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Drift dispersal of mayfly nymphs in the presence of chemical and visual cues from diurnal drift- and nocturnal benthic-foraging fishes

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SUMMARY

1. The drift of *Baetis thermicus* nymphs in the presence of chemical, visual and hydrodynamic cues, considered individually and in combination, produced by different predatory fishes was examined experimentally in laboratory streams. Masu salmon (*Oncorhynchus masou*) and freshwater sculpin (*Cottus nozawae*) are typical drift- and benthic-foraging fishes, respectively.
2. Observations of fish swimming in the streams revealed differing diel periodicity between the species; sculpin were nocturnal foragers and salmon diurnal.
3. The drift rate of *Baetis* by night increased in the presence of chemical cues from sculpin, with other cues having no interactive effects. In contrast, the drift rate increased primarily in the presence of both chemical and, particularly, visual cues from salmon, although no additional effects were found for any non-visual cues. Visual cues could enable *Baetis* to assess precisely the predation risk from foraging salmon by day, whereas *Baetis* could not use visual cues to detect sculpin either at night, because of the low light intensity, or during the day, because of the low activity of sculpin at that time.
4. In natural streams, which are often inhabited by several predatory fish employing different modes of foraging, invertebrates may be able to precisely assess the risk and effectively to avoid predators by using cues unique to each.

Keywords: *Baetis* nymphs, diurnal drift-foraging fish, drift dispersal, laboratory experiments, nocturnal benthic-foraging fish, predator cues

Introduction

Most animals can assess predation risk, and thus alter their behaviour so as to reduce encounters with predators (Lima & Dill, 1990). This can incur costs associated with the reduced opportunities for feeding, however (Krebs & Kacelnik, 1991). Therefore, prey behaviour should represent a trade-off between avoiding predators and maximizing foraging success (Lima & Dill, 1990). In addition, animals often occur in natural communities with multiple predator species employing a variety of foraging modes. Hence, the risk of predation may vary greatly among habitats, seasons, days or even times of day (e.g. McIntosh & Townsend, 1995). To maximize fitness, prey animals should assess risk where possible from any cues available from the predators (Sih, Englund & Wooster, 1998). Until recently, however, most empirical studies have examined prey responses to single predator species only (see reviews by Sih, 1987).

In lotic systems, benthic invertebrates may reduce risk by occupying different habitats when in the presence of predators (Power, 1984; Kohler & McPeek, 1989; McIntosh & Townsend, 1996) or altering their behaviour (Culp & Scrimgeour, 1991; Flecker, 1992; Forrester, 1994; Wooster & Sih, 1995; Miyasaka &

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Nakano, 1999). Proximate causes of such anti-predatory responses include visual, chemical and hydrodynamic cues produced by both vertebrate (Tikkanen, Muotka & Huhta, 1994, 1996) and invertebrate predators (Peckarsky, 1987; Scrimgeour, Culp & Cash, 1994). Most studies have shown that non-visual signals from predators, e.g. chemical and hydrodynamic cues, dramatically changed prey behaviour in aquatic habitats, where turbid or dark environments often precluded the use of visual cues (see review by Dodson *et al*., 1994). Whereas the concentration of a chemical cue from predators may remain as long as the predator is present (McIntosh, Peckarsky & Taylor, 1999), visual and hydrodynamic cues might change temporally, even within a 24-h period, according to the foraging activity of the predators and/or light intensity. Therefore, the utility of each cue to prey, in assessing predation risk precisely, would depend upon the foraging modes of the predators. Nevertheless, few studies have attempted to compare the effects of various cues produced by predators having different foraging modes (Williams & Moore, 1985).

Some stream-dwelling mayflies may drift away from habitat patches with high predation risk (Kohler, 1985; Forrester, 1994; Miyasaka & Nakano, 1999). Although drift behaviour could represent a potential cost to the nymph in terms of relocation to a new habitat with unknown food resources, the direct risk of predation probably outweighs the benefit of staying within a profitable food patch (Lima & Dill, 1990). Many predatory fishes are patchily distributed in streams (Poff & Ward, 1990; Townsend & Hildrew, 1994; Urabe & Nakano, 1999) and could affect the spatial distribution of invertebrates because of direct predation and/or the avoidance behaviour of prey (Crowl *et al*., 1997). Because visually foraging fishes pose a risk to drifting individuals (Allan, 1978; Wilzbach, Cummins & Hall, 1986; Angradi & Griffith, 1990), mayflies usually exhibit nocturnal periodicity (Douglas, Forrester & Cooper, 1994; Rader, 1997). However, the presence of nocturnal, benthic-foraging fishes has also been found to increase nocturnal mayfly drift (Culp, Glozier & Scrimgeour, 1991; Miyasaka & Nakano, 1999). The nocturnal drift of mayfly nymphs was caused either by direct attacks or by non-contact approaches of nocturnal benthic-foraging cyprinids (Culp *et al*., 1991). Sympatric diurnal and nocturnal foraging fishes could both influence nocturnal drift of mayflies. Because these two types of fish predator differ considerably in foraging modes, e.g. method, and level and diel periodicity of activity, mayflies may be expected to enter stream drift in response to the different cues arising from the two types of predator.

In this study, we examined experimentally the flexible drift dispersal of *Baetis thermicus* (Ueno) nymphs in a laboratory stream in the presence of chemical, visual and hydrodynamic cues, presented individually and in combination, produced by a diurnal, drift-foraging fish, the masu salmon (*Oncorhynchus masou* Brevoot), and a nocturnal, benthic-foraging fish, the freshwater sculpin (*Cottus nozawae* Snyder).

Methods

Test animals

The laboratory experiment was conducted from 17 May to 15 June 1998, at a laboratory of the Tomakomai Experimental Forest of Hokkaido University (TOEF), Hokkaido, Japan. Test individuals of both *B. thermicus* and two species of predatory fishes, masu salmon and freshwater sculpin, were collected in the second order Betsubetsu Stream (12 km long, 3–6 m wide and 1–2% gradient) in south-western Hokkaido, Japan (42°37′N, 141°20′E) 2 days before each daily experimental trial (see below). Both fish species were common in the stream, with *Baetis* being a dominant benthic invertebrate (H. Miyasaka & S. Nakano, unpublished data). Mean *Baetis* density in the stream, estimated from 10 samples collected with a 100-μm mesh Surber sampler (25 cm × 25 cm quadrat, 1.0 m long; Urabe-Kagaku, Sapporo, Japan), was 228 ± 24 (SE) m^{-2} (range = 80–448). Water temperature in the stream ranged from 8 to 12 °C during the sampling period. *Baetis* nymphs were captured using an electrofishing technique (Model-12, Smith-Root Inc., Vancouver, WA, U.S.A.), which has been widely employed to collect mayfly nymphs and does not affect their subsequent behaviour (see McIntosh & Townsend, 1996; Kuhara, Nakano & Miyasaka, 1999). To minimize the difference in susceptibility to predators among the various body sizes of *Baetis*, we used nymphs of more or less the same average body size as test individuals. The mean body length and head width of test nymphs, which were randomly subsampled from the test individuals, was 6.9 ± 1.9 (SE) mm ($n = 35$) and 1.0 ± 0.2 mm, respectively. Both fish species were also captured using the same electrofishing unit as above. The mean body weight of juvenile masu salmon was 11.7 ± 0.6 (SE) g (live mass) and of freshwater sculpin 11.4 ± 0.6 g ($n = 126$ for both species), with the former being 10.8 ± 0.1 (SE) cm in fork length and the latter 9.8 ± 0.2 cm in total length. All of the experimental animals were then transferred to the TOEF facilities and stocked separately in aerated aquaria (under a 14L : 10D light regime and a constant water temperature at 9 °C) until required. To standardize hunger levels in both *Baetis* and the fishes, all were starved for 24-h prior to experimentation. Individuals of both *Baetis* and two fish species were used only once during the experiment.

Laboratory stream system

Experimental reaches (2.20 m long, 0.20 m wide and 0.15 m depth; 0.44 m^2 area) were created by isolating portions of each of five stream tanks constructed of polyvinyl bicarbonate (Fig. 1). Each experimental reach was blocked at its upstream end by a fine mesh screen (1 mm aperture) which was impassable for both fishes and *Baetis*, and at its downstream end by a coarse mesh screen (10 mm aperture), which kept the fishes within the reach but allowed *Baetis* to pass through. The latter were collected as they drifted out of the experimental reach, in a 1-mm-mesh drift-net (20 cm × 20 cm mouth opening, 30 cm long) placed just downstream from the coarse mesh screen. An observation window (2.8 m long × 0.25 m wide), made of transparent polyvinyl bicarbonate, allowed observers who sat in a darkened observation room next to each stream tank, to record the behaviour of the fishes and *Baetis*. To exclude any residual chemical cues of fishes, the stream tanks were filled with ground water. Water temperature in the tanks were maintained at 9 °C by using thermostatically controlled chilling and heating units during the experimental period. Circular water flow in the tank was maintained by three air-lift pumps, one each being located at the end of the experimental reach and the third on the opposite side of the reach (Fig. 1). To regulate water velocity, flow was generated by currents through two pipes (2 cm diameter), which were connected with an air-lift pump located at the upstream end of the experimental reach. Water velocity, measured at 11 locations in each reach, was similar among the stream tanks [22.3 ± 1.5 (SE) cm s^{-1} at mid water column, $n = 55$], but heterogeneous within reaches (range = 8.7–64.2 cm s^{-1}).

Eleven unglazed ceramic plates (19 cm × 19 cm area, 1 cm thickness) were placed in each experimental reach so as to leave a 5-cm space beneath to serve as both refuges from fishes (below) and sources of periphyton (on top) for *Baetis*. The plates had been placed on the streambed of the Horonai Stream running through TOEF (see Miyasaka & Nakano, 1999, for description of stream environment) for 1 month, enabling sufficient natural periphyton to have become established by the beginning of the experiments. The periphyton attached to the sides and undersurface of the plates was brushed off to ensure that only the top of the plates would provide food for *Baetis* during the experiment. The mean periphyton biomass, which was randomly subsampled from the plates used in the experiment, was 0.24 ± 0.01 (SE)

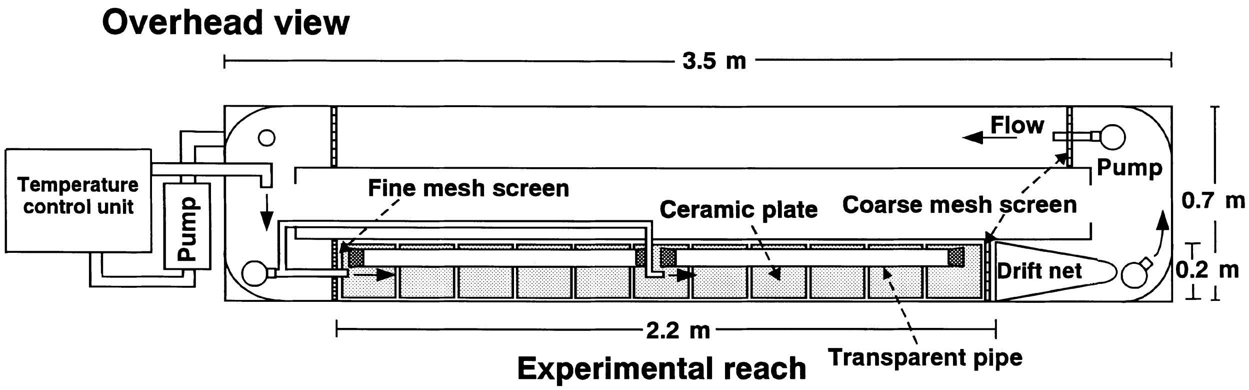

Fig. 1 Diagram of the stream tank used in the experiment.

ash-free dry mass (AFDM) mg cm^{-2} ($n = 54$, upper surface only). To avoid depletion of the periphyton by *Baetis* grazing, the plates were replaced for every experimental trial. The five stream tanks, which were located in an otherwise completely darkened laboratory, were illuminated (2700 lux at water surface) by two 100-W fluorescent bulbs 1.5 m above each tank from 05.00 to 19.00 hours (i.e. 14L : 10D light regime), using a time controller. This light regime was very close to that in the catchment of the stream where the test animals were collected.

Experimental design

The drift response of *Baetis* nymphs to various cues of salmon and sculpin was examined. The experiments were conducted separately for each fish species, emphasizing five fish cue treatments for each: (1) control with no fish, and treatments with (2) visual cues of fish, (3) chemical cues of fish, (4) visual plus chemical cues of fish (hereafter termed visual + chemical) and (5) freely swimming fish (i.e. visual + chemical + hydrodynamic). Each treatment was replicated six times in random order for each fish species. The stream tank was washed using bleaching powder and the water replaced completely for each trial.

To equalize fish density in keeping with the various cues in the experimental reach (0.44 m^2 area), we altered the number of introduced fish for each treatment in the stream tank (2.45 m^2 area). In the visual + chemical + hydrodynamic cue treatments, four individuals of each species were introduced into the experimental reach (0.44 m^2 area), thereby resulting in fish densities of 9.1 m^{-2}, which were near the upper range reported for juvenile salmonids of similar body size (Grant & Kramer, 1990) and also found for sculpin in natural streams (H. Miyasaka & S. Nakano, unpublished data). In addition, 19 individual fish were stocked in the tank on the opposite side of the experimental reach, resulting in a fish density of 9.4 m^{-2} for the overall stream tank (2.45 m^2 area; Fig. 1). The visual cue treatment was provided by two individual fish held in each of two transparent acrylic resin pipes (8 cm diameter, 1.0 m long) with silicon plugs at both ends so that water exchange did not occur between the pipe and the stream tank. The pipes were filled with water containing sufficient oxygen for fish survival during the experiment and placed in a row parallel to the flow over the ceramic plates, so that *Baetis* could see the fish in the pipes. A 1-cm space between the pipes and the tops of the plates allowed easy observation of *Baetis* on the surface of the plates. To standardize any turbulence effect created by the pipes, two pipes filled with water were similarly positioned in the other treatments. In the chemical cue treatment, 23 individual fish were introduced into the opposite side of the experimental reach in the tank. Therefore, although *Baetis* could neither see the fish nor perceive hydrodynamic cues, the circulating water flow transported fish chemical cues to the experimental reach. The visual + chemical cue treatment was effected by combining the above individual treatment techniques. All fishes introduced into the experimental reach, which were individually marked with different coloured ribbon-tags after being anaesthetized with 2-phenoxyethanol, were introduced to each experimental reach 24 h before each daily trial so as to become acclimatized to the experimental conditions. To equalize the hunger levels of introduced fishes, the fishes were not given any food during the acclimation period.

Each experimental reach was stocked with 110 individuals of *Baetis* 24 h after the establishment of the fish cue treatments. This density (250 m^{-2}) was approximately equal to the mean value observed in the Betsubetsu Stream where *Baetis* were collected. Subsequently, the current velocity was gradually accelerated up to the experimental conditions, over a 30-min period from the start of the experiment. *Baetis* individuals entering the drift net during this 30-min period were restocked to the reach. The set up of each experiment was completed by 07.00 hours, and drift sampling and fish observation started at 08.00 hours for every trial (see below).

Observations and sample analyses

The number of *Baetis* individuals drifting out the experimental reach was recorded. In each daily trial, individuals caught in the drift net were collected at six times (08.00, 12.00, 16.00, 20.00, 24.00 and 04.00 hours). To examine differences in drift response of *Baetis* among the treatments, drift data were expressed as the proportion of individuals captured by the drift net by day (08.00, 12.00 and 16.00 hours; hereafter termed daytime drift rate) and by night (20.00, 24.00 and 04.00 hours; night-time drift rate) to the total number introduced initially. An analysis of daytime drift rates, however, was not undertaken because the drift rate was too low to enable testing of the treatment effects [2 ± 0.4 (SE)%].

To examine diel changes in the feeding activity of masu salmon and freshwater sculpin, we observed the behaviour of four individuals of each species freely swimming in the experimental reach during the visual + chemical + hydrodynamic cue treatments and four individuals caged in the transparent pipes during the visual and visual + chemical cue treatments. Fish individuals were observed during the same six times as the *Baetis* drift observations for each daily trial. The horizontal location of each fish focal position and focal position height (distance between the plates and fish snout) were recorded five times on 1 : 5 scale maps, at 2-min intervals (i.e. 8-min total) in each of the six observation times for each of the experimental reaches. For each individual in each observation time, four distances were measured between each pair of consecutive positions and totalled. Total distance was taken as movement distance [cm (8 min)$^{-1}$], although comprising straight line measurements, it was an underestimation of the actual fish path. We also calculated mean focal position height (cm) for each individual in each observation time, and then obtained the mean values of both movement distance and focal position height of both fish species for daytime (08.00, 12.00 and 16.00 hours) and night-time (20.00, 24.00 and 04.00 hours). Dim red light was used only for the fish observations in the laboratory; otherwise, the laboratory was in complete darkness during the night-time period. To minimize the bias of dim red light used for the night-time observations focusing on the visual cues of fish during the night-time, we made the observations as quickly as possible. In reality, the period of the observation with the dim red light was shorter than 1 min. We used a portable spotlight with red filter (approximately 8 cm of lightspot in diameter), and turned the spotlight on the fish only.

At the end of each trial, the stomach contents of the fishes in the visual + chemical + hydrodynamic cue treatment were collected by stomach pumping with a 2-mL pipette so as to flush prey items from the entire stomach region (Giles, 1980). This enabled a count of the number of *Baetis* eaten by the fishes during the experiment. Under experimental conditions, both fish species consumed relatively low proportions of the total *Baetis* nymphs introduced initially [masu salmon, 2 ± 2 (SE)%; freshwater sculpin, 2 ± 1, $n = 6$ for both]. Accordingly, direct predation data was ruled out from the analyses.

Statistical analyses

For statistical analyses on both fish and *Baetis* behaviour, stream tank means were used as replicates. To examine diel periodicity in the activity levels of the two fishes, both movement distance and focal position height of fish freely swimming in the experimental reach and caged in the transparent pipes were analysed with repeated-measures two-way ANOVA, with fish species and condition (caged or uncaged) as between-subjects, and time period as within-subject, factors. To analyse the effects of the various fish cues on *Baetis* behaviour, we examined the night-time drift rate of *Baetis* using two-way ANOVA with fish species and cues as factors. This analysis was conducted excluding the control treatment, which lacked a fish cue. One-way ANOVAs were used to test for the effect of cue treatments separately for each fish species, including the control treatments. Student–Newman–Keuls multiple comparison tests were carried out to assess the differences among the fish cues when significant effects were encountered.

$\text{Log}_{10}(x + 1)$ transformations for exact values and arcsine transformations for percentages were made in order to standardize variances and improve normality, if necessary, to satisfy the assumptions of the ANOVA model. All statistical tests were two-tailed. For all statistical tests, the α-value of 0.05 was used for statistical significance. All analyses were conducted using the statistical package StatView (version J 5.0, Abacus Concepts Inc., Berkeley, CA, USA).

Results

Behaviour of two predatory fish

Diel periodicity in activity was completely different between salmon and sculpin (Fig. 2). The repeated-measures two-way ANOVA revealed a significant diel-by-species interaction effect on movement distance (Table 1). Salmon activity during the daytime was greater than that at night, whereas the night-time activity of sculpin was greater than during the day (Fig. 2). Other within-subject

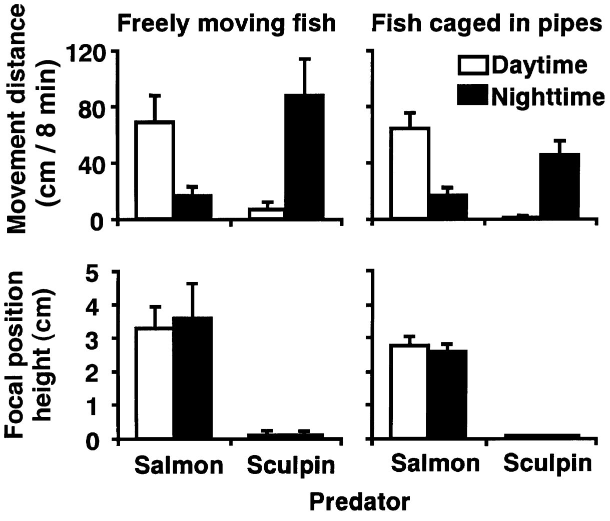

Fig. 2 Diel changes in behavioural activities of masu salmon and freshwater sculpin under two experimental conditions. Data given as mean ± 1 SE ($n = 6$).

effects, diel, diel-by-condition and diel-by-species-by-condition interactions, were not significant (Table 1). The diel periodicities in movement distances of both fish species did not differ with presence or absence of the transparent pipes. In the between-subject effects, neither condition nor species-by-condition interaction effects were significant; the movement distance of both species was unaffected by the presence of the transparent pipes. A non-significant species effect on the movement distance revealed that overall activity did not differ between the fish species.

The repeated-measures two-way ANOVA revealed that species, condition and species-by-condition effects all impacted significantly on the focal position height of the two fish, with no within-subject effects being significant (Table 1). The focal position height of salmon was significantly greater than that of sculpin, but no diel changes were found in either species (Fig. 2).

Night-time drift rate of Baetis *nymphs*

The night-time drift rate of *Baetis* was increased by partial different fish cues between salmon and sculpin (Fig. 3). Two-way ANOVA revealed that species ($F_{1,40} = 14.36$, $P < 0.001$), cues ($F_{3,40} = 12.52$, $P < 0.001$) and species-by-cues interaction ($F_{3,40} = 11.45$, $P < 0.001$) effects were all significant factors affecting the night-time drift rate of *Baetis*.

Both visual and chemical cues of salmon increased the night-time drift rate of *Baetis*, the influence of the visual cues being greater (Fig. 3). In masu salmon experiments, drift rates were significantly affected by the presence of fish cues (one-way ANOVA, $F_{4,25} = 13.93$, $P < 0.001$; Fig. 3). Drift rates in treatments including any of the salmon cues were significantly greater than those in the control ($P < 0.05$ for all combinations, by Student–Newman–Keuls). The drift rate for the chemical cue treatment was significantly lower than for any other treatments with salmon cues ($P < 0.05$ for all combinations), although no significant differences were found among the visual, visual + chemical and visual + chemical +

Table 1 Results of repeated-measures two-way ANOVA on the behavioural activities, movement distance and focal position height of sculpin and salmon under the two experimental conditions: freely moving in the experimental reach and fish caged in transparent pipes

		Movement distance			Focal position height		
Source	d.f.	Mean squares	*F*	*P*	Mean squares	*F*	*P*
Between-subjects							
Species	1	0.48347	1.53361	0.225	4.28451	361.47442	< 0.001
Condition	1	1.21145	3.84280	0.059	0.13156	11.09931	0.002
Species × condition	1	0.24593	0.78012	0.384	0.05980	5.04536	0.032
Error	32	0.31525			0.01185		
Within-subjects							
Diel	1	0.00014	0.00057	0.981	0.00119	0.01554	0.901
Diel × species	1	12.45559	50.63954	< 0.001	0.00344	0.66369	0.421
Diel × condition	1	0.15645	0.63606	0.431	0.00249	0.48175	0.493
Diel × species × condition	1	0.71055	2.88882	0.099	8.65×10^{-8}	0.00002	0.997
Error	32	0.24597			0.00518		

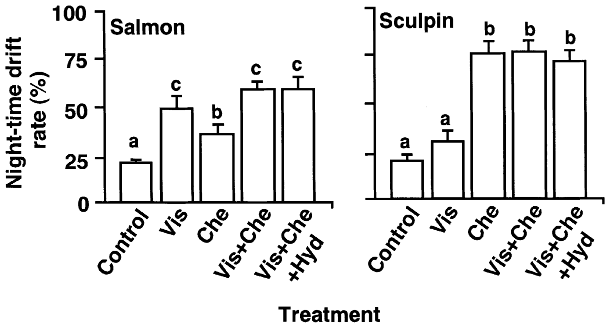

Fig. 3 Effects of various cues from masu salmon and freshwater sculpin on the night-time drift rate of *Baetis thermicus* nymphs. Data given as mean ± 1 SE ($n = 6$). Different letters indicate statistically significant differences within each fish treatment. Fish cues treatments: Vis: visual cues; Che: chemical cues; Vis + Che: visual and chemical cues; Vis + Che + Hyd: visual, chemical and hydrodynamic cues.

hydrodynamic cue treatments ($P > 0.05$ for all combinations).

In contrast to the salmon experiments, only the chemical cue of sculpin resulted in a high drift rate of *Baetis* (Fig. 3). In the freshwater sculpin experiments, night-time drift rates of *Baetis* were affected significantly by the presence of fish cues (one-way ANOVA, $F_{4,25} = 31.41$, $P < 0.001$; Fig. 3). In all except the visual cue treatment, the night-time drift rates were significantly greater than in the control ($P < 0.05$ for all combinations, by Student–Newman–Keuls). Non-significant differences among the chemical, visual + chemical and visual + chemical + hydrodynamic cue treatments were found ($P > 0.05$ for all combinations).

Discussion

In our laboratory experiments, predator cues to which *Baetis* responded behaviourally, differed somewhat between sculpin and salmon. Observations of movement distances revealed the diel periodicity of foraging activities to differ considerably between the fish species in spite of the experimental conditions (i.e. freely moving or caged); sculpin was a nocturnal forager and salmon diurnal. Such experimental findings were consistent with the diel periodicity of foraging activity observed for each fish species in natural streams (Inoue & Nakano, 1994; Miyasaka & Nakano, 1999). Moreover, the position in the water column also differed between the species, with salmon having a greater focal position height than sculpin. These differences in behavioural mode between the fishes could be responsible for differences in the effects of the visual cues given.

Both chemical and visual cues of salmon caused an increased drift rate of *Baetis*, the latter cue inducing the greater response. Neither chemical nor hydrodynamic cues had an effect additional to that of the visual cue, because the drift rate in the visual cue treatment did not differ from those in visual + chemical and visual + chemical + hydrodynamic cue treatments. It is clear, therefore, that *Baetis* perceives salmon primarily by visual cues. Such cues are readily available to *Baetis* for a precise assessment of the risk of predation by salmon, as a result of the salmon swimming actively to hold position in the water column by day. However, the response of *Baetis* to salmon at night might be because of the dim red light used for the observations. Heise (1992) indicated that mayfly nymphs could detect red light, so the red light allowed the prey to see the fish although it was not moving around at night. In our results of visual cues treatment, *Baetis* could not detect the presence of predation risk by sculpin, which moved actively during the night. It seems that the effect of visual cues from salmon, which did not moved around, at night was smaller than that during the day. The nocturnal response in the *Baetis* nymphs to visual cues from salmon might come from a memory of the predation risk by salmon during the day.

In contrast, the presence of chemical, but not visual, cues of sculpin induced the higher night-time drift rate of *Baetis*. However, visual and hydrodynamic cues did not have effects on the drift rate, additional to that of the chemical cue, the rate not differing between the chemical, visual + chemical and visual + chemical + hydrodynamic cue treatments. Although this result provides evidence for *Baetis* using only chemical cues to detect sculpin, any effect of a separate hydrodynamic cue could not be tested and remains unknown. *Baetis* could not utilize visual cues for detection of sculpin either by night or by day, because of low light intensity during the night and the inactivity of sculpin during the day.

Most experimental studies on predator–prey interactions in aquatic systems have shown that behavioural shifts of prey animals occurred in response to the presence of chemical and/or hydrodynamic cues from predators (see review by Dodson *et al.*, 1994). In contrast to these cues, the sole effect of a visual cue from a predatory fish on an invertebrate species has never been clearly shown, although Tikkanen *et al.* (1994) found that visual cues from a cyprinid fish had additional effect to that of the chemical cue on mayfly drift in a laboratory experiment. Because prey invertebrates are unlikely to perceive chemical cues from downstream fishes in natural streams, such cues being transported downstream only (McIntosh *et al.*, 1999), they would be vulnerable to both downstream and overhead drift-foraging fish (in this case, masu salmon) rather than upstream ones, because most of the latter feed facing upstream. Therefore, prey invertebrates may not make precise decisions for avoiding predation by salmon (positioned downstream) using chemical cues only. Moreover, prey invertebrates in natural streams are likely to have less than complete information on predatory fish from chemical cues, when the latter are upstream and the cues dispersed by eddies and/or turbulent water conditions. Accordingly, when the predatory fish can be seen by the mayflies in the clean water and in daylight, visual assessment for ascertaining predation risk, combined with other cues, might improve the overall efficiency with which water-column, drift-feeding fishes are detected. The drift rate of *Baetis* increased in the presence of salmon during the night-time, although the latter was inactive and the light intensity apparently too low for visual detection by *Baetis*. It is considered to perceive visual cues from salmon during daylight when the fish is active, drift being suppressed by day because of the predation risk (Douglas *et al.*, 1994). Similarly, some experiments have reported an increased nocturnal drift rate of *Baetis* under conditions of high density of diurnal drift-foraging fishes (Williams, 1990; Douglas *et al.*, 1994; Forrester, 1994). Also, in a natural stream with these predators, Miyasaka & Nakano (1999) showed an increase in the nocturnal drift rate in some mayfly species including *Baetis*.

The study led us to conclude that the cues used by *Baetis* for predator-avoidance varied with the predatory fishes, primarily because of differences in the availability of such cues. In natural streams, which are often inhabited by several predatory fish species employing various foraging modes, prey invertebrates may be able to precisely assess and effectively to reduce predation risk by using unique cue to each predator type.

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