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INTERPOPULATION VARIATION IN MAYFLY ANTIPREDATOR TACTICS: DIFFERENTIAL EFFECTS OF CONTRASTING PREDATORY FISH¹

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Abstract. Introduced brown trout (*Salmo trutta*) have replaced native common river galaxias (*Galaxias vulgaris*) as the principal predators in many streams in the Taieri River system, New Zealand. Brown trout and common river galaxias present prey with contrasting predation risks as galaxias forage mainly at night using mechanical cues and trout present a higher predation risk during the day by foraging using visual cues. To determine if this change has affected the behavior of a siphonurid mayfly, *Nesameletus ornatus*, we compare the behavior of *N. ornatus* nymphs from three neighboring streams that have different fish predation regimes (trout, galaxias, fishless) when confronted with all possible predation regimes in the laboratory (trout, galaxias, no fish). *N. ornatus* from a trout stream were consistently nocturnally active whether trout, galaxias, or no fish were present. In contrast, when mayflies from streams without trout were confronted with trout, no consistent diel periodicities in their behavior were observed. However, when mayflies from streams without trout were tested with and without galaxias they altered their behavior according to the presence/absence of the native predator. The possibility that *N. ornatus* accumulates evolutionary experience of trout through adults flying between streams may be ruled out: mayflies with no possible experience of trout did not respond differently to those from streams without trout but with the possibility of migrating from trout streams close by. The presence of different predatory fish may have resulted in differential trade-offs between foraging and predator avoidance. The probability of mayflies leaving food patches was higher during the day in the presence of trout. In contrast, the probability was higher during the night in the presence of galaxias. Trout and galaxias were also associated with differential reductions in the number of mayflies on the substrate surface and the proportion of mayflies on food patches, with consequent effects on time spent foraging. These responses indicate that both the history of the prey population and the nature of the predation risk have considerable influence on antipredator behavior and indicate a possible important influence on stream communities of predatory fish through sublethal effects on prey behavior.

Key words: diel periodicity; drift; fixed behavior; *Galaxias vulgaris*; *Nesameletus ornatus*; New Zealand; positioning; predator avoidance; sublethal effects; *Salmo trutta*; streams; trade-offs.

INTRODUCTION

Despite the fact that insectivorous fish often consume large numbers of prey in streams (Allen 1951, Hildrew and Townsend 1982, Allan 1983), their principal influences may occur through sublethal effects (sensu Peckarsky et al. 1993) on prey (Dill 1987, Peckarsky et al. 1993). To lower the risk of predation, prey may be forced to occupy different habitats, forage at different times, make changes to their level of activity, or alter their foraging behavior (Charnov et al. 1976, Stein and Magnuson 1976, Stein 1977, Milinski and Heller 1978, Sih 1980, 1982, Cooper 1984, Townsend and Winfield 1985, Gilliam and Fraser 1987, Rahel and Stein 1988, Sih and Moore 1990, Scrimgeour and Culp 1994).

Predatory fish may alter prey behavior in streams by affecting prey movements and/or positioning. Stream

macroinvertebrates, especially mayflies (Ephemeroptera), are typically highly mobile and are often found moving in the water column. Nocturnal peaks in this phenomenon of "drift" (see reviews by Waters 1972, Müller 1974, Brittain and Eikeland 1988) have been interpreted as an evolutionary response to minimize predation by visually hunting fishes during the day (Allan 1978, 1984, Malmqvist 1988, Flecker 1992, Douglas et al. 1994, but see Elliott 1967, Bishop and Hynes 1969, Kovalak 1978 for alternative hypotheses). The hypothesis is supported by observations that the larger, more vulnerable size classes show an increased propensity to drift at night (Allan 1978, 1984) and by a positive correlation between the magnitude of predation risk and the degree of diel periodicity in drift (Flecker 1992). Variation in the propensity to drift may be expected to be linked to changes in positioning or activity of invertebrates on the stream bed, but published results are conflicting. Some studies have reported correlations between drift and diel positioning changes (Allan et al. 1991), but nocturnal drift patterns

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have also been recorded that are negatively associated or unassociated with patterns in positioning or activity (Kohler 1983, Statzner and Mogel 1985, Allan et al. 1986, Casey 1987). If predators affect positioning they may force trade-offs with foraging by restricting access to the more productive upper surfaces of stones. If predators affect drift activity they may restrict movement between patches since drift is a major component of search behavior while foraging (Kohler 1985); this could force prey to trade off staying in a poor patch with the risk of moving to a new one.

In many New Zealand streams introduced trout have replaced native fish as the major predators (Crowl et al. 1992) causing a far-reaching change in the predation regime. In the Taieri River system, brown trout (*Salmo trutta* L.) are found in most suitable habitats, but native common river galaxias (*Galaxias vulgaris* Stokell) are found as isolated populations above waterfalls that trout cannot climb, while in some streams no predatory fish are present (Townsend and Crowl 1991). Brown trout forage from positions in the water column (Fausch and White 1981) predominantly on drifting prey (Elliott 1973, Ringler 1979, McNicol et al. 1985, Glova et al. 1992). They have been observed to feed during both the day and the night (Jenkins 1969, Elliott 1970, Ringler 1979, Glova and Sagar 1991, Glova et al. 1992) but have a higher probability of catching prey during the day (Jenkins 1969; A. R. McIntosh, unpublished data). Thus, like most visually feeding salmonids they present the greatest predation risk during the day (Metz 1974, Allan 1978, Ringler 1979, Allan 1981, Walsh et al. 1988, Angradi and Griffith 1990). In comparison, common river galaxias are benthic fish that have considerably lower feeding rates than brown trout (A. R. McIntosh, unpublished data) and are mostly active at night, taking prey items from both the drift and the benthos (Cadwallader 1975a, b, Glova et al. 1992, McIntosh et al. 1992). We compare the behavior of *Nesameletus ornatus* nymphs from three neighboring streams in the Taieri River (South Island of New Zealand) that have different fish predation regimes (trout, galaxias, fishless) when confronted with all possible predation regimes in the laboratory (trout, galaxias, no fish). *N. ornatus* is a widely distributed (Winterbourn et al. 1981, Winterbourn and Gregson 1989) grazing mayfly (Winterbourn et al. 1984) that is a very capable swimmer. It is found in the diet of both common river galaxias (Cadwallader 1975b, c, Glova and Sagar 1989, Glova et al. 1992; A. R. McIntosh, unpublished data) and brown trout (Burnet 1969, Hopkins 1970, Glova et al. 1992; A. R. McIntosh, unpublished data).

We expected that differences in the antipredator behavior of *N. ornatus* would be related to the history of the prey population and the contrasting predation risks presented by trout and galaxias. Prey that have evolved in isolation from a predator may lack appropriate predator avoidance abilities (Sih 1992), but prey that have some evolutionary experience of a predator may have

an inherited predisposition to respond when a predator is present (Tulley and Huntingford 1987, Magurran 1990). *N. ornatus* may respond to all predators present in the area if its adult stages can accumulate some evolutionary experience by flying between streams. We used the response of *N. ornatus* from a stream on Stewart Island, 35 km south of the South Island of New Zealand, as a control for intercatchment flight. Trout have not been introduced to Stewart Island (Chaderton 1988) and mayflies with poor flying abilities, such as *N. ornatus*, are unlikely to be able to fly from the mainland, so Stewart Island mayflies have no possible experience of trout.

In our experiments we tested the following hypotheses: (1) that *N. ornatus* behaves differently in the presence of predators that hunt using different sensory modes, (2) that predation history affects *N. ornatus* behavior, (3) that *N. ornatus* trades off predator avoidance with acquiring resources.

METHODS

Mayflies and predatory fish were captured using electrofishing techniques (Townsend and Crowl 1991) from three neighboring streams with similar physical characteristics in the Taieri River system, one containing no fish (Burgan Stream, NZMS 260 H43 721114), one containing *G. vulgaris* but not *S. trutta* (Stony Creek, NZMS 260 H43 683089), and one containing *S. trutta* but not *G. vulgaris* (Deep Stream, NZMS 260 H44 752995). Mayflies were also collected from Mill Creek on Stewart Island (NZMS 336-10 14J), a stream containing banded kokopu (*G. fasciatus* Gary) and koaro (*G. brevipinnis* Günther). Banded kokopu and koaro are also native galaxiids that are predominantly nocturnal foragers (Glova and Sagar 1989, McDowall 1990). Predatory fish used in the experiments were adult *G. vulgaris*, 75–85 mm total length, and juvenile *S. trutta*, 90–120 mm total length. It should be noted that the taxonomic status of some populations of *G. vulgaris* is under review (R. M. Allibone et al., unpublished manuscript). The genetic type used in our work is referred to as the lower Taieri type. Mayflies were late-instar *N. ornatus* larvae without black wing pads (i.e., not immediately about to emerge), 10–13 mm in length (identified from reared adults according to Phillips 1930). Mayfly populations were housed in separate aerated aquaria (30 × 30 × 40 cm), galaxias in a recirculating aquarium (100 × 50 × 30 cm), and trout in a large recirculating tank (200 × 200 × 30 cm), all under a 10D:14L light regime. We advanced the laboratory light regime by 1 h (compared to the environmental light regime) for our convenience and all animals were held under this light regime for at least 3 d before being used in the experiments. Mayflies were fed ad libitum on green unicellular algae grown on unglazed tiles and fish were fed ad libitum on a combination of meal worms, mosquito larvae, and *N. ornatus* once a day.

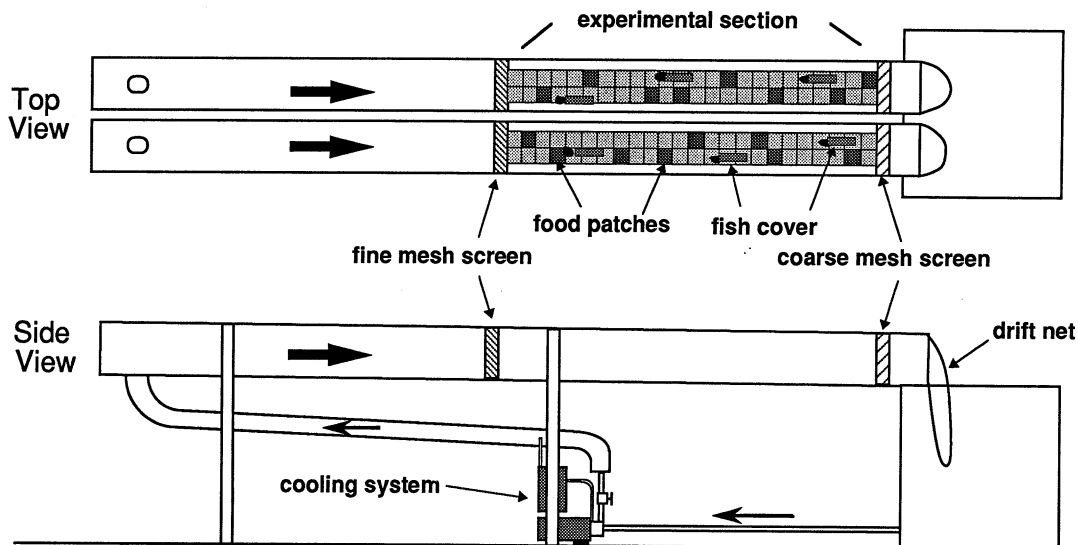


FIG. 1. Diagram of the stream channels used in the experiments (not to scale).

Stream channels

Four 6 m long channels were constructed from sections of PVC (polyvinyl chloride) plastic pipe cut longitudinally in half (diameter 35 cm and depth 17.5 cm) and connected in pairs to two reservoir tanks (Fig. 1). Dechlorinated tapwater was supplied at 14°C, to give a maximum depth of 15 cm and a mean (± 1 SE) current velocity of 18 (± 0.6) cm/s (maximum 20 cm/s, minimum 15 cm/s). A 2.6 m long experimental section in each channel was defined by a fine mesh grill (2.5 mm aperture) that stopped fish and mayflies from swimming upstream and a coarse mesh grill (7 mm aperture) that kept fish in but allowed mayflies to move out to be caught in a net suspended at the downstream end.

In the experimental section of each channel, we placed gravel covered by a layer of 48 unglazed ceramic tiles (10 \times 10 cm). Of nine tiles provisioned with green algae for each trial, eight were distributed in a consistent pattern throughout the channel to act as food patches (Fig. 1) and one was randomly selected for algal quantification to assess food availability between trials. The ash-free dry mass of algae on the tops of tiles was calculated after drying at 60°C for 24 h and ashing at 550°C for 1 h. The bottom of tiles was thoroughly scrubbed to ensure food was not available on these surfaces. Short pieces of PVC pipe, each associated with a small cobble, provided cover for the fish (Fig. 1).

We ran four replicate trials during the day and night of each predator and prey combination; each mayfly or fish was used once only. Trials were run in random order and treatments were rotated among channels. However, the same predator treatment was always run at the same time in both channels of each pair to avoid mixing predator chemicals since channels were connected in pairs to the water tanks. After each trial the

channels were washed, the gravel and tiles were changed, and the water replaced.

Experimental protocol

The experiments took place during January and February 1992 (the austral summer), with "Day" experiments starting at 1000 and "Night" experiments starting at 2030 (1 h after the lights went out). Fish were introduced without food (1 trout/channel \approx 1 trout/m² or 3 galaxiids/channel \approx 3 galaxiids/m²) 24 h before the start of trials to acclimatize. These densities are within the natural range found in the wild (Townsend and Crowl 1991; A. R. McIntosh, *unpublished data*). We started each trial by lowering the current velocity to <5 cm/s and gently pouring 30 mayflies (creating a density commonly found in the wild) into the central region of the experimental section. The velocity was then slowly increased to 18 cm/s over a 5-min period; any mayflies drifting out during the following 10 min were returned to the channel by the above process or replaced if they drifted out more than once. Experiments were ended after 3 h by removing the fish and recovering mayflies from the channels.

Assessing behavior

The behavior of fish and mayflies was recorded on videotape using an infrared light sensitive camera (JVC model TK 5310EG, Victor Company of Japan Limited, Tokyo, Japan) mounted above the experimental section. With the aid of infrared light, which mayflies and fish are unlikely to detect (Lythgoe 1988, Heise 1992), we were able to follow fish and mayfly movements during day and night in the middle portion (110 cm long, covering 42% of the area) of the experimental section of each channel. Behavior was described from the last 2 h of videotape by scoring movements and

TABLE 1. The mean (± 1 SE) consumption of *Nesameletus ornatus* by one trout or three galaxias per trial out of a total of 30 mayflies.

Predator	Prey population	Time			
		Day		Night	
		Mean	SE	Mean	SE
Trout	No fish	4.5	2.53	5.75	2.72
	Galaxias	1.75	1.18	2.5	1.55
	Trout	2.0	1.08	1.75	1.18
	Stewart Island	3.5	1.19	1.75	1.18
Galaxias	No fish	2.0	1.35	1.25	0.75
	Galaxias	1.0	0.40	1.25	0.48
	Trout	2.0	0.91	0.75	0.48
	Stewart Island	1.25	0.95	0.5	0.5

position in relation to the grid formed by the tiles on the bottom of the channel. We measured fish activity in terms of the number of times a fish passed through the field of view and the number of attempted and successful captures of *N. ornatus* in the field of view. The mean number of mayflies visible on the tops of tiles was recorded every 5 min. All interpatch (between tile) mayfly movements were recorded in terms of the starting patch, destination, and any associated intra- or interspecific interactions. At the end of trials we classified mayflies as drifted out, remaining in the channel, or missing. We assumed those missing to have been eaten by fish because no mayflies were unaccounted for in trials without fish. From these data we were able to evaluate mayflies not visible, calculated as the total number of mayflies (30) minus those visible, those drifted out, and those consumed. This can only be regarded as a relative measure because the number visible was a mean from the 2 h of videotape, while the number drifting and the number eaten were totals. The number not visible will also have included individuals on top of the tiles but out of view of the video camera, but since these will have comprised a small and constant proportion over the trials because mayflies were consistently distributed throughout the channel, our figure gives a relative index across treatments of the number under the substrate.

Statistical analysis

In order to fully elucidate the effects due to predation regime and prey history we conducted three sets of analyses on *N. ornatus* behavior. First, we examined the behavior of *N. ornatus* from the trout stream by testing the effect of different predator cues (trout vs. galaxias vs. no fish) and time (day vs. night) in a two-factor ANOVA. Second, we considered the behavior of *N. ornatus* from streams without trout, when confronted with brown trout, in a two-factor ANOVA that tested the effect of predation history (fishless stream vs. galaxias stream vs. Stewart Island stream) and time (day vs. night). Finally, we investigated the behavior of *N. ornatus* from streams without trout, but this time

when confronted with galaxias or no fish, in a three-factor ANOVA that tested the effect of predator cues (galaxias vs. no fish), predation history (fishless stream vs. galaxias stream vs. Stewart Island stream) and time (day vs. night). Data were checked for homogeneity of variance and normality and square root, logarithmic, or angular (in the case of proportions) transformations were used where necessary to satisfy the assumptions of analysis of variance. All factors were treated as fixed effects. The ash-free dry mass of periphyton from food patches (mean ± 1 SE = 1.097 ± 0.08 g/m²) was initially included as a covariate in these analyses to determine if food levels in trials were different between treatments but was later excluded because it was not significant. Minitab (version 8.2, Minitab, State College, Pennsylvania, USA) statistical software was used for all analyses.

RESULTS

Predator behavior

The fish consumed a relatively small and variable proportion of the total *N. ornatus* present (Table 1). Our experiments were not designed as feeding trials, however (their short duration and the disturbance to fish caused when adding prey limited feeding), and no conclusions can be drawn from consumption data about the relative vulnerability of *N. ornatus* to trout and galaxiids. Nevertheless, differences in timing and style of foraging by trout and galaxiids are consistent with our contention that they present quite different predation risks. Both were active during the day and the night but galaxias foraged predominantly at night while trout tended to forage more during the day, as indicated by a significant interaction ($F_{1,60} = 13.60$, $P < 0.001$) in the number of passes fish made through the experimental section (Fig. 2). Distinct differences were also observed in the methods employed by trout and galaxiids to capture prey. Foraging trout maintained position in the middle of the water column and moved around a relatively small area in the channel. They

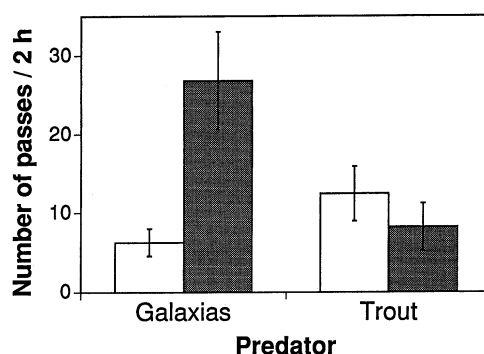


FIG. 2. The activity of one brown trout or three common river galaxias during the day (unshaded bars) and night (shaded bars) as indicated by the mean (± 1 SE) number of passes per trial through the video camera's field of view.

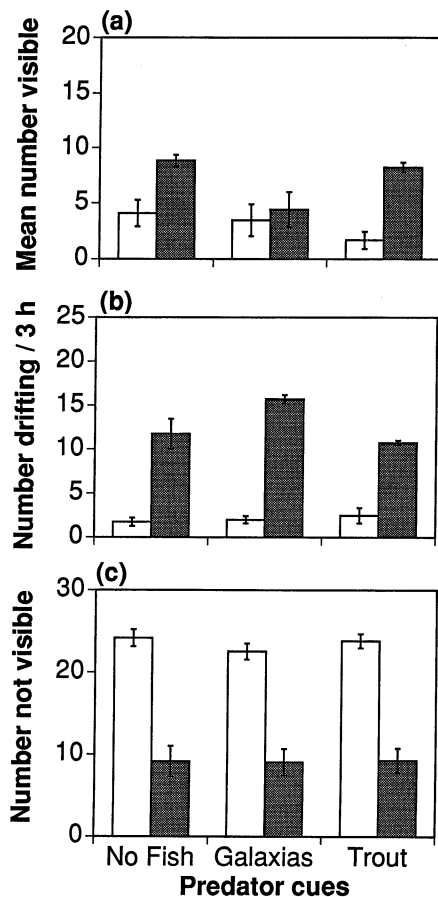


FIG. 3. (a) The mean (± 1 SE) number of mayflies visible; (b) the mean (± 1 SE) number of mayflies drifting out of the channels; and (c) the number of mayflies not visible during a trial for trials with mayflies from the stream with trout during the day (unshaded bars) and night (shaded bars) in different fish predator treatments. Data for the number not visible are means (± 1 SE) calculated from the total number of mayflies (30) minus the number eaten, the number drifting out, and the mean number visible.

preyed upon swimming and stationary *N. ornatus* during the day, but were never observed to attack stationary *N. ornatus* at night. In comparison, foraging galaxiids did not spend long in the water column but made circuits of the channel, moving 30–40 cm, waiting for 4 or 5 s, and then moving again. They regularly encountered *N. ornatus* stationary on the substrate (i.e., swam within 2 cm) but were only observed to attack *N. ornatus* that had moved previously.

Interpopulation variation in prey behavior

The response of *N. ornatus* to our manipulations of the predation regime depended on the predation history of the prey population. *N. ornatus* from the stream with trout displayed a consistent behavioral pattern that did not change despite our alterations of the predation regime (Fig. 3). The majority of mayflies were not visible during the day but moved onto the tops of

tiles during the night (Fig. 3a, c). Grazing trails in the algae on top of the tiles indicated that mayflies were feeding while on the substratum surface. This positioning periodicity was associated with a night drift periodicity (Fig. 3b). It is likely that the disturbance created by nocturnal foraging by galaxias was responsible for mayflies drifting out more quickly, leading to a smaller mean number visible in the galaxias treatment. *N. ornatus* from the trout stream did not change their positioning periodicity even when all predatory fish were absent. For each of the variables measured, analysis of variance indicated that time had a significant effect but there was no effect of predator treatment and no significant interactions (Table 2).

This pattern of behavior is distinct from those of mayfly populations from all streams without trout when confronted with brown trout predators (Fig. 4). Mayflies from the Taieri stream containing galaxias drifted at a higher rate than those from Stewart Island or the Taieri stream containing no fish, but none of these mayflies showed a behavioral response in the form of a positioning periodicity to the presence of trout (indicated by the lack of a significant effect of time in the analysis, Table 3). Furthermore, the behavior of mayflies from Stewart Island was not consistently different from that of mayflies from the streams adjacent to the trout stream in the Taieri River system.

In comparison to the inflexible responses of mayflies from the trout stream, mayflies from streams without trout changed their behavior according to the presence and absence of the native predator (Fig. 5). In the presence of galaxias there was a reduction in the mean number visible compared to the treatment with no fish (Fig. 5a, b), as indicated by a significant predator effect (Table 4). A nocturnal drift periodicity was established in the galaxias treatment (Fig. 5c, d), shown by a significant predator effect, a significant time effect, and a significant interaction between predator and time (Ta-

TABLE 2. Analysis of variance results for the three variables measured in trials with *Nesameletus ornatus* from the stream with trout during the day and the night (time) in the presence of trout, galaxias, or no fish (predator cues).

Source of variation	df	F	Prob.
Mean number visible			
Predator cues	2	2.53	0.108
Time	1	19.38	<0.001
Predator cues \times time	2	3.20	0.065
Number drifting			
Predator cues	2	1.45	0.261
Time	1	131.88	<0.001
Predator cues \times time	2	1.05	0.369
Number not visible			
Predator cues	2	0.10	0.906
Time	1	104.89	<0.001
Predator cues \times time	2	0.08	0.927
Error	18
Total	23

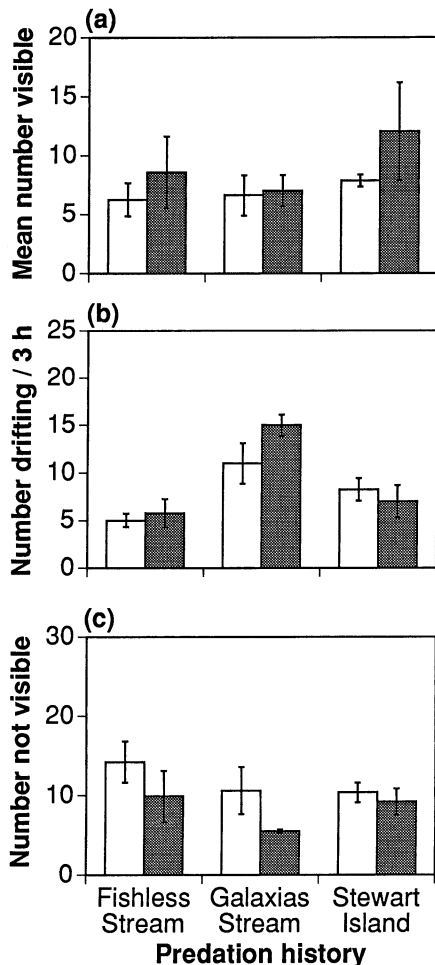


FIG. 4. (a) The mean (± 1 SE) number of mayflies visible; (b) the mean (± 1 SE) number of mayflies drifting out of the channels during a trial; and (c) the number of mayflies not visible for trials with mayflies from streams lacking trout during the day (unshaded bars) and night (shaded bars) when confronted by brown trout. Data for the number not visible are means (± 1 SE) calculated from the total number of mayflies (30) minus the number eaten, the number drifting out, and the mean number visible.

ble 4). A periodicity in the number not visible was also apparent when galaxias were present compared to the treatment without fish (Fig. 5e, f), resulting in a significant interaction between predator and time (Table 4).

The source of the prey population also affected the patterns of prey behavior observed in the presence of galaxias or no fish. Although the number visible decreased in the presence of galaxias, each population maintained its characteristic positioning periodicity (Fig. 5a, b). A significant interaction between prey and time, but not a significant three-way interaction (Table 4), indicates that different prey populations have different positioning periodicities. In the case of the number drifting out of the channels (Fig. 5c, d) the source

of the prey population had a significant effect and there was a significant interaction between prey population and predator (Table 4). Thus, different prey populations had characteristic drift rates and responded to the presence of galaxias differently (Table 4). Finally, there was a significant interaction between prey population and time in determining the number not visible, but not a significant three-way interaction (Fig. 5e, f and Table 4); this indicates that although the presence of galaxias resulted in a night periodicity, different prey populations had distinguishable periodicities in the number not visible.

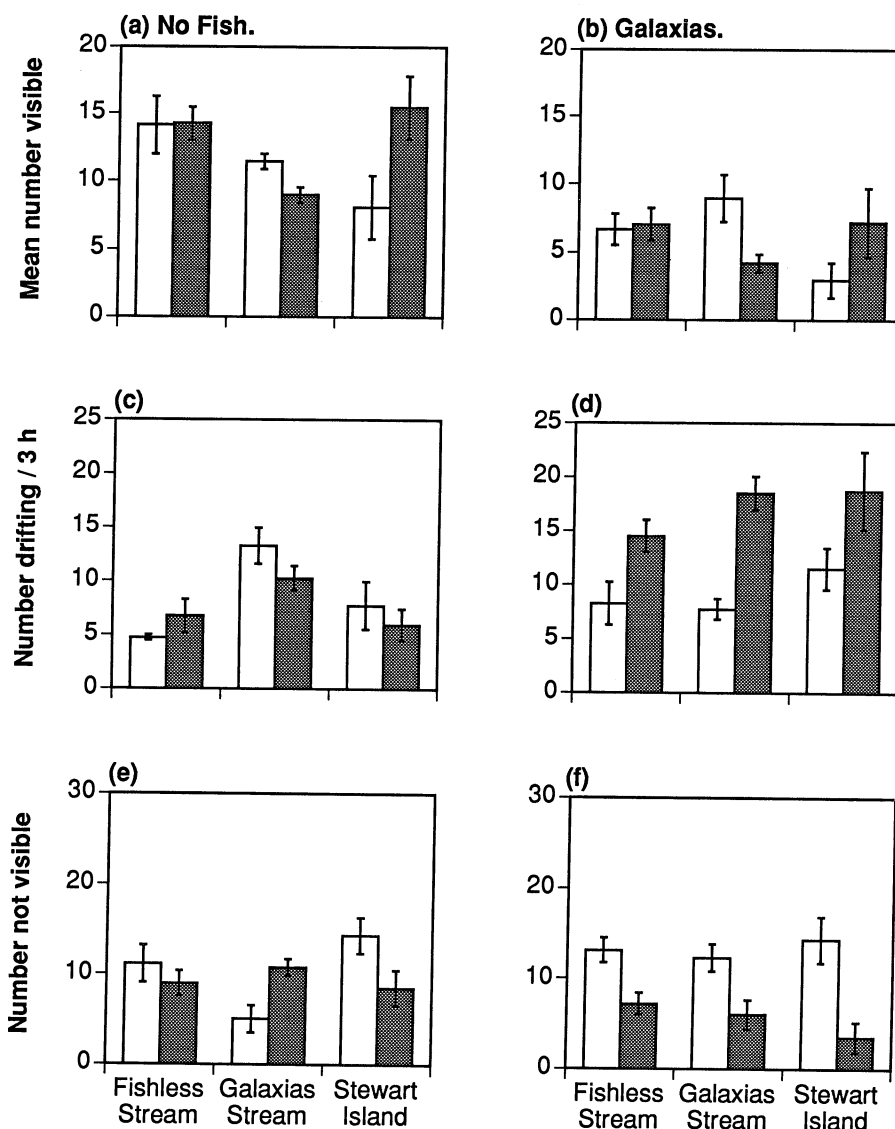
Trade-offs in prey behavior

When the behavior of mayflies from each prey population from the Taieri River system, confronted with their own predation regime, was examined, we found considerable differential influences on prey foraging. We considered the probability of leaving a patch, expressed as the ratio of the total number leaving a patch to the mean number of mayflies present in a patch. These ratios were lower for patches with food (Fig. 6a) than patches without food (Fig. 6b). Predators had a significant effect on the probability of leaving patches with food ($F_{2,18} = 4.58$, $P < 0.05$) and there was a significant interaction between predator treatment and time ($F_{2,18} = 3.87$, $P < 0.05$). However, there was no significant relationship between predator treatment and the probability of a mayfly leaving a patch without food. *N. ornatus* were very unlikely to leave patches with food in the fishless treatment but were considerably more likely to vacate a food patch in the trials with predatory fish, especially when the fish was active, that is, during the day in trout trials and during the night in galaxiid trials (Fig. 6a).

As well as affecting the number of mayflies on the substrate surface, predators also affected their distri-

TABLE 3. Analysis of variance results for the three variables measured in trials with *Nesameletus ornatus* from Stewart Island, the stream with galaxias and the stream with no fish (predation history) during the day and the night (time) in the presence of brown trout.

Source of variation	df	F	Prob.
Mean number visible			
Predation history	2	0.25	0.778
Time	1	0.26	0.614
Predation history \times time	2	0.03	0.974
Number drifting			
Predation history	2	12.96	<0.001
Time	1	0.51	0.484
Predation history \times time	2	1.40	0.271
Number not visible			
Predation history	2	1.44	0.263
Time	1	3.57	0.075
Predation history \times time	2	0.38	0.691
Error	18
Total	23



Predation history

FIG. 5. (a) and (b) The mean (± 1 SE) number of mayflies visible; (c) and (d) the mean (± 1 SE) number of mayflies drifting out of the channels; and (e) and (f) the number of mayflies not visible for trials with mayfly populations from streams without trout in the presence of no fish (a, c, and e) or galaxias (b, d, and f) during the day (unshaded bars) and night (shaded bars). Data for the number not visible are means (± 1 SE) calculated from the total number of mayflies (30) minus the number eaten, the number drifting out, and the mean number visible.

bution among patches. The proportion of mayflies in food patches was significantly affected by predator treatment ($F_{2,18} = 10.22$ $P < 0.001$). This proportion was lower in the galaxiid and trout treatments compared to the treatment with no fish, irrespective of time (Fig. 7).

DISCUSSION

Variations in mayfly behavior

The different responses to our manipulation of predation regime indicate that the variation in predation

risk in streams with introduced brown trout, native common river galaxias, and no fish has resulted in *N. ornatus* from these streams adopting quite different antipredator strategies. *N. ornatus* from the stream where brown trout were present drifted out of the channels more at night. This nocturnal drift periodicity was associated with a strong nocturnal positioning periodicity and, unlike the behavior of prey from other streams, did not alter despite our manipulations of the predation regime. Trout pose the greatest predation threat during the day (Jenkins 1969, Metz 1974, Allan 1978, 1981, Ringler 1979, Walsh et al. 1988, Angradi

TABLE 4. Analysis of variance results for the three variables measured in trials with *Nesameletus ornatus* from Stewart Island, the stream with galaxias and the stream with no fish (predation history) in the presence of galaxias or no fish (predator cues) during the day and the night (time).

Source of variation	df	F	Prob.
Mean number visible			
Predation history	2	2.72	0.079
Predator cues	1	36.66	<0.001
Time	1	0.85	0.363
Predation history \times predator cues	2	0.99	0.382
Predation history \times time	2	8.47	0.001
Predator cues \times time	1	0.53	0.471
Predation history \times predator cues \times time	2	0.22	0.805
Number drifting			
Predation history	2	5.16	0.011
Predator cues	1	23.55	<0.001
Time	1	10.14	0.003
Predation history \times predator cues	2	4.52	0.018
Predation history \times time	2	0.42	0.659
Predator cues \times time	1	15.13	<0.001
Predation history \times predator cues \times time	2	1.49	0.240
Number not visible			
Predation history	2	1.15	0.327
Predator cues	1	0.47	0.495
Time	1	16.67	<0.001
Predation history \times predator cues	2	1.96	0.156
Predation history \times time	2	6.20	0.005
Predator cues \times time	1	15.58	<0.001
Predation history \times predator cues \times time	2	1.95	0.157
Error	36
Total	47

and Griffith 1990, Glova and Sagar 1991, Glova et al. 1992; A. R. McIntosh, *unpublished data*) so by restricting its foraging and movement to the night, *N. ornatus* is likely to reduce the risk of predation. Nocturnal increases in drift were not just a result of changes in positioning, however, as drift rates were low during the day when quite large numbers of *N. ornatus* were foraging on the substrate surface in trials with galaxias or no fish. An increase in search behavior by mayflies at the onset of foraging could help explain the enhancement of drift during the night; drift is often an important component of interpatch search behavior (Kohler 1985).

The inflexible nature of this strategy, even in the complete absence of all physical and chemical cues from predators, indicates it may have become fixed or canalized (*sensu* Stearns 1989). However, this might not be the case if the response to changes in the predation regime has a latency period greater than the duration of the experiments (i.e., 3 h) or if the behavior is a plastic response cued early in development through a developmental switch (*sensu* Stearns 1989) or conversion (*sensu* Smith-Gill 1983).

Inflexible antipredator strategies have previously been described for zooplankton vertical migrations (Neill 1992), but have also been recorded for diel drift periodicities and feeding periodicities in mayflies (Ciborowski et al. 1977, Ciborowski 1983, Kohler 1985, Cowan and Peckarsky 1994). Fixed strategies may re-

duce the threat of predation, but they are also likely to have costs because prey cannot take advantage of temporal and spatial reductions in predation threat (Havel 1987, Sih 1987). A number of explanations are possible for the evolution of these strategies. In this case, phylogenetic constraints, which prevent other patterns of behavior, can be ruled out since *N. ornatus* from other streams do not have fixed diel patterns. Stein (1979) suggested that a fixed strategy may evolve when costs are low, but this is unlikely to be true here, since we found that predator avoidance by *N. ornatus* substantially reduced potential foraging time. A relatively low benefit of flexibility in a constant environment (Levins 1968, Glasser 1979) is a more likely explanation. Neill (1992) found that the diel vertical migration pattern of a calanoid copepod, *Daptomus kenai*, was flexible to the temporally variable predation threat from *Chaoborus* spp. phantom midges, but was inflexible to the relatively constant and predictable threat from visually foraging juvenile cutthroat trout, *Oncorhynchus clarki*. This explanation may account for some of the selection pressure for a fixed behavior in *N. ornatus*, since trout population densities in the Taieri River system are relatively stable between sampling occasions (C. R. Townsend, *unpublished data*). However, studies of microhabitat use by trout in streams indicate that considerable spatial variation in predation threat can be expected, since trout are highly selective in the microhabitats they occupy (Fausch and White 1981, Hearn

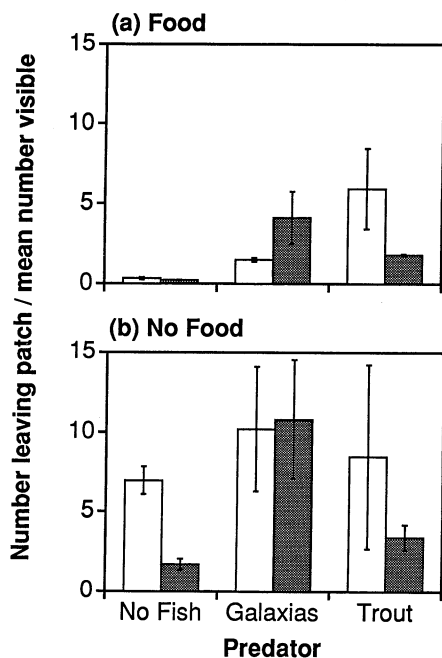


FIG. 6. The mean (± 1 SE) probability of *Nesameletus ornatus* leaving (a) a food patch and (b) a patch without food during the day (unshaded bars) and night (shaded bars) in trials with different predators. These probabilities are calculated from the total number leaving patches during the trial divided by the mean number present in patches during the trial.

1987, McIntosh et al. 1992). Thus, a constant predation threat is unlikely to be solely responsible. Just as important may be a prohibitively high cost of gathering information to assess predation risk (Sih 1987). When a visual predator such as brown trout is present, the chances of being preyed upon while assessing threat on the substrate surface can be expected to be high, particularly for a large mobile mayfly like *N. ornatus*. The cost (a high probability of predation) of assessing predation risk may, therefore, outweigh any advantage gained by being able to adapt to fluctuations in the threat of predation.

When *N. ornatus* from streams without trout were confronted with trout, no consistent positioning or drift periodicities were observed. Furthermore, the behavioral response of mayflies from the Stewart Island stream, where there was no possibility of any previous experience of trout, was not consistently different from that of prey from streams in the Taieri River system. Although adult *N. ornatus* from streams in the Taieri River system could conceivably fly between streams with different predation regimes, they do not appear to accumulate evolutionary experience that allows them to respond to the introduced predator.

The response of *N. ornatus* in streams lacking trout differs from that found in other parts of the world where there are native salmonid fishes. Cowan and Peckarsky (1993) found that *Baetis bicaudatus* from a fishless

stream in Colorado gained a nocturnal feeding periodicity when water from a stream containing native brook and stocked rainbow trout was added and Douglas et al. (1994) found that *B. coelestis* in three fishless streams in California decreased their day drift when caged native rainbow trout were added to the streams. Andersen et al. (1993) found that *Gammarus pulex* L. changed their behavior immediately after brown trout were introduced to two previously fishless Danish streams. Because New Zealand has no native fishes from the family Salmonidae, New Zealand mayflies may be relatively "naïve" to the threat posed by these predators.

In contrast to the lack of reaction to introduced brown trout, *N. ornatus* from Stewart Island, the galaxias stream, and the stream without fish changed their behavior according to the presence and absence of the native predator, the common river galaxias. When predatory fish were absent, no consistent drift or positioning periodicities were observed, but when common river galaxias were present mayflies from these streams without trout drifted out of the channels more often at night. However, this nocturnal increase in drift was not associated with a distinct nocturnal positioning periodicity as observed in mayflies from the trout stream. Instead, increases in drift at night can be accounted for by an increase in the frequency of interactions between galaxias and *N. ornatus*. The foraging pattern of *G. vulgaris* was typical of fish that use mechanical sensory systems to detect and capture prey (Hoekstra and Janssen 1985, Montgomery and Milton 1993). Foraging galaxias frequently disturbed mayflies and *N. ornatus* generally left a patch after an encounter by entering the water column. This behavior may appear risky, but we observed no reaction by *G. vulgaris* to mayflies swimming behind them, which is where their movements generally took them. Culp et al. (1991) have also emphasized the role of direct interactions

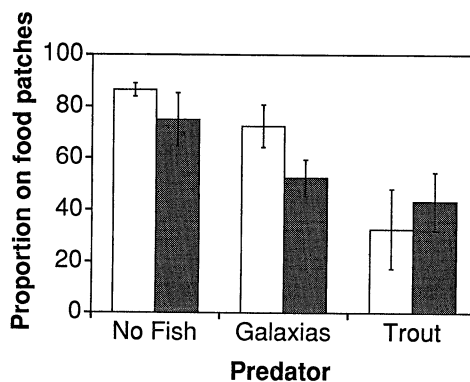


FIG. 7. The proportion of mayflies on food patches during the day (unshaded bars) and night (shaded bars) in trials with different predators. Data are means (± 1 SE) calculated from the number of mayflies on food patches in the camera's field of view divided by the total number visible in the video camera's field of view.

between fish and prey in their study of longnose dace (*Rhinichthys cataractae*) and the mayfly *Paraleptophlebia heteronea*. Nocturnal foraging by the fish caused the mayfly to flee by taking to the water column, resulting in nocturnal peaks in drift. The reactions of *P. heteronea* were similar to those of *N. ornatus* except *P. heteronea* fled before physical contact could occur.

The flexible nature of the antipredator strategy used by *N. ornatus* when confronted with galaxias, in comparison to that used by *N. ornatus* from the trout stream, is probably a reflection of differences in predation threat. Compared to trout, the risk of predation by galaxias of a mayfly on the substrate surface can be expected to be considerably less because galaxias rely more on mechanical cues to detect prey. Thus, in galaxias streams a flexible antipredator strategy may be advantageous given the lower cost of sampling the predation threat.

N. ornatus from the Stewart Island stream and the fishless stream responded to the presence of common river galaxias without any experience of this predator from their stream, but prey from streams without trout did not change their behavior when confronted with trout. Two levels of explanation could account for this difference. First, *G. vulgaris* and *N. ornatus* have had a long coevolutionary history, enabling *N. ornatus* to accumulate the evolutionary experience that would allow it to respond to the presence of galaxias, whereas brown trout are a relatively recent introduction to New Zealand. However, *N. ornatus* in the trout stream have been able to evolve inflexible antipredator behaviors in the relatively short time since trout were introduced to New Zealand in the late 1860s (Thomson 1922). Second, the foraging behavior of *G. vulgaris* is much more likely to provoke an escape response from *N. ornatus* than that of *S. trutta*. Trout spend most time foraging in the water column, whereas galaxias are more strongly associated with the benthos. Thus, *N. ornatus* on the substrate surface are more likely to be physically disturbed by galaxias than trout.

The differences observed between prey populations in their response to the presence and absence of galaxias indicate that although there was a general response to the presence of galaxias, behaviors characteristic of individual prey populations were still able to be detected. It seems that prey from different streams have behavior patterns that predispose them to respond in a certain way to a change in the predation regime. For example, the drift response of *N. ornatus* from the galaxias stream when confronted with galaxias was much stronger than that of *N. ornatus* from the Stewart Island stream or the stream without fish.

Trade-offs in mayfly behavior

Antipredator behavior can have important implications for prey if their ability to capture resources or reproduce is affected. Other workers have also suggested that predator avoidance by stream invertebrates might have associated costs (Kohler 1983, Culp et al.

1991, Flecker 1992, Peckarsky et al. 1993). In our case, the consequences for *N. ornatus* of the behavioral modifications caused by predatory fish are likely to be reductions in time spent foraging.

In nature, as in our experiment, the distribution of algal resources is characterized by large increases in the quality and quantity on the tops of stones compared with the bottoms. This dichotomy will potentially result in a severe reduction in resources available to prey forced to occupy the undersides of stones. The effect of positioning changes, such as those associated with trout, could therefore be a reduction in the algal food resources available during the day. By avoiding the top surfaces of stones during the day *N. ornatus* reduced its foraging time in our experiments by as much as half. Where resources are patchily distributed, as in streams (Pringle et al. 1988), any restrictions on movement may lead to decreases in foraging efficiency (net energy intake) by increasing interpatch search time (Krebs and Davies 1984, Stephens and Krebs 1986). In our experiments, the proportion of mayflies on food patches decreased as the restrictions on mayfly behavior increased. When mayfly positioning and drift were restricted during the day by trout, only a very small proportion of mayflies was found on food patches compared to trials with no fish. Disturbances by fish that resulted in mayflies abandoning food patches also caused a reduction in the proportion of mayflies on food patches.

As the extent of behavioral changes forced upon prey by predators has been realized (Kerfoot and Sih 1987), the need to understand the consequences for the structure and functioning of communities has also become more prominent (Dill 1987, Flecker 1992). In this context, it is important to know whether the effects of behavioral trade-offs filter down to lower trophic levels. In experiments conducted in situ stream channels in a small New Zealand stream, Flecker and Townsend (1994) found that the presence of fish resulted in a reduction in grazing by invertebrates and a subsequent increase in algal biomass with trout exerting a stronger effect than galaxias. It is clear from our experiments that predatory fish have a large influence on the behavior of *N. ornatus*. Further investigations of the effect of predatory fish on the behavior of stream macroinvertebrates are likely to reveal more important influences on stream communities through their sublethal effects on prey.

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