Oecologia (1999) 118:99–106

Hitoshi Miyasaka · Shigeru Nakano

Effects of drift- and benthic-foraging fish on the drift dispersal of three species of mayfly nymphs in a Japanese stream

Received: 27 April 1998 / Accepted: 5 October 1998

Abstract Differences in the effects of two common predatory fishes, rainbow trout (*Oncorhynchus mykiss*) and freshwater sculpin (*Cottus nozawae*), on drift dispersal of the nymphs of three mayfly species, *Baetis thermicus*, *Cinygmula* sp., and *Paraleptophlebia chocorata*, were examined by manipulative field experiments using stream enclosures in a northern Japanese stream. The diel periodicity of prey consumption rate differed considerably between the two fishes; the prey consumption of the drift-foraging trout was greater at both dawn and dusk, whereas the benthic-foraging sculpin showed a higher consumption rate at night. The drift propensity at night was much greater than during the day for all the mayfly species in each of the trout, sculpin and fishless treatments, as well as under natural conditions with both fishes present. The nighttime drift propensities of the epibenthic grazers, *B. thermicus* and *Cinygmula* sp., were greater in the sculpin treatment than in trout and fishless treatments, and they did not differ between the trout and fishless treatments. By contrast, the nighttime drift propensity of *P. chocorata*, an infaunal collector-gatherer, did not differ among the treatments. The daytime drift propensity did not differ among the treatments for any of the mayfly species. Thus differences in drift response to the predatory fishes could be related to the characteristic microhabitats of the mayfly species. Moreover, the experiments demonstrated that benthic-foraging sculpin had greater overall effects on prey drift than drift-foraging trout.

H. Miyasaka (✉)[1] · S. Nakano
Tomakomai Research Station, Hokkaido University Forests,
Takaoka, Tomakomai, Hokkaido 053-0035, Japan,
e-mail: jin@orange.lowtem.hokudai.ac.jp,
Fax: +81-144-332173

Present address:
[1] Biodiversity Group, Institute of Low-Temperature Science,
Hokkaido University, Sapporo, Hokkaido 060-0019, Japan

Key words Predator-prey interactions · Sublethal effects · Fish foraging modes · Manipulative field experiments · Stream enclosures

Introduction

Predation has generally been thought of as an important factor affecting the abundance and size structure of prey populations (Murdoch and Oaten 1975; Spiller and Schoener 1990) and the species composition of the prey assemblage (Paine 1980; Kerfoot and Sih 1987), with most studies emphasizing the role of lethal effects, i.e., direct predation. Predators, however, also have potentially important sublethal effects on prey, by modifying their morphology (Harvel 1990) and life history traits (Crowl and Covich 1990). Moreover, predators have a strong impact on much prey behavior because prey can reduce predation pressure either by avoiding encounters with predators or by escaping after such an encounter (Sih 1987; Lima and Dill 1990). In recent years, much of the focus on predator effects has shifted from the direct influence on prey abundance to the sublethal effects on prey behavior (Kerfoot and Sih 1987; Flecker 1992). Several studies have pointed out that behavioral effects may often be more costly to prey populations than direct predation, which generally affects only small proportions of the population (Huang and Sih 1990; Werner and Anholt 1996).

In lotic systems, various predators have a variety of sublethal effects on prey behavior (see reviews by Kerfoot and Sih 1987; Wooster and Sih 1995). Thus, despite the fact that predatory fish often consume large numbers of stream insects (Flecker 1984), their principal influences may occur through sublethal effects (Cooper et al. 1990). To lower the risk of fish predation, stream insects may occupy different habitats (Kohler and McPeek 1989; McIntosh and Townsend 1996), change their activity levels (Kohler and McPeek 1989; Forrester 1994a, b) or alter their foraging behavior (Sih 1980). In particular, the influence of predatory fish on the downstream dispersal "drift" of some insect species has received considerable attention from stream ecologists (see Allan 1995). Many manipulative field experiments have demonstrated that predatory fish can alter prey insect densities by inducing changes in dispersal behavior as well as by direct removal by predation (e.g., Gilliam et al. 1989; Dudgeon 1991; Power 1992; Forrester 1994a, b). Moreover, recent theoretical studies have indicated that frequent dispersal of prey insects into and out of a local area can swamp the local effects of predation (swamping hypothesis), with the extent of prey dispersal providing an explanation for variations in the apparent effects of predators on local prey density (Cooper et al. 1990; Lancaster et al. 1991). To date, however, the majority of such experiments, except that by Forrester (1994a, b), have been carried out using cages covering small patches of the streambed. Small-scale experiments may strongly bias the evaluation of the magnitude of dispersal in mobile prey such as stream insects (Englund and Olsson 1996). To improve understanding of the sublethal effects of predators on the drift dispersal of stream insects, it is crucial that experimental manipulations are undertaken on a suitable scale.

Although drift dispersal of insects is influenced by various abiotic and biotic factors, including the presence of predators, in most streams, far greater numbers of insect species undergo drift at night than during the day (see Allan 1995). Such nocturnal drift has been interpreted as a response for avoiding predation by fish that feed in the water column during the day (e.g., Douglas et al. 1994; Rader 1997). However, most natural streams are inhabited not only by diurnal drift foragers, but also by benthic foragers with various diel periodicities in activity. Therefore, prey insects usually face a number of potential predators that may use a variety of search and capture strategies. Thus, drift dispersal is possibly situation dependent and might change in response to the presence of different types of predatory fish (McIntosh and Townsend 1994). Nevertheless, only a few studies have attempted to compare such effects among multiple predatory fishes occurring in sympatric conditions (see review by Dahl and Greenberg 1996).

In the present study, using stream enclosures, we examined differences in the sublethal effects on the nymphs of three mayfly species, *Baetis thermicus*, *Cinygmula* sp., and *Paraleptophlebia chocorata*, induced by two common predatory fishes, namely rainbow trout (*Oncorhynchus mykiss*) and freshwater sculpin (*Cottus nozawae*), which are characterized by different foraging modes. The focus was primarily on the drift response to the different predatory fish.

Methods

Study site

The study was conducted in the Horonai Stream running through the Tomakomai Experimental Forest (TOEF), southwestern Hokkaido, Japan (42°43′N, 141°36′E), during the summers of 1995 and 1996. This small, cold spring-fed stream (14 km long, 2–5 m wide and $<1\%$ gradient), which discharges directly into the Pacific Ocean, is characterized by pyroclastic substrates which have their origin in the past volcanic activities of Mount Tarumae (Sakuma 1987). A 1-km stretch of the stream 1.5–2.5 km downstream from the headwater spring was selected as a study reach for investigating the drift dispersal of the mayfly nymphs. Approximately 94% of the stream width was shaded by riparian forest canopies in the study reach, where daily water temperature was approximately 9°C during summer. Mean habitat variables over the study period included 3.6 m stream width, 22 cm water depth, 42 cm/s water current velocity and 0.27 m^3/s stream discharge.

Dominant fish species found in the stream included rainbow trout (the average density in 3425-m reaches was 0.3 m^{-2}) and freshwater sculpin (0.8 m^{-2}; S. Nakano, unpublished data). The former species was accidentally introduced into the stream approximately 30 years ago from a local fish hatchery, while sculpin was native to the stream. The stream was also inhabited by small numbers of introduced white-spotted charr (*Salvelinus leucomaenis*) and Dolly Varden (*S. malma*), and native masu salmon (*O. masou*), three-spine stickleback (*Gasterosteus aculetus*) and loach (*Noemachelius balbatulustoni*).

Insect sampling under natural conditions

Drifting insects were collected on 25 July and 10 August 1995, using 185-μm-mesh drift-nets (25 × 25 cm mouth opening, 1 m net length) at two sites 50 m apart, which were near the center of the study reach. At each sampling site, four drift-nets were placed across the stream for 20 min every 4 h (2000, 2400, 0400, 0800, 1200, and 1600 hours) over a 24-h period, with care being taken to sample the entire water column from the streambed to the water surface. Current velocities at the net openings were measured using a portable current meter (Tanida et al. 1985). In addition, 12 benthos samples were collected on the same days as the drift samples, using a 225-μm-mesh Surber net sampler (25 × 25 cm quadrat, 1 m net length) in 5- to 25-m upstream reaches of each drift sampling site. Both the drift and benthos samples were immediately preserved in 5% buffered formalin solution.

Fish sampling and estimation of prey consumption rate under natural conditions

To analyze diel periodicity of fish foraging, rainbow trout and freshwater sculpin were collected with electrofishing (Model 12, Smith-Root, Vancouver, Canada) every 4 h (2000, 2400, 0400, 0800, 1200 and 1600 hours) over a 24-h period just downstream from the drift sampling sites on the same days. Electrofishing proceeded upstream until six or more specimens of each fish species had been captured, within a period of less than 1 h. Captured fishes were anesthetized with 2-phenoxyethanol, fork lengths (FLs) of trout and total lengths (TLs) of sculpin were measured to the nearest 0.1 cm, and the fishes were weighed to the nearest 0.1 g wet mass. The stomach contents were collected by stomach pumping with a 2-cm^3 pipette to flush prey items from the entire stomach region (Giles 1980). Stomach content samples were preserved in 5% buffered formalin solution until analysis. The biomass of each sample was measured as dry mass to the nearest 0.01 mg after drying at 60°C for 24 h.

To show the diel periodicity of prey consumption rate, we estimated the dry mass of prey consumed by each trout and sculpin during each 6-h sampling period over a 24-h period, following Elliott and Persson (1978):

$$C_t = (S_t - S_0 e^{-Rt}) R_t \,/\, (1 - e^{-Rt})$$

where C is the dry mass (mg) of prey consumed per 100 mg dry mass of fish in a sampling interval of t h, S_0 and S_t are the mean dry mass of prey in the stomach of 100 mg dry mass of fish at the beginning and end of the interval, respectively, and R is the rate of gastric evacuation. The dry mass of captured fish was estimated from the wet mass measured according to simple linear regressions (H. Miyasaka and S. Nakano, unpublished data). Gastric evacuation rates were estimated as 0.042 in rainbow trout and 0.086 in freshwater sculpin at 9°C following Elliott's (1972) equation (H. Miyasaka and S. Nakano, unpublished data). Since water temperature was stable throughout the experimental period, we assumed the gastric evacuation rates to be constant over the 24-h period. Finally, the daily prey consumption rate of total and benthic invertebrates was calculated for each species.

Field experiments

Field experiments to test the effects of different predatory fishes on the drift dispersal of three mayfly nymphs were conducted over two consecutive summers, 18–31 August 1995 and 17–30 June 1996, using six 25-m-long enclosures constructed along the study reach. Each enclosure was separated from adjacent enclosures by over 50 m unmanipulated reach. Both ends of each enclosure were blocked by 10-mm polypropylene mesh, which prevented fishes from entering or leaving the enclosures. Most stream insects, however, were unlikely to have had their movements impeded. Fishes were removed from all enclosures by nine electrofishings. Two enclosures were subsequently randomly selected for stocking with trout (hereafter termed trout treatment), two with sculpin (sculpin treatment) and the remaining two left fishless as a control (fishless treatment).

We released either 39–43 trout or 75–132 sculpins in each enclosure (Table 1). Under natural conditions, the daily prey consumption rate of rainbow trout (8.00–9.07 mg dry mass/100 mg dry mass of fish, $n = 2$) was approximately twice that of sculpin (3.61–4.20 mg dry mass/100 mg dry mass of fish, $n = 2$). However, the daily prey consumption rate of aquatic invertebrates was nearly identical between rainbow trout (2.71–3.69 mg, $n = 2$) and sculpin (see above), since terrestrial invertebrates contributed to 62.5% of the trout diet but were absent in the sculpin diet. In addition, the average standing crop of freshwater sculpin and rainbow trout was almost the same in the Horonai Stream (approximately 11 g wet mass/m^2; H. Miyasaka and S. Nakano, unpublished data). Therefore, the number of fish in each enclosure was adjusted to keep fish standing crop at approximately the same level (15 g wet mass/m^2). This was done to equalize the direct predation effect on stream invertebrates between the two fish treatments. Abiotic characteristics of the stream enclosures were similar to those of natural reaches and did not vary much among the treatments (Table 1). Both drift and benthos sampling were undertaken twice, on the 2nd and 14th days of the experiments in both 1995 and 1996, using the same sampling protocols as those used under natural conditions. The drift samples were collected at the downstream end of each enclosure.

Analyses of drift and benthos samples

Both stream drift and benthos samples were sieved once with 225-µm mesh to equalize the minimum size of insects, and examined under a binocular microscope. Benthic density was expressed as the number of insects per unit area of the streambed (m^2). Three dominat mayfly nymphs in the samples collected under natural conditions ($n = 48$) were *B. thermicus* (mean benthic density ± 1 SE = 738 ± 67/m^2), *Cinygmula* sp. (2554 ± 332/m^2) and *P. chocorata* (1569 ± 238/m^2). These species accounted for approximately 37% of the total number of benthic invertebrates. In the present study, only drift dispersal of these three species of mayflies was examined. Drift density was expressed as number of insects drifting per 100 m^3 water, following Smock (1996). We subsequently estimated the drift propensity of each mayfly species, dividing the mean drift density by mean benthic density, following Forrester (1994b).

Statistical analysis

In both the natural and experimental studies, we obtained mean drift and benthic density for each study site (or enclosure) on each sampling day with the four drift-nets and 12 benthos samples (subsamples) being pooled. We then calculated drift propensity. For the unmanipulated field study, mean values of the drift propensity on the two sampling dates were compared among the mayfly species and between daytime (0800, 1200 and 1600 hours) and nighttime (2000, 2400 and 0400 hours) with a repeated-measures two-way ANOVA with the two sampling sites as replicates. To examine the diel periodicity of foraging success in each fish species, prey consumption rates were compared between daytime and nighttime using a one-way ANOVA. Contrasts (means comparisons test) were carried out to assess differences among the mayfly species when significant main effects were encountered.

A repeated-measures three-way ANOVA was used to test for the effects of fish treatment (sculpin vs trout vs fishless), time period (daytime vs nighttime) and block (year; 1995 vs 1996) on the drift propensity of the three mayfly species recorded on day 2 and 14 of the experiments. The two experimental reaches were considered replicates for this test. When all within-subject effects were not significant for each of the above ANOVAs, differences among treatments were assessed by constrasts. Analyses were conducted using the statistical package Super ANOVA version 1.11 (Abacus Concepts).

All statistical tests were two-tailed. $\mathrm{Log}_{10}(x + 1)$ transformations for exact values were made in order to standardize variances and improve normality if necessary, to satisfy the assumptions of the ANOVA model. For all tests, the α-value of 0.05 was used for statistical significance.

Table 1 Habitat characteristics of stream reaches with different experimental treatments (n = sample size)

Variables	Treatment					
	Trout		Sculpin		Fishless	
	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n
Fish standing crop (g/m^2)	14.21 ± 0.08	4	14.28 ± 0.09	4	–	–
Fish density (number/m^2)	0.41 ± 0.03	4	1.13 ± 0.13	4	–	–
Fish body length (mm)	141 ± 2	154	102 ± 1	386	–	–
Fish body weight (g)	35.3 ± 1.4	154	14.3 ± 0.4	386	–	–
Canopy shade (%)	93.8 ± 1.5	20	90.6 ± 1.4	20	88.1 ± 1.6	20
Area (m^2)	94.0 ± 6.6	4	100.5 ± 5.7	4	90.0 ± 5.9	4
Width (m)	3.5 ± 0.1	20	3.8 ± 0.1	20	3.5 ± 0.1	20
Depth (cm)	21.6 ± 1	20	20.6 ± 1	20	22.0 ± 1	20
Current velocity (cm/s)	46 ± 1	20	40 ± 1	20	42 ± 1	20
Discharge (m^3/s)	0.27 ± 0.01	4	0.26 ± 0.02	4	0.27 ± 0.01	4
Water temperature (°C)	8.7 ± 0.4	24	8.6 ± 0.5	24	8.7 ± 0.6	24

Results

Drift dispersal of mayflies under natural conditions

Under natural conditions, the three species of mayfly nymphs showed clear nocturnal habits in drift propensity, although the propensity differed among the species (Fig. 1). The repeated-measures two-way ANOVA revealed that species, time, and species × time interaction were all significant, whereas no within-subject effects were significant (Table 2). The significant interaction effect revealed that the magnitude of nocturnal drift propensity differed among the species. The drift propensities of *B. thermicus* and *P. chocorata* were both significantly higher than that of *Cinygmula* sp., and the first-mentioned species also showed a significantly higher propensity than *P. chocorata* (contrasts, $P < 0.001$ for all the combinations; Fig. 1). In each of the mayfly species, the drift propensity increased dramatically between 1600 hours and 2000 hours (just after sunset), remaining relatively high until 2400 hours, and decreased drastically after 0400 hours (just before sunrise; Fig. 1).

Foraging activities of fishes under natural conditions

The diel periodicity of foraging activities clearly differed between trout and freshwater sculpin (Fig. 2). The nighttime prey consumption rate of sculpin was significantly greater than during the day (one-way ANOVA, $F_{1,10} = 26.413$, $P < 0.001$). In contrast, the prey consumption rate of trout did not differ significantly between day and night ($F_{1,10} = 0.543$, $P = 0.478$). Despite the lack of statistically significant diel changes, the lack of prey consumption by trout between both 2000 and 2400 hours, and 0800 and 1200 hours indicated bimodal foraging activity with more prey consumed just around dawn and dusk than at other times.

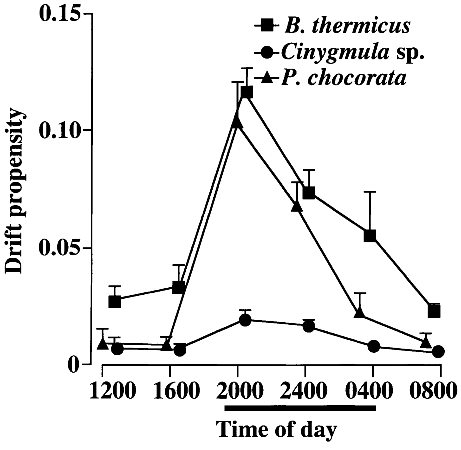

Fig. 1 Diel changes in the drift propensity (drift density divided by benthic density) of three species of mayfly nymphs sampled over a 24-h period under natural conditions in the Horonai Stream. *Thick horitontal bar* under *x*-axis indicates nighttime. Data given as means ± 1 SE

Table 2 Repeated-measures ANOVA for the drift propensity (drift density divided by benthic density) of three mayfly species under natural conditions

Source	*df*	Mean square	*F*	*P*
Between subjects				
Species	2	0.006	436.998	< 0.001
Time	1	0.012	956.121	< 0.001
Species × time	2	0.002	159.554	< 0.001
Error	6	0.00001		
Within subjects				
Date	1	0.00003	0.459	0.523
Date × species	2	0.000008	0.111	0.897
Date × time	1	0.0003	5.355	0.060
Date × species × time	2	0.00018	2.471	0.165
Error	6	0.00007		

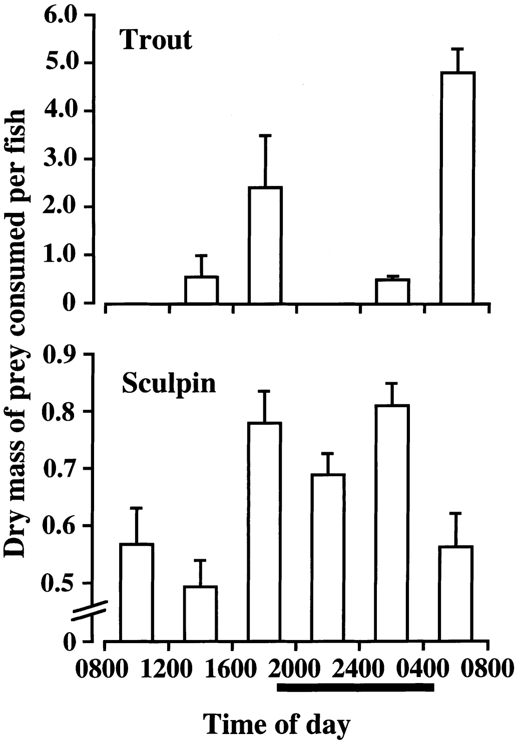

Fig. 2 Diel changes in the prey consumption rate (mg dry mass/100 mg dry mass of fish) of rainbow trout (**a**) and freshwater sculpin (**b**) under natural condistions in the Horonai Stream. *Horizontal bar* under *x*-axis indicates nighttime. Data given as means ± 1 SE

Drift dispersal of mayflies under experimental conditions

In the drift propensities of three mayflies, a clear nocturnal habit was observed under experimental conditions (Fig. 3). The diel periodicities were similar among the fish treatments, being consistently low during the day

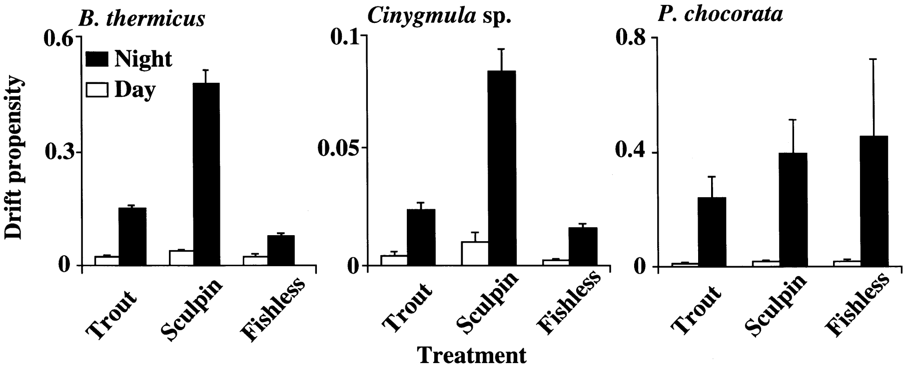

Fig. 3a–c Effects of experimental treatments on the drift propensity (drift density divided by benthic density) of three species of mayfly nymphs. Data given as means ± 1 SE

Table 3 Repeated-measures ANOVA for the drift propensity (drift density divided by benthic density) of three mayfly species under experimental conditions

Source	*df*	*B. thermicus*			*Cinygmula* sp.			*P. chocorata*		
		Mean square	*F*	*P*	Mean square	*F*	*P*	Mean square	*F*	*P*
Between subjects										
Fish	2	0.022	15.981	< 0.001	0.001	4.440	0.028	0.003	0.251	0.781
Time	1	0.054	39.687	< 0.001	0.003	10.242	0.005	0.146	13.928	0.002
Year	1	0.004	2.785	0.113	0.001	4.990	0.039	0.063	6.013	0.025
Fish × time	2	0.012	8.495	0.003	0.001	2.677	0.098	0.002	0.195	0.825
Error	17	0.001			0.002			0.010		
Within subjects										
Date	1	0.0003	0.479	0.494	0.00009	2.101	0.165	0.004	1.446	0.246
Date × fish	2	0.002	3.324	0.057	0.000007	0.169	0.846	0.0003	0.144	0.867
Date × time	1	0.0000005	0.001	0.977	0.00004	0.962	0.341	0.004	1.709	0.209
Date × year	1	0.0004	0.678	0.422	0.00009	2.100	0.166	0.016	6.154	0.024
Date × fish × time	2	0.00002	0.046	0.955	0.000006	0.144	0.867	0.0003	0.134	0.876
Error	17	0.001			0.000004			0.003		

but high at night, as indicated by a significant time effect (Table 3). There was a significant year effect in both *Cinygmula* sp. and *P. chocorata*, but not in *B. thermicus* (Table 3). This was probably due to the 1996 experiment being conducted 2 months earlier in the year than the 1995 experiment. No significant within-subject effects were evident for the drift propensities of either *B. thermicus* or *Cinygmula* sp. (Table 3). The only significant date by year interaction effect was for *P. chocorata.*

The drift propensities of *B. thermicus* and *Cinygmula* sp. were significantly affected by the fish treatments, but no treatment effect was observed for *P. chocorata* (Table 3). Nighttime drift propensity of *B. thermicus* in the sculpin treatment was significantly higher than that in the trout ($P < 0.001$) and fishless treatments ($P < 0.001$), although no significant difference was found between the trout and fishless treatments ($P = 0.134$; Fig. 3). The daytime drift propensity of this mayfly, however, was not significantly different among the fish treatments ($P > 0.325$ for all the combinations). A significant fish × time interaction effect indicated that the effect of sculpin depends on the time of day (Table 3). Similarly, the nighttime drift propensity of *Cinygmula* sp. in the sculpin treatment was significantly higher than that in the trout ($P = 0.008$) and fishless ($P = 0.003$) treatments with non-significant differences being found between the trout and fishless treatment ($P = 0.660$). The daytime drift propensity of *Cinygmula* sp. did not differ significantly among the fish treatments ($P > 0.659$ for all the combinations). There was no significant effect of fish × time interaction (Table 3). Thus, in both *B. thermicus* and *Cinygmula* sp., greater nocturnal drift than in the fishless treatment occurred only in the sculpin treatment. In contrast, no such trend was observed in *P. chocorata*, where the drift propensity did not differ among the fish treatments (Table 3, Fig. 3). No significant fish × time interaction effect was detected for the drift propensity of *P. chocorata.*

Discussion

In the present study, all three species of mayfly nymphs, *B. thermicus*, *Cinygmula* sp. and *P. chocorata*, showed a pronounced nocturnal drift in both the manipulated treatments and under natural conditions in which both species of predatory fish were present. Nocturnal drift peaks in stream insects have often been interpreted as an evolutionary response to minimize predation risk from visually hunting, drift-foraging fishes during the day (see review by Allan 1995). In the Horonai Stream, the prey consumption rates of rainbow trout were high at dawn and dusk, decreasing around noon and midnight. Most stream salmonids are visual foragers, preying primarily upon drifting invertebrates while maintaining focal points in the water column (Angradi and Griffith 1990; see Kitano et al. 1993 for rainbow trout in the Horonai Stream). In such drift foragers, the foraging efficiency generally decreases with lower light intensity (Robinson and Tash 1979). Thus, the above "risk-of-predation hypothesis" can at least partly explain the nocturnal periodicity of mayfly drift in the Horonai Stream.

Although rainbow trout is an exotic species in the Honorai Stream, masu salmon, which is native to the stream, is also a typical drift-foraging salmonid (Nakano 1995), and it may have similar effects on the drift behavior of mayflies. Flecker (1992) examined drift behavior in a series of Andean streams where non-native trout had established resident populations of varying abundance and showed that predation by the trout governed the nocturnal drift of mayflies. In addition, Malmqvist (1988) demonstrated that adaptive response in drift behavior, i.e., nocturnal drift, had evolved in mayfly nymphs within 25 years after successful introduction of non-native trout. These findings suggest a rapid evolutionary response of stream insects to novel predation risks.

In contrast to rainbow trout, sculpin consumed prey at night as well as during the day, their prey consumption rate at night being greater than during the day. The foraging mode adopted by sculpin is known to be quite different from salmonids, the former foraging on benthic prey directly on the streambed (Greenberg 1991). Such benthic-foraging fishes have been generally found to be able to visually search the benthos under relatively low light intensity (see Broadway and Moyle 1978), although Kohler and McPeek (1989) suggested greater prey consumption during the day in a different sculpin species. In addition, a sculpin has been shown to feed well in total darkness by means of a well-developed lateral line system (Hoekstra and Janssen 1986). Thus, the diel change in prey consumption rate of sculpin resulted from greater prey hunting at night in the present study. The high nighttime foraging of sculpin on the substrate may be linked to the greater likelihood of mayflies entering stream drift at night when most mayflies become exposed on the surface of the substrate (Kohler 1985; Kohler and McPeek 1989). Since mayfly nymphs try to escape the benthic-foraging sculpins, these fish may increase the nocturnal drift of mayfly nymphs.

The present field experiments revealed differences in the relative contributions of the predatory fishes to the mayfly drift. The nighttime drift propensities of *B. thermicus* and *Cinygmula* sp. increased in the presence of freshwater sculpin, although their daytime propensities were not influenced by the sculpins. Plastic behavioral responses (i.e., increased nocturnal drift) in stream insects have previously been shown to be induced by the nighttime foraging activities of either fish (Culp et al. 1991; McIntosh and Townsend 1994) or invertebrate predators (Peckarsky and Cowan 1995; Peckarsky 1996). We argue that the presence of sculpin, which actively search for prey on the streambed, often disturbs mayflies at night, causing the nocturnal drift of the mayflies to increase because of an increasing frequency of encounters. Additionally, various studies have shown that the general activity levels of stream insects decrease and refuge use increases in response to the presence of predators at night (Andersson et al. 1986; McIntosh and Townsend 1996). McIntosh and Townsend (1996), for instance, found both increased refuge use and increased drift in a mayfly species in response to greater frequency of attack by a benthic-foraging galaxid at night. Previous experiments in laboratory channels showed similar sublethal effects of sculpin on nymphs of the two mayflies, *B. thermicus* and *Epeorus uenoi* (H. Miyasaka and S. Nakano, unpublished data). Further, laboratory experiments by Culp et al. (1991) showed that most nocturnal drift entries of mayfly nymphs occurred either from direct attacks or from non-contact approaches by nocturnal benthic-foraging cyprinids.

In contrast, the presence of trout in the present study did not influence drift propensity either at night or during the day. This stands in contrast to Forrester's (1994a,b) studies which found that the nighttime drift propensity of two mayflies increased in experimental reaches containing high densities of trout. The different results in our study may be attributed partly to the relatively low density of the trout ($0.41/m^2$) compared to Forrester's (1994a,b) experiments ($0.88–1.56/m^2$). Laboratory studies which completely controlled the predator cue have clearly demonstrated that the nocturnal drift of stream insects increased in response to the presence of trout (Culp and Scrimgeour 1993; Cowan and Peckarsky 1994; McIntosh and Peckarsky 1996; but see Peckarsky and McIntosh 1998). Rainbow trout mainly utilize the water column while foraging, with only occasional attacks on the substrate during the day, when stream insects are less active (see Kohler 1985). Such feeding behavior in trout may not induce avoidance behavior by benthic prey. We may conclude that the difference in drift propensity in the presence of freshwater sculpin and rainbow trout may partly reflect variations in predator feeding behavior. The higher density of sculpin than trout in the enclosures, however, could also influence the results. If drift behavior of mayfly species is promoted by increased frequency of encounters with predators as found in a study on invertebrate predators (Peckarsky and Cowan 1995), then drift propensity in the sculpin treatment may be greater than that in the trout treatment simply due to the higher density of sculpins.

In the present field experiments, the presence of sculpins influenced the drift propensities of *B. thermicus* and *Cinygmula* sp., whereas that of *P. chocorata* did not differ among the treatments. This result suggests that the difference in drift response to the predatory fishes could be related to the microhabitats characteristic of each mayfly spcies. *B. thermicus* and *Cinygmula* sp. are categorized as epibenthic grazers-scrapers, which generally forage on preiphyton on the substrate surface, whereas *P. chocorata* is an infaunal collector-gatherer which forages primarily upon detritus-filled interstitial spaces in the substratum (Merritt and Cummins 1984).

Frequent drift dispersal of potential prey insects into and out of a local area of streambed has been suggested as swamping the direct effects of predation (Cooper et al. 1990; Lancaster et al. 1991). Moreover, to date it has been emphasized that drift-foraging fish strongly affect the magnitude of drift by stream insects (e.g., Allan 1978; Douglas et al. 1994; Forrester 1994a), while less attention has been paid to the role of benthic-foraging fish. The direct predation effects on stream invertebrates were likely similar between sculpin and trout during summer in the Horonai Stream, where both the standing crop and prey consumption rate were nearly equal between the two fish species. Nevertheless, the present experiments suggest that, through their greater sublethal effects, sculpins had a greater influence than trout on the magnitude of drift dispersal of mayflies. Dahl and Greenberg (1996) pointed out that benthic foragers have greater effects on benthic prey density than drift-foraging predators because of the greater predation pressure upon benthic prey by the former. This study predicts that variations in the impact of the two types of predatory fish on mayfly populations primarily result from differences in sublethal effects on the nymphs.

Acknowledgements We are sincerely grateful to A.P. Covich, Y. Taniguchi, U.G. Rainhardt, N. Kuhara and Y. Miyake for critical comments on an early draft of the manuscript. We also express our sincere thanks to members of the TOEF Stream Ecology Group for invaluable advice during the field studies. We are also grateful to K. Ishigaki, T. Aoi and other staff of the Tomakomai Research Station, Hokkaido University Forests, for their logistical support. This research was funded by the Japan Ministry of Education, Science, Sport and Culture (grant nos. 08454246, 08406011 and 09NP1501 to S. Nakano) and Ministry of Agriculture, Forestry and Fisheries of Japan.

References

Allan JD (1978) Trout predation and the size composition of stream drift. Limnol Oceanogr 23:1231–1237

Allan JD (1995) Stream ecology. Chapman & Hall, London

Andersson KG, Brönnark C, Herrmann J, Malmqvist B, Otto C, Sjörstrom P (1986) Presence of sculpin (*Cottus gobio*) reduces drift and activity of *Gammarus pulex* (Amphipoda). Hydrobiologia 133:209–215

Angradi TR, Griffith JS (1990) Diel feeding chronology and diet selection of rainbow trout (*O. mykiss*) in the Henrys Fork of the Snake River, Idaho. Can J Fish Aquat Sci 47:199–209

Broadway JE, Moyle PB (1978) Aspects of the ecology of the prickly sculpin, *Cottus asper* Richardson, a persistent native species in Clear Lake, California. Environ Biol Fish 3:337–343

Cooper SD, Walde SJ, Peckarsky BL (1990) Prey exchange rates and the impact of predators on prey populations in streams. Ecology 71:1503–1514

Cowan CA, Peckarsky BL (1994) Diel feeding and positioning periodicity of a grazing mayfly in a trout stream and a fishless stream. Can J Fish Aquat Sci 51:450–459

Crowl TA, Covich AP (1990) Predator-induced life-history shifts in a freshwater snail. Science 247:949–951

Culp JM, Scrimgeour GJ (1993) Size-dependent diel foraging periodicity of a mayfly grazer in streams with and without fish. Oikos 68:242–250

Culp JM, Glozier NE, Scrimgeour GJ (1991) Reduction of predation risk under the cover of darkness: avoidance responses of mayfly larvae to a benthic fish. Oecologia 86:163–169

Dahl J, Greenberg L (1996) Impact on stream benthic prey by benthic vs drift feeding predators: a meta-analysis. Oikos 77:177–181

Douglas PL, Forrester GE, Cooper SE (1994) Effect of trout on the diel periodicity of drifting in baetid mayflies. Oecologia 98:48–56

Dudgeon D (1991) An experimental study of the effects of predatory fish on macroinvertebrates in a Hong Kong stream. Freshwater Biol 25:321–330

Elliott JM (1972) Rates of gastric evacuation in brown trout, *Salmo trutta* L. Freshwater Biol 2:1–18

Elliott JM, Persson L (1978) The estimation of daily rates of food consumption for fish. J Anim Ecol 47:977–991

Englund G, Olsson T (1996) Treatments effects in a stream fish enclosure experiment: influence of predation rate and prey movements. Oikos 77:519–528

Flecker AS (1984) The effects of predation and detritus on the structure of a stream insect community: a field test. Oecologia 64:300–305

Flecker AS (1992) Fish predation and the evolution of invertebrate drift periodicity: evidence from neotropical streams. Ecology 73:438–448

Forrester GE (1994a) Influences of predatory fish on the drift dispersal and local density of stream insects. Ecology 75:1208–1218

Forrester GE (1994b) Diel patterns of drift by five species of mayfly at different levels of fish predation. Can J Fish Aquat Sci 51:2549–2557

Giles N (1980) A stomach sampler for use on live fish. J Fish Biol 16:253–261

Gilliam JF, Fraser DF, Sabat AM (1989) Strong effects of foraging minnows on a stream benthic invertebrate community. Ecology 70:445–452

Greenberg LA (1991) Habitat use and feeding behavior of thirteen species of benthic stream fishes. Environ Biol Fish 31:389–401

Harvel CD (1990) The ecology and evolution of inducible defenses. Q Rev Biol 65:323–340

Hoekstra D, Janssen J (1986) Lateral line receptivity in the mottled sculpin (*Cottus bairdi*). Copeia 1986:91–96

Huang C, Sih A (1990) Experimental studies on behaviorally mediated, indirect interactions through a shared predator. Ecology 71:1515–1522

Kerfoot WC, Sih A (1987) Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover

Kitano S, Nakano S, Inoue M, Shimoda K, Yamamoto S (1993) Feeding and reproductive ecology of exotic rainbow trout *Oncorhynchus mykiss* in the Horonai Stream in Hokkaido, northern Japan (in Japanese with English summary). Nippon Suisan Gakkaishi 59:1837–1843

Kohler SL (1985) Identification of stream drift mechanisms: an experimental and observational approach. Ecology 66:1749–1761

Kohler SL, McPeek MA (1989) Predation risk and foraging behavior of competing stream insects. Ecology 70:1811–1825

Lancaster J, Hildrew AG, Townsend CR (1991) Invertebrate predation on patchy and mobile prey in streams. J Anim Ecol 60:625–641

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Malmqvist B (1988) Downstream drift in Madeiran Levadas: tests of hypotheses relating to influence of predators on the drift of insects. Aquat Insects 10:141–152

McIntosh AR, Peckarsky BL (1996) Differential behavioural responses of mayflies from streams with and without fish to trout odour. Freshwater Biol 35:141–148

McIntosh AR, Townsend CR (1994) Interpopulation variation in mayfly anti-predator tactics: differential effects of contrasting predatory fish. Ecology 75:2078–2090

McIntosh AR, Townsend CR (1996) Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behavior? Oecologia 108:174–181

Merritt RW, Cummins KW (1984) An introduction to the aquatic insects of North America, 2nd edn. Kendall/Hunt, Iowa

Murdoch WW, Oaten A (1975) Predation and population stability. Adv Ecol Res 9:1–131

Nakano S (1995) Competitive interactions for foraging microhabitats in a size-structured interspecific dominance hierarchy of two sympatric stream salmonids in a natural habitat. Can J Zool 73:1845–1854

Paine RT (1980) Food webs: linkage, interaction strength and community infrastructure. J Anim Ecol 49:667–685

Peckarsky BL (1996) Alternative predator avoidance syndromes of stream-dwelling mayfly larvae. Ecology 77:1888–1905

Peckarsky BL, Cowan CA (1995) Microhabitat and activity periodicity of predatory stoneflies and their mayfly prey in a western Colorado stream. Oikos 74:513–521

Peckarsky BL, McIntosh AR (1998) Fitness and community consequences of avoiding multiple predators. Oecologia 113:565–576

Power ME (1992) Habitat heterogeneity and the functional significance of fish in river food webs. Ecology 73:1675–1688

Rader RB (1997) A functional classification of the drift: traits that influence invertebrate availability to salmonids. Can J Fish Aquat Sci 54:1211–1234

Robinson FW, Tash JC (1979) Feeding by Arizona trout (*Salmo apache*) and brown trout (*Salmo trutta*) at different light intensities. Environ Biol Fish 4:363–368

Sakuma T (1987) Characterization of soil in the Tomakomai Experimental Forest, especially on the characteristics of the organic horizons and their alteration following the partial cutting (in Japanese with English summary). Res Bull Hokkaido Univ For 44:749–760

Sih A (1980) Optimal behavior: can animals balance two conflicting demands? Science 210:1041–1043

Sih A (1987) Predators and prey lifestyles: an evolutionary and ecological overview. In: Kerfoot WC, Sih A (eds) Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, pp 203–204

Smock LA (1996) Macroinvertebrate movements: drift, colonization, and emergence. In: Hauer FR, Lamberti GA (eds) Methods in stream ecology. Academic Press, New York, pp 371–390

Spiller DA, Schoener TW (1990) A terrestrial field experiment showing the impact of eliminating the top predator on foliage damage. Nature 347:469–470

Tanida K, Yamashita K, Rossiter A (1985) A portable current meter for field use. Jpn J Limnol 46:219–221

Werner EE, Anholt BR (1996) Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. Ecology 77:157–169

Wooster D, Sih A (1995) A review of the drift and activity responses of stream prey to predator presence. Oikos 73:3–8