

Do different predators affect distance, direction, and destination of movements by a stream mayfly?

Angus R. McIntosh and Colin R. Townsend

Abstract: We observed the directions and distances travelled by *Nesameletus ornatus* mayfly nymphs in stream channels (current velocity 18 cm·s⁻¹) with either Eldon's galaxias (*Galaxias eldoni*), brown trout (*Salmo trutta*), or no fish. Short (<20 cm) upstream movements were most common, but movements up to 90 cm in both directions were recorded. Predators had no significant impact on movement direction or distance compared with controls when all movements were considered. Only movements in direct response to galaxias were significantly longer and more likely to be in a downstream direction than movements not directly associated with galaxias. In most cases the frequency of downstream drift distances fitted a negative exponential model. Our results showed that when current and turbulence were low, *N. ornatus* could have considerable control over their movement.

Résumé : Nous avons observé les directions et distances de déplacement de nymphes d'éphémère *Nesameletus ornatus* dans des chenaux (vitesse de courant de 18 cm·s⁻¹) où se trouvaient des galaxias de Eldon (*Galaxias eldoni*), des truites brunes (*Salmo trutta*) ou aucun poisson. Des déplacements courts (<20 cm) vers l'amont étaient le plus souvent notés, mais des déplacements dans les deux directions et pouvant atteindre 90 cm ont aussi été notés. Les prédateurs n'avaient pas d'effet appréciable sur la direction ou la distance des déplacements, par rapport aux témoins, si l'on tient compte de tous les déplacements. Seuls les déplacements en réaction aux galaxias étaient significativement plus longs et plus souvent en direction de l'aval que les déplacements non directement associés à ces poissons. Dans la plupart des cas, la fréquence des déplacements de dérive en aval correspondait à un modèle exponentiel négatif. Nos résultats montrent que les *N. ornatus* peuvent exercer un très important contrôle sur leurs déplacements lorsque le courant et la turbulence étaient faibles.

[Traduit par la Rédaction]

Introduction

Movement in the water column of streams is of major importance to the ecology of streams (Brittain and Eikeland 1988; Allan 1995; Palmer et al. 1996; Rader 1997). Many studies have investigated macroinvertebrate drift in streams, but we still have a limited knowledge of the distances moved. Estimates of drift distance have been obtained by calculating the rate at which drift subsides downstream from an experimental disturbance, a stream blockage, or a release that launches individuals into the water column. These techniques have yielded results that fit well to a negative exponential function (McLay 1970; Elliott 1971; Larkin and McKone 1985; Allan and Feifarek 1989; Lancaster et al. 1996). Nevertheless, they offer limited opportunities to identify behavioural control of drift distance and destination, to

measure upstream movement, and to discriminate between single and multiple movements of individuals.

Many factors have been shown to affect the rate or density of drift that can be measured at a certain point in a stream including flow, light, benthic density, invertebrate predators, benthic fish, drift-feeding fish, substrate, life history stage, and food (Anderson 1966; Walton et al. 1977; Ciborowski 1983; Kohler 1985; Malmqvist and Sjöström 1987; Culp et al. 1991; Poff and Ward 1991; Poff et al. 1991; Flecker 1992; Rader 1997). These factors may affect the distance moved, the direction of movement, and the destination of individual macroinvertebrates, but few of these possibilities have been investigated.

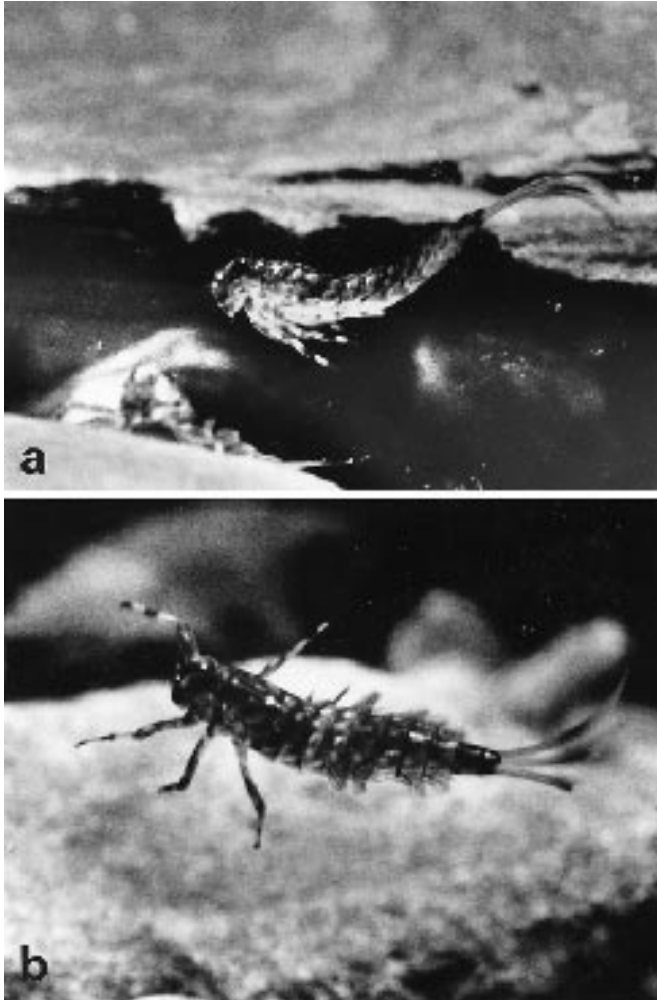
We have shown previously that predatory fish have a large influence on the propensity of a highly mobile New Zealand mayfly, *Nesameletus ornatus* Eaton, to drift (McIntosh and Townsend 1994). *Nesameletus ornatus* from a stream with introduced brown trout (*Salmo trutta*) avoided moving in the water column during the day and moved predominantly at night, even when trout were absent. Nymphs from a stream with a native benthic fish, Eldon's galaxias (*Galaxias eldoni* McDowall), swam away after encounters with the fish and, since the galaxias were more active at night, the drift rate was higher at night. In comparison, the movement of nymphs from a fishless stream was unrestricted and showed no diel pattern. It is possible that as well as influencing the rate of *N. ornatus* drift, these preda-

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A.R. McIntosh¹ and C.R. Townsend. Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand.

¹Author for all correspondence at the following address:
Department of Zoology, University of Canterbury,
Private Bag 4800, Christchurch, New Zealand.
e-mail: a.mcintosh@zool.canterbury.ac.nz

Fig. 1. *Nesameletus ornatus* nymphs move in the water column of streams either (a) by swimming upstream or downstream using dorsoventral oscillations of their body with limbs tucked close to the body or (b) by floating downstream in the current, "parachuting" with limbs outstretched.



tory fish may also affect the direction and distance of movements. We observed *N. ornatus* in laboratory stream channels in this study to determine how the predation regime influences the distance and direction of *N. ornatus* movements.

Methods

Nesameletus ornatus nymphs and predatory fish were collected from three neighbouring streams in the Taieri River system that contained (i) no fish (Burgan Stream), (ii) Eldon's galaxias but no trout (Stony Creek), and (iii) brown trout but no galaxias (Deep Stream, see McIntosh and Townsend 1994 for additional information). The Stony Creek population of galaxias, called *G. vulgaris* by McIntosh and Townsend (1994), has now been described as a new species, *G. eldoni* (McDowall 1997). Predatory fish used were adult Eldon's galaxias, 75–85 mm total length, and juvenile brown trout, 90–120 mm total length. The mayflies were late-instar *N. ornatus* without black wing pads (i.e., not about to emerge), 10–13 mm in length. The three mayfly populations were housed in

separate aerated aquaria and the fish in separate recirculating tanks, all under a 10 h dark : 14 h light regime. While in captivity, mayflies were fed ad libitum green unicellular algae grown on tiles and fish were fed ad libitum meal worms, mosquito larvae, and *N. ornatus*.

Four 6-m-long stream channels were constructed from plastic pipes cut longitudinally in half (35 cm diameter and 17.5 cm depth) and connected in pairs to two reservoir tanks (see fig. 1 in McIntosh and Townsend 1994). Dechlorinated tap water was supplied at 14°C to give a maximum depth of 15 cm and a mean (\pm SE) current velocity at two-thirds depth of 18 ± 0.6 cm·s⁻¹ (maximum 20 cm·s⁻¹, minimum 15 cm·s⁻¹). A 2.6-m-long experimental section in each channel was defined with a fine-mesh grill (2.5-mm aperture) at the upstream end that stopped fish and mayflies from swimming upstream and a coarse-mesh grill (7-mm aperture) at the downstream end that was impermeable to fish but allowed mayflies to move out of the section to be caught in a net suspended at the end of the channel.

In the experimental section of each channel, we placed gravel covered by a layer of 48 unglazed ceramic tiles (10 × 10 cm). Prior to experiments, some tiles were placed in an outdoor recirculating tank to allow algal colonisation. For each trial, eight tiles provisioned with green algae were distributed evenly throughout the channel to act as food patches. The bottom of each tile was thoroughly scrubbed to ensure that food was not available on these surfaces. Short pieces of PVC pipe with a small cobble in front provided cover for the fish in the channels.

The experiments took place during January and February 1992 (the austral summer), with "day" experiments starting at 10:00 and "night" experiments starting at 20:30 (1 h after the lights went out). Fish were introduced without food (one trout per channel ≈ 1 ·m⁻² or three galaxias per channel ≈ 3 ·m⁻²) 24 h before the start of trials to acclimatise. These densities are high compared with densities in the wild (Townsend and Crowl 1991). We started each trial by lowering the current velocity to <5 cm·s⁻¹ and gently pouring 30 mayflies (similar to densities found in the wild, A.R. McIntosh, unpublished data) into the central region of the experimental section. The velocity was then slowly increased to 18 cm·s⁻¹ over a 5-min period; any mayflies drifting out during the following 10 min were returned to the channel or replaced if they immediately drifted out again. Experiments were ended after 3 h by removing the fish and recovering mayflies from the channels.

The behaviour of fish and mayflies was recorded on videotape using an infrared light sensitive camera (JVC model TK 5310EG) mounted above the experimental section. With the aid of infrared light, which is unlikely to be detected by mayflies and fish (Lythgoe 1988; Heise 1992), we followed fish and mayfly movements during day and night in the middle portion (110 cm long) of the experimental section of each channel. Behaviour and distance moved were described from the last 2 h of videotape by estimating movement distance in relation to the grid formed by the tiles on the bottom of the channel. Only those movements taking place completely within the video camera's field of view were considered. In the trials with galaxias, movements of mayflies were classified as a direct response to a fish if the movement occurred within 2 s of the fish passing within 5 cm of the mayfly.

We ran four replicate trials during the day and night with prey from each of the three streams together with the fish predation regime found at that location, i.e., four replicate day and night trials with nymphs from Stony Creek with galaxias, nymphs from Burgan Stream with no fish, and nymphs from Deep Stream with trout. Each mayfly or fish was used once only. Trials were run in random order and treatments were rotated among channels. After each trial the channels were washed, the gravel and tiles changed, and the water replaced. Green unicellular algae formed a uniform mat; there were no significant differences among treatments in the

Fig. 2. Frequency distributions of distances moved in the water column by *N. ornatus* nymphs in the presence of trout, galaxias, or no fish during day and night in laboratory stream channels. Frequencies are for all replicates combined.

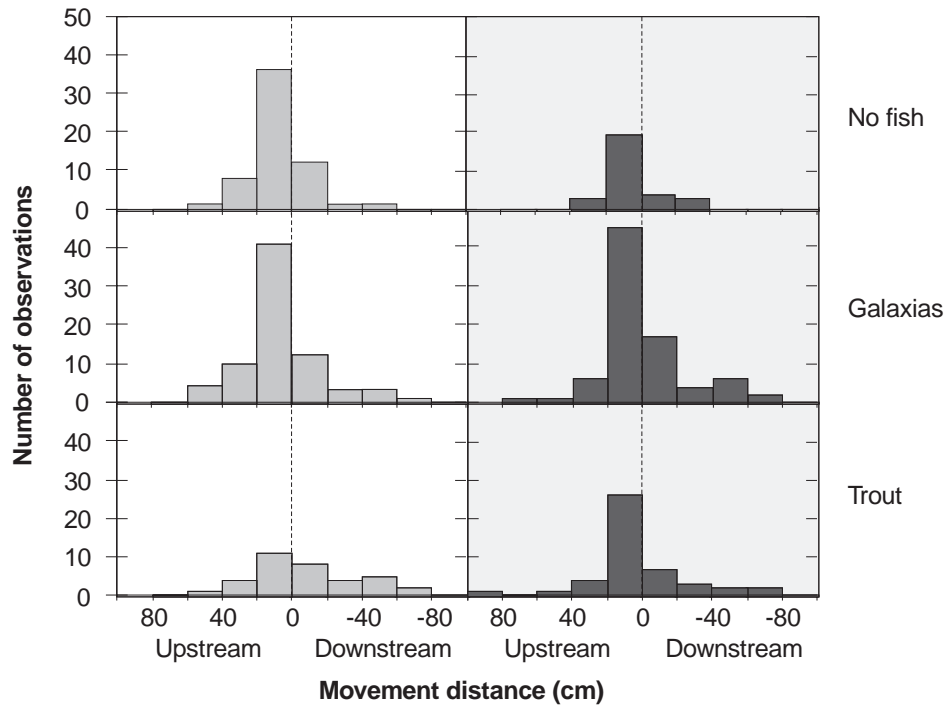


Table 1. Results of split-plot ANOVA on $\ln(x + 1)$ -transformed movement distances of *N. ornatus* mayfly nymphs in trials with either no fish or galaxias or trout (fish) during day or night (time) and moving either upstream or downstream (direction).

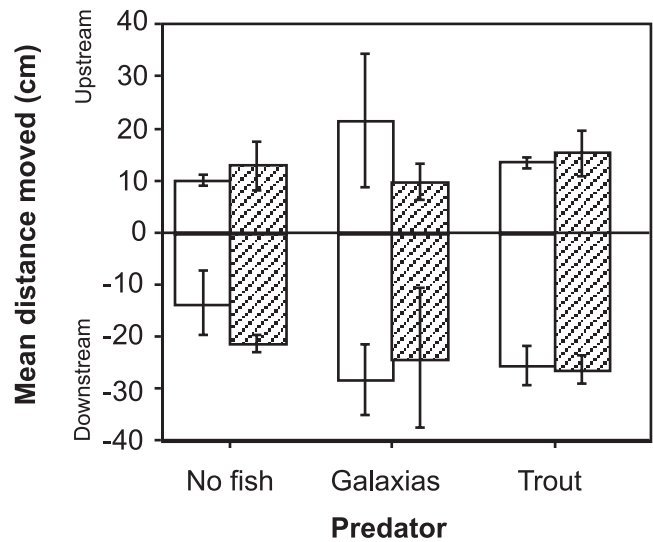
Source	df	MS	F	p
Time	1	0.1055	0.124	0.73
Fish	2	1.1475	1.350	0.28
Time × fish	2	0.1575	0.185	0.83
Rep(time × fish)	18	0.8498		
Direction	1	0.6912	0.856	0.37
Direction × time	1	0.1342	0.166	0.69
Direction × fish	2	0.5786	0.717	0.50
Direction × time × fish	2	0.3526	0.437	0.65
Error	18	0.8071		

Note: The main and interactive effects of time and fish were tested with the rep(time × fish) MS term, and the main and interactive effects of direction were tested with the error MS term. Rep, replicates; df, degrees of freedom; MS, mean square; F, likelihood ratio; p, probability.

abundance of algae, and mean (\pm SE) algal ash-free dry mass was $1.097 \pm 0.08 \text{ g}\cdot\text{m}^{-2}$ (McIntosh and Townsend 1994).

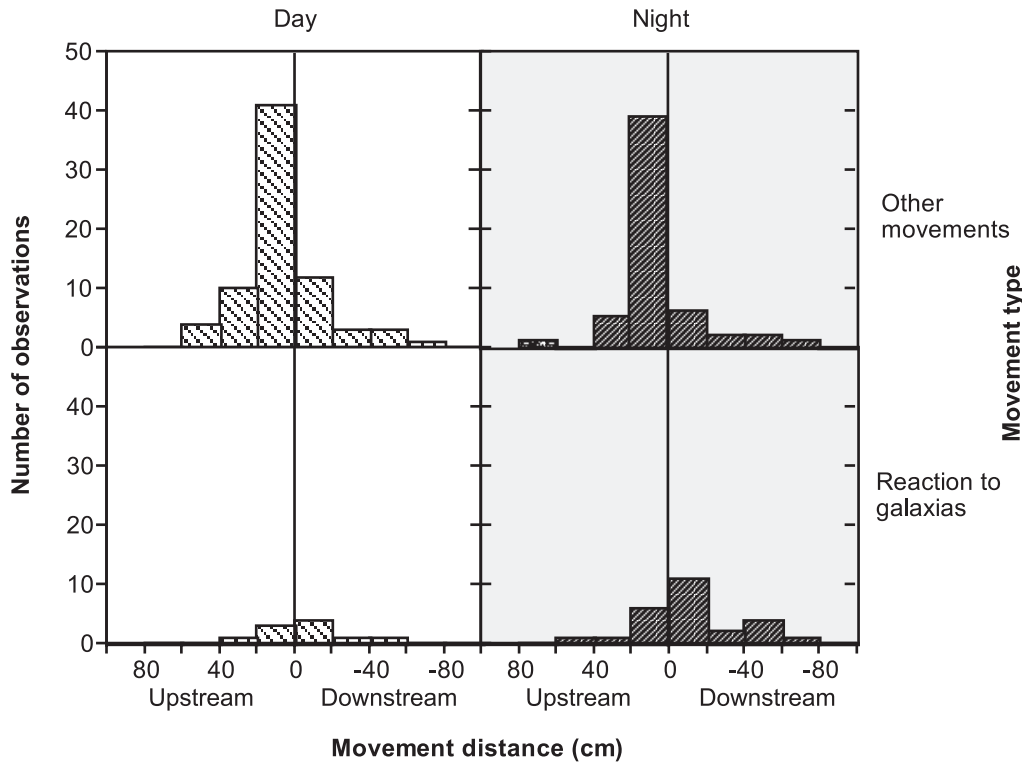
Frequency distributions combining the distances moved from all four replicate trials for a treatment were constructed for each treatment to show differences in distance and direction. Each frequency distribution potentially contained multiple movements from the same nymph, influenced by the same fish (when fish were present). To avoid the possibility that individual nymphs or fish could influence the outcome of the analysis, mean movement distances from the four replicate trials for each predation regime during day and night were analysed statistically with split-plot ANOVA (using Statistica software). In the ANOVA model the direction of movement (either upstream or downstream) was treated as a split-plot factor and the replicate data points used were the mean of movement distances measured in each trial.

Fig. 3. Mean (\pm SE) distances moved upstream and downstream by *N. ornatus* mayfly nymphs in the presence of trout, galaxias, or no fish during the day (open bars) and night (hatched bars) in laboratory stream channels.



To compare the distances of downstream movements measured in our experiments with those from other studies, we fitted a negative exponential decay model to the decline in drift downstream of a starting point (McLay 1970). For each treatment, we used the combined movements from the four trials to count the number of nymphs remaining in the water column at increasing distances downstream of their entry point. Using least squares regression, the negative exponential model was fitted to the relationship between distance downstream of the starting point and the number of nymphs still drifting. Each regression included movement distances from four trials involving different fish and mayflies. We

Fig. 4. Frequency distributions of distances moved by *N. ornatus* resulting from either interactions with galaxias or movements not associated with galaxias. Movements resulting from interactions with galaxias occurred within 2 s of a galaxias passing within 5 cm of a nymph whereas all other movements were not so associated with galaxias.



tested for between-treatment differences in the fit of the model using ANCOVA (Systat 1992).

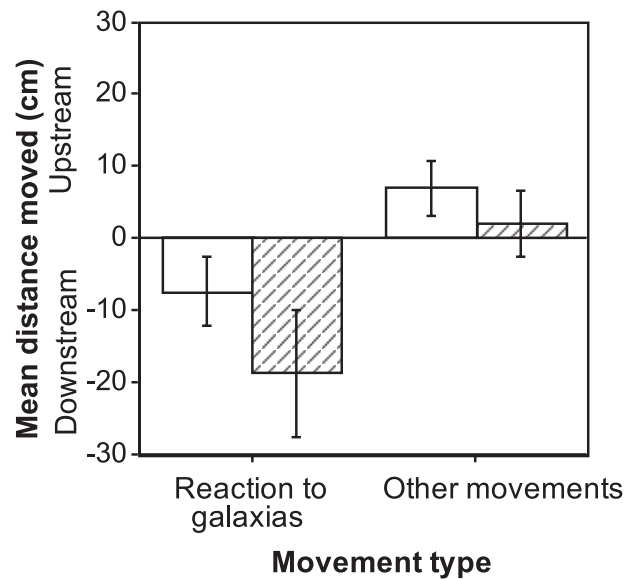
Results

Few direct interactions were observed between trout, which often held station off the substratum, and mayflies. In contrast, galaxias foraged from benthic positions and moved around more at night, often disturbing mayflies from the substratum. After galaxias had passed close to an *N. ornatus*, it usually swam away in the opposite direction. *Nesameletus ornatus* either swam using dorsoventral oscillations of their bodies (Fig. 1a) or held their legs out in a “parachute” fashion and were carried passively by the current (Fig. 1b). Swimming was used for both upstream and downstream movements, but parachuting was downstream only.

Short (<20 cm) upstream movements were the most common, but *N. ornatus* moved up to 90 cm in both downstream and upstream directions (Fig. 2). The high frequency of short movements and the lack of long movements (>80 cm) indicate that there was a low probability of missing long movements because of our limited field of view. The frequency distributions of distances moved indicated that there were few substantial differences between day and night and among predator treatments (Fig. 2). Mean distances moved were similar among treatments (Fig. 3), and there were no significant effects on movement distance relating to the predation regime or time of day or interactions between them (Table 1).

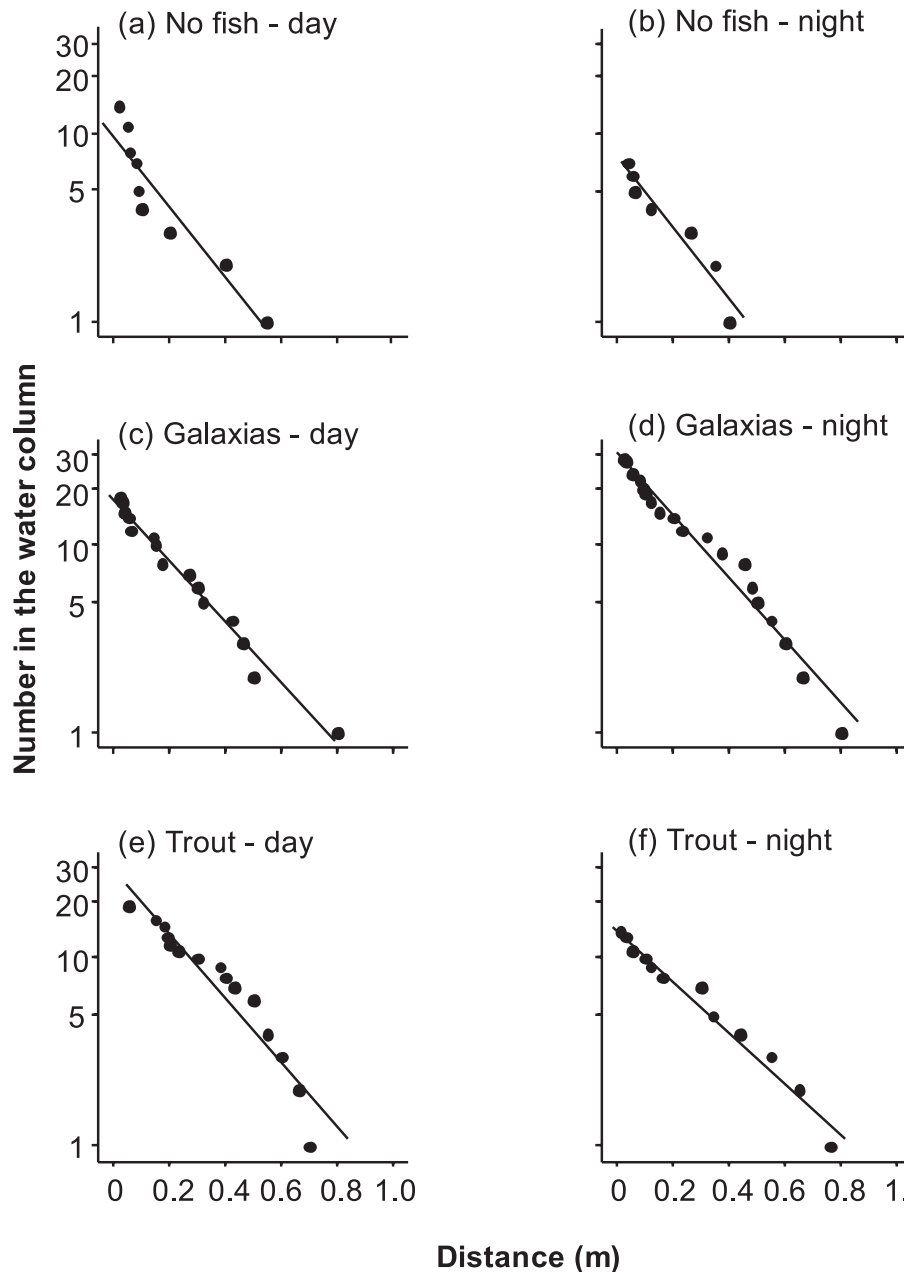
Movements by *N. ornatus* occurring shortly after interac-

Fig. 5. Mean (\pm SE) distances moved by *N. ornatus* resulting from either interactions with galaxias or movements not associated with galaxias. See the legend to Fig. 4 for additional details.



tions with galaxias were more likely to be in the downstream direction than other movements, especially during the night (Figs. 4 and 5). Analysis using Mann-Whitney *U*-tests indicated a significant difference between movements associated with reactions to passing galaxias and those not associated with galaxias.

Fig. 6. Fit to a negative exponential model (described in Table 2) of the downstream movements of *N. ornatus* in stream channels with either (a and b) no fish, (c and d) galaxias, or (e and f) trout during day and night. The line indicates the negative exponential model fitted. Note that the y-axis has a \log_e scale.



rectly associated with galaxias during the night ($U = 15$, $p = 0.04$) but not during the day ($U = 10$, $p = 0.16$).

The rate of nymphs leaving the water column and landing on the substratum decreased with increasing distance downstream and provided a good fit to the negative exponential model in most cases (Fig. 6; Table 2). However, it should be noted that in some treatments the relationship appears to depart from the negative exponential model, since the data do not have a linear relationship (Figs. 6a, 6b, and 6d). In all cases the rate of return to the substratum (i.e., β , the slope of the regression line) was very fast ($\beta < -3.00$), indicating that *N. ornatus* did not move large distances. The rate of return of nymphs to the substratum did not differ significantly among treatments (ANCOVA, $F_{5, 65} = 2.156$, $p > 0.05$).

Discussion

Our observations from laboratory channels indicate that *N. ornatus* nymphs can control their movement direction, distance, and destination. In particular, *N. ornatus* commonly moved short distances upstream by swimming. Upstream movement of stream inhabitants has been reported frequently for a wide range of taxa (Söderström 1987) and may be more important than current work on invertebrate movement in streams suggests.

Increases in current velocity and turbulence are likely to reduce the movement control of stream invertebrates and increase the probability of longer downstream movements (Elliott 1971; Allan and Feifarek 1989; Lancaster et al.

Table 2. Summary of regression equations describing the negative exponential relationship between the number of *N. ornatus* nymphs in the water column and the distance moved downstream.

Treatment	R^2	Slope (estimate \pm SE)	y-Intercept (estimate \pm SE)	df	F	p
No fish, day	0.87	-4.32 \pm 0.63	9.8 \pm 1.2	1, 7	47	<0.001
No fish, night	0.93	-4.35 \pm 0.55	8.3 \pm 1.1	1, 5	63	<0.001
Galaxias, day	0.98	-3.73 \pm 0.15	17.3 \pm 1.1	1, 13	636	<0.001
Galaxias, night	0.97	-3.85 \pm 0.17	30.9 \pm 1.0	1, 17	516	<0.001
Trout, day	0.91	-3.93 \pm 0.35	30.3 \pm 1.2	1, 13	128	<0.001
Trout, night	0.97	-3.12 \pm 0.17	14.3 \pm 1.1	1, 10	358	<0.001

Note: Treatments indicate different predator and time combinations. The slope and y-intercept are β and N_0 , respectively, in the equation $\ln N = \ln N_0 - \beta X$ (or $N = N_0 e^{-\beta X}$), where N is the number of nymphs in the water column, β is the rate of return to the substratum, X is the distance downstream of the starting point, and N_0 is the total number of nymphs entering the water column initially (following the notation of Lancaster et al. 1996). R^2 refers to the coefficient of determination for regression models; see Table 1 for additional abbreviations.

1996). The flow in our stream channels was, of course, much more homogeneous and the current velocity (18 cm s⁻¹) slower than in many areas of real streams. Nevertheless, the physical environment of streams is patchy and areas of slow current velocity and less turbulent hydraulic conditions are common. Thus, we contend that control of water column movement on the scale seen in our channels is possible in real streams in areas where hydraulic conditions are conducive.

Impact of predators on distance moved

Although fish influence the drift rate of *N. ornatus* (McIntosh and Townsend 1994), we found no difference in the mean distances that *N. ornatus* moved in trials with different predators. This indicates that the nocturnal increases in drift associated with galaxias and trout reported previously (McIntosh and Townsend 1994) are not caused by significant increases in drift distance at night but are related to their propensity to leave the substratum. These observations are in accord with those of Allan and Feifarek (1989) who found that *Baetis* nymphs, which display nocturnal peaks in the frequency of drift, did not have longer drift distances at night. They support the argument that nocturnal increases in drift rates are due to changes in the propensity to enter the drift associated with predator avoidance (Flecker 1992; Douglas et al. 1994; Tikkanen et al. 1994) and are not the result of nymphs drifting longer distances because they become disoriented at night (Statzner and Mogel 1985).

In contrast, movements specifically associated with galaxias encounters resulted in movements that were more likely to be downstream and longer than those not associated with galaxias encounters. Foraging galaxias probably rely on mechanical cues to capture prey, they generally forage in an upstream direction, and they have relatively short reaction distances (McIntosh and Townsend 1995). Thus, a *N. ornatus* nymph is likely to decrease its risk of predation by moving further away and in a direction in which the fish will have difficulty detecting it. Furthermore, passive drift in a parachute fashion may decrease the production of hydrodynamic cues that this predator responds to.

Water column movement in streams

The rates of return to the substratum calculated from the negative exponential model in these experiments are much

faster than those reported for most other taxa (McLay 1970; Elliott 1971; Larkin and McKone 1985; Lancaster et al. 1996). This is likely to be due in part to the behaviour, morphology, and large size of *N. ornatus*. Large invertebrates and those that can swim or alter their body posture are better able to control their movement in the water column (e.g., Madsen 1968; Corkum 1978; Ciborowski and Corkum 1980; Otto and Sjöström 1986; Wilzbach et al. 1988; Allan and Feifarek 1989; Poff et al. 1991; Rader 1997). However, the different methods used in this study are also likely to produce faster return rates. Our observations were made in an artificial environment that was conducive to a high degree of movement control. Field measurements of macroinvertebrate movement are typically only done in riffles where drift nets work efficiently. Field measurements will also be affected by flow heterogeneity and faster currents, which affect transport distances (Poff et al. 1991; Lancaster et al. 1996). Furthermore, macroinvertebrates launched into the water column by an experimenter may have different behaviour than those emigrating without interference, and catches downstream of a release or a blockage also potentially include multiple movements. Thus, our observations describe different aspects of invertebrate movement (e.g., upstream movement) than those measured using drift nets and described by the negative exponential model. Our study was not intended to compare the negative exponential model with other models that could be fitted to drift distances, but our results in Fig. 6 show obvious nonlinearity, which indicates departure from the negative exponential model. Allan and Feifarek (1989) also found significant deviations about the regression line in 29% of their regressions despite high R^2 values. These findings indicate that stream ecologists should not assume that drift distances will always conform to a negative exponential model.

The debate over whether drift results from "active" entry to the water column or "passive" dislodgement (e.g., Campbell 1985; Allan et al. 1986; Wilzbach 1990; Poff et al. 1991) has spawned much work on the movement of stream organisms in the water column. However, we are still a long way from explaining the patchy distributions of organisms found in streams (Pringle et al. 1988; Palmer et al. 1996). We concur with Palmer et al. (1996) that we need to learn much more about invertebrate movement in streams before we can understand the patchy distributions found in streams.

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