Substrate Attachment by Drifting Aquatic Insect Larvae

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SUBSTRATE ATTACHMENT BY DRIFTING AQUATIC INSECT LARVAE[1]

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Abstract. A series of laboratory experiments was designed to evaluate sediment type and illumination as factors affecting substrate attachment by 3 species of drifting aquatic insect larvae. Stone or cobble sediment patches with (natural) or without (sterile) an epilithic food resource were placed in artificial stream channels. Larvae of *Stenacron interpunctatum* (Ephemeroptera), *Acroneuria abnormis* (Plecoptera), and *Chimarra aterrima* (Trichoptera) were drifted over these patches. Attachment was partitioned into (1) settling and (2) failure to return to the drift (delayed drift). Significant sediment effects on settling were observed with *S. interpunctatum* and *C. aterrima*, for the former only during daylight. For all 3 species, significantly fewer animals settled in darkness. Significant delayed drift occurred in both *S. interpunctatum* and *C. aterrima*, but only in darkness, off sterile sediments, for the former. These results suggest that invertebrate drift may function as a direct, one-way link between substrate specific faunal associations.

A similar experiment tested the effect of a predator (*A. abnormis*) on substrate attachment by drifting prey (*S. interpunctatum*). No predator effect was observed on either settling or delayed drift of the prey.

Repeating the first series of experiments with killed animals allowed an evaluation of the relative importance of behavior and morphology in substrate attachment. A sediment effect was observed only in *A. abnormis*, and no settling differences were observed between *S. interpunctatum* and *C. aterrima*, species of strikingly different morphology. Killed animals rarely reentered the drift after settling. For these species, settling and delayed drift were much more a function of behavior than of morphology.

Key words: Acroneuria; *aquatic insect larvae;* Chimarra; *Ephemeroptera; invertebrate drift; Plecoptera; sediment type;* Stenacron; *substrate attachment; Trichoptera.*

INTRODUCTION

The existence of stream benthos in substrate specific associations is well documented (see Cummins 1966 for a review; Ulfstrand 1968, Egglishaw 1969). Several studies and laboratory investigations (Madsen 1968, Cummins and Lauff 1969, Higler 1975) have identified sediment particle size as a principal determinant of the distribution of stream benthos.

Invertebrate drift, within stream migration, hyporheic migration, and flight by aerial adults are the 4 types of movement involved in the development, maintenance, and coupling of benthic associations (Williams and Hynes 1976). The most intensively investigated of these movements has been invertebrate drift, the downstream transport of benthic invertebrates in streams. Since Needham's (1928) discovery of drift, numerous investigators have shown that most taxa engage in drifting during at least part of their life cycle.

Drift can be partitioned into entry into the drift, drifting downstream, and return to the substrate. Factors affecting entry into the drift and the kinds of animals actually in the drift have been well studied (see Waters 1972 and Müller 1974 for reviews). The distance travelled by drifters before returning to the substrate has also been examined (Waters 1965, McLay 1970, Elliot 1971, Keller 1975, Luedtke and Brusven 1976, Otto 1976). A significant question remains unanswered: does differential settling occur directly from the drift? If so, then substrate-specific associations may begin forming directly from the drift. If not, movement by the other methods mentioned above assumes greater importance.

This paper presents results from a series of experiments designed to evaluate attachment from the drift. Sediment particle size, food level, illumination, and predation were evaluated as factors influencing return to substrate. Use of both living and dead individuals of 3 taxa allowed the relative importance of behavior and morphology to be addressed. All experiments were conducted in artificial stream channels during June and July of 1977.

MATERIALS AND METHODS

Experimental animals

Three species of aquatic insect larvae were selected to provide a variety of sizes, morphologies, feeding habits, and swimming abilities. All animals were collected in New Hope Creek, North Carolina, USA (for a description of the creek, see Hall 1972).

Stenacron interpunctatum (Say) (Ephemeroptera:

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Heptageniidae) has been collected in the drift by Mason et al. (1973). In work done in North Carolina, Mark Luckenbach (*personal communication*) found that this mayfly consumed detritus and diatoms. Edmunds et al. (1976) reported that the genus probably feeds by collecting, and Cummins (1973) described a closely related species, *Stenacron fuscum,* as feeding by scraping. *Acroneuria abnormis* (Neuman) (Plecoptera: Perlidae) was another species selected. The feeding and drifting habits of this large, carnivorous stonefly were discussed by Walton et al. (1977). The third species, *Chimarra aterrima* Hagen (Trichoptera: Philopotamidae), is a net-spinning caddisfly (Ross 1944) feeding primarily on filtered detritus (Cummins 1973, Williams and Hynes 1973). A closely related species, *Chimarra obscura,* has been collected in the drift by Mason et al. (1973) and Cloud and Stewart (1974).

Fresh animals were collected for each experiment, and individual *S. interpunctatum* and *C. aterrima* were used once. Extreme drought made obtaining *A. abnormis* difficult, and individuals were occasionally reused the same day. A variety of instars from each species was randomly assigned to experimental treatments.

Artificial stream channels

Experiments were conducted in 2 Plexiglas®, recirculating stream channels (3.1 metres long × 0.25 metres wide × 0.15 metres deep). Filtered water (No. 60 sieve, 250 μm opening) from New Hope Creek was used to maintain depth at 3 centimetres. Current velocity was 20 cm/s. The channels were illuminated by 40-W fluorescent bulbs. Temperature was maintained at a constant 20°C.

Sediment type and illumination

Stones (20- to 50-millimetre diameter, Phi = −4, −5) and cobbles (75- to 150-millimetre diameter, Phi = −6, −7) from a riffle in New Hope Creek were transported in buckets of stream water to the laboratory. Phi classification is after Cummins (1962). Some of these natural sediments were then scrubbed and oven-dried at 150°C for 1 h. This provided 4 sediments, 2 naturally conditioned and 2 without a potential food resource. The scrubbed and dried sediments will be referred to as "sterile." Fresh natural sediments were gathered daily. An additional sterile sediment, stones (20- to 50-millimetre diameter) from a quarry, was added to the *S. interpunctatum* experiment.

A second factor was illumination. Animals were kept on a natural photoperiod, and experiments were conducted in the afternoon using fluorescent lighting and repeated after 2100 h in complete darkness. During nighttime work, a red lamp was used in brief pulses for necessary data gathering, but animals to be used later were not exposed to this light source.

To initiate each experimental run, either 15 *S. interpunctatum,* 15 *C. aterrima,* or 10 *A. abnormis* were simultaneously poured into the stream channel immediately upstream from a sediment patch (20 cm × 25 cm × 2 cm). Animals were poured from a 300 ml widemouth glass jar containing 75 ml of stream water. Animals drifting off the patch were caught in a downstream screen (250 μm opening). Data were collected as number of animals drifting off the patch during a given time period. Drift was counted immediately (0 time), at 1 min, 5 min, and thereafter at 5-min intervals for a total of 30 min. The sediment patch and all remaining animals would then be removed, a new patch added, and the procedure repeated.

To attach to the substrate a drifter must settle and then resist any factors tending to induce further drift. Therefore, the data could be meaningfully separated into 2 components, immediate drift (animals failing to settle on the substrate) and delayed drift (animals drifting after first settling on the substrate). I considered 0- and 1-min drift as immediate. By including 1-min drift I accounted for animals which failed to settle on the substrate but were temporarily caught in eddies. Animals drifting during the 1- to 5-min interval could not always be placed with certainty in either category (especially at night). Therefore, delayed drift was defined as that occurring between 5 and 30 min and included only animals drifting after first settling on the substrate.

Thus, for each species a completely randomized factorial experiment was run. For *A. abnormis* and *C. aterrima,* the 2 factors were sediment type (4 levels) and illumination (2 levels). Each treatment combination was replicated 4× giving a total of 32 experimental runs (4 × 2 × 4). The additional sediment type (quarry stones) and an additional replicate increased the number of experimental runs for *S. interpunctatum* to 50 (5 × 2 × 5). For each species, immediate and delayed drift were analyzed by analysis of variance. Because delayed drift was partially a function of the number of animals still in a sediment patch after 5 min, delayed drift was first divided by the number of animals in the patch after 5 min. Analysis of variance then followed arcsin square root transformation (this homogenizes the variance of proportional data).

Presence of predator

Another experiment tested the effect of a predator in the substrate on settling by drifting prey. *Stenacron interpunctatum,* a natural food of *A. abnormis,* were released upstream from sediment patches containing 10 *A. abnormis.* Each treatment combination was replicated 4× but the experiment was otherwise conducted and analyzed exactly as above. This experiment was then combined with the earlier 2-factor *S. interpunctatum* study into a completely randomized 3-factor experiment with a total of 72 experimental runs.

Killed animals

A final series of experiments allowed a further evaluation of the importance of behavior and morphology

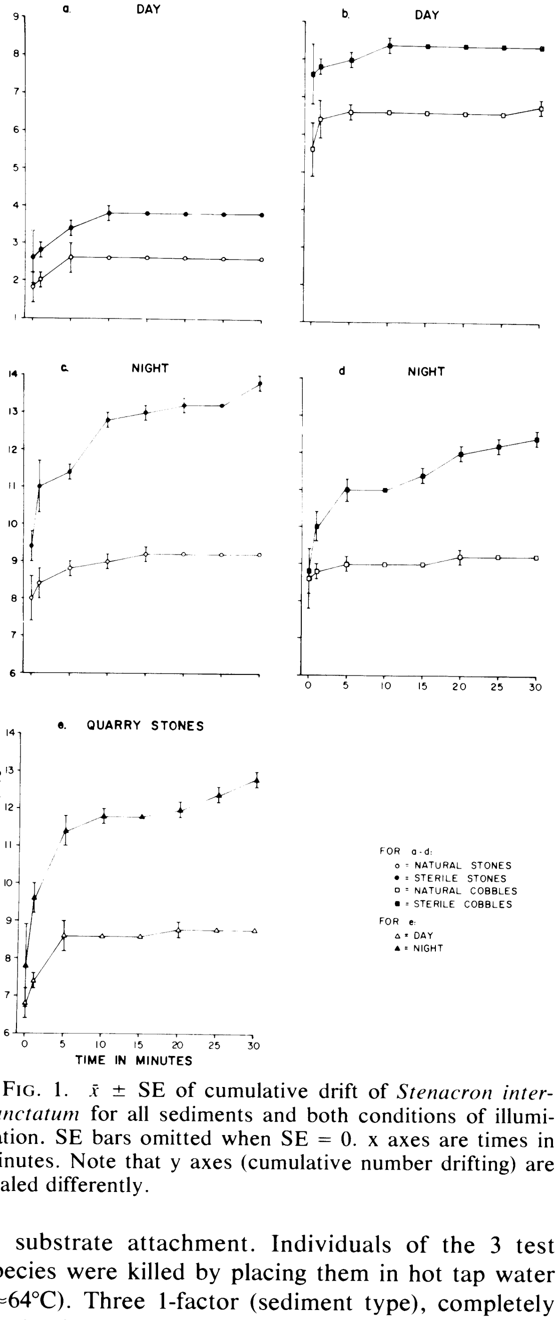

FIG. 1. $\bar{x}$ ± SE of cumulative drift of *Stenacron interpunctatum* for all sediments and both conditions of illumination. SE bars omitted when SE = 0. x axes are times in minutes. Note that y axes (cumulative number drifting) are scaled differently.

in substrate attachment. Individuals of the 3 test species were killed by placing them in hot tap water ($\approx$64°C). Three 1-factor (sediment type), completely randomized experiments were conducted and analyzed as above. Four replicates for each sediment resulted in 16 experimental runs for each test species.

RESULTS AND DISCUSSION

Though the techniques used in these experiments were chosen to minimize trauma to the test animals, handling could produce unusual behavior. Any interpretation of the results must be done with this in mind.

Sediment type and illumination

Stenacron interpunctatum.—Data from the *S. interpunctatum* experiment are plotted in Fig. 1 as $\bar{x}$ ± SE of cumulative number drifting off the sediment patches during the 30-min test periods. The figures are arranged to facilitate comparisons between the natural and sterile members of the stone and cobble sediment pairs under the 2 conditions of illumination.

These plots strongly support the partitioning of the data into immediate drift (0–1 min) and delayed drift (5–30 min). The curves for sterile sediments at night (quarry stones included) are strikingly steeper in slope than are all other curves. In fact, delayed drift off sterile sediments at night nearly denuded these sediments in 30 min. This indicates that settling on the substrate and resistance to drift after settling warrant separate consideration.

During the day, *S. interpunctatum* was more successful at settling on stone sediments than on the others, but these differences disappeared at night (Fig. 1). For all sediments, fewer animals settled at night.

Immediate drift (cumulative 1 min) was analyzed by analysis of variance, and the sediment, illumination, and sediment × illumination effects were strongly significant ($P < .001$, $P \ll .001$, and $P < .001$, respectively). The sediment effect was partitioned by Tukey's HSD (Steel and Torrie 1960). During the day, significantly fewer *S. interpunctatum* drifted immediately off the 2 stone sediments than off the other sediments ($P = .05$). The lack of any significant differences at night helps explain the significant interaction term.

For delayed drift (drift during the 5- to 30-min interval), the sediment, illumination, and sediment × illumination effects were all highly significant ($P < .001$ for each). Substantial delayed drift occurred at night off the sterile sediments even though relatively few animals were still available to drift. In all other experimental runs, animals once attached to the substrate tended to remain there. The sediment effect was partitioned by Tukey's HSD ($P = .05$, Steel and Torrie 1960), and at night significantly greater delayed drift occurred off sterile stones and quarry stones than off the other sediments. Drift off sterile stones at night was also greater than that off sterile cobbles. The lack of any significant differences during the day helps explain the significant interaction term.

Thus, sediment type significantly affected settling of *S. interpunctatum* from the drift during the daytime and delayed drift at night. Presence of an epilithic food resource did not affect settling, but the sharply higher delayed drift off sterile sediments at night strongly suggests a food-level response.

Delayed nighttime drift of *S. interpunctatum* off sterile sediments soon removed most of those previously settled. This suggests that this species would not colonize a substrate (from the drift or otherwise) unless epilithic resources were adequate. During rising water, newly covered sediments could provide migrants with temporary refuges from predation and competition. *Stenacron interpunctatum* and similarly

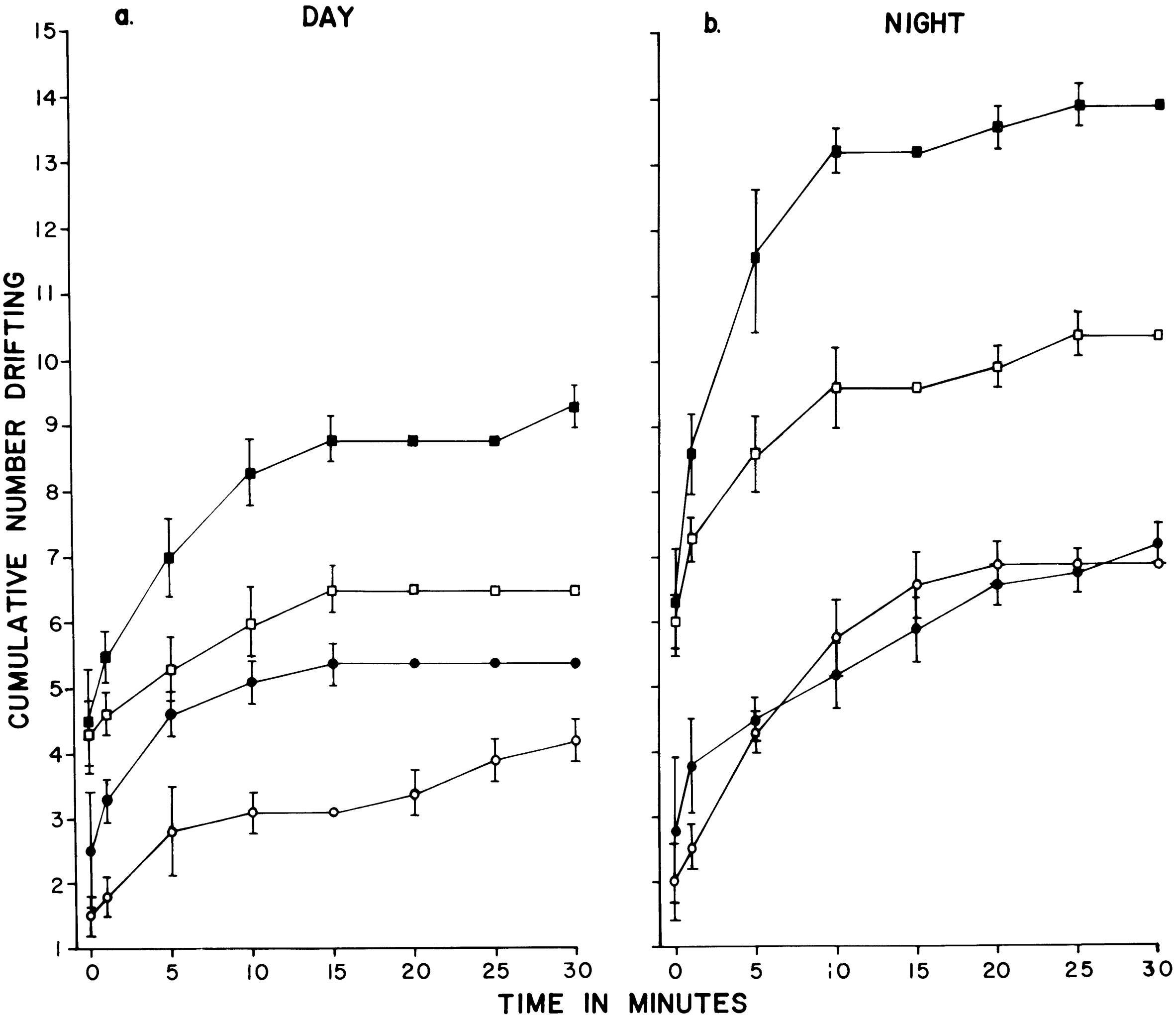

FIG. 2. $\bar{x}$ ± SE of cumulative drift of *Chimarra aterrima* for all sediments and both conditions of illumination. SE bars omitted when SE = 0. Open symbols = natural sediments, closed symbols = sterile sediments. Circles = stones, squares = cobbles.

behaving species might not colonize these substrates until suitable epilithic resources developed.

Acroneuria abnormis.—*Acroneuria abnormis* was much more successful at attaching to the substrate than was *S. interpunctatum*. On all sediments and under both conditions of illumination, most animals attached immediately to the substrate (Table 1). In only 2 of the 32 experimental runs did an animal drift after the 0 time period, 1 from natural cobbles during the day and 1 from sterile cobbles at night. Delayed drift essentially did not occur in this species. Walton et al. (1977) reported that at a similar current velocity and density, 2 or fewer *A. abnormis* drifted off stone and cobble sediments in 24 h.

By analysis of variance, no evidence was found for any sediment effect on settling (P = .43), but significantly more immediate drift occurred at night (P = .004). *Acroneuria abnormis*, a strong swimmer, indiscriminantly settled on the sediments, but the species settled less effectively at night.

Walton et al. (1977) found that entry into the drift by *A. abnormis* off stones and cobbles was strongly influenced by density and sediment type but was independent of velocity. They suggested that this was a response to intraspecific competition for interstitial spaces. These findings all indicate that biological fac-

TABLE 1. $\bar{X}$ ± SE (n = 4) for immediate drift (cumulative 1 min) of *Acroneuria abnormis*

	Sediment			
Illumination	Natural stones	Sterile stones	Natural cobbles	Sterile cobbles
Day	0.25 ± 0.25	0.25 ± 0.25	0.50 ± 0.29	1.50 ± 0.64
Night	2.50 ± 1.19	1.50 ± 0.64	2.50 ± 0.87	2.75 ± 1.10

tors may be more important than physical factors in influencing drift of this species.

Chimarra aterrima.—Under both conditions of illumination, distinct differences in settling of *C. aterrima* occurred as a function of sediment type, and *C. aterrima* was less successful at settling at night (Fig. 2). By analysis of variance the sediment and illumination effects were both significant ($P \ll .001$ and $P = .002$, respectively), but the interaction was not ($P = .18$).

Fewer *C. aterrima* attached to cobbles than stones under both conditions of illumination. During the day, immediate drift was significantly greater (by Tukey's HSD, $P = .05$, Steel and Torrie 1960) off sterile cobbles than off natural stones. At night, immediate drift off the 2 cobble sediments was significantly greater than that off the 2 stone sediments. Thus, a significant sediment effect occurred both during the day and in darkness. This contrasts with the *S. interpunctatum* experiment where, at night, no evidence was found for a significant sediment effect.

The propensity for settled *S. interpunctatum* to remain attached to all sediments during the day and to natural sediments at night was not shared by *C. aterrima* (compare Fig. 1 with Fig. 2). Substantial delayed drift occurred off most sediments under both conditions of illumination. Most taxa drift in a diel periodicity with substantially greater drift occurring at night (Waters 1972, Müller 1974). Waters (1972) reported that most exceptions to this generalization are caddisflies, and *C. aterrima* may also be a day-active caddisfly.

For delayed drift of *C. aterrima,* the sediment and illumination effects were significant ($P = .002$ and $P = .003$, respectively), but the interaction was not ($P = .26$). Significantly more delayed drift occurred at night, and by Tukey's HSD ($P = .05$, Steel and Torrie 1960), delayed drift at night was significantly greater off sterile cobbles than that off natural sediments. Differences in delayed drift during the day were not significant.

Settling of *C. aterrima* was not affected by presence of an epilithic food resource. However, delayed drift at night off sterile cobbles was significantly greater than that off natural cobbles, suggesting a food-level response.

In summary, each of the 3 test species demonstrated a distinctly different pattern of substrate attachment. A clear sediment effect on settling of *S. interpunctatum* during the day disappeared at night. Sediment type did not influence settling of *A. abnormis,* but a significant sediment effect occurred with *C. aterrima* under both conditions of illumination. Significant delayed drift of *S. interpunctatum* occurred only at night from sterile sediments. *Acroneuria abnormis* did not engage in delayed drift, and substantial delayed drift of *C. aterrima* occurred during the day and at night off most of the sediments. These findings emphasize the importance of investigating a variety of taxa before generalizations concerning the total fauna should be made.

Physical properties of an animal (size, shape, and density) and behavior (swimming ability) were identified by McLay (1970) as the principal factors determining the distance that animal will drift. Elliott (1971) and Luedtke and Brusven (1976) similarly stressed behavior, and Elliott (1971) also discussed the importance of aquatic macrophytes as a natural filter for drift. To these factors can now be added sediment particle size. On a species-specific basis, sediment type can apparently strongly influence return to the stream bottom.

Enhanced delayed drift by *S. interpunctatum* off all sterile sediments at night and by *C. aterrima* off sterile cobbles at night likely was a food-level effect. *Stenacron interpunctatum* probably feeds on epilithic material (Cummins 1973, Edmunds et al. 1976). *Chimarra aterrima* usually harvests detritus captured in its nets, but the species will feed on epilithic material (Williams and Hynes 1973). Hildebrand (1974) and Keller (1975) have shown that a reduced level of epilithic food resources will induce drift in species dependent on these resources. Hildebrand (1974) also found that hydropsychid caddisfly larvae, normally net spinners, drifted in response to epilithic food level.

Hildebrand (1974) assumed that increased searching activity at low food levels increased exposure to current, and increased drift resulted from accidental dislodgment. An alternative explanation is deliberate desertion of an unsatisfactory habitat. *Chimarra aterrima* was much more difficult to dislodge manually from a stone or cobble than was *S. interpunctatum,* yet it was quite likely to engage in delayed drift. Edington (1965) observed hydropsychid caddisfly larvae swimming away from the substrate when preferred current velocities were altered. Williams and Hynes (1973) reported that *C. aterrima* in a Canadian stream preferred velocities of >40 cm/s. In my experiments, this species may have been deliberately deserting an unfavorable habitat (insufficient current velocity).

Altered behavior under conditions of reduced illumination has been implicated as contributing to nocturnal increases in drift. Hughes (1966) reported that larvae of a baetid mayfly used a dorsal light response (a general orientation response in many animals) for orientation, and without an overhead light source the nymphs could not efficiently land on the substrate. He suggested that this might be a general phenomenon and could contribute to increased nocturnal drift. Elliott (1971) reported that distance drifted at night by 4 taxa (3 mayflies and 1 amphipod) did not increase significantly over daytime distance. He felt that this weakened Hughes' (1966) hypothesis.

A significant nocturnal increase in immediate drift (decreased settling) was observed in all 3 test species. Even *A. abnormis,* a strong swimmer, was less adept at attaching to the substrate at night. Luedtke and

TABLE 2. $\bar{X} \pm$ SE (n = 4) for drift during each time interval of *Stenacron interpunctatum* off sediments with a predator (10 *Acroneuria abnormis*/sediment patch)

Illumination	Time (min)	Sediment			
		Natural stones	Sterile stones	Natural cobbles	Sterile cobbles
Day	0	2.7 ± 0.3	2.7 ± 0.5	6.0 ± 2.0	7.8 ± 1.4
	1	0.5 ± 0.3	0.8 ± 0.5	0.3 ± 0.3	. . .
	5	0.3 ± 0.3	1.7 ± 0.9	0.7 ± 0.5	0.7 ± 0.5
	10	0.3 ± 0.3	1.3 ± 0.6	0.3 ± 0.3	0.3 ± 0.3
	15	. . .	0.3 ± 0.3	. . .	. . .
	20	0.7 ± 0.5	. . .	. . .	. . .
	25	. . .	. . .	. . .	0.3 ± 0.3
	30	. . .	. . .	. . .	. . .
Night	0	5.5 ± 1.6	7.8 ± 1.2	7.3 ± 0.5	8.5 ± 1.7
	1	0.5 ± 0.3	1.0 ± 0.4	0.7 ± 0.2	1.5 ± 0.6
	5	1.3 ± 0.6	1.5 ± 0.3	0.3 ± 0.3	1.3 ± 0.9
	10	0.3 ± 0.3	0.5 ± 0.5	0.5 ± 0.3	0.3 ± 0.3
	15	0.3 ± 0.3	0.3 ± 0.3	0.3 ± 0.3	0.3 ± 0.3
	20	0.8 ± 0.5	0.3 ± 0.3	. . .	1.0 ± 0.4
	25	0.7 ± 0.3	. . .	. . .	0.3 ± 0.3
	30	0.5 ± 0.3	0.8 ± 0.3	. . .	. . .

Brusven (1976) found that return to substrate rates for 4 taxa (2 stoneflies, 1 mayfly, and 1 caddisfly) were sharply reduced in darkness. These findings suggest a nocturnal increase in distance drifted. Further studies with more taxa are needed to reconcile the apparent contradiction between these findings and Elliott's (1971).

Further investigation of the sensory cues used by drifters in settling is also needed. The sensory information allowing *S. interpunctatum* to settle differentially in the daytime was no longer available at night. Though fewer *C. aterrima* settled at night, a significant sediment effect also occurred at night.

Presence of a predator

Data for the *S. interpunctatum*-with-a-predator (10 *A. abnormis*/sediment patch) experiment are presented in Table 2. To evaluate the effect of the predator, compare Table 2 with Fig. 1. Notice that for most corresponding sediment and illumination comparisons, settling and delayed drift were similar with or without *A. abnormis*. The overall pattern of sediment and illumination differences observed in the earlier experiment (without the predator) held with the predator.

The 2 experiments were combined to form a 3-factor experiment (sediment type, illumination, and predator) and immediate drift was analyzed by analysis of variance. Although the sediment and illumination effects were highly significant ($P \ll .001$ for both) no evidence was found for a predator effect ($P = .72$). An analysis of variance of delayed drift also produced no evidence for a predator effect ($P = .39$).

The lack of any discernible predator effect on return to substrate may have been due to predator density. Keller (1975) found that, at a lower density than I used, presence of a predator did not influence drift of a heptageniid mayfly. Work in progress by me indicates that substantially greater densities of *A. abnormis* are required to enhance drift of *S. interpunctatum*.

Killed animals

As expected, killed animals were less likely to settle on sediment patches than were live animals (compare Table 3 with Fig. 1, Table 1, and Fig. 2). However, killed animals once in the substrate tended to remain there. Delayed drift occurred in only 14 of 48 experimental runs, and in none of those 14 did >1 animal drift.

A separate analysis of variance of immediate drift for each species indicated that a significant sediment effect occurred only in *A. abnormis*, ($P = .002$). The P-values for *S. interpunctatum* and *C. arterrima* were .39 and .41, respectively. By Tukey's HSD (Steel and Torrie 1960) at the $P = .05$ level, immediate drift of *A. abnormis* was significantly less off natural stones than that off both cobble sediments.

No differences in tendency to settle were observed between killed *S. interpunctatum* and killed *C. aterrima*, 2 species of strikingly different morphology. The overall average percentage drifting immediately was 76.3% for the former and 75.0% for the latter. On a percentage basis, drift of killed *A. abnormis* off cobble sediments approached that of the other 2 species off

TABLE 3. $\bar{X} \pm$ SE (n = 4) of immediate (cumulative 1 min), 5 min, and total (cumulative 30 min) drift of killed animals

Species	Time	Sediment			
		Natural stones	Sterile stones	Natural cobbles	Sterile cobbles
	1 min	11.0 ± 1.5	10.5 ± 1.5	13.0 ± 1.1	11.3 ± 0.8
Stenacron interpunctatum	5 min	11.5 ± 1.5	10.5 ± 1.5	13.0 ± 1.1	11.5 ± 0.6
	30 min	11.5 ± 1.5	10.7 ± 0.8	13.0 ± 1.1	11.8 ± 0.5
	1 min	2.5 ± 0.3	4.5 ± 0.9	5.8 ± 0.7	7.0 ± 0.4
Acroneuria abnormis	5 min	3.0 ± 0.4	4.5 ± 0.9	5.8 ± 0.7	7.0 ± 0.4
	30 min	3.7 ± 0.3	4.8 ± 0.8	6.3 ± 0.8	7.3 ± 0.5
	1 min	10.2 ± 1.4	12.3 ± 0.6	11.5 ± 0.6	11.0 ± 0.0
Chimarra aterrima	5 min	10.5 ± 1.3	12.3 ± 0.6	12.0 ± 0.7	11.5 ± 0.5
	30 min	11.0 ± 1.6	12.3 ± 0.6	12.3 ± 0.5	11.5 ± 0.5

all sediments. This similarity occurred in spite of the significantly greater length and volume of *A. abnormis*.

These findings strongly suggest that, for the test species, settling on the substrate and entry into the drift were much more a function of behavior than of morphology. Delayed drift in killed animals was rare, but delayed drift by living *S. interpunctatum* at night nearly denuded the sterile substrates. Living *C. aterrima* actively engaged in delayed drift off most substrates under both conditions of illumination.

CONCLUSIONS

The importance of substrate and the associated specific faunas to a variety of processes in streams is well recognized. Rate of leaf-litter breakdown (Reice 1974), life-cycle length (Thorup 1963), and morphometric development (Svensson 1975) have all been reported as varying with substrate type. My results suggest that substrate-specific associations may begin forming directly from the drift. Drift may occasionally function as a direct, 1-way link connecting similar associations. Lowered energy cost of migration is a probable advantage to animals employing drift in this manner.

Other factors of probable importance to substrate attachment from the drift include current velocity, area of sediment patch and competition. Studies of these factors and their interactions with sediment type, food level, illumination, and predation would enhance our understanding of the substrate attachment process. A major goal of these studies should be determining the relative importance of the types of population movements occurring in streams. This could then be profitably integrated with results from microdistribution studies such as those of Rabeni and Minshall (1977). A thorough understanding of the formation and maintenance of substrate specific associations would be a major contribution to stream ecology.

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