Predation by Paragnetina fumosa (Banks) (Plecoptera: Perlidae) on Mayflies: The Influence of Substrate Complexity

ABSTRACT: An experiment was conducted to determine if substrate complexity influenced the rate of predation by *Paragnetina fumosa* on several of its naturally occurring mayfly prey species. Rates of predation were evaluated in circular plexiglass streams on three substrate types: (1) sand alone (0.5-2.0 mm); (2) one layer of pebbles (3-5 cm) 25-50% embedded in sand; and (3) sand covered by one layer of unembedded pebbles. The predation rate was lower on the complex substrate (pebbles unembedded in sand) than on the simple substrate (sand alone). The response on the pebble embedded in sand substrate was intermediate. The differences in predation rates among the various substrates are attributed to the availability of spatial refuge.

INTRODUCTION

The distribution, abundance and behavior of stream-dwelling aquatic insects are influenced by the morphometric characteristics of a stream, such as current velocity, depth and especially, substrate composition (Minshall, 1984). The functional significance of substrate type to insects has traditionally been related to the trapping of organic matter for food and the provision of shelter from current. Little attention has been given to the function of substrate in providing spatial refuge from predators.

A few studies have investigated the role of substrate in determining fish predation rates on macroinvertebrates. Brusven and Rose (1981) found that insect predation by the torrent sculpin (*Cottus rhotheus*) in laboratory streams was significantly lower on complex substrates (cobble over sand) relative to less complex substrates (sand alone and cobble half embedded in sand). Ware (1972) found that intensity of predation and total macroinvertebrate (amphipod) consumption by rainbow trout (*Salmo gairdneri*) in glass aquaria were inversely related to substrate complexity. However, Flecker and Allan (1984) reported, in a field manipulation, that fish did not reduce insect abundance on substrates offering limited spatial refuge as compared to more complex substrates.

A recent review (Peckarsky, 1984) noted that few studies have investigated the influence of substrate refuges in insect-insect predator-prey interactions. The purpose of this experiment was to determine if substrate complexity (*i.e.*, availability of spatial refuge) influences the rate of predation by a stonefly predator, *Paragnetina fumosa* (Banks), on some of its naturally occurring mayfly prey. The hypothesis tested was that predation rate would be inversely related to substrate complexity.

MATERIALS AND METHODS

Organisms were collected with a D-frame net from Sinking Creek, Giles County, Virginia. On the first sampling trip, several predacious species were collected and returned to the laboratory for gut analysis in order to determine the preferred prey item(s) for each species. After this initial survey, one stonefly species (*Paragnetina fumosa*) and species of two mayfly families (Baetidae and Heptageniidae) were selected to serve respectively as predator and prey in the subsequent experiment.

The experiment was conducted in circular plexiglass streams powered by air bubbles (Mackay, 1981). Rates of predation were tested in the streams on three different substrate types: (1) 2 cm of sand alone (0.5-2.0 mm); (2) one layer of pebbles (3-5 cm) inserted into 2 cm of sand (25-50% embedded); and (3) 2 cm of sand covered by one layer of unembedded pebbles. Pebbles, when present, were placed as close together as possible in order to form interstitial refuges between them. However, sand filled nearly all of the interstitial spaces in the pebble embedded in sand treatment. Four streams were established for each substrate type. One stream in each group contained prey but no predators and served as a control; the other three streams in each group were test streams containing both predators and prey. The average number of control stream prey items unaccounted for at the end of the experiment was subtracted from the number of prey items eaten in each test stream in order to adjust for nonpredatory losses.

One species of prey, *Baetis vagans* (3-4 mm length), was easily separated from other mayflies in the field and served as the principal prey item—10 per artificial stream. In addition, two size classes, small (3-6 mm) and large (9-11 mm), of heptageniid naiads were used as prey items—five small and two large in each artificial stream. The heptageniid prey included: *Epeorus rubidus*, *E. dispar*, *Stenonema sinclari*, *Stenacron interpunctatum* and *Leucrocuta* sp. The predator, *Paragnetina fumosa*, was collected in two size classes, medium (15 mm) and large (25 mm)—one medium and two large individuals were placed in each test stream.

Predator and prey organisms were collected and returned to the laboratory in slightly iced stream water. Prey organisms were subsequently placed in the artificial streams, while predators were starved in separate holding tanks for 48 hr. After 48 hr, the predators were placed in the treatment streams and allowed to interact with the prey. Qualitative observations of predator foraging behavior and prey escape behavior were made during the period of predator-prey interaction. The experiment was terminated after 72 hr, and the number of prey items missing (presumed eaten) was determined. The data were analyzed statistically using a one-way ANOVA and Duncan's Multiple Range Test for the separation of means.

RESULTS AND DISCUSSION

The mean number of nonpredatory losses in the control streams was 1.0 for *Baetis vagans* and 0.7 for the heptageniid species. These losses (10% of initial densities) were due primarily to adult emergence.

The overall ANOVA was significant ($P \leq 0.05$) for *Baetis vagans*, but was not significant for the heptageniids (Table 1). For *B. vagans* the rate of predation on the sand substrate was significantly higher than that on the unembedded pebble substrate; the predation rate on the embedded pebble substrate was intermediate. Although the overall ANOVA was not significant for the heptageniid prey, the predation rate was inversely related to substrate complexity.

During qualitative observations, no encounters between predator and prey were observed in the unembedded pebble treatment. In this treatment, the predators were observed moving across the tops of the pebbles while the prey remained in the interstitial spaces between the pebbles. Several observations of predator-prey interaction in the sand and embedded pebble treatments indicated that *Paragnetina fumosa* searches for prey by sweeping its antennae slowly across the substrate as it moves into the current. Antennal contact with a prey item elicited a rapid movement towards the prey accompanied by grasping motions with the prothoracic legs. *Baetis vagans* and the heptageniids exhibited different escape responses when touched by the predator's antenna. When *B. vagans* was contacted, the naiads actively entered the drift, which may partially explain the predominance of *Baetis* species in the drift of many streams. In contrast, the heptageniids rapidly crawled away over the substrate. No successful captures were observed.

The results of this study suggest that the predation rate of *Paragnetina fumosa* on mayfly prey items is inversely related to substrate complexity. The availability of spatial refuge in the unembedded pebble substrate resulted in the lowest predation rates for both *Baetis vagans* and the heptageniids. In contrast, the sand and pebble embedded in sand treatments offered relatively less spatial refuge from the predators and higher predation rates were exhibited. It is apparent that the often overlooked factor of embeddedness and other aspects of substrate complexity should be included in studies of insect-substratum relationships. Results from the embedded pebble treatment indicate that even moderate sedimentation could affect insect distribution and abundance because of increased predation rates. Further experiments are needed to determine the relative importance of food availability, exposure to current, exposure to predators and other factors in determining substrate preference by aquatic insects.

TABLE 1.—Number of mayflies eaten ($\overline{X}$ + 1 SE) by *Paragnetina fumosa* during 72 hr of interaction on three substrate types: S = sand; PE = pebbles embedded in sand; PU = unembedded pebbles on sand. Initial densities were 10 and 7 per replicate for *Baetis vagans* and the heptageniid species, respectively. F and P values are associated with a one-way ANOVA (df = 2,6). Means with the same superscript are not significantly different based on Duncan's Multiple Range Test ($P < 0.05$)

	Substrate type				
Prey	S	PE	PU	F	P
Baetis vagans	$6.0^{a} \pm 1.0$	$4.7^{ab} \pm 0.9$	$1.7^{b} \pm 0.9$	5.78	.039
Heptageniidae	5.6 ± 0.3	4.3 ± 1.0	2.9 ± 0.9	2.82	.137

LITERATURE CITED

BRUSVEN, M.A. AND S.T. ROSE. 1981. Influence of substrate composition and suspended sediment on insect predation by the torrent sculpin *Cottus rhotheus*. *Can. J. Fish. Aquat. Sci.*, **38**:1444-1448.

FLECKER, A.S. AND J.D. ALLAN. 1984. The importance of predation, substrate, and spatial refugia in determining lotic insect distribution. *Oecologia*, **64**:306-313.

MACKAY, R.J. 1981. A miniature laboratory stream powered by air bubbles. *Hydrobiologia*, **83**:383-385.

MINSHALL, G.W. 1984. Aquatic insect-substratum relationships, p. 358-400. *In*: V.H. Resh and D.M. Rosenberg (eds.). The ecology of aquatic insects. Praeger Publishers, New York.

PECKARSKY, B.L. 1984. Predator-prey interactions among aquatic insects, p. 196-254. *In*: V.H. Resh and D.M. Rosenberg (eds.). The ecology of aquatic insects. Praeger Publishers, New York.

WARE, D.M. 1972. Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density, and prey size. *J. Fish. Res. Board Can.*, **29**:1193-1201.

KURT W. PONTASCH, University Center for Environmental and Hazardous Materials Studies and Department of Biology, Virginia Polytechnic Institute and State Univ., Blacksburg 24061.
Submitted 27 May 1987; accepted 6 August 1987.

JOSEPH GROSSFIELD

Dr. Joseph Grossfield of the Biology Department of City College of New York died December 12, 1987. He was a graduate of CCNY and taught at Purdue University before joining its faculty. He worked on behavioral genetics of *Drosophila* and more recently of striped bass and other migratory fish. Dr. Grossfield also served as Associate Editor for Genetics and Cytology of the American Midland Naturalist from 1974-1978.