

# Stream drift as a consequence of disturbance by invertebrate predators

## Field and laboratory experiments

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**Summary.** We carried out an experimental field study in a Swedish stream in order to determine whether mobile predators enhance the drift of stream insects. We increased the density of nymphs of the predaceous perlid stonefly, *Dinocras cephalotes*, in an experimental section of a stream up to densities in another more densely populated part of the same stream. The drift of several benthic species increased significantly compared to a control section where *D. cephalotes* were rare. Experiments carried out in September showed a strongly elevated drift response in nymphs of the mayfly *Baetis rhodani* only, whereas May experiments resulted in increased drift in *B. rhodani* as well as the amphipod *Gammarus pulex*, the stonefly *Leuctra fusca*, chironomids, and the total number of drifting animals. In September, we found that the drift response of *Baetis rhodani* to predator disturbance was dependent on the size of mayfly nymphs; small nymphs appeared in greater numbers in the drift nets than did large nymphs. A subsequent laboratory analysis of drift lengths of *B. rhodani* nymphs supported the hypothesis that small nymphs travel in the drift for longer than do large nymphs, particularly in darkness. We suggest that morphological constraints in vision or swimming performance, or both, cause small nymphs to drift longer. In May, size-dependent drift was less obvious, probably because the size of the nymphs was considerably greater than in September.

**Key words:** Benthos – Drift – Experiments – Predators – Stream

The phenomenon of drift has been extensively studied over the last 30 years. During that time different schools have advocated that drift is either a consequence of active entry of the organisms to the water column (e.g. Chaston 1972), or a passive phenomenon linked to the eroding powers of the moving water (Elliott 1967). This controversy is still unsolved (e.g., Allan et al. 1986). It is clear, however, that the drift of animals always includes a behavioural component (Wiley and Kohler 1984), and that a number of factors elicit drift; Statzner et al. (1984) list 16 different factors governing drift. For example, when resources become limiting in populations of growing larvae, drift may act as a means for dispersal (Waters 1972; Müller 1974).

Only rarely have such hypotheses been tested experimentally.

The idea that predators may cause benthic invertebrates to drift downstream is not new (e.g. Corkum and Clifford 1980; Walton 1980), and several experimental approaches have been implemented. However, these have been conducted either under extremely high predator densities (Walton 1980) or with species that have a low propensity to drift (Keller 1975; Walton 1978). There is presently little realistic experimental evidence that predators can cause drift. Corkum and Clifford (1980) noted that large, in contrast to small, *Baetis tricaudatus* Dodds nymphs increased their drift rate in the presence of the predatory stonefly *Isogenoides elongatus* (Hagen) in a simple aquarium system. Corkum and Pointing (1979) found increased drift of *Baetis vagans* McDunnough when the nymphs were exposed to the stonefly predator *Paragnetina media* (Walker), and Malmqvist (1986) obtained similar results using two species of *Baetis* and stonefly predators. Wiley and Kohler (1981), using a time-lapse cinematographic technique in a field study, observed that *Rhyacophila* caused blackfly larvae to enter the drift. Peckarsky (1980) found that stonefly contacts with baetids, in particular, resulted in evasive behaviour, including primarily swimming and drifting. To our knowledge, the latter two studies are the only ones examining predator-caused drift in natural or seminatural environments.

If individuals benefit from adopting a drift behaviour, the advantage may differ among e.g. size-classes within a species. Allan (1978, 1984) hypothesized that large insects should avoid drifting in daytime since they then would be easy prey for visually hunting predators, notably fish. Small insects, however, are less in danger from fish predators that selectively prefer large invertebrate prey (Allan 1978; Ringler 1979). Consequently, one would expect that selection for nocturnal drifting behaviour will be greater in large animals. However, we believe similar effects may also arise because of morphological constraints associated with body size, i.e., due to the less well-developed swimming ability and/or vision of small species, and of young stages.

In this study we observed the response of a natural benthic community to the experimental addition of a predaceous perlid stonefly, *Dinocras cephalotes* (Curtis), whose feeding and behaviour have been documented previously in field and laboratory investigations (Malmqvist and Sjöström 1980, 1984; Sjöström 1985a, 1985b). We monitored changes in drift rates in a control and an experimental sec-

tion of a South Swedish stream both during the day and the night, and at two different seasons. We paid special attention to the influence of the predators on the size distribution of drifting *Baetis rhodani* Pictet, the dominant species of mayfly nymph. In order to better understand mechanisms underlying the observed drift patterns of this species we designed a laboratory experiment to study how the drift distances of a size-range of *B. rhodani* nymphs varied following disturbance by the predaceous stonefly.

## Materials and methods

### i. The field experiment

We conducted the field experiment in a fairly homogeneous riffle section of the stream Klövbäcken in southern Sweden (55°08'N, 13°08'E).

We subdivided the experimental area into two parallel sections, each 2 m wide and 6 m long, using sheet-metal that was pressed approximately 10 cm into the substrate and reaching above the water surface. Four weeks prior to the start of the first experiment, we took quantitative samples [modified Neill sampler, area: 0.05 m<sup>2</sup>, N=10] immediately upstream from the experimental sections to ascertain the approximate natural density of *Dinocras cephalotes*. The mean density ( $\pm$ S.D.) of *D. cephalotes* was estimated as  $4.0 \pm 8.4$  ind/m<sup>2</sup>. On this occasion we set up the two drift sampling units (without attaching drift nets); one in each of the parallel sections' downstream part. Each unit consists of an "organ" of 12 tubes (diam. 115 mm) onto which drift nets are easily attached.

Experiments were run on 23–26 September 1985 and 13–16 May 1986. On each occasion, drift was sampled in the experimental and control sections for two nights and two days prior to predator introduction, and again the day and night after the introduction. In both seasons we transferred 500 *D. cephalotes* (size range: 15–23 mm, September; 15–29 mm, May) from an area 2.5 km upstream where the stonefly densities had been estimated as  $57 \pm 65$  ind/m<sup>2</sup> (mean  $\pm$  S.D., Neill sampler, 0.05 m<sup>2</sup>, N=47; Malmqvist and Sjöström, unpubl.) on an earlier occasion. We introduced the stonefly nymphs to the experimental section in the early afternoon of the third day using a mixed implanta-

tion strategy: some were dropped into the stream upstream and in the experimental section, others were allowed to move freely from the stream margin to deeper water, others again were introduced via coarse-meshed nets held on the stream bed. We observed that single stoneflies drifted through the whole section during the introduction. In both September and May the experimental and control sections were sampled (Neill sampler, 0.05 m<sup>2</sup>, N=10) in the morning following the predator introduction to evaluate the effectiveness of the introduction.

Each drift net was 50 cm deep and had a mesh width of 0.20 mm. The drift nets always operated for 60 min. We measured the current speed in the centre of the aperture of each net at the beginning and the end of the exposure time; the mean was used for calculation of the water volume passing through the individual nets. We collected day drift between 16<sup>00</sup>–17<sup>00</sup> h (September), 17<sup>00</sup>–18<sup>00</sup> h (May), and night drift between 20<sup>00</sup>–21<sup>00</sup> h (September, sunset 19<sup>00</sup> h), 22<sup>30</sup>–23<sup>30</sup> h (May, sunset 21<sup>05</sup> h) (all times daylight saving times). Drift tends to peak shortly after nightfall (Allan and Russek 1985) and we consequently performed our night drift measurements in the early night. The drift samples were preserved in 70% alcohol in the field. We sorted the samples in the laboratory, taking special care not to miss any of the very small animals. Identification was made to species level, except for the limnephilids, chironomids, and oligochaetes. We measured the head width of *Baetis rhodani* nymphs to the nearest 0.1 mm using a dissecting microscope and an ocular micrometer.

Log ( $x$ ) or log ( $1 + x$ ) transformed data of the drift densities were used in all statistical analyses.

### ii. The laboratory experiments

We conducted the experiments in a small circular, white plastic aquarium (outer diam 120 mm, inner diam 40 mm), provided with a translucent pebble substratum. Current was created by compressed air blown from two tubes at opposite sides of the aquarium. Current speed was approximately 20 cm/s at the outer margin where the speed was highest. We immersed the aquarium in an outer, transparent water bath for temperature control ( $12 \pm 1^\circ$ ) and mounted an infra-red sensitive video camera vertically over the aquarium and

**Table 1.** The benthic densities of invertebrates (No. m<sup>-2</sup>) in the experimental and control sections on the day following predator introduction in the two seasons. In all cases N=10 samples each of 0.05 m<sup>2</sup> area

Taxon	September 1985				May 1986			
	Control		Experiment		Control		Experiment	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
<i>Gammarus pulex</i>	1755	1719	440	399	188	106	154	20
<i>Baetis rhodani</i>	1299	565	579	266	586	446	538	286
Trichoptera	392	162	319	215	180	58	306	220
<i>Dinocras</i>	3	7	19	24	6	10	8	10
Other Plecoptera	120	94	52	34	480	461	757	432
Coleoptera	465	357	133	118	140	76	155	90
Diptera	977	961	384	294	1700	868	988	578
Mollusca	73	210	33	35	7	10	9	14
Others	77	94	34	30	531	335	504	514

**Table 2.** Mean drift densities (No. 100 m<sup>-3</sup>, N=12 for each mean) of some important taxa in the two sections in September 1985. Day 1 and 2 are prior to, and day 3 follows predator introduction to the experimental section

Taxa	Experiment						Control					
	Day 1		Day 2		Day 3		Day 1		Day 2		Day 3	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
<i>G. pulex</i>	10.3	9.9	8.2	9.0	14.0	11.7	13.6	10.6	12.5	16.1	17.7	21.4
Simuliidae	3.2	6.1	5.5	6.1	5.7	6.4	8.3	12.4	10.7	16.3	3.3	5.3
Chironomidae	166.8	95.2	114.9	58.5	112.3	38.9	177.4	110.2	114.0	62.4	127.3	50.7
<i>L. hippopus</i>	5.2	15.3	2.5	5.0	1.4	3.3	2.0	6.9	0	0	0.7	2.3
<i>Baetis rhodani</i>	2.4	5.8	2.7	5.2	8.2	12.9	10.3	12.7	5.8	10.5	11.8	16.9
Others	20.3	15.9	15.7	13.5	24.3	21.9	31.3	22.4	16.5	14.3	17.6	13.8
	Night 1		Night 2		Night 3		Night 1		Night 2		Night 3	
<i>G. pulex</i>	50.3	35.7	52.8	39.4	62.3	38.0	47.8	55.2	64.4	37.2	62.3	26.9
Simuliidae	18.8	16.7	15.7	14.9	27.4	16.7	35.5	22.6	16.5	23.6	19.2	16.9
Chironomidae	971.1	431.6	712.0	229.6	792.0	220.7	1218.3	607.3	810.8	243.3	755.3	268.6
<i>L. hippopus</i>	51.2	35.5	23.4	21.3	35.8	31.3	49.4	29.1	35.4	21.3	28.9	20.8
<i>Baetis rhodani</i>	61.8	37.2	43.3	39.6	110.1	44.8	63.3	38.1	34.9	21.6	45.8	31.3
Others	68.1	34.4	85.1	39.8	73.6	39.0	99.2	68.0	59.3	39.1	68.8	40.1

**Table 3.** Mean drift densities (No. 100 m<sup>-3</sup>, N=12 for each mean) of some important taxa in the two sections in May 1986. Day 1 and 2 are prior to, and day 3 follows predator introduction to the experimental section

Taxa	Experiment						Control					
	Day 1		Day 2		Day 3		Day 1		Day 2		Day 3	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
<i>G. pulex</i>	18.7	15.9	17.8	12.4	17.3	14.9	11.5	5.3	15.4	11.0	8.6	10.7
<i>Baetis rhodani</i>	3.0	7.6	0	0	4.3	7.2	4.4	4.8	3.6	4.5	8.3	8.7
<i>Brachyptera risi</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leuctra fusca</i>	2.3	5.5	6.8	7.8	3.9	5.0	7.3	8.5	3.3	6.3	3.9	7.8
Simuliidae	2.5	5.9	2.1	3.8	0.6	2.0	0	0	0.8	2.9	0.9	3.2
Chironomidae	102.5	37.1	86.5	35.9	121.8	46.7	87.6	32.5	135.7	42.0	159.3	69.2
Others	8.7	9.8	3.9	9.1	5.8	5.5	8.1	17.6	7.4	8.4	4.5	6.8
	Night 1		Night 2		Night 3		Night 1		Night 2		Night 3	
<i>G. pulex</i>	15.8	13.9	14.2	10.9	45.7	17.8	23.4	24.8	22.4	14.0	38.6	29.9
<i>Baetis rhodani</i>	4.3	6.2	4.2	5.9	35.3	25.1	15.1	15.3	23.5	17.0	38.6	35.1
<i>Brachyptera risi</i>	1.1	2.5	2.6	5.1	6.6	7.2	1.7	3.9	6.0	7.0	5.4	9.2
<i>Leuctra fusca</i>	9.9	8.7	9.7	7.9	32.6	21.0	11.7	11.6	12.5	10.1	21.3	16.3
Simuliidae	3.3	4.3	4.8	7.2	5.8	9.7	2.3	4.1	7.1	8.2	2.8	6.6
Chironomidae	86.9	30.7	92.3	58.1	226.4	123.3	204.8	105.9	186.3	81.0	248.7	164.7
Others	14.4	12.8	7.3	5.9	16.5	16.0	24.2	16.4	13.2	14.3	10.3	15.0

an infrared light source under the aquarium. Two differently sized *Baetis rhodani* individuals were acclimatized in the aquarium for 30 min before each trial. We followed the drift behaviour of the mayfly nymphs on video tape recordings after the addition of a single *Dinocras* nymph. We measured the time in drift, from entry to exiting, with a stop watch for 5–15 min of observation, yielding approximately 20 estimates of drift time for each mayfly. We assume that there is a positive relationship between time and distance drifted. Also, we classified whether or not drift entry was a result of contact with the predator. In total, we performed 10 trials in total darkness and 8 trials in light (250 lux).

## Results

The initial survey of the area immediately upstream from the experimental section that was subsequently used in the experiments was carried out on 28 August 1985. This survey revealed that the densities of *D. cephalotes* were low in this part of the stream (8 ind/m<sup>2</sup> and 0 ind/m<sup>2</sup> immediately upstream the control and experimental sections, respectively), possibly because the substratum was finer and differently packed from that of the densely populated parts further upstream.

If all of the introduced stonefly nymphs were to have stayed within the experimental section, and if we assume

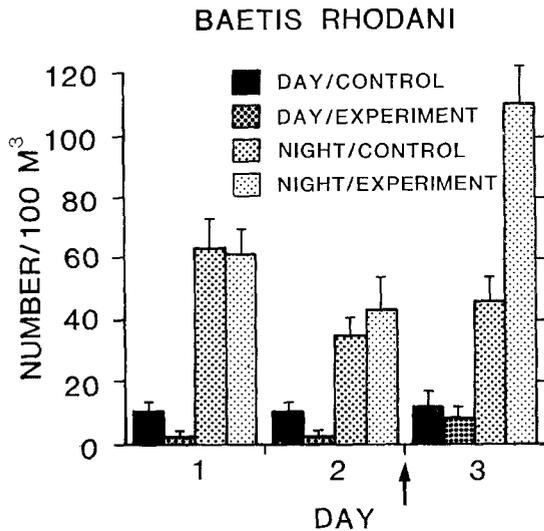


Fig. 1. The drift of *Baetis rhodani* in the two sections during the September experiment. Day 1 and 2 represent the drift before the experimental addition of stonefly nymphs (arrow). The vertical bars indicate one standard error

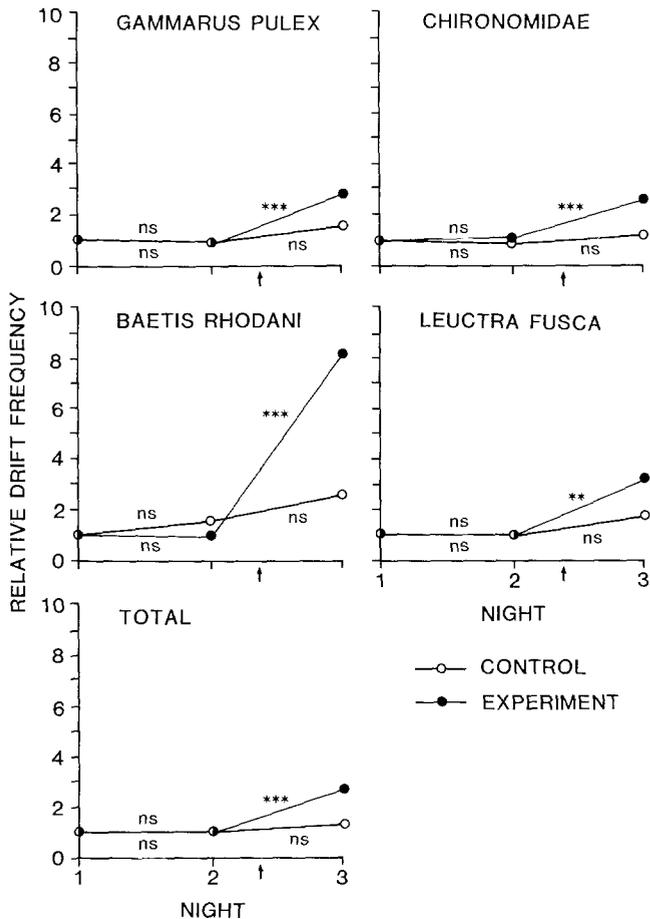


Fig. 2. The night drift rate of various taxa, as well as that of all drifting invertebrates combined in relation to drift on the first night. First night densities in both control and experimental sections were set=1. Open dots represent the control section and filled dots the experimental section, arrows indicate predator introduction. ns = non-significant ( $P > 0.05$ ), \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ . Comparisons of nights 2 and 3 vs night 1 were made using t-tests, and the significance levels for these comparisons are denoted in the graph between night 1 and 2, and 2 and 3, respectively

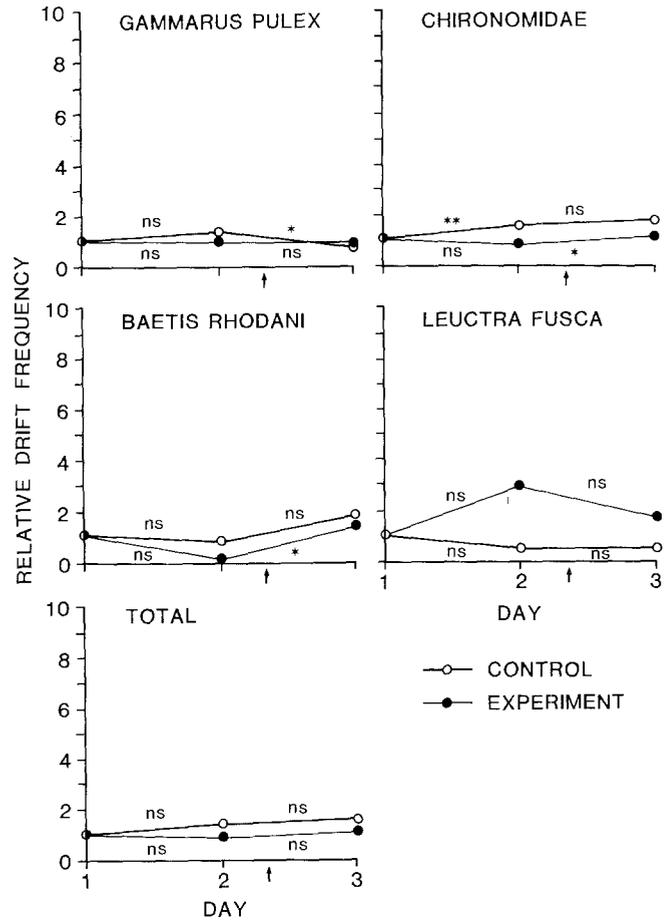


Fig. 3. The day drift rate of various taxa and all drifting invertebrates combined in relation to drift on the first day. Symbols as in Fig. 2

that the quantitative sampling gives an absolute estimate of density, we would expect to find 40 *D. cephalotes* nymphs per m<sup>2</sup> at the end of the experiment. The densities per m<sup>2</sup> that we did find were 19 (September) and eight (May), respectively (Table 1). While these densities may seem low, we consider these results acceptable since we observed some losses during the process of introduction, and since emigrations is likely to have occurred during the many hours of darkness after the night drift was sampled.

The drift rate in general was considerably higher at night than during the day for most taxa and this tendency was stronger in the autumn than in the spring (Tables 2 and 3).

Nighttime drift expressed as numbers 100 m<sup>-3</sup> did not show significant differences between the control and experimental sections before the introduction of predators in the September experiment, except for limnephilids (higher in control, two-way Anova,  $F_{1,44} = 5.99$ ,  $P < 0.05$ ). Following predator introduction the night drift of *Baetis rhodani* increased more than twofold compared with the control (repeated one-way Anova  $F_{1,22} = 17.82$ ,  $P < 0.001$ ; Fig. 1). There was no significant increase in all taxa combined nor of any other individual taxon. Daytime drift was not significantly different for any taxa between the experimental and control sections.

In the May experiment the conditions (substrate, current speed, etc.) had apparently changed to such a degree that the drift rates in the experimental part deviated signifi-

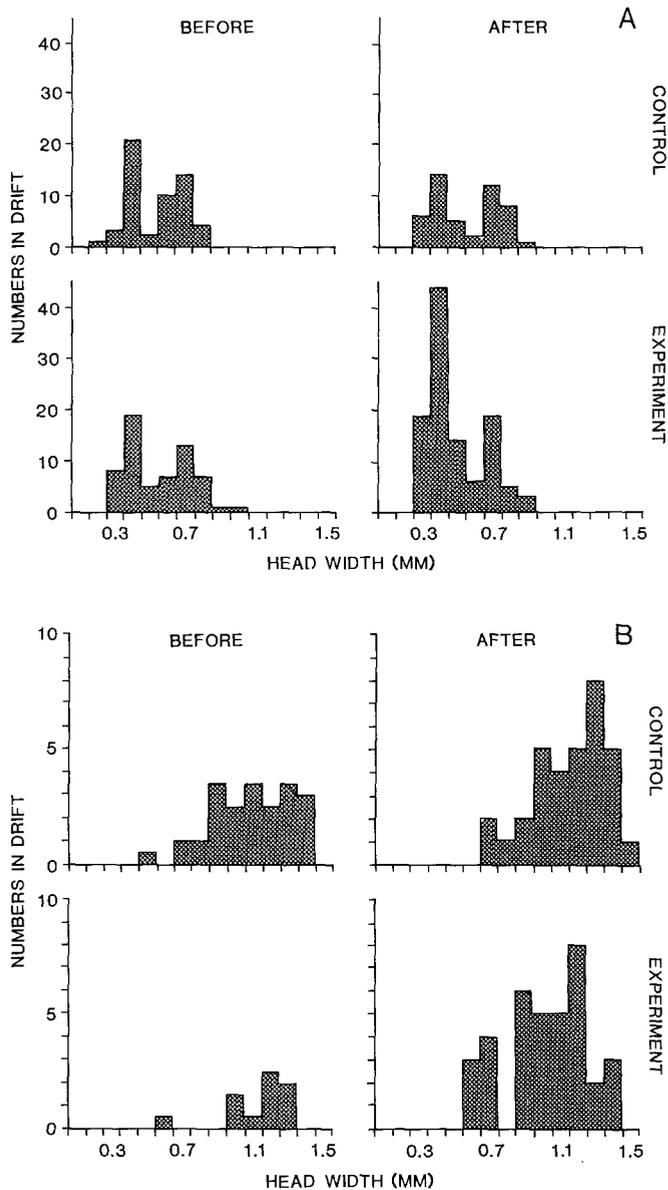


Fig. 4 A, B. Head width of drifting *Baetis rhodani* in the field experiment, before and after predator introduction in the control and experimental sections in September (A), and May (B)

cantly from those in the control section before the experimental introduction. This was the case for *B. rhodani* (two-way Anova,  $F_{1,44} = 14.98$ ,  $P < 0.001$ ), chironomids ( $F = 34.51$ ,  $P < 0.001$ ), and all taxa combined ( $F = 37.25$ ,  $P < 0.001$ ) by night, and for *B. rhodani* ( $F = 8.47$ ,  $P < 0.01$ ) by day (Table 3). There were, however, no significant differences among the different days in the control section or between the two days preceding introduction in the experimental section. Therefore, it was possible to use data from the days prior to the introduction in the experimental section as controls. Also, we compared control and experimental sections by setting the drift densities on Day 1 equal to one and then regarding the relative changes the following days. On this occasion several taxa [Chironomidae ( $t = 4.24$ ,  $P < 0.001$ ), *Baetis rhodani* ( $t = 4.63$ ,  $P < 0.001$ ), *Leuctra fusca* L. ( $t = 2.66$ ,  $P = 0.014$ ), *Gammarus pulex* L. ( $t = 3.85$ ,  $P = 0.001$ )], and all taxa combined ( $t = 5.11$ ,  $P < 0.001$ ) showed significantly higher drift in the experimental section at night

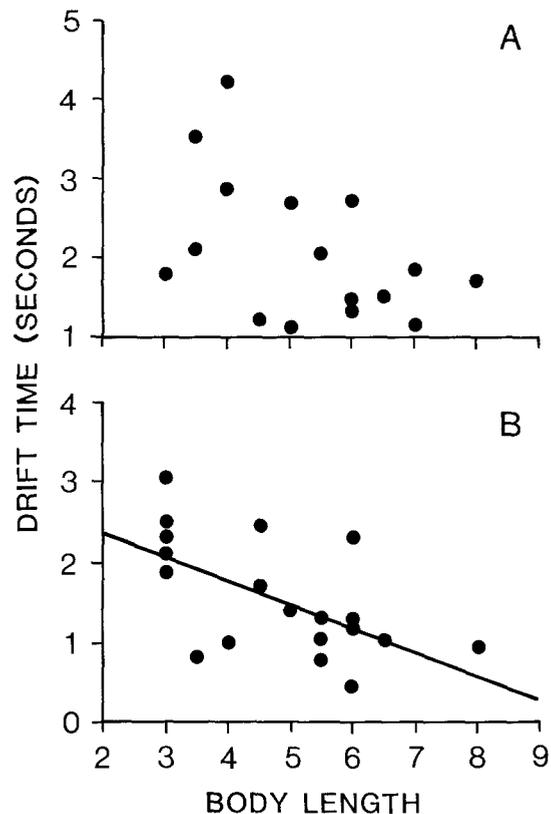


Fig. 5. A The duration of individual drift bouts of *Baetis rhodani* nymphs after encounters with *Dinocras cephalotes* nymphs in light conditions. The relationship is not significant ( $N = 16$ ,  $r = -0.46$ ,  $P > 0.05$ ). B The duration of individual drift bouts of *Baetis rhodani* nymphs after encounters with *Dinocras cephalotes* nymphs in darkness. There is a significant correlation between duration and body length ( $N = 20$ ,  $r = -0.60$ ,  $P < 0.05$ )

(Fig. 2). Also in May, the drift rate during the day of the predator addition did not increase (Fig. 3). The somewhat irregular patterns of relative drift rates during daytime are probably an artifact due to low numbers of drifting animals (Table 3).

In September, the mean ratio between the numbers  $\cdot 100 \text{ m}^{-3}$  of *Baetis rhodani* captured in the drift nets during the night vs. during the day prior to predator introduction was 9.51, while this ratio was 4.44 in May (ratios calculated as the mean ratio of all night drift densities to all day drift densities, excluding the experimental section on Day 3). The mean size of *B. rhodani* (head width  $\pm$  S.D.) was 0.46 mm at night ( $\pm 0.16$ ) and 0.35 mm ( $\pm 0.11$ ) during the day in September. In May, the mean head width of the drifting *B. rhodani* was larger than in September, and the difference between day and night was less obvious and reversed, viz 1.01 mm ( $\pm 0.22$ , night) and 1.05 mm ( $\pm 0.21$ , day).

Benthic sampling on the morning following the experiment showed that benthic densities differed to some extent between the control and experimental sections (Table 1). More important, the densities of *Dinocras* showed that a reasonable number had been present during the experimental period in September. In May, however, few *Dinocras* remained in the experimental section when sampling was performed the following morning.

In the September experiments the addition of predators resulted in increased drift of small *B. rhodani* in particular,

while larger nymphs did not increase their drift rate (Fig. 4A,  $G$ -test corrected for continuity;  $G_{\text{adj}}=29.7$ ,  $P < 0.001$ ). In May, when small nymphs were rare, the drift rate increases were unrelated to size in this species (Fig. 4B,  $G_{\text{adj}}=2.80$ ,  $P > 0.05$ ).

The laboratory experiments showed that in darkness small *Baetis* nymphs drifted longer, on average, than did larger nymphs in the presence of *Dinocras* (Fig. 5B). The same tendency, although not significant, was observed in the experiments carried out in daylight (Fig. 5A). In light conditions, 80.2% of the observed drift responses ( $N=177$ ) took place upon physical contact with the predator and 19.8% were before contact. In darkness, 98.0% of all registered drift ( $N=267$ ) was upon contact. The observed difference between light and dark conditions was highly significant ( $X^2_{(1)}=64.68$ ,  $P < 0.001$ ). Not all of the observed reactions in *B. rhodani* were expressed as drift behaviour. In 20% of the evasive responses (light: 19.7%, darkness: 20.1%) the mayfly nymphs did not drift but moved locally only, either by some rapid steps to the side or, more rarely, by a small jump. The relative frequency of local movements was unrelated to the size of the mayflies.

## Discussion

In relation to other factors that influence drift entry predator disturbance may have been underestimated previously (cf. Peckarsky 1980). Laboratory experiments have shown that up to 72% of the drift of *Baetis rhodani* may be caused by hunting *Dinocras cephalotes* (Malmqvist 1986) and we observed approximately 60–90% increases in drift rate in the present field experiment.

There are inherent difficulties in replicating field experiments (Hurlbert 1984), which are applicable also to our approach. Field experiments are costly to carry out, and identical conditions are never met in different samples, neither in time nor space. Despite these constraints the results of our field and laboratory experiments are consistent with the hypothesis that predator-induced drift is a real and important phenomenon for certain prey taxa.

Predators may cause either an increase or a decrease in prey activity depending upon whether the contact between the predator and prey is direct or indirect. For example, a lowered rate of movement can be viewed as a secondary defence (sensu Edmunds 1974) against predation, lowering the likelihood of encountering a predator (Stein and Magnuson 1976; Sih 1984; Andersson et al. 1986; Malmqvist, unpublished work). In addition, low prey mobility will draw less attention from visual predators. *Dinocras cephalotes* is a strictly nocturnal predator, inactive by day, relying predominantly on tactile cues for prey detection (Sjöström 1985b). The behavioural data reported here suggest that prey drift following direct predator-prey contacts were the mechanism underlying the observed pattern of nocturnal drift increase with predator addition. These data further suggest that nocturnal drift reflects an increased feeding activity of *Dinocras*. None of the different prey taxa showed reduced drift activity in this study, supporting that drift was the major response. We do not believe that indirect contacts, for example chemical cues caused the observed increase of the nighttime drift. In a laboratory study, Malmqvist (1986) found an increased nighttime drift of *B. rhodani* when exposed to free *D. cephalotes*, whereas constrained predators had no significant influence on the drift

of the mayfly. This is in accordance with the results of the present laboratory study, in which we found that almost all (98%) of the drift entries of *B. rhodani* were elicited upon direct contact.

Agile species, that escape by swimming, such as baetid mayflies and *Gammarus pulex*, would be expected to redistribute at a high rate, while prey species that run on the substrate (e.g. heptageniid mayflies, Peckarsky 1982), species that are protected by cases (e.g. caddis larvae, Otto Svensson 1980), or those that are in some other way safe from hunting stonefly nymphs (e.g. beetles, Malmqvist and Sjöström 1984) would be comparatively rarer in the drift. This prediction was largely confirmed. We did, however, expect blackfly larvae to drift in response to the increased number of hunting predators. It is possible that the simuliid density was too low to detect a pattern (Tables 2 and 3). Alternatively, the blackflies might drift but use their anchor threads to return to their original site instead of drifting into the nets (D.D. Hart, unpublished work, cf. Wotton 1986).

Allan (1978, 1984) suggested that small insects face less risk of being preyed upon by fish than do large insects. This relative risk should be reflected in their drift rates, so that small insects would drift at any time of the day, while large ones would occur in the drift mainly at night. Support for this contention has been given by Newman and Waters (1984), Skinner (1985), and Andersson et al. (1986). When analysing the diel size composition of drifting *Baetis rhodani* nymphs before the introduction of *Dinocras cephalotes*, we found that the size distribution in September was in agreement with Allan's hypothesis, in that large nymphs dominated in the night drift. However, upon introduction of *D. cephalotes*, the small *B. rhodani* nymphs increased their drift far more than did large ones (Fig. 4), suggesting either size-selective encounters by the predator, or size-dependent escape behaviour by the prey. Our laboratory experiment suggested yet another explanation, namely that small *Baetis rhodani* experience longer drift bouts because they have less advanced swimming abilities than large nymphs. They also have less developed eyes, resulting in decreased resolution and light sensitivity (Sherk 1978; Sjöström 1985), because of a positive relationship between the number of ommatidia and body size in hemimetabolous insects (Sherk 1977; Cloarc 1984, Sjöström 1985). We expect such ontogenetic constraints to cause small nymphs to be relatively less able to detect and settle on suitable places on the stream bed. Thus, the increase in drift of small *Baetis* with *Dinocras* addition may reflect elevated drift net catches due to longer drift distances, rather than increased initiation of drift by contact with stoneflies.

Statzner and Mogel (1985) observed a discrepancy between the size distribution of *Baetis buceratus* Eaton individuals leaving artificial substrates in the field, and that of individuals caught in drift nets. They presented age-related differences in drift behaviour, especially disorientation in darkness, as one likely explanation, another being size-dependent stress by water current causing greater dislodgement of large larvae. Our laboratory experiments in infrared light do not support a disorientation hypothesis since the *B. rhodani* nymphs did not show any obvious size-dependent differences in behaviour, apart from greater drift lengths in comparison with light conditions. Due to shallow depth in the experimental aquarium (1–2 cm), compared to a natural stream, where the swimming distance needed

for a drifting animal to resettle might be substantially greater, the importance of swimming capacity in relation to vision is likely to have been underestimated.

An investigation by Campbell (1985) showed that the sinking time of *Baetis rhodani* was greater for small nymphs than for large ones, as a result of both physical (dead nymphs) and behavioural (live nymphs) causes. Among small nymphs, upward swimming and 'parachuting' resulted in long drift bouts. However, Campbell's observations were made on animals added to the water surface, while in our investigation, they were allowed to enter the drift 'naturally'. Nevertheless, the same size-dependent mechanisms might have been operational also in the present study illustrating the complexity of the drift-settling process.

In the laboratory experiments *Baetis* drifted before contact with the predator in about 20% of the cases in daylight, while virtually no drift before contact was registered in infrared light. Thereby we conclude that vision may play an important part in the predator detection by *Baetis* and that the sight of an approaching predator may cause the mayflies to drift. Moving an object over the water surface elicited extensive drift of *B. rhodani* in a shallow, fast-flowing stream (Malmqvist, unpublished work). Sjöström (1985b) also presented evidence for visual detection of hunting *Dinocras cephalotes* by *Baetis rhodani*.

In conclusion, the field experiment demonstrated clear differences in drift activity between the experimental and control sections following predator introduction. As it was impossible to make true replicates we cannot statistically ascribe these differences to the introduction of *Dinocras*. However, because the results from the two field experiments and the laboratory experiment are all consistent we feel confident in our conclusion that the downstream drift of benthic invertebrates in streams is, to some extent, governed by the disturbance caused by hunting stonefly nymphs. Some species that comprise agile components of the benthos, e.g. *Baetis rhodani*, are especially prone to drift away under such circumstances. From this study, it is clear that the patterns of drift are further complicated by different responses among instars and their seasonal occurrence. The reasons for drift are certainly numerous, and the mechanism proposed here is only one possible cause of drift, disturbance by predator is probably important wherever perlid stoneflies, or other similarly mobile predators, e.g. perlodid stoneflies, are relatively abundant.

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