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PREDATION RISK AND THE FORAGING BEHAVIOR OF COMPETING STREAM INSECTS¹

STEVEN L. KOHLER² AND MARK A. MCPEEK
W. K. Kellogg Biological Station, Michigan State University,
Hickory Corners, Michigan 49060 USA

Abstract. Invertebrates that graze periphyton growing on stones in coldwater streams in Michigan are at greatest risk of predation from a benthic-feeding fish (the mottled sculpin, *Cottus bairdi*) while on the top surface of substrates, where periphyton is most abundant, and during the day, when sculpin feed most actively. We conducted laboratory experiments with larvae of two strong exploitative competitors for periphyton (the mayfly *Baetis tricaudatus* and the caddisfly *Glossosoma nigrrior*) to test if and how their foraging behavior was affected by presence of sculpin when sculpin were not allowed to attack prey. We incorporated four experimental factors in a factorial design: sculpin presence/absence, the abundance (low, high) of food that was patchily distributed on the top surface of substrates, grazer hunger level (fed, starved), and time of day (day, night).

In feeding trials, *Baetis* was much more vulnerable than *Glossosoma* to sculpin predation. Similarly, only the foraging behavior of *Baetis* was strongly affected by the presence of sculpin. *Baetis* larvae responded to the presence of sculpin by: (1) significantly reducing the time spent on the top surface of substrates, and their movement rate while moving within and between food patches, and (2) significantly increasing the proportion of time spent in food patches, and the proportion of individuals that left the substrate by drifting downstream. *Baetis* larvae accepted greater risk of predation (by spending more time on top) when food abundance on top was high and when larvae had been starved for 27 h. Also, *Baetis* behavior was strongly affected by sculpin presence during the day but not at night. Collectively, these results suggest that *Baetis* larvae made adaptive compromises between feeding and avoiding sculpin. In contrast, *Glossosoma* behavior was not affected by the presence of sculpin. *Glossosoma* responded most strongly to alterations in food density and their own hunger level.

Our results suggest that the presence of sculpin, even though the fish consumed no larvae, might indirectly affect the outcome of competitive interactions between *Baetis* and *Glossosoma* through the grazers' differential behavioral responses to the predator.

Key words: *Baetis*; competition; conflicting demands; *Cottus*; foraging behavior; *Glossosoma*; indirect effects; predation risk; predator avoidance; trade-offs.

INTRODUCTION

Field experiments in stony streams generally have not supported the hypothesis that fish predation has strong direct effects on the abundances or species composition of stream benthos (reviewed by Allan 1983, Thorp 1986). These results have been obtained in experiments when fish fed largely on drifting prey (Allan 1982) and when they fed directly on benthic prey (e.g., Reice 1983, Flecker and Allan 1984, Reice and Edwards 1986). Exceptionally strong mortality effects of fish on benthos in stony streams have been observed only when fish were introduced to a previously fishless headwater stream (Griffith 1981). Similar results have been observed in lentic systems; effects of fish have been pronounced where fish were previously rare or absent (e.g., Hall et al. 1970, Crowder and Cooper 1982, Post and Cucin 1984). In systems containing fish,

effects on the size structure of benthic populations are often strong, while effects on benthic densities and species richness are generally weak (Thorp 1986, Mittlebach 1988).

Predators can nonetheless have strong effects on prey community structure through their effects on prey behavior (see Kerfoot and Sih 1987). For example, predator-induced changes in habitat use can lead to increased intra- and interspecific competition among refuging prey (Mittlebach 1981, 1988, Werner et al. 1983). Morin (1986) suggested that understanding the complex interactions among predators and competing prey may require an understanding of the behavioral ecology of predator-prey interactions.

The responses of prey to the presence of predators can significantly affect prey fitness. Prey behavior that maximizes fitness should represent a compromise between the potentially conflicting demands of avoiding predators and maximizing feeding rate (Sih 1980, 1982, Werner et al. 1983). This conflict is most pronounced when the best feeding sites also have the highest mor-

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² Present address: Illinois Natural History Survey, 607 E. Peabody Drive, Champaign, Illinois 61820 USA.

tality risk. Because habitats can vary temporally as well as spatially in both foraging profitability and predation risk, complex decisions may be required to reach an adaptive compromise. A number of recent studies demonstrate that prey use less profitable feeding sites in the presence of predators (e.g., Stein and Magnuson 1976, Milinski and Heller 1978, Grubb and Greenwald 1982, Sih 1982, Werner et al. 1983, Holmes 1984, Kotler 1984, Power et al. 1985, Holomuzki 1986), and several studies suggest prey may adaptively balance the trade-off between foraging gain and predation risk (Sih 1980, Lima 1985, Lima et al. 1985, Gilliam and Fraser 1987, Abrahams and Dill 1989). Few studies have examined prey behavior when predation risk varies temporally and spatially among habitats that differ in foraging profitability.

There is strong evidence that predators influence the behavior of lotic invertebrates on both evolutionary and ecological time scales. For example, ontogenetic changes in invertebrate drift behavior appear to have evolved in response to size-selective feeding by visual fish predators. Large size classes, which are preferentially fed upon by drift-feeding fish, drift predominantly at night when risk of predation is low, while the drift of small size classes generally is aperiodic (Allan 1978, 1984, Newman and Waters 1984). The behavior of several invertebrates is affected by the presence of predators, even when predator attacks are not allowed. For example, distributions and activity levels of several mayflies are affected by the presence of predaceous stoneflies (Peckarsky 1980, Peckarsky and Dodson 1980), and the amphipod *Gammarus* shows reduced activity in the presence of trout (Williams and Moore 1982, 1985) and sculpin (Andersson et al. 1986).

We studied interactions between a visual, benthic-feeding fish, the mottled sculpin (*Cottus bairdi*), and the larvae of two periphyton-grazing stream insects, the mayfly *Baetis tricaudatus* and the caddisfly *Glossosoma nigrior*, that are strong exploitative competitors for food (McAuliffe 1984, S. L. Kohler, *unpublished manuscript*). Grazing invertebrates in streams feed largely on stony substrates that contain two distinct habitats: the top and bottom surfaces. The top surface of substrates supports relatively high periphyton availability and high risk of predation by sculpin while the bottom surface supports relatively low periphyton availability and low predation risk. Therefore, grazers are confronted with a conflict situation when in the presence of sculpin (i.e., the best feeding sites have the greatest risk of predation). Risk of sculpin predation should also vary on a diel basis, as mottled sculpin largely feed during the day (Wiley 1980). We conducted laboratory experiments to test: (1) if the grazers respond behaviorally to the presence of sculpin when direct predatory attacks are prevented and, if so, (2) whether grazers make adaptive compromises between feeding and minimizing predation risk. We also determined the relative vulnerability of *Baetis* and

Glossosoma to sculpin predation to help evaluate mechanisms responsible for differential behavioral responses of the grazers to risk of predation by sculpin.

METHODS

Study animals

Baetis tricaudatus Dodds (Ephemeroptera: Baetidae) and *Glossosoma nigrior* Banks (Trichoptera: Glossosomatidae) often dominate the community of periphyton-grazing invertebrates in coldwater streams in Michigan (S. L. Kohler, *personal observation*). Both species are bivoltine in southwest Michigan. Each species has a generation in which aquatic larvae develop in the summer with terrestrial adults present in late summer to early fall, and a second generation in which larvae develop from fall through spring and adults emerge in late spring. The larvae of both species are quite mobile, although *Baetis* is more likely to enter the water column and drift downstream. This is partly because *Glossosoma* larvae build a large portable case out of sand grains that is structurally similar to a turtle shell. *Baetis* larvae do not build a case. Case building is thought to be an antipredator adaptation in *Glossosoma* and many other caddisflies (Wiggins 1977, Otto and Svensson 1980), but alternative hypotheses generally have not been rigorously tested (but see Williams et al. 1987). Both species inhabit hard substrates (primarily stones) and graze periphyton from such substrates throughout the day and night (S. L. Kohler, *personal observation*).

The fish fauna of small, coldwater streams is generally quite simple, consisting largely of trout and sculpin. Since trout feed primarily on animals drifting downstream in the water column (Chapman and Bjornn 1969, Jenkins et al. 1970, Elliott 1973), sculpin are the major benthic-feeding visual predators in such systems. Sculpin are considered to be ambush predators (Daniels and Moyle 1978, Brusven and Rose 1981, Kratz and Vinyard 1981), and their diets are frequently dominated by mobile prey including many mayflies, caddisflies, midges (Diptera: Chironomidae), and crustaceans (Amphipoda and Isopoda) (Koster 1937, Dineen 1951, Bailey 1952, Petrosky and Waters 1975). *Baetis* and *Glossosoma* commonly occur in sculpin diets (Petrosky and Waters 1975, Wiley 1980). Few direct observations of sculpin feeding behavior have been reported. We have assumed that grazers should be at greatest risk of sculpin predation while on the top surface of substrates because: (1) sculpin are too large to access prey inhabiting the bottom surface of most stony substrates, and (2) other benthic invertebrates (e.g., predaceous stoneflies) are reported to be at greatest risk of predation by sculpin while on the top surface (Soluk and Collins 1988).

Experimental design

The experimental design incorporated 16 treatments in a $2 \times 2 \times 2 \times 2$ factorial structure. The experimental

factors were sculpin presence/absence, food abundance (low, high) on the top surface of substrates, grazer hunger level (fed, starved), and time of day (day, night). Each treatment was replicated three times. Food abundance and forager hunger level were included in the design because: (1) grazer foraging behavior is affected by these factors (e.g., Hart 1981, Kohler 1984, 1985), and (2) we were interested in whether these factors modified grazer responses to the presence/absence of sculpin (cf. Cerri and Fraser 1983, Dill and Fraser 1984, Holbrook and Schmitt 1988). Time of day was included because risk of sculpin predation should be greater during the day than at night.

Trials were conducted in two identical, recirculating artificial streams that followed the design of Vogel and LaBarbera (1978). Each stream consisted of a Plexiglas channel ($1.2 \times 0.15 \times 0.15$ m) and a return circuit of 7.6 cm diameter polyvinyl chloride pipe. A net was positioned at the downstream end of each channel to capture drifting larvae. Two flow collimators 25 cm apart at the upstream end of each channel created a 375-cm² enclosure for sculpin. Each collimator was an array of 2.5-cm long pieces of plastic drinking straw glued together and oriented with the straw openings parallel to the current. This arrangement prevented direct interactions between the sculpin and the grazers, and likely isolated the sculpin visually from the potential prey. A single stone (≈ 100 cm² top surface) was scrubbed, autoclaved, and placed in each enclosure to provide a substrate for the sculpin. Channels were filled with well water to a depth of 8 cm (total water volume = 25 L). The water was changed periodically during the experiments. The streams were housed in a greenhouse where water temperature was maintained at $13.2 \pm 0.9^\circ\text{C}$ (mean ± 1 SD, $n = 18$). Fluorescent lights were used to maintain a 13:11, L:D cycle.

Four trials were conducted per day during February and March 1987. To minimize any residual effects of sculpin on the sculpin-absent treatments, we performed all sculpin-present treatments in one channel and all sculpin-absent treatments in the other channel. The channel that received the sculpin-present treatments was selected by coin toss. With this constraint, treatments were randomly interdispersed over time. Daytime trials commenced at 1330 and were terminated at 1600. Nighttime trials began at 1930, 0.5 h before lights were turned off, and were terminated at 2200. Trials were relatively short to minimize effects of food depletion on grazer behavior.

Because we did not randomize the sculpin presence/absence treatment with respect to stream channels, we needed to test whether effects attributed to sculpin presence/absence were due to channel effects (e.g., position of the channels in the room, inherent differences between channels, etc.). After completing the main experiment, we drained and thoroughly cleaned both channels. Channels were refilled and a small amount of bleach was added to each to remove residual odors.

The channels were then flushed for several hours, drained, and allowed to dry for 2 d before being refilled. The sculpin was placed in the channel from which it had previously been absent, and we repeated the following two treatments three times each: sculpin present, low food, fed grazers, day; sculpin absent, low food, fed grazers, day. These treatments were chosen because, based on observations made during the main experiment, we expected the effect due to sculpin presence/absence to be large.

Procedures

Baetis and *Glossosoma* larvae were collected from Spring Brook, Kalamazoo County, Michigan and held in the greenhouse in a 95-L flowing-water rearing tank (Gee and Bartnik 1969) for ≈ 1 mo before being used in a trial. Periphyton was cultured on artificial substrates in similar tanks, and the rearing tank contained several such substrates. These substrates were changed periodically, before food depletion became pronounced. At least 1 d prior to being used in a trial, larvae were transferred to a tank containing periphyton at ambient Spring Brook levels. Animals to be starved were transferred to small flowing-water chambers (Wiley and Kohler 1980) that did not contain periphyton and held for 27 h before being used in a trial. Fifth-instar *Glossosoma* larvae and mature *Baetis* larvae (without black wing pads) were used in all trials.

Sculpin were seined from Augusta Creek, Kalamazoo County, Michigan (sculpin were also present in Spring Brook) and held in the greenhouse in well-aerated 20-L buckets containing large stones from Augusta Creek. One large sculpin (standard length [SL] = 75 mm) was used in all experimental trials while four smaller fish (SL: 60–65 mm) were held for use in a prey vulnerability experiment (see Methods: Prey Vulnerability). The diets of sculpin in these size classes are very similar (Wiley 1980, S. L. Kohler, *personal observation*). The larger sculpin was periodically transferred to a bucket for feeding. Sculpin were fed stream insects (including *Baetis* and *Glossosoma* from the experimental trials) and *Gammarus*.

Grazers fed on substrates that supported either low or high periphyton standing crops. Substrates were molded from concrete and measured $9 \times 11 \times 2$ cm. The low food treatment used substrates containing ambient Spring Brook periphyton levels. The high food treatment was obtained by removing all grazers from substrates, placing the substrates on platforms that elevated them slightly above the stream bottom (to prevent colonization by *Glossosoma*), and collecting the substrates 10 d later (see Lamberti and Resh 1983, Kohler 1984). We created periphyton patches on substrates by scraping periphyton from the top surface to form a 6×7 array of 0.25-cm² patches, each patch separated by 1 cm of bare substrate (see Kohler 1984). We performed this manipulation so that various aspects of grazer foraging behavior (e.g., search rate with-

in and between food patches, patch revisitation, etc.) could be readily observed (see Hart 1981, Kohler 1984). Periphyton was also scraped from substrate sides to ensure that food was present only on the top surface. Periphyton scraped from the top of a substrate was rinsed into a jar and used to estimate standing crop in patches. Aliquots were drawn onto precombusted glass fiber filters (Whatman GF/F) which were immediately frozen. Filters were later dried at 102° for 24 h, weighed, combusted at 550° for 1 h, and reweighed to obtain ash-free dry mass (AFDM).

One substrate was placed in each experimental stream 0.6 m downstream of the sculpin enclosure. Ten *Glossosoma* larvae were first placed on each substrate. Ten *Baetis* larvae were then put into each stream by pouring them from a beaker through a funnel over the substrate. This was done in still water so that the larvae could attach to the substrate without being transported downstream. The current velocity (measured 2 cm above the substrate with a Gurley pygmy current meter) was then gradually increased to 30 cm/s. Larvae that had not become established were reintroduced to the substrate in still water and the current was again slowly increased. This procedure was repeated as necessary for 5 min, after which larvae that had not become established on the substrate were discarded. Larvae that subsequently drifted were sampled at the end of the trial. Since night trials were started shortly before lights were turned off, we have assumed that drift during this lighted period was negligible. Other studies suggest this is a reasonable assumption (Kohler 1985).

The foraging behavior of larvae was recorded using 8-mm time-lapse cinematography (Wiley and Kohler 1981, Kohler 1984, 1985). A low-intensity, short-duration strobe flash provided sufficient light for exposures but did not affect the behavior of *Baetis* or *Glossosoma* at the filming rate used (4 frames/min) (Wiley and Kohler 1981).

Films were analyzed frame by frame using an 8-mm analytical projector. The film record of the last 90 min of each trial was analyzed. We will refer to the preceding 1-h period as the pretrial period. Since we were unable to measure the feeding rate of individuals directly, we analyzed components of foraging behavior highly correlated with feeding rate. These included the proportion of individuals on the top surface of the substrate, the time spent by individuals on top, movement rate within and between food patches and the overall movement rate of larvae, the proportion of time on top spent in food patches, the encounter rate with patches (i.e., number of patches encountered per hour of between-patch search), and the proportion of patches that were revisited before a different patch was located. Revisitation of the most recently grazed patch (see Kohler 1984) was not included when patch encounter rates were estimated. We also analyzed the proportion of *Baetis* larvae that drifted during the trial. *Glossosoma* larvae did not drift. Since visual predators often

use movement as a cue to detect the presence of prey (Ware 1973, Kratz and Vinyard 1981), some of these parameters (e.g., movement rate between food patches) should also be correlated with the probability of detection by sculpin.

Larvae readily moved among the top, side, and bottom surfaces of the substrates. As in previous studies (Kohler 1984, 1985), we had no difficulty in following the movements of individual larvae while they were on the top surface. Individuals were followed until they moved off the top surface, and they were not considered if they subsequently returned to the top. Film analysis methods differed slightly for *Baetis* and *Glossosoma*. For *Baetis* movement analyses, individuals were followed and their location at each frame was recorded using a sonic digitizer and microcomputer. Movement rates calculated from such records were normalized by the body length of each individual and are reported as body lengths (BL) moved per hour. (*Baetis* movement rates expressed as moves per hour give qualitatively identical results.) Because several aspects of *Glossosoma*'s behavior make it difficult to analyze their movements in terms of distance moved, we simply recorded the number of movements made within and between food patches (reported as moves per hour). For both species, at least two individuals were randomly chosen for analysis per trial whenever possible. We also calculated the proportion of individuals on the top surface differently for each species. Because *Baetis* larvae moved off the substrate by drifting downstream during trials, the proportion of *Baetis* on top was calculated as the mean number on top during the last 10 min of a trial divided by the number on the substrate at the end of the trial. Because *Glossosoma* did not drift, the proportion of *Glossosoma* on top was simply the mean proportion on top during the 90-min period.

Statistical analyses

For the variables of the behavior of animals while on the top surface of the substrate (overall movement rate, within-patch movement rate, between-patch movement rate, proportion of time in patches, encounter rate with patches, and proportion of patches revisited) we used a weighted mean of the responses observed for all animals digitized in a replicate as the value for that replicate. Each animal's response was weighted by the time it spent on the top surface of the substrate. We assumed that the behavior of animals spending more time on top would be more representative of their responses to the treatments than animals that remained on top for only a few minutes. A simple arithmetic mean was calculated for the time spent on the top surface of the substrate. Variables expressed as proportions were arcsine transformed to satisfy homogeneity-of-variances assumptions of variance analyses (Sokal and Rohlf 1981).

For each variable we initially performed an analysis of covariance, including periphyton AFDM as a covariate and all possible first-, second-, and third-order interaction terms in the analysis, to account for any variance due to differences in periphyton standing crops within the food level treatments. Periphyton AFDM was not a significant covariate in any analysis ($P > .05$ for all analyses), and was therefore omitted. Four-way analyses of variance were then performed, including all possible first-, second-, and third-order interaction terms in the analysis. Only 1 of the 85 second- and third-order interaction terms was significant at $P < .05$. Because this result is likely to result by chance alone, we omitted the second- and third-order interaction terms from the analysis (Sokal and Rohlf 1981). Results are presented for analyses of variance that include all main effect and first-order interaction terms.

We tested for channel effects by comparing the two treatments performed after the sculpin had been switched between channels to the analogous treatments in the main experiment. For each variable we performed a two-way analysis of variance, including terms for the identity of the channel, the presence or absence of the sculpin, and the interaction of these two terms in the analysis.

Prey vulnerability

We examined the relative vulnerability of *Baetis* and *Glossosoma* larvae to sculpin predation. Feeding trials were done in 23-L plastic tubs containing two substrates with periphyton densities comparable to the low food treatments in the main experiment. A large airstone and deflector plate in one end of the tub created a current during the trial (Gee and Bartnik 1969). Twenty mature *Baetis* (without black wing pads) and 20 fifth-instar *Glossosoma* larvae were placed on the substrates and allowed to acclimate for 4 h. One sculpin (SL: 60–65 mm) was then added to the tub and allowed to feed for 41 h. The fish was then removed and the tub thoroughly searched for all surviving larvae.

Sculpin feeding was evaluated using Manly's preference index, α , calculated for *Baetis* (Manly 1974, Chesson 1978, 1983) as

$$\alpha_B = \frac{\ln((N_B - C_B)/N_B)}{\ln((N_B - C_B)/N_B) + \ln((N_G - C_G)/N_G)}$$

where N_B and N_G are the initial numbers of *Baetis* and *Glossosoma*, respectively, and C_B and C_G are the numbers of *Baetis* and *Glossosoma* consumed by the sculpin, respectively (Chesson 1983). This index ranges from 0.0 to 1.0. A value of $\alpha_B > 0.5$ indicates that *Baetis* larvae were more vulnerable to the sculpin than *Glossosoma* larvae. The feeding of four sculpin was evaluated. We calculated α_B for each sculpin and used these values in a t test to test the null hypothesis of $\alpha_B = 0.5$ (no differences in vulnerability) (Chesson 1983).

TABLE 1. Periphyton biomass on the top surface of substrates at the start of experimental trials.

Source	df	ss	F	P
Model	10	467 513	5.84	<.0001
Time of day	1	17 404	2.18	.1487
Sculpin	1	469	0.06	.8101
Hunger level	1	169	0.02	.8853
Food level	1	404 985	50.62	<.0001
Time \times sculpin	1	357	0.04	.8337
Time \times hunger	1	27 027	3.38	.0741
Time \times food	1	1474	0.18	.6702
Sculpin \times hunger	1	13 233	1.65	.2064
Sculpin \times food	1	1925	0.24	.6266
Hunger \times food	1	469	0.06	.8101
Error	37	296 041		
Total	47	763 554		

B. Periphyton ash-free dry mass ($\mu\text{g}/\text{cm}^2$) in the food level treatments.

Treatment	n	Mean	SE
Low food	24	221.5	16.0
High food	24	405.2	19.9

RESULTS

Prey vulnerability

Sculpin largely fed on *Baetis* larvae during the feeding trials ($\alpha_B = 0.98 \pm 0.01$ [mean ± 1 SE]; $t_3 = 111.6$, $P < .001$ for the null hypothesis of $\alpha_B = 0.5$). Only 0–5% of the *Glossosoma* were eaten during the trials, but >95% of the *Baetis* larvae were eaten in each trial.

Behavior of grazers

No consistent differences were found in the behavior of individuals between the main experiment and the second experiment (after the sculpin had been switched between channels) that could be associated with the stream channels ($P > .05$ for all response variables, both species). Also, there were no significant channel \times sculpin presence/absence interactions for either prey species, indicating that the effect of sculpin presence/absence did not depend on the stream channel in which the sculpin was placed. Therefore, we will consider only the results of the main experiment below.

Periphyton abundance in food patches in the high food treatment was nearly twice that present in the low food treatment, and no strong patterns of variation in food abundance were detected among the remaining treatments (Table 1).

Baetis behavior.—The presence of sculpin affected nearly all components of *Baetis* foraging behavior that were considered (Table 2). Individuals were less likely to move onto the top surface of a substrate (where periphyton was present) with sculpin present, and those that moved to the top spent less time there than in the absence of sculpin. While on top, movement rates of individuals while searching for food patches (between-

TABLE 2. Summary of the responses of *Baetis* larvae to the main effects of the experimental treatments. Degrees of freedom for the *F* tests are 1,36 (except where noted otherwise) rather than 1,37 as the design would dictate because no larvae were observed on the top surface in one trial. BL = body lengths.

Response variable		Treatment							
		Sculpin		Food level		Hunger level		Time of day	
		Present	Absent	Low	High	Fed	Starved	Day	Night
Proportion on top surface†	Mean	0.514	0.762	0.539	0.746	0.572	0.698	0.571	0.704
	(SE)	(0.069)	(0.038)	(0.062)	(0.052)	(0.069)	(0.053)	(0.072)	(0.047)
	<i>F</i>	13.1***		12.8**		3.1		3.2	
Time spent on top surface (min)‡	Mean	55.5	69.6	49.1	76.0	53.0	72.1	56.2	68.9
	(SE)	(5.7)	(4.0)	(4.9)	(3.5)	(5.7)	(3.5)	(5.2)	(4.6)
	<i>F</i>	14.7***		53.2***		26.8***		11.9**	
Overall movement rate (BL/h)	Mean	74.9	112.2	114.6	74.2	92.6	95.3	100.1	88.1
	(SE)	(6.9)	(7.8)	(8.3)	(6.0)	(9.3)	(7.4)	(8.8)	(7.8)
	<i>F</i>	20.1***		23.8***		0.1		2.2	
Within-patch movement rate (BL/h)	Mean	40.7	51.1	51.1	41.6	43.5	48.8	49.6	43.0
	(SE)	(1.9)	(2.6)	(2.4)	(2.4)	(2.4)	(2.6)	(2.6)	(2.3)
	<i>F</i>	15.6***		11.0**		3.8		5.2*	
Between-patch movement rate (BL/h)	Mean	140.3	188.0	195.7	134.9	171.2	158.3	164.4	164.9
	(SE)	(14.3)	(15.5)	(17.5)	(10.7)	(19.9)	(10.4)	(17.0)	(14.5)
	<i>F</i>	6.1*		11.2**		0.6		0.0	
Proportion time in patches	Mean	0.625	0.538	0.546	0.614	0.600	0.562	0.548	0.612
	(SE)	(0.029)	(0.026)	(0.027)	(0.028)	(0.026)	(0.030)	(0.026)	(0.030)
	<i>F</i>	6.2*		3.0		1.4		2.6	
Encounter rate with patches (no./h)	Mean	20.1	27.8	27.8	20.8	24.2	24.1	23.7	24.6
	(SE)	(2.3)	(2.5)	(2.6)	(2.3)	(2.8)	(2.4)	(2.4)	(2.7)
	<i>F</i>	4.2*		3.8		0.0		0.0	
Proportion of patches revisited	Mean	0.307	0.272	0.226	0.350	0.273	0.304	0.247	0.329
	(SE)	(0.038)	(0.034)	(0.035)	(0.033)	(0.040)	(0.032)	(0.033)	(0.037)
	<i>F</i>	0.3		7.8**		0.7		3.7	
Proportion drifting	Mean	0.255	0.099	0.216	0.133	0.261	0.100	0.146	0.209
	(SE)	(0.043)	(0.032)	(0.043)	(0.037)	(0.043)	(0.032)	(0.041)	(0.041)
	<i>F</i>	11.9**		2.1		10.8**		1.7	

* .05 > *P* > .01; ** .01 > *P* > .001; *** *P* ≤ .001.

† *df* = 1,33; results from four trials were discarded because larvae were disturbed as the trials were terminated.

‡ *df* = 1,37.

patch movement rate) and while feeding in patches (within-patch movement rate) were significantly reduced in the presence of sculpin. As a result of reduced movement rates, the rate that larvae encountered food patches was reduced in the sculpin treatments relative to the no-sculpin treatments. Although most measures of activity level were lower with sculpin present, the proportion of larvae that drifted during a trial was over 2.5× as great in the sculpin treatments as in the no-sculpin treatments.

Baetis behavior with respect to the food level, hunger level, and time-of-day treatments generally was consistent with results obtained in previous studies (Table 2; cf. Kohler 1984, 1985). The proportion of individuals on the top surface and the time spent by individuals on top was greater at the high food level, at night, and in treatments with starved larvae. Movement rates were strongly affected by food level but not by hunger level or time of day. In contrast to Kohler (1985), drift of starved larvae was significantly less than that of fed larvae. High drift of starved larvae in Kohler (1985) may have resulted from food depletion during trials, since independent day and night trials were not conducted, as in the present study.

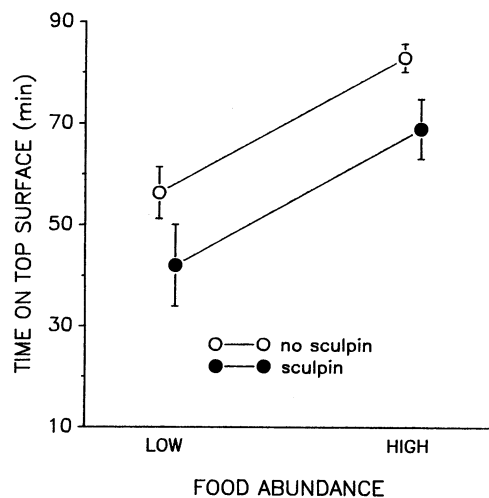


FIG. 1. The proportion of *Baetis* larvae on the top surface of the substrate (mean ± 1 SE) during the day and night in the sculpin and no-sculpin treatments.

TABLE 3. Summary of first-order interaction effects for *Baetis*. Interactions not marked by an asterisk were not significant ($P > .05$). As in Table 2, degrees of freedom for the F tests are 1,36 except where noted otherwise.

Response variable	Interaction					
	Sculpin × time	Sculpin × food	Sculpin × hunger	Hunger × food	Hunger × time	Food × time
	F values					
Proportion on top surface†	22.4***	2.7	1.1	0.0	0.0	0.1
Time spent on top surface‡	4.7*	0.0	20.1***	6.8*	0.5	0.9
Overall movement rate	4.9*	0.9	2.2	3.9	0.4	0.3
Within-patch movement rate	5.9*	0.5	0.1	0.1	0.1	0.6
Between-patch movement rate	1.3	1.3	0.7	9.0**	0.0	0.4
Proportion time in patches	1.1	0.0	0.3	2.7	1.5	4.2*
Encounter rate with patches	1.3	0.3	0.2	2.4	0.0	0.4
Proportion of patches revisited	-1.1	0.2	3.7	0.7	0.0	2.0
Proportion drifting†	0.1	0.8	0.4	3.2	0.1	0.4

*.05 > P > .01; **.01 > P > .001; *** P ≤ .001.

† df = 1,33.

‡ df = 1,37.

First-order interaction effects among the treatments for *Baetis* are summarized in Table 3. We will concentrate on interactions involving sculpin presence/absence, since these are of interest in interpreting how foragers respond to conflicting demands (e.g., Cerri and Fraser 1983, Fraser and Huntingford 1986, Holbrook and Schmitt 1988). The proportion of larvae on the top surface was high in day and night trials in the absence of sculpin. With sculpin present, the proportion on top decreased substantially during the day, but not at night (Fig. 1).

Although all of the experimental factors affected the time spent by *Baetis* larvae on top (Table 2), none of the factors acted independently (Table 3). The time spent by larvae on top was significantly reduced with sculpin present only during the day. At night, larvae spent about the same amount of time on top with sculpin present as they did with sculpin absent during the day and night (Fig. 2A). Starved larvae stayed on

top significantly longer than fed larvae in the sculpin treatment, but not in the no-sculpin treatment (Fig. 2B).

Significant interactions between sculpin presence/absence and time-of-day treatments for movement rates of larvae while on top (Fig. 3) are less indicative of compromises in *Baetis* foraging behavior than are the interactions previously discussed. Within-patch and overall movement rates of larvae were significantly lower during the day in the sculpin treatment than in the no-sculpin treatment, but not at night. The absence of differences at night primarily resulted from reductions in movement rate at night in the no-sculpin treatment and only slightly from nocturnal increases in the sculpin treatment.

No significant interactions between the sculpin presence/absence and food level treatments occurred (Table 3), even though these treatments strongly affected several aspects of *Baetis* behavior (Table 2). In general,

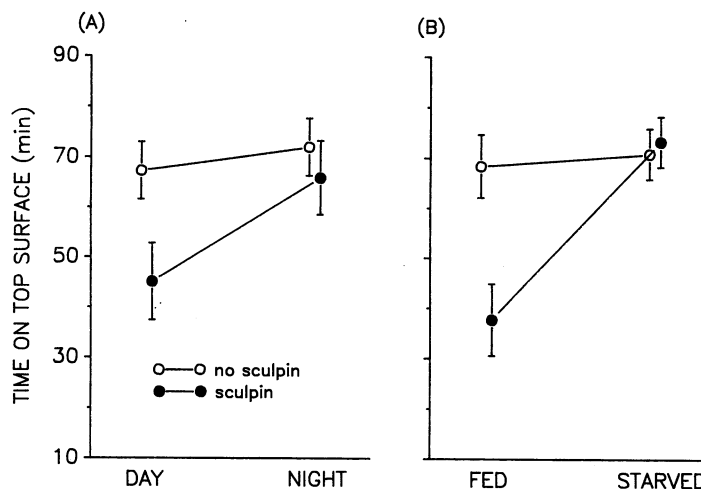


FIG. 2. The time spent by *Baetis* larvae on the top surface of the substrate (mean ± 1 SE) in the sculpin and no-sculpin treatments: (A) during the day and night, and (B) for fed and starved larvae.

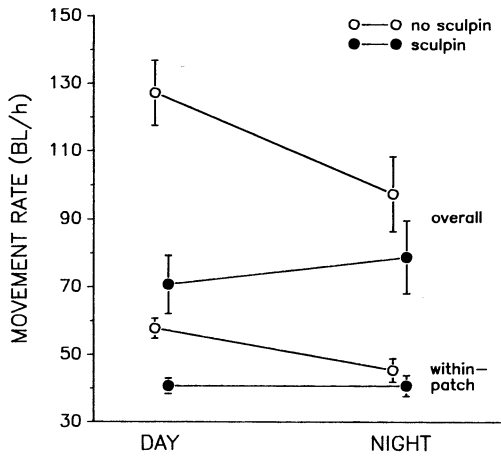


FIG. 3. Overall and within-patch movement rates of *Baetis* larvae (mean \pm 1 SE) during the day and night with sculpin present and sculpin absent. Movement rate is expressed as body lengths (BL) moved per hour.

components of *Baetis* behavior (e.g., time spent by larvae on top) were reduced in the sculpin treatment relative to the no-sculpin treatment, and the amount of reduction was constant across food levels (Fig. 4). *Baetis* larvae spent significantly more time feeding on the top surface in the high food treatments than in the low food treatments, both with sculpin absent and with sculpin present (Fig. 4A).

Although we restricted our analyses to the final 90 min of 2.5-h trials, *Baetis* responses to the presence of sculpin were immediate. The number of fed larvae on top in low-food-day treatments with sculpin present was significantly fewer than with sculpin absent within the first 5 min of the 1-h pretrial period, and this difference became more pronounced over time (Fig. 5). As for data from later in the trials, effects of sculpin

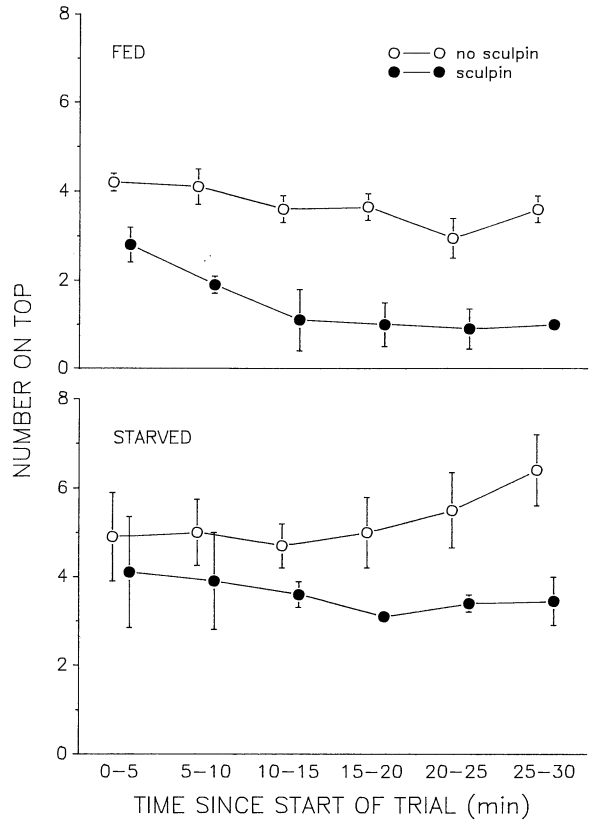


FIG. 5. Changes in the number of *Baetis* larvae on the top surface of the substrate (mean \pm 1 SE, $n = 3$) during the first 30 min of the 1-h pretrial period in low-food daytime trials with sculpin present and sculpin absent.

presence/absence ($F_{1,8} = 17.8, P < .01$ from a repeated measures ANOVA) and hunger level ($F_{1,8} = 16.2, P < .01$) on the number of larvae on top during the first 30 min of the pretrial period were highly significant, while

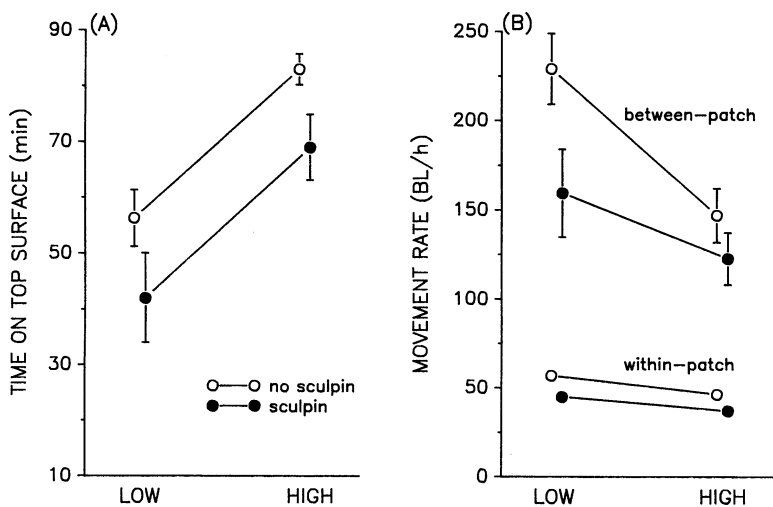


FIG. 4. (A) The time spent by *Baetis* larvae on the top surface of the substrate (mean \pm 1 SE) in low and high food treatments with sculpin present and sculpin absent. (B) Within- and between-patch movement rates of *Baetis* larvae (mean \pm 1 SE) in low and high food treatments with sculpin present and sculpin absent. Movement rate is expressed as body lengths (BL) moved per hour.

TABLE 4. Summary of the responses of *Glossosoma* larvae to the main effects of the experimental treatments. Degrees of freedom for the *F* tests are 1,37 except where noted otherwise.

Response variable		Treatment							
		Sculpin		Food level		Hunger level		Time of day	
		Present	Absent	Low	High	Fed	Starved	Day	Night
Proportion on top surface	Mean	0.655	0.684	0.590	0.748	0.576	0.763	0.588	0.751
	(SE)	(0.043)	(0.052)	(0.051)	(0.038)	(0.042)	(0.045)	(0.052)	(0.036)
	<i>F</i>		0.3		7.8**		11.0**		8.4**
Time spent on top surface (min)	Mean	87.1	85.4	82.5	90.0	86.5	86.0	84.0	88.5
	(SE)	(1.8)	(3.4)	(3.7)	(0.0)	(2.0)	(3.4)	(3.7)	(0.9)
	<i>F</i>		0.2		3.6		0.0		1.3
Overall movement rate (moves/h)	Mean	48.0	49.8	56.3	41.6	47.4	50.5	52.0	45.9
	(SE)	(3.8)	(4.8)	(4.1)	(3.9)	(4.5)	(4.2)	(4.6)	(3.9)
	<i>F</i>		0.1		7.1*		0.3		1.2
Within-patch movement rate (moves/h)	Mean	36.3	37.9	42.8	31.4	36.1	38.1	39.3	34.9
	(SE)	(4.0)	(4.1)	(4.1)	(3.6)	(4.1)	(4.0)	(4.5)	(3.5)
	<i>F</i>		0.1		4.8*		0.1		0.7
Between-patch movement rate (moves/h)	Mean	74.5	72.5	77.3	69.7	75.5	71.5	80.2	66.8
	(SE)	(4.2)	(5.1)	(4.4)	(4.9)	(3.9)	(5.4)	(4.5)	(4.5)
	<i>F</i>		0.1		1.5		0.4		4.6*
Proportion time in patches	Mean	0.570	0.610	0.565	0.616	0.597	0.583	0.611	0.569
	(SE)	(0.033)	(0.028)	(0.029)	(0.032)	(0.028)	(0.034)	(0.029)	(0.032)
	<i>F</i>		0.8		1.4		0.1		0.9
Encounter rate with patches (no./h)	Mean	1.4	1.7	1.6	1.5	1.5	1.6	1.8	1.3
	(SE)	(0.2)	(0.4)	(0.2)	(0.4)	(0.3)	(0.3)	(0.3)	(0.2)
	<i>F</i>		0.3		0.0		0.1		1.6
Proportion of patches revisited†	Mean	0.903	0.902	0.868	0.934	0.966	0.833	0.889	0.917
	(SE)	(0.043)	(0.042)	(0.046)	(0.039)	(0.018)	(0.056)	(0.043)	(0.042)
	<i>F</i>		0.0		1.3		5.1*		1.3

* .05 > *P* > .01; ** .01 > *P* > .001.

† df = 1,35; larvae did not encounter a patch and/or leave the only patch encountered in two trials.

that of the time since the start of the pretrial period was not ($F_{5,40} = 1.3$, $P > .05$). The interaction terms were not significant ($P > .05$).

Glossosoma behavior.—The behavior of *Glossosoma* larvae did not differ between the sculpin and no-sculpin treatments (Table 4), although two first-order interaction terms involving sculpin presence/absence were significant. *Glossosoma* responses to the food, hunger, and time-of-day treatments were similar to those of *Baetis* (Table 4). The proportion of larvae on top increased with increasing food abundance and hunger level, and was greater at night than during the day. Larvae on top at the start of a trial generally stayed there throughout the trial. As with *Baetis*, movement rates were lower in high food than in low food treatments. When on top, *Glossosoma* and *Baetis* rarely were not moving, but *Glossosoma* was much less active (in terms of distance moved per time) than *Baetis*. For example, *Baetis* encountered patches at a rate over 15 × as great as did *Glossosoma* (cf. Tables 2 and 4).

There were significant interactions between the sculpin presence/absence and hunger level treatments for two components of *Glossosoma* movement rate (Table 5; Fig. 6). Results of this form (Fig. 6) were classified by Fraser and Huntingford (1986) as "improbable outcomes" of experiments on behavioral responses of prey to predation risk, and are not readily interpreted in the context of compromises between feeding and avoiding predators.

DISCUSSION

Our results show substantial differences between two prey species that are known to be strong exploitative competitors in their responsiveness to the presence of a shared predator. We will consider: (1) the adaptive significance, for both species, of observed responses to predation risk, (2) the mechanisms used to detect and avoid predators, and (3) the implications of observed behavioral responses to predation hazard for the organization of the prey community.

Numerous studies have shown that prey species or size classes that are more vulnerable to predators exhibit stronger antipredator behavioral responses (reviewed in Stein 1979, Sih 1987). This appears clearly to be true in the system we considered. When allowed to feed on *Baetis* and *Glossosoma* larvae, sculpin largely consumed *Baetis*. Virtually all aspects of *Baetis* foraging behavior considered were affected by sculpin presence, while the behavior of *Glossosoma* larvae was unmodified.

Although fifth-instar *Glossosoma* are larger than mature *Baetis* larvae and some evidence suggests that sculpin are size-selective predators (Gilson and Benson 1979, Newman and Waters 1984), *Glossosoma* was much less vulnerable to sculpin than was *Baetis*. One explanation for this reduced vulnerability is that *Glossosoma*'s stone case deters predation by sculpin. Of course, *Glossosoma*'s case could have this present-day

TABLE 5. Summary of first-order interaction effects for *Glossosoma*. Interactions not marked by an asterisk were not significant ($P > .05$). As in Table 4, degrees of freedom for the F tests are 1,37 except where noted otherwise.

Response variable	Interaction					
	Sculpin × time	Sculpin × food	Sculpin × hunger	Hunger × food	Hunger × time	Food × time
	F values					
Proportion on top surface	0.8	0.0	0.0	0.6	0.6	0.0
Time spent on top surface	0.7	0.2	0.9	0.0	0.0	1.3
Overall movement rate	0.1	0.6	5.6*	2.1	0.7	1.2
Within-patch movement rate	0.2	0.2	3.9	3.2	0.3	5.8*
Between-patch movement rate	0.0	0.1	4.2*	1.8	1.6	0.0
Proportion time in patches	2.6	0.7	2.6	0.1	0.0	0.3
Encounter rate with patches	0.1	1.1	0.0	1.2	0.5	1.5
Proportion of patches revisited†	1.3	1.6	0.8	0.0	0.2	3.6

*.05 > P > .01.

† $df = 1,35$.

function whether case-building behavior in *Glossosoma* evolved in response to predation pressure (Wiggins 1977, Otto and Svensson 1980) or as a mechanism to facilitate respiration (Williams et al. 1987). However, occupation of a case alone does not appear to be sufficient to deter attacks from sculpin. For example, Gilson and Benson (1979) found that mottled sculpin in a West Virginia stream exhibited feeding biases for two stone-case-building limnephilid caddisflies, *Pycnopsyche* sp. and *Neophylax concinnus*. A more satisfactory explanation of the differential vulnerability

of *Glossosoma* and *Baetis* to sculpin requires consideration of prey and predator behaviors that may affect predator-prey encounters and predator attacks.

Sculpin are generally considered to be ambush predators that detect prey visually (Daniels and Moyle 1978, Brusven and Rose 1981, Kratz and Vinyard 1981). Such predators generally rely heavily on prey movement to detect prey (Ware 1973). Movement rate (distance moved per time) appears more important than movement per se in affecting encounter rates between sculpin and potential prey. For example, Kratz and Vinyard (1981) studied the feeding biases of piute sculpin, *Cottus beldingi*, for three invertebrate species that were active throughout feeding trials. Sculpin largely consumed the prey species that had the highest movement rate. The case-building caddisflies (*Neophylax*, *Pycnopsyche*) that were highly vulnerable to mottled sculpin in Gilson and Benson's (1979) study are relatively large and active. In fact, the feeding behavior of *Neophylax* is quite similar to that of *Baetis* (S. L. Kohler, *personal observation*). While *Baetis* and fifth-instar *Glossosoma* larvae are active virtually 100% of the time throughout the day and night (S. L. Kohler, *personal observation*), the movement rate of *Baetis* is much greater than that of *Glossosoma*, as evidenced by substantial differences in patch encounter rates. As a result, sculpin should have much higher encounter rates with *Baetis* than with *Glossosoma* (when densities of both species are similar), which would help to account for observed sculpin feeding biases.

While *Glossosoma*'s relatively low average movement rate appears to result in part from constraints imposed on movement by the unique design of glososomatid cases, *Glossosoma* is nonetheless capable of high movement rate (S. L. Kohler, *personal observation*). Therefore, it is interesting to consider whether predation by visual predators, such as sculpin, has influenced the evolution of an overall life-style in *Glossosoma* that involves relatively low movement rate. Comparative studies of *Glossosoma* behavior (and that of other invertebrates) among streams with and with-

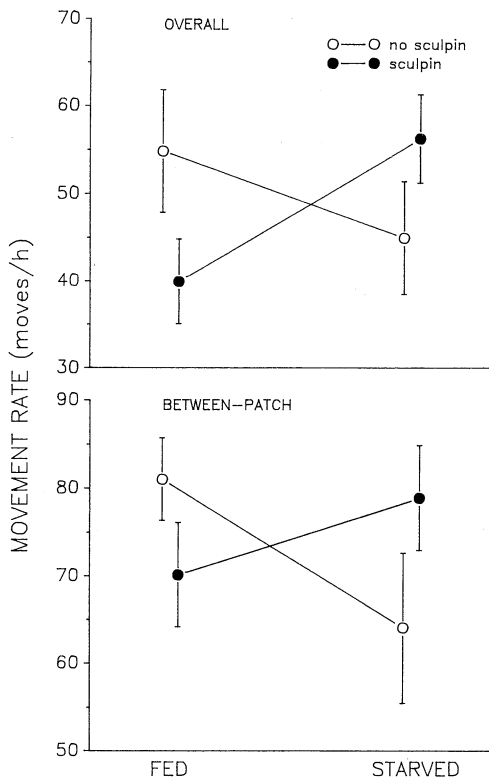


FIG. 6. Movement rates of fed and starved *Glossosoma* larvae (mean \pm 1 SE) with sculpin present and sculpin absent.

out benthic-feeding fish would be instructive in that regard.

The degree of response of *Baetis* larvae to sculpin presence was not independent of other factors, especially time of day and larval hunger level. A major effect of sculpin presence was to suppress *Baetis* use of the risky, top surface (where food was present) during the day, but not at night. Larval behavior, in terms of the number of larvae that used the top surface and the time individuals spent feeding on top, was similar at night with sculpin present to that observed during the day and night with sculpin absent. Similarly, the presence of sculpin strongly reduced the time spent on the top surface by fed larvae but not by starved larvae. These responses suggest *Baetis* made adaptive compromises between feeding and avoiding sculpin, for reasons that will be considered below.

Mottled sculpin appear to concentrate their feeding activities during the daytime. Wiley (1980) found that virtually all sculpin collected during the day in a cold-water Michigan stream had fresh stomach contents, while <40% of the individuals collected at night had fresh contents. Less than 15% of sculpin collected from Spring Brook just prior to dawn on each of two dates had fresh stomach contents, while >70% of fish collected in late morning or late afternoon had recently fed (S. L. Kohler and M. A. McPeck, *personal observation*). Therefore, benthic invertebrates should be at greatest risk to mottled sculpin predation during the day. By concentrating feeding activities at night with sculpin present and utilizing the top surface throughout the day and night in the absence of sculpin, *Baetis* individuals should effectively minimize the long-term probability of death per unit of food reward obtained (Gilliam and Fraser 1987). Holomuzki (1986) discussed similar diel patterns of habitat use by larval salamanders. Salamander larvae used shallow, vegetated areas of ponds where food was most abundant during the day and moved to deeper, open areas at night when predaceous diving beetles were most active in shallow areas. With beetles absent, larvae remained in shallow areas throughout the day and night. Other examples of diel shifts in habitat use in response to spatial and temporal variation in food availability and predation risk are probably numerous (e.g., diel vertical migration of zooplankton) and deserve greater attention from a perspective of the trade-offs between foraging gain and predation risk.

The notion that benthic invertebrates in streams exhibit diel shifts in microhabitat use enforced by risk of predation (i.e., individuals move from the bottom to top of substrates at night to feed when predation risk is low) was, at one time, widely accepted by stream ecologists (e.g., Elliott 1967, 1968, Bishop 1969, Waters 1972). Such diel habitat shifts were thought to be fixed by evolution. Our results, along with recent field studies of diel patterns in microhabitat use (Kohler 1983, Allan et al. 1986), suggest that stream invertebrates are much

more plastic in their behavior than previously thought. Such plasticity should itself be adaptive, because it allows individuals to modify their behavior to changing circumstances (Dill 1983, 1987).

Sih (1987) suggested that the optimal amount of time that prey individuals spend exposed to predators should increase with prey hunger level. Behavior of *Baetis* in the sculpin treatments supports this prediction. Starved individuals behaved with sculpin present as if the sculpin were absent by spending considerably more time on the top surface than fed larvae. Larvae made trade-offs between risk of starvation and risk of predation in a manner consistent with Sih's (1987) qualitative predictions. Similar results were obtained by Dill and Fraser (1984), in which drift-feeding coho salmon moved greater distances (at greater risk of predation) to capture drifting prey when hungry than when satiated.

Baetis larvae assessed food abundance on the top surface and risk of predation independently. Nonetheless, larvae clearly made compromises between feeding and avoiding sculpin. For example, the time spent feeding on the top surface was reduced in the presence of sculpin, but increased at the higher food level by the same amount in both the sculpin present and sculpin absent treatments. Larvae were willing to accept greater predation risk (by spending more time on top) when food availability on top was high than when food availability was low. Similar results have been obtained in other studies (Sih 1980, Cerri and Fraser 1983, Fraser and Huntingford 1986, Gilliam and Fraser 1987, Holbrook and Schmitt 1988), but, as in our experiments, the extent that such behavior balances the conflicting demands of feeding and minimizing predation risk has generally not been quantitatively addressed. Only Gilliam and Fraser (1987) and Abrahams and Dill (1989) have attempted to predict the increase in food availability necessary to compensate for an increase in predation risk. It is encouraging that, in both cases, the behavior of foragers agreed quite well with model predictions.

The adaptiveness of *Baetis* behavior cannot be evaluated without information concerning the costs (in terms of mortality rate) and benefits (in terms of feeding rate) of different behavioral options, and using such information, in conjunction with an optimality model, to predict how behavior should change with changing circumstances (e.g., Ydenberg and Houston 1986, Gilliam and Fraser 1987). *Baetis* larvae clearly made trade-offs between feeding and avoiding sculpin. More importantly, larvae behave in the presence of sculpin as if the sculpin were not present when risk of predation should be lowest (at night) and when the risk of starving to death is relatively high. Such behavioral flexibility should confer greater benefits to individuals (in terms of low long-term probability of death per unit of food obtained) than fixed strategies in which predators are either always or never avoided when present. In that regard, *Baetis* larvae appear to respond to spatial and

temporal variation in food abundance and predation risk in an adaptive manner.

Baetis larvae were able to detect a sculpin's presence even though the sculpin was not allowed to attack prey. A growing number of freshwater studies suggests such abilities may be diverse among vulnerable invertebrate prey (e.g., Peckarsky 1980, Townsend and McCarthy 1980, Williams and Moore 1982, 1985, Andersson et al. 1986, Holomuzki and Short 1988). As in our experiment, Peckarsky's (1980) study suggested that the magnitude of insect prey responses to noncontact stimuli from stonefly predators was positively correlated with prey vulnerability to stonefly predation. Similar correlations have been observed in marine systems (e.g., Fishlyn and Phillips 1980), where a large body of evidence indicates that prey use chemical cues to detect predators (e.g., Feder 1972, Mackie and Grant 1974, Phillips 1978). While our results suggest *Baetis* used chemical cues to detect sculpin, we cannot completely reject other mechanisms (e.g., visual detection). Irrespective of the specific mechanism by which prey detect predators, a major benefit to prey of having abilities to respond to noncontact stimuli from predators is that it allows prey to detect a predator's presence and respond accordingly before the predator detects the prey.

Upon detecting a predator's presence, prey can minimize the probability of being eaten by reducing movement, becoming most active when the predator is inactive, or utilizing more protected habitats (Sih 1985). *Baetis* used all of these options. Shifts in habitat use by *Baetis* (and other stream invertebrates) can be accomplished by two contrasting means. Individuals can move to relatively low risk microhabitats (e.g., the bottom surface of substrates), or they can leave the habitat by entering the water column and drifting downstream. *Baetis* drift was greater in the presence of sculpin than in the no-sculpin treatment. This is in contrast to results of previous studies in which drift of *Gammarus* decreased in response to noncontact stimuli from trout (Williams and Moore 1982, 1985) and sculpin (Andersson et al. 1986). Other studies have reported increased prey drift in the presence of a potential predator (Corkum and Pointing 1979, Corkum and Clifford 1980, Walton 1980, Malmqvist and Sjöström 1987), but drift probably resulted from contact encounters with the invertebrate predators used (see Peckarsky 1980). Of the three immediate responses *Baetis* can make upon detecting a sculpin's presence (i.e., reduce movement, move to a more protected microhabitat, drift), drifting is probably the most risky, especially during the day, since other fish (e.g., trout) prey effectively on drifting animals. It is perhaps not surprising then that the proportion of *Baetis* individuals that drifted, even in the presence of sculpin, was generally low. It will be interesting to explore if and how the use of different predator avoidance mechanisms should vary with changing circumstances (e.g., how should the use of drift change with variation in perceived quality of the

prey's immediate feeding habitat and/or the perceived intensity of predation hazard). We know of no models that address such issues, although Sih (1982) suggested it should be possible to make simultaneous predictions concerning the optimal mechanism for avoiding predators as well as for the optimal degree of predator avoidance. Such models may be useful in interpreting variation among prey in responses to similar predation hazards.

Sculpin-induced habitat shifts by *Baetis* (via movement to more protected microhabitats) could lead to increased encounters with refuging invertebrate predators, such as stoneflies, that are also vulnerable to sculpin predation (Soluk and Collins 1988). Whether such common occupancy of refuges leads to increased *Baetis* mortality should depend on when and where invertebrate predators commonly feed and how they respond to the presence of sculpin. Soluk and Collins (1988) found that *Baetis* mortality in the presence of mottled sculpin and the predaceous stonefly *Agneta capitata* did not differ from treatments where only sculpin were present, largely because *Agneta* consumed fewer *Baetis* with sculpin present than with sculpin absent. Therefore, under some circumstances, the presence of sculpin may actually reduce *Baetis* mortality from invertebrate predation. The behavior of both predators and their prey requires greater attention to understand the mechanisms responsible for such positive indirect effects (with respect to *Baetis*) of sculpin presence.

Nonlethal effects of sculpin on prey behavior may also affect competitive interactions among its prey. In some systems, predator-induced occupancy of refuges can enhance competition among prey (Peckarsky and Dodson 1980, Mittlebach 1984, 1988, Mittlebach and Chesson 1987). If prey species differ in their vulnerability to a predator and respond accordingly to the predator's presence, predators could produce the opposite effect in some communities (Sih 1982, 1987). This appears to be a likely indirect result of predation risk in the sculpin-*Baetis*-*Glossosoma* system. The major effects of sculpin on *Baetis* in our experiments were to reduce the number of individuals that used the top surface and the time they spent feeding there. The overall result of these effects should be a reduction in the impact of *Baetis* on the periphyton food resource that it shares with *Glossosoma*. In the absence of sculpin, *Baetis* and *Glossosoma* exhibit strong exploitative competition for periphyton, with *Baetis* having a stronger competitive effect on *Glossosoma* than *Glossosoma* has on itself and *Glossosoma* having a weaker competitive effect on *Baetis* than *Baetis* has on itself (S. L. Kohler, unpublished manuscript). These patterns result because, at natural densities, *Baetis* is able to drive periphyton standing crop to lower levels than is *Glossosoma*. In the presence of sculpin, the competitive effect of *Baetis* on *Glossosoma* should be weaker because the impact of *Baetis* on periphyton levels should

be less than with sculpin absent. The effect of *Baetis* on itself should be stronger with sculpin present because *Baetis* individuals should spend more time feeding in relatively unprofitable habitats. We are currently testing these predictions in laboratory and field experiments. Since sculpin densities are often high (i.e., >2 individuals/m²; Petrosky and Waters 1975, Wiley 1980), effects of sculpin on prey foraging behavior may well be as important as the direct consumption of prey in structuring prey communities in streams.

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