulted in a greater than 70% chance of a type II error (i.e. not rejecting a false null hypothesis) for males compared with a less than 3% chance for females. There was also a significant block effect for males because *Baetis* in the east block of tanks emerged earlier than they did in the central and west blocks. Nonetheless, we conclude from our data that delayed emergence only occurred in females and in treatments with stoneflies.

Indirect effects of predators on algal abundance mediated through *Baetis* behaviour

At the end of the 3-week experiment, there were obvious visual differences in the distribution and abundance of

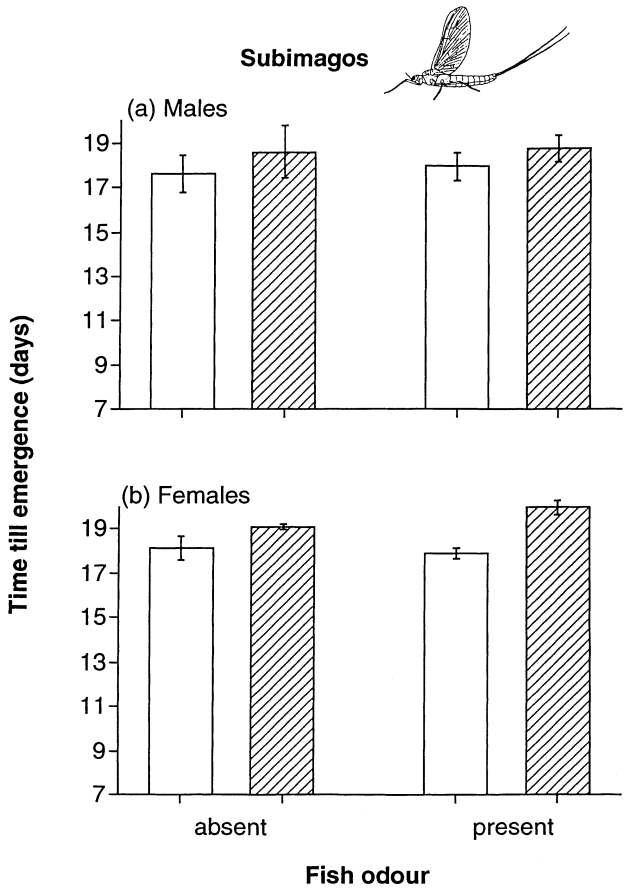

Fig. 5 Mean ± SE number of days from the start of the experiment to emergence from tanks with (*hatched bars*) and without (*open bars*) stoneflies, in the presence and absence of brook trout odour for ten male (**a**) and ten female (**b**) *Baetis*. The first individual emerged on day 7 and the last on day 20

Table 5 Results of factorial ANOVA for the mean time to emergence (days) for male and female *Baetis* in tanks with and without stoneflies and in the presence and absence of fish odour. Data were not transformed

	Source	*d.f.*	Mean square	*F*	*P*
Males					
	Stonefly	1	2.386	2.84	0.143
	Fish	1	0.1995	0.24	0.644
	Stonefly × Fish	1	0.011	0.012	0.914
	Block	2	5.669	6.74	0.029
	Error	6	0.841		
Females					
	Stonefly	1	7.151	19.16	0.002
	Fish	1	0.271	0.73	0.419
	Stonefly × Fish	1	0.884	2.26	0.171
	Error	8	0.372		

algae among treatments. Tanks with both predator cues appeared uniformly green, while other tanks had more patchy algal distributions on the rocks. The algal community that established was comprised of an overstory of filamentous cyanobacteria (largely *Mougotia*, *Oscillatoria* and *Spirogyra*), underlain by a diatom layer

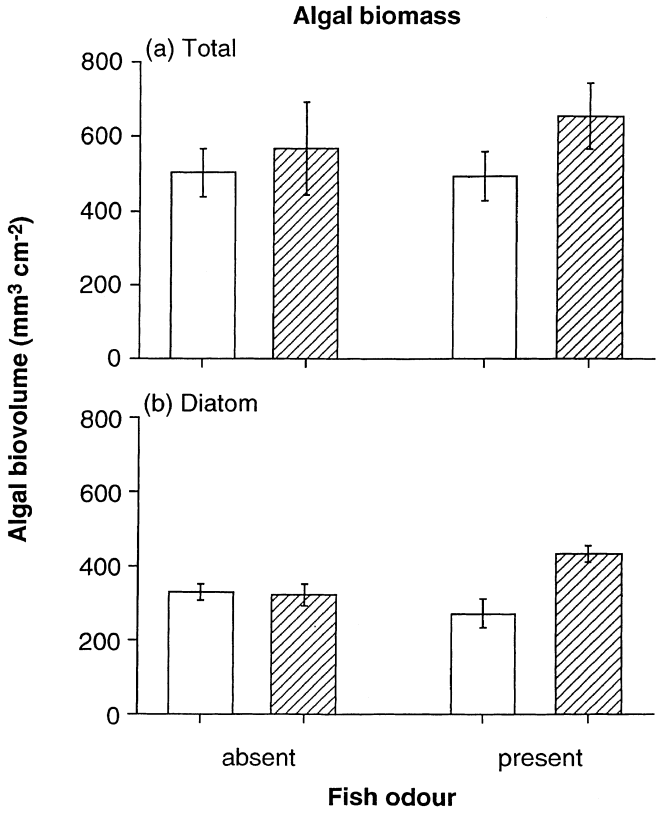

Fig. 6 Mean ± SE total algal (**a**) and diatom (**b**) biovolumes for tanks with (*hatched bars*) and without (*open bars*) stoneflies in the presence and absence of trout odour

dominated by *Acnanthes*, *Navicula* spp., *Cymbella*, *Gomphonema*, *Fragilaria*, *Meridion* and *Hannea*. Total algal biovolume (all taxa) and diatom biovolume were between 30–35% higher in tanks with both predators than in all other treatments (Fig. 6). Significant stonefly effects for both total algae and diatom biovolume and a significant interaction between fish odour and stoneflies for diatom biovolume (Table 6) indicated that stoneflies significantly affected diatom biomass only when fish odour was present.

Discussion

Alterations in prey behaviour caused by the presence of predators are common, particularly in streams (see reviews by Lima and Dill 1990; Wooster and Sih 1995), but their influence on population- and community-level processes in any type of community has only recently been investigated empirically (Huang and Sih 1991; Fraser and Gilliam 1992; Werner 1992; Billick and Case 1994; Wootton 1994a, b; Hill and Lodge 1995; Ball and Baker 1996; Werner and Anholt 1996). Information is particularly lacking in situations where more than one predator influences prey behaviour. In this study we have shown that predator-prey interactions can be modified by the presence of more than one predator

Table 6 Multivariate and univariate ANOVAs for total algal biovolume and diatom algal biovolume in tanks with and without stoneflies and in the presence and absence of fish odour. Data were not transformed

Response variable	Source	*d.f.*	Wilks' lambda	Mean square	*F*	*P*
MANOVA	Stonefly	2, 5	0.1545		13.68	0.009
	Fish	2, 5	0.5988		1.67	0.277
	Stonefly × Fish	2, 5	0.1757		11.73	0.013
	Block	4, 10	0.0365		10.59	0.001
Total algae	Stonefly	1		38 460	10.89	0.016
	Fish	1		4 536	1.28	0.300
	Stonefly × Fish	1		7 455	2.11	0.196
	Block	2		85 346	24.16	0.001
	Error	6		3 532		
Diatoms	Stonefly	1		17 426	21.03	0.004
	Fish	1		2 175	2.63	0.156
	Stonefly × Fish	1		21 200	25.58	0.002
	Block	2		7 456	8.99	0.016
	Error	6		828		

species, and have far-reaching consequences, influencing not only the population dynamics of the prey species but also other components of the biotic community.

The threat of predation from visually feeding fish restricted mayfly search behaviour during both day and night by reducing movement around the tanks. Such reduced grazer movement can result in lower food intake (Culp and Scrimgeour 1993; Cowan and Peckarsky 1994), depending on patch quality and the rate of exploitation of algae during nocturnal feeding periods. By a different mechanism, encounters with benthic predators forced mayflies to flee from food patches. This disruption could reduce the proportion of mayflies occupying high-quality patches (McIntosh and Townsend 1994; Scrimgeour and Culp 1994b) or cause them to suspend foraging (Culp et al. 1991; Peckarsky 1996) thereby reducing food intake (Peckarsky et al. 1993; Scrimgeour et al. 1994). Thus, we would expect predator-induced alterations in movement and activity to reduce mayfly foraging efficiency, growth rates and fecundity, representing complex trade-offs between resource acquisition and predator avoidance (Peckarsky 1996).

As predicted, our data showed that the presence of trout cues caused both male and female mayflies to mature at smaller sizes than those in control treatments with no predators. While a fecundity cost of small size in female mayflies is widely recognised (Sweeney 1978; Peckarsky et al. 1993), reduced mating success in small male mayflies has only been demonstrated for one species (Flecker et al. 1988). Thus, our data suggest that trout-induced changes in foraging behaviour of mayflies may have important sublethal effects on mayfly fitness. Notably, the impact of fish odour on *Baetis* growth was due to relatively small changes in the magnitude of nocturnal movement observed in our experiments and not to alterations in the diel periodicity itself. Thus, we would predict a much greater impact of fish on the growth of fishless-stream mayflies, which show more dramatic qualitative differences in diel drift periodicity in the presence and absence of trout cues (McIntosh and Peckarsky 1996; A.R. McIntosh and B.L. Peckarsky, submitted).

Interestingly, the potential fitness costs to *Baetis* of reduced growth rates and size at emergence in the presence of stoneflies in this study were comparable to those measured in previous studies at a much smaller scale (Peckarsky et al. 1993). Analysis of demographic parameters from different experiments using a common currency (change in rate of population growth) also indicated that the sublethal costs of predator avoidance were greater than direct losses to predation by either trout or stoneflies, but that the impact of direct mortality by trout predation was four times higher than that by stoneflies (McPeek and Peckarsky, in press).

Since only stoneflies caused delayed emergence of mayflies, stoneflies may have greater sublethal and indirect effects on *Baetis* fitness than trout. However, stonefly-induced mortality was low (Kerans et al. 1995) and had very little impact on *Baetis* fitness (McPeek and Peckarsky, in press), suggesting that the benefit of staying in the stream longer to achieve larger size and fecundity may outweigh the mortality cost of increased exposure to predation by stoneflies in fishless streams. However, delayed emergence in the presence of stoneflies could reduce mayfly fitness by several other mechanisms. Delayed development may expose mayflies to warmer temperatures resulting in higher metabolic costs (Sweeney and Vannote 1978; Sweeney 1978), and smaller and less fecund adults emerging later in the adult flight period (B.L. Peckarsky, unpublished data). Further, infection rates of mermithid parasites are seasonal, increasing as water temperatures rise throughout the summer. Late-emerging *Baetis* risk much higher rates of parasitism than those emerging earlier in the summer (Vance and Peckarsky 1996). Finally, we suspect that the timing of available oviposition sites (protruding rocks in streams) might be an important factor limiting recruitment of *Baetis* to the next generation (Caudill and Peckarsky 1996). Delayed emergence may carry an additional cost if nearby oviposition sites have been filled thereby increasing chances of predation on females dispersing to other locations in search of suitable oviposition sites.

Since trout and predatory stoneflies coexist in Rocky Mountain streams, their effects on common prey pop-

ulations are not independent. Release from predation by trout has been given as a possible explanation for higher densities of large predatory stoneflies in fishless streams (Allan 1975; Harvey 1993). Feltmate and Williams (1991) attributed lower densities of predatory stoneflies in a manipulated section of an Ontario stream containing fish to a combination of direct predation by trout and emigration of stoneflies. In contrast, we observed that stonefly movement within the tanks was suppressed by trout cues, although they could not emigrate from tanks. Further, we have no evidence that these predator-induced changes in stonefly activity affect stonefly growth rates (Duvall and Williams 1995). In fact, *Megarcys* from fishless streams near RMBL emerged significantly smaller and had lower fecundities than those from trout streams (Taylor et al., in press). These data suggest that factors other than presence of fish, such as stonefly density, are responsible for fitness differences of stoneflies from fish and fishless streams.

It is also noteworthy that stoneflies and trout had biologically equivalent effects on the maturation size of mayflies. The combined effect of both predators on mayfly growth was neither additive nor different from that of each predator separately. Other studies have shown that the impact of a particular predator can be modified by other predator species (Soluk and Collins 1988; Huang and Sih 1991; Resetarits 1991; Wissinger and McGrady 1993; Scrimgeour and Culp 1994b; Werner and Anholt 1996). Unlike other studies, our experiments were designed to measure changes in prey fitness due solely to predator-induced behavioural changes, and were not confounded by changes in abundance of the prey or the two predator species. The non-additivity of impacts of the two predators on prey growth represents an interaction modification (sensu Wootton 1994a) where the impact of one species on another is modified by a third. Here, trout odour not only reduced *Baetis* drift rates directly but also altered the impact of stoneflies on *Baetis* drift, resulting in a reduction in stonefly-induced *Baetis* movement.

As our study shows, pairwise species interactions may not provide accurate predictions about the nature of the entire community (Werner and Anholt 1996). Natural complexity makes it difficult for ecologists to understand the structure of ecological communities (Alder and Morris 1994; Billick and Case 1994; Wootton 1994b). Our study indicates that more thorough knowledge of species interactions can be used to understand how predation effects propagate at the population and community levels. Theoreticians have typically used per capita population growth rate as the currency to examine the outcome of pairwise species interactions (Abrams 1995). Billick and Case (1994) argue that this parameter is also the best way to examine more complex multiple-species interactions. Data generated in our study show that trout and stoneflies induced similar, non-additive reductions in *Baetis* size at maturity, and can be used in demographic models to determine the relative effects of multiple predators on per capita population growth rate (McPeek and Peckarsky, in press). Further, careful observation of behavioural interactions among both predators and their prey provided a mechanism to explain the non-additivity of effects of multiple predators. Thus, we concur with Wootton (1994a) that knowledge of per capita population growth rates and the mechanisms producing them in a community will provide the most insight into the complexity of ecological systems.

The visual difference between algal communities that developed in different tanks was pronounced, and our algal biomass data may provide preliminary evidence for a behavioral trophic cascade. In treatments with both predator cues, total algae and diatom biomass accumulated at a greater rate than in treatments with only one predator cue or no predators. These data are not consistent with the alternative explanation that nutrients in the water supplied to the trout odour treatments elevated algal biomass, because tanks with fish odour did not have higher algal biomass than tanks without trout odour. Top-down effects of predators on algal abundance have been demonstrated previously in stream ecosystems (Power et al. 1985; Power 1990; Flecker and Townsend 1994; McIntosh and Townsend 1996). However, in most of those studies the mechanism of the trophic cascade is attributed to predator-induced changes in the abundance of the intermediate (grazer) species.

In our study, changes in the primary producers could be completely attributed to effects of predators on prey behaviour, because predators were not allowed to feed on prey in our experiment and we have no evidence that presence of non-feeding stoneflies causes mayfly mortality (Peckarsky et al. 1993). McIntosh and Townsend (1996) argued that increases in algal abundance in their stream channels with fish were the result of changes in grazer behaviour because they found no significant differences in grazer abundance between channels with and without fish. Schmitz et al. (1997) also prevented consumption by a predator (spiders) and observed impacts on the biomass of primary producers (grasses) that resulted exclusively from changes in predator-induced changes in the behaviour of consumers (grasshoppers).

Our behavioural data are insufficient to resolve the specific mechanisms explaining observed effects on algal biomass, because the behaviours quantified may not accurately reflect mayfly grazing pressure on algal resources, and we cannot be certain that mayfly behaviours observed during the first week were maintained over the course of the experiment. For example, if the number of visible mayflies corresponded directly to mayfly grazing rates, then we would have expected decreases in algal biomass in tanks with stoneflies (Fig. 3b). In fact, we observed just the opposite (Fig. 6), because many of the mayflies on substratum surfaces were probably avoiding stoneflies rather than foraging. Further confounding behavioural resolution of cascading effects was that high numbers of mayflies in the drift could result in either decreased or increased mayfly grazing rates, depending on the cause of that drift. Previous studies have shown that when stoneflies induce

high drift rates mayfly grazing rates are reduced (Peckarsky et al. 1993), but numbers of mayflies on high-quality food patches are not affected (Peckarsky 1996). In contrast, when trout suppress mayfly drift rates, mayflies are prevented from using drift as a foraging movement (to disperse to new food patches; Kohler 1985), which would consequently reduce grazing rates (Cowan and Peckarsky 1994). Thus, the predator-induced shifts in prey behavior observed in this study cannot be used as mechanistic explanations for the responses of the algal community to experimental treatments. Direct measurements of *Baetis* grazing rates are needed to resolve the mechanism producing a behavioural cascade.

Finally, since our study was conducted in a simplified experimental system, we must interpret results with caution. Trophic cascades may appear primarily where there are distinct and simplified trophic levels, and be uncommon in more complex food webs or in more complex habitats (Power 1992; Polis and Strong 1996). Further research is necessary to determine whether the behavioural trophic cascade observed in our simplified experimental systems occurs in natural habitats.

In summary, we have shown that by forcing mayflies to leave algal patches or by restricting their ability to move, predators caused trade-offs between foraging and predator avoidance that resulted in sublethal reductions in prey fitness comparable to those measured in previous experiments at smaller scales. Furthermore, the nature of the trade-off was altered considerably by the combination of predators present. The predator-mediated changes in behaviour also indirectly altered algal abundance through a behavioural trophic cascade. Thus, predators exerted selection pressure on prey by influencing their behaviour, which has a large potential to alter prey fitness thereby affecting prey population dynamics and the abundance and distribution of resources at the community level.

The implications of this study broadly suggest that carefully controlled experiments can reveal the details of mechanisms of complex predator-prey interactions that result in interaction modifications. It is possible that trade-offs detected in small-scale experimental systems are rare in natural systems because of complexity or heterogeneity in resources, habitats and predation risk (Peckarsky et al. 1997). Nevertheless, the importance or relevance of the trade-offs we have observed at small scales depends on whether they occur in real systems. Recent investigations in Rocky Mountain streams indicate that differences in the fitness of mayflies from fish and fishless streams may be observed at the scale of stream reaches, but that effects of stoneflies on prey fitness are obscured by other factors (B.L.P. unpublished data). Eventually we hope to determine how resource heterogeneity, habitat heterogeneity and variation in predation risk affect prey distribution and behaviour. We suggest that by combining observations in natural streams with detailed mechanistic studies carried out at appropriate scales, we will ultimately clarify the role of complex interactions in determining patterns of community structure.

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