HYDROBIOLOGIA

The Influence of Substrate Particle Size on the Microdistribution of Stream Macrobenthos

by

KENNETH W. CUMMINS & GEORGE H. LAUFF

Kellogg Biological Station Michigan State University, USA

The Influence of Substrate Particle Size on the Microdistribution of Stream Macrobenthos

by

KENNETH W. CUMMINS & GEORGE H. LAUFF

Kellogg Biological Station Michigan State University, USA

INTRODUCTION

The great majority of research conducted on organism-substrate relationships is attributable to marine ecologists (e.g. CRAWFORD, 1937; TEST, 1945; POMERAT & NEISS, 1946; HOLME, 1949, 1954; JONES, 1950; LOOSANOFF et al., 1951; SWAN, 1952; PRATT, 1953; BADER, 1954; WILSON, 1955, 1958; PARKER, 1956; SANDERS, 1956, 1958, 1960; WIESER, 1956, 1957a, 1957b, 1959, 1960a, 1960b; WILLIAMS, 1958; CLARK & HADERLIE, 1960; SANDERS, et al., 1962; BUCHANAN, 1963; DRISCOLL, 1967. An important feature of many of these investigations on marine benthos has been the inclusion of critical laboratory experiments.

A lesser number of investigations specifically aimed at various aspects of organism-substrate relationships have been completed by freshwater ecologists (see review by CUMMINS, 1966). Most of these have concerned lentic waters. In an early study, KERECKER & LANCASTER (1933) worked on the littoral fauna of western Lake Erie associated with basic substrate types which they described and photographed. RAWSON (1941) related lake substrates and productivity and MILNE (1943) discovered a relationship between the nature of the sediments on which caddisflies were found in Saskatchewan Lakes and their case building requirements. HUNT (1953) and LYMAN (1956) concluded from their studies in Michigan lakes that

substrate was critical in determining mayfly distribution patterns. HENSEN (1954) studied substrate relations of deepwater benthos in Cayuga Lake and related invertebrate distributions (HENSEN, 1962) to actual physical analyses in the Straits of Mackinac (LAUFF et al., 1961b). CORBELLA et al., (1956) correlated the distribution of benthic populations with the chemical nature of lake sediments, especially the sedimentation of "planktonic debris". BEATY & HOOPER (1958) sorted sediments of Sugarloaf Lake, Michigan, by wet sieving into five categories which they correlated with benthic distributions. BRINKHURST (1967) and JOHNSON & MATHESON (1963) related chemical and textural characteristics to invertebrate distributions in Lake Huron and Lake Ontario, respectively.

Of particular interest are the papers of SUBLETTE (1957, 1958) on the bottom fauna of Lake Texoma, Oklahoma and Chaplin's Lake, Louisiana, which contain good discussions of organism-substrate relationships. Also, the investigations of MARZOLF (1962, 1966) on the deepwater amphipod *Pontoporeia* are excellent since they represent the correlation of field and laboratory studies and include sediment analysis with special emphasis on the role of bacteriobenthos.

Among the first stream ecologists to investigate the relationship between benthic distribution patterns and the nature of the substrate were PERCIVAL & WHITEHEAD (1929). They recognized seven basic substrate types and found that certain animal species were consistently associated with each. HUNT (1930) also recognized the importance of substrate type in determining stream benthos distributions. Although ADAMS (1901) recognized the significance of differences in erosional and depositional habitats to stream faunas, and ELLIS (1936) discussed the importance of erosion silt to mussel distributions in depositional regions of lotic waters, the full statement of the "erosion-deposition concept" in stream ecology is attributed to MOON (1939). In rapidly flowing water (erosional) all but the coarse substrate units are washed away, resulting in characteristic fauna adapted for attachment, clinging or avoidance of the current. In regions of reduced flow (depositional) fine sediments are deposited and the organisms are variously adapted to deal with such an environment.

WENE (1940) appears to have been the first stream investigator to employ actual sediment analysis in a study of organism-substrate relationships. He correlated the distribution of midge larvae with the the occurrence of five particle size ranges. LINDUSKA (1942) concluded that substrate types, which he described, were most critical in determining mayfly distributions in Rattlesnake Creek, Montana. PENNAK & VAN GERPEN (1947) visually recognized four substrate types in a Colorado trout stream and described the benthic fauna

146

associated with each. SCOTT (1958) measured three dimensions of stones with which caddisfly larvae were associated in the River Dean and SCOTT & RUSHFORTH (1959) and SCOTT (1960, 1966) have suggested that a factor, termed cover fraction (Cvf), which relates the size of stones and the portion of a sample area covered with stones, can be employed as an index of benthic macroinvertebrate density. KAMLER & RIEDEL (1960) collected the larger substrate units, sorted them into size classes and counted the number of particles; these data were correlated with the distribution of benthic species from streams in the Tatra Mountains of Poland. A combination of substrate particle size analysis of field samples and laboratory experiments were utilized by ERIKSEN (1961, 1963a, 1963b, 1964a, 1964b, 1966) and CUMMINS (1961, 1964, 1966) in investigations of aquatic insects in Fleming Creek, Michigan. Substrate responses were included in experiments by BOVBJERG (1959, 1964) on density dependent dispersal of crayfish populations in a laboratory stream. FELDMETH (1966) also considered the importance of substrate in experiments concerned with respiratory responses of a stream limnephilid caddisfly. THORUP (1966) investigated substrate-stream benthos relationships in several Danish springbooks and reviewed a major portion of the European literature on the subject.

· A number of investigators have studied substrate relations, at least indirectly, by providing substrates for colonization in the natural environment (e.g. MOON, 1940; WENE & WICKLIFF, 1940; ALBRECHT, 1953: CIANFICCONI & RIATTI, 1957; DENDY, 1963; BREWER & GLEASON, 1964).

Very few papers have appeared in which stream organism-substrate relations have been investigated under laboratory conditions. (SHELFORD, 1914; ERIKSEN, 1961; CUMMINS, 1961, 1964; LAUFF & CUMMINS, 1964; see also, review by CUMMINS, 1966). The present paper is intended as a contribution to this experimental area, although some preliminary field data have been included for correlative purposes.

METHODS

Description of Field Study Area

Fleming Creek is a small spring-fed stream in southeastern Michigan with a drainage area limited to northeastern Washtenaw County. The stream ranges from 5 to 10 meters in width and is shallow enough for detailed analyses, averaging about 30 cm in depth

with some pools a meter or more deep. The water is relatively free from pollution as there are few dwellings along its course and only restricted areas of cultivated crops. The principle study area is essentially undisturbed since it is within the confines of the University of Michigan Botanical Gardens.

Due to the calcareous nature of the drainage area, alkalinity determinations average about 230 ppm $CaCO_3$. Temperatures range from near 0° C in the winter to about 25° C in the summer, with springs and vegetation cover causing local variations; diurnal fluctuations up to three degrees have been measured. Determinations of oxygen concentration indicate a general saturation from surface to bottom at all seasons, attributable to the shallowness of the stream and its numerous riffle areas. Further descriptions of Fleming Creek are given in CUMMINS (1961, 1964) and ERIKSEN (1960, 1961).

Field Samples and Stream Sediments

A large number of preliminary field collections and observations were made, and all ten species were reared in the laboratory prior to conducting experiments. In conjunction with the laboratory experiments, quantitative field samples were taken approximately every two weeks from July 30, 1959 through June 7, 1960. Data obtained from these quantitative field samples provided a basis for the interpretation of experimental results.

The quantitative field samples were taken with a 10 cm diameter cylinder which retained both substrate materials and organisms. (For a complete description of sampling sites and procedures see CUMMINS, 1961). The animals were removed by hand sorting and with the elutriating device described by LAUFF et al. (1961a). Particle size analysis of substrate samples was accomplished by decantation of silt and clay, separation of silt and clay by centrifugation and dry sieving of the very fine sand and coarser particle sizes into 11 categories according to the Wentworth Scale (WENTWORTH, 1922, see Table I). A modified classification was adopted in which the granule and a portion of the pebble categories of the Wentworth Scale have been replaced by a gravel category (CUMMINS, 1962). The phi scale (negative log to the base 2 of the particle size diameter in millimeters) and corresponding millimeter size categories are compared in Table I. Complete discussions of the sampling and analysis techniques are presented in CUMMINS (1961, 1962).

Sediments used in the experimental studies were collected from Fleming Creek, washed, oven dried at 40° C and sorted by dry sieving into eight particle size classes. The categories were 1/8, 1/4, 1/2, 1, 2, 4, 8 and 16 mm size classes. (Actually each of these designations

148

TABLE I
Substrate particle size terminology and categories*

Modified classification (CUMMINS, 1961)	Wentworth classification		Phi Scale
	Name	Particle size range in mm	
Boulder	Boulder	> 256	− 8
Cobble	Cobble	64−256	− 6, − 7
Pebble ——————— Gravel	Pebble	32−64 16−32 8−16 4−8	− 5 − 4 − 3 − 2
	Granule	2−4	− 1
Very coarse sand	Very coarse sand	1−2	0
Coarse sand	Coarse sand	0.5−1	1
Medium sand	Medium sand	0.25−0.5	2
Fine sand	Fine sand	0.125−0.25	3
Very fine sand	Very fine sand	0.0625−0.125	4
Silt	Silt	0.0039−0.0625	5, 6, 7, 8
Clay	Clay	< 0.0039	9

*After CUMMINS (1962).

indicates the sediment retained on a given screen having the stated size openings; thus, for example, the 1/2 mm class consisted of particles having least diameters slightly less than 1 mm to slightly greater than 1/2 mm).

The silt fraction ($< 1/16 > 1/256$ mm) was separated from coarser and finer material by settling time, each separation involving about 20 decantations. The silt was then over dried at 40° C, wetted, aerated for 24 hours, allowed to settle and a final decantation of finer material made. This procedure yielded a size class of natural stream silt with a total volatile solids content averaging about 5% by weight as determined by loss of weight on ignition at 600° C.

Experimental Animals

The ten species of aquatic macro-invertebrates selected for the detailed analysis of substrate responses are given in Table II along with the general habitat types in which the species are found in Fleming Creek and the life stages utilized in the experiments.

TABLE II

Taxa, general habitat types, and life stages of the ten species of Fleming Creek macro-invertebrates used in experimental studies

Order	Species	General Habitat Type	Life Stage*
Plecoptera	*Perlesta placida* (Hagen)	Riffle	Nymphs
Ephemeroptera	*Ephemera simulans* Walker	Intermediate**	Nymphs
	Caenis latipennis Banks	Pool	Nymphs
Megaloptera	*Sialis vagans* Ross	Pool	Larvae
Trichoptera	*Pycnopsyche lepida* (Hagen)	Intermediate	Larvae
	Pycnopsyche guttifer (Walker)	Pool	Larvae
	Helicopsyche borealis Hagen	Riffle	Larvae
Coleoptera	*Stenelmis crenata* Say	Riffle	Adults
Diptera	*Tipula caloptera* Loew	Riffle	Larvae
Pulmonata	*Helisoma anceps* Menke	Intermediate	Adults

*Full grown nymphs and larvae were used.
**Intermediate between pool and riffle community types.

These particular species were selected to provide representatives of riffle, pool and intermediate communities and because of their abundance in Fleming Creek as well as the ease with which live specimens could be sorted from related species in the field. In addition, all ten species are common stream inhabitants widely distributed in eastern North America.

Experimental animals were collected from Fleming Creek with dip nets and nesting screens prior to each series of trials and maintained in aerated containers on natural stream substrates at 20° C under conditions of constant low level illumination. Between experiments the animals were placed in enamel trays on an aluminium screen substrate at the particular experimental temperature.

Laboratory Experiments

Model Stream. Experiments on substrate preference were conducted in a flowing water system, described elsewhere (LAUFF & CUMMINS, 1964), composed of two fiber-glassed plywood troughs

150

arranged one above the other, and a reservoir. A centrifugal pump was utilized to raise water from the reservoir through plastic pipes to the upper trough, and the volume of water flowing to and through the troughs controlled by gate valves. Suspended materials were continuously removed by glass wool filters installed at several locations in the system. Current velocities corresponding to various gate valve settings at a given pitch were determined with a pigmy current meter (CORBETT, 1955). Aluminum trays (27 x 15 x 2.5 cm) designed to fit into the model stream were employed for studying responses of the ten macroinvertebrate species to substrate particle size. The trays were filled with the eight size classes of stream sediments described above and tray-length aluminum clips used to join them together; substrates were smoothed over to minimize barriers between trays. At each end of the series of eight substrate trays, a tray covered with aluminum screen provided a buffer zone between the substrates and the end retaining screens used to prevent escapement from the experimental area – thus, animals merely selecting the upstream or downstream ends of the enclosure were not counted in a substrate tray. In addition, aluminum half-trays constructed to fit inside the full length trays allowed half of each particle size to be altered by covering it with a skim of silt. In this manner, the importance of silt in modifying substrate selection, as previously determined with full length trays, could be evaluated (see LAUFF & CUMMINS, 1964 for a description and figures of the tray system).

The presence of partitions between substrates did not appear to influence substrate selection since the animals were noted to move over the substrate surface; the partitions were necessary to maintain particle size categories in discrete ranges and to reduce the amount of sieving required for replicate experiments. Both direct observation and recovery of marked individuals established the ability of all species tested to move the length of the experimental area (122 cm, or eight trays) during a 24 hour period.

Control of Physical, Chemical and Biological Conditions. The aquarium room used to house the flowing water system was kept essentially at outdoor temperatures throughout most of the year. During the summer a cooling unit was employed to maintain water temperatures close to those in the field during the period of experimental work (19° C to 25° C).

An average current velocity of 3 cm/sec was maintained in the flowing water system throughout the experimental trials. Except during those experiments conducted in complete darkness (covered trough), illumination was by natural lighting and followed the normal photoperiod of the season.

In order to keep the quantities of organic material and associated bacterial populations as low as possible, glass wool filters were installed in the model stream during experiments and the sediments were washed and the trough scrubbed down after each experiment. Since a small amount of sediment tended to be lost from each tray upon removal from the trough, substrate materials were added after every two or three trials. Following every 10 to 20 experiments, the trays were emptied and refilled with new sediments.

Experimental Design. Two groups of animals (groups I and II) were alternately introduced into each of three arrangements of the substrate trays; these were two graded series, one with the largest particle size (16 mm) at the upstream end of the trough, the other with the largest size downstream, and one series with the particle sizes alternated. Beginning at the upstream end, the alternate tray arrangement by particle size was 1, 8, 1/4, 2, 1/2, 16, 1/8 and 4 mm. When introduced, each experimental group was divided equally among the eight substrate trays. In some cases, it was necessary to replace individuals of a given group which had died or escaped from the system during the course of an experiment. If additional animals were not immediately available, the group was increased when animals became available. The numbers of animals used in full-tray series experiments are listed for each species by tray type (half or full), tray arrangement and group in Table III. In contrast to the six experiments completed with each series in the three tray arrangements under conditions of a normal 24 hour photoperiod, one experiment of longer duration (48 to 96 hours) and one in complete darkness (covered trough) were conducted. Finally, the two experiments using both groups (I and II) of a given species were designed and conducted to evaluate the role of learning in the observed substrate responses. At the end of an initial experiment, the individuals in one or two of the trays were reintroduced into the same tray series. If the distribution of the reintroduced animals was not statistically different (Kolmogorov-Smirnov one-sample test; SIEGEL, 1956; pp. 47—52) from that of the total initial group, the effect of learning on tray selection was disregarded.

In order to evaluate effects of siltation upon the responses of the ten species, the half-tray system described above was employed. The portion of each particle size enclosed in the half-tray was covered with a skin of silt approximately 1 mm thick. This was accomplished with a large bulb pipette when the trays were submerged and in place. The positions of the silted half-trays were alternated along the length of each tray arrangement resulting in a checkerboard pattern. The procedure utilized in the full length, non-silted substrate tray ex-

TABLE III

Numbers of animals of each species used in substrate preference experiments presented by tray, arrangement group and non-silted (full tray) and silted (half tray) sediments. (See text for further explanation).

Species	Tray Arrangement	Coarse Upstream		Coarse Downstream		Alternate	
		Group I	Group II	Group I	Group II	Group I	Group II
Perlesta	Full trays	16	24	16	16	16	16
placida	Half trays	16	64	16	16	32	32
Helicopsyche	Full	16	32	24	24	24	24
borealis	Half	16	48	32	32	32	32
Stenelmis	Full	48	40	40	40	40	40
crenata	Half	48	96	48	48	32	48
Tipula	Full	24	24	24	24	16	24
caloptera	Half	16	16	16	32	16	16
Caenis	Full	24	48	40	40	40	40
latipennis	Half	48	64	48	32	48	48
Pycnopsyche	Full	24	24	24	24	24	24
guttifer	Half	16	16	48	16	16	16
Sialis	Full	40	32	32	24	24	24
vagans	Half	32	32	32	32	32	32
Ephemera	Full	24	40	40	48	48	48
simulans	Half	96	32	96	32	96	32
Pycnopsyche	Full	24	24	24	24	24	24
lepida	Half	16	48	16	16	16	16
Helisoma	Full	48	48	48	48	40	48
anceps	Half	48	48	48	48	48	48

periments was followed, except the numbers of animals introduced differed (these numbers are also summarized for each species by tray arrangement and group in Table III). An equal number of animals was introduced into each half-tray in any given trial; thus total number of animals was 16 or a multiple of it.

Only the animals recovered in the substrate trays have been included in the results of the full and half-tray experiments. Those animals recovered under the trays, on the sides of the trough, on terminal screen trays, on end retaining screens, or outside the experimental area are not included in the substrate selection data presented below. Although no attempt was made to introduce the animals in any particular orientation with respect to current direction, the points of introduction were spread out over the surface of each substrate tray.

Statistical Analyses. A number of statistical analyses were employed to determine significant differences in the distribution

of animals in the substrate preference experiments. (A probability of 0.01 was selected as the level of rejection of the null hypothesis). Bias attributable to tray arrangement or to the reuse of individuals was sought with the chi-square test for k independent samples (SIEGEL, 1956; pp. 174—179). The Kolmogorov-Smirnov one-sample test (SIEGEL, 1956: pp. 47—52) was employed to evaluate the effects of long term experiments (48 to 96 hours), trials in complete darkness (covered trough) and the two trial learning tests described above.

None of the species showed significant differences between the results of the usual 24 hour trials and longer term (48 to 96 hours) experiments. Bias due to reusing individuals could not be demonstrated statistically for any of the ten species and, indeed, no learning was demonstrated using the two trial learning tests. Only *Pycnopsyche lepida* showed a significant difference between trials in complete darkness (covered trough) and normal photoperiod experiments in the same tray arrangement.

The results obtained for six of the ten species in the full-length tray experiments indicated definite bias due to substrate tray position when evaluated by the chi-square test for k independent samples. Therefore, all the results have been grouped by tray arrangement for the evaluation of this bias, due presumably to current direction as well as the character of neighboring trays.

The significance of particle size selection by the ten macroinvertebrate species in the full-tray series of experiments was evaluated with the Kolmogorov-Smirnov one-sample test. Probability values are summarized in Table V along with probabilities determined in the comparisons of results obtained in the full-tray series and the non-silted half-trays, and those of the non-silted and silted half-tray series (latter probability values also derived with Kolmogorov-Smirnov one-sample test).

RESULTS AND DISCUSSION

Fast-water Species

Perlesta placida (HAGEN).   The predaceous nymphs of *P. placida* are quite common in eastern North America where they usually inhabit the rapid portions of streams and rivers and are found among coarse substrate materials (CLASSEN, 1931; FRISON, 1935; LAUFF et al., 1961c), although the nymphs do show some tolerance for slower water (HARDEN & MICKEL, 1952). The general patterns of substrate selection by *P. placida* nymphs were given previously (LAUFF &

154

TABLE IV

Probability values for the substrate preference experiments
(Kolmogorov – Smirnov one-sample test)

Species	Tray Arrangement	Significance of Particle Size Selection in Full Trays	Comparison Between Full Trays and Non-Silted Half Trays	Comparison Between Silted and Non-silted Half Trays
Perlesta placida	Coarse Upstream	< .01	< .01	< .01
	Coarse Downstream	< .01	< .01	< .01
	Alternate	< .01	> .20	< .20
Helicopsyche borealis	Coarse Upstream	< .01	< .01	< .20 > .15
	Coarse Downstream	> .20	> .20	> .20
	Alternate	< .15 < .10	< .05 > .01	> .20
Stenelmis crenata	Coarse Upstream	< .01	> .20	< .15 > .10
	Coarse Downstream	< .01	< .20 < .15	< .05 > .01
	Alternate	< 0.1	< .20	> .20
Tipula caloptera	Coarse Upstream	< .01	> .05 < .01	> .20
	Coarse Downstream	< .01	< .20	> .20
	Alternate	< .01	> .20 < .15	> .20
Caenis latipennis	Coarse Upstream	< .01	> .20	< .15 < .10
	Coarse Downstream	> .20	> .20	< .05 > .01
	Alternate	< .01	> .20	> .20
Pycnopsyche guttifer	Coarse Upstream	< .01	> .20	> .05 < .01
	Coarse Downstream	< .01	< .05 > .01	< .20
	Alternate	< .01	> .20	< .20
Sialis vagans	Coarse Upstream	< .01	< .20	> .20
	Coarse Downstream	< .01	< .15 > .10	> .20
	Alternate	< .01	> .20	> .20
Ephemera simulans	Coarse Upstream	< .20	< .01	< .10 > .05
	Coarse Downstream	< .20	< .01	< .15 > .10
	Alternate	< .10 < .05	> .20	< .01
Pycnopsyche lepida	Coarse Upstream	< .01	< .05	< .05 > .01
	Coarse Downstream	< .01	< .20	> .20
	Alternate	< .01	> .20	> .20
Helisoma anceps	Coarse Upstream	< .01	> .01	> .20
	Coarse Downstream	< .05 > .01	> .20	> .20
	Alternate	> .20	> .20	< .01

155

CUMMINS, 1964) but are included in the present paper for comparative purposes and more detailed discussion.

P. placida nymphs showed a significant selection (Table IV) for the three largest particle sizes (4, 8 and 16 mm; Fig. 1) in the full length tray series of experiments. The nymphs exhibited a tendency to move downstream as evidenced by the recovery of a few in the 1/8 mm sediment tray when it occupied the terminal downstream position and the reinforced selection of the 16 mm particle size (62.5%) when it was at the downstream end. Also, the largest selection for the 4 mm particle size occurred when it was in the downstream position. Thus, although bias due to tray position was not statistically significant at the .01 level (p = <.05> .01), current direction did influence substrate selection. The importance of neighboring fine particle sizes can be seen by the selection of the 2 mm substrate which occurred only when it was bordered by 1/4 and 1/2 mm sizes in the alternate try arrangement (Fig. 1).
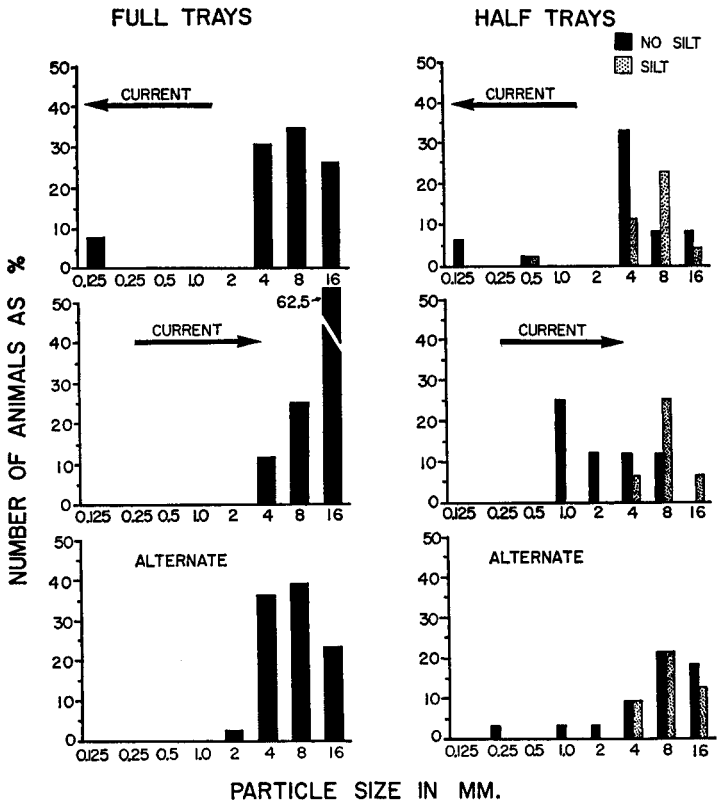
Fig. 1. Substrate particle size selection by *Perlesta placida* nymphs.

There is no significant difference between the full-tray and non-silted half-tray results when the alternate series are compared, but a few more nymphs were recovered in the fine sediments. However, the results are significantly different when the coarse upstream and coarse downstream series are compared. The results of the coarse downstream half-tray (non-silted) experiments showed a selection for the 1 and 2 mm sediments not previously encountered.

When the recoveries in the non-silted half-trays are compared, it is apparent that almost all nymphs recovered from the 2 mm and finer sizes had selected the non-silted sediments. The selection for silted and non-silted half-trays in the alternate series was about the same, while the results of the graded series were quite different. More nymphs selected the non-silted half of the 4 mm particle size when the trays were arranged in graded series but selection for the silted side of the 8 mm substrate was greater than that for the non-silted portion. Although no nymphs were recovered from the non-silted half of the 16 mm substrate in the coarse downstream trials, an essentially equal preference for silted and non-silted 16 mm substrate is obtained when the results of all three tray arrangements are totaled.

Thus, in general, the nymphs of *Perlesta placida* selected coarse particle sizes, tended to move with the current, and showed a tendency to select a smaller particle size when it was surrounded by less favorable finer sediments. Silting of the substrates resulted in an increased selection for non-silted fine particle sizes when compared to the full-tray results. Although the silted portion of the 4 mm substrate was less suitable, silt had little or no effect on the selection of the 16 mm particles and the silted half of the 8 mm substrate was actually preferred. Therefore, silt in the intersticies of finer sediments appears to be unfavorable for *P. placida* nymphs but makes less difference in coarse substrates where some filling between the particles may actually be preferable, as indicated by the recoveries in the silted 8 mm sediment (Fig. 1).

Since none of the 59 quantitative samples taken during 1959—1960 contained *P. placida* nymphs, the Mdø values (median diameters in phi units) given for natural substrates in Table V were taken from another source (limnology class data, 1961; Department of Zoology, University of Michigan) and are to be regarded only as rough estimates. An average median diameter range for these field samples of ø – 3 to ø – 4 (8—16 mm) agrees well with the experimental results. The peak diameter range (i.e., most abundant particle size by weight) of ø – 4 to ø – 7 (16—64 mm) included substrates more coarse than those tested experimentally.

Helicopsyche borealis HAGEN. The herbivorous (or omnivorous)

157

larvae of the caddisfly *H. borealis* (CUMMINS et al., 1966; 1968; COFFMAN, 1967) are usually described as inhabitants of clear, swift, stony streams (LLOYD, 1921; BEETEN, 1934; ROSS, 1944; PENNAK, 1953). The larvae have also been taken from the rocky shores of glacial lakes (VORHIES, 1909; ROSS, 1944).

The only significant selection encountered in the full-tray series experiments occurred in the coarse upstream tray arrangement in which the largest numbers of larvae were recovered from the 1/8 and 1/4 mm particle sizes. In the coarse downstream and alternate tray arrangements more larvae tended to be recovered on the 16 mm pebbles and the three finest substrates (1/2, 1/4, 1/8 mm), although the selection was not statistically significant (Table IV). Observations of moving larvae during the experiments revealed that those introduced or entering on to the finer sediments were unable to leave the trays due
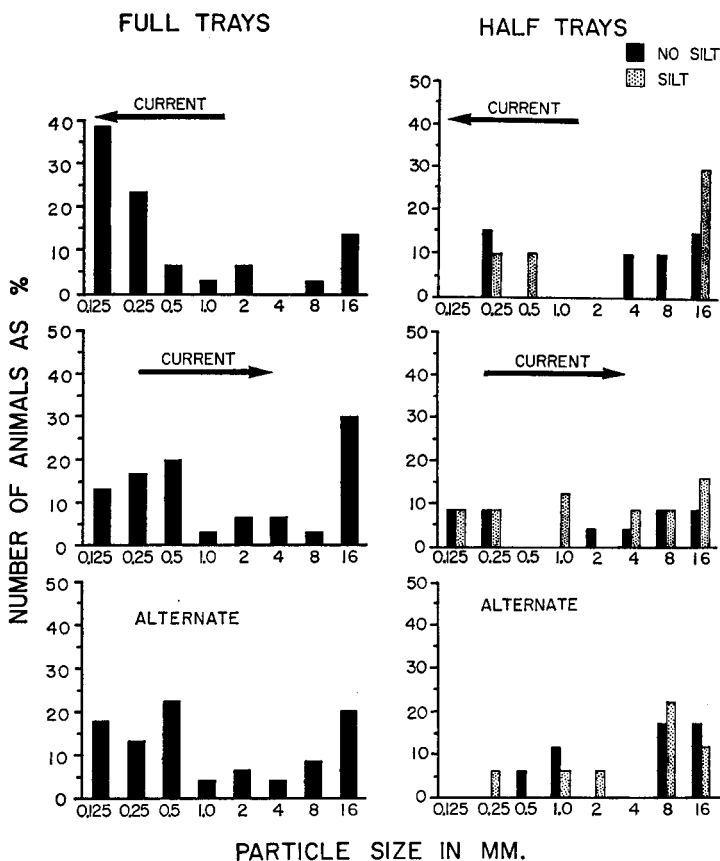
Fig. 2. Substrate particle size selection by *Helicopsyche borealis* larvae.

158

to locomotory difficulties. Since the apparent selection for the three finer sediments was due to an inability of the larvae to move on these substrates, actual selection was indicated for the 16 mm particle size (Fig. 2). A slight tendency (p value for bias due to tray arrangement was $< .20 > .10$) for the larvae to move downstream was indicated by the largest recoveries in the fine sediments when they were at the downstream end and the greatest selection for the 16 mm substrate when it was in the terminal downstream position.

When full-tray and non-silted half-tray results are contrasted, the only significant difference is between the coarse upstream trials (Fig. 2; Table IV). Apparently, a silt covering altered the ability of larvae to escape from the 1/2 mm and finer particle sizes. Indeed, observations indicated that larvae moved somewhat more readily over the silted surfaces, and was reflected in reduced recoveries in the non-silted halves of the trays, probably due to a reduction in the surface area of immobility by one-half. No statistically significant difference was observed between recoveries from the silted and non-silted sections in the half-tray series of experiments.

In general, then, the larvae of *H. borealis*, which were unable to locomote on non-silted fine sediments, showed a non-significant tendency to select the 16 mm pebble substrate and move with the current. Presence of silt made no difference in substrate selection, but observations indicated that locomotion was favored on the silted surfaces of fine sediments.

The Mdø values of the field samples containing *H. borealis* larvae were in the gravel and pebble range (Table V), with the sample containing the most larvae having a Mdø value of -1.4. Peak phi values were in the gravel-pebble-cobble range. A preponderance of coarse substrate materials in all samples containing *H. borealis* larvae indicates the general riffle habitat occupied by this species in Fleming Creek. The lack of a strong selection by larvae for coarse substrate materials in the experiments indicates the secondary influence of substrate particle size on micro-habitat selection. It seems likely that the larvae of *H. borealis* are generally confined to riffle areas and coarse substrates in the field by food requirements; that is, it is probably the food organisms of this caddisfly that selectively grow on coarse sediments in riffles.

Stenelmus crenata SAY. The riffle beetle *S. crenata* is characteristically found in the rapid portions of streams on coarse substrates where it presumably feeds on periphytic algae and detritus (PENNAK, 1953; EDMONDSON, 1959; ARNETT, 1960; DILLON & DILLON, 1961; also see data for *S. beameri* in CUMMINS et al., 1966, 1968 and COFFMAN, 1967).

TABLE V

Median and peak particle size diameters in phi (ø) units for quantitative field samples

Species	Number of Samples	Md ø for sample(s) containing largest no. of animals	Range of Md ø values (all samples containing animals); fine and coarse limits	Peak ø value for samples containing largest number of animals	Range of peak values (all samples containing animals); fine and coarse limits
*Perlesta placida**	5	− 3 to − 4		− 4 to − 7	
Helicopsyche borealis	16	− 1.4	− 1.4, − 4.3	− 3	− 3, − 6
Stenelmis crenata	5	− 1.4	− 1.4, − 3.3	− 3	− 3, − 5
Tipula caloptera	5	− 1.4	+ 4.7, − 3.8	− 3	+ 5, − 5
Caenis latipennis	34	− 2.4	+ 5.2, − 4.6	− 3	+ 5, − 6
Pycnopsyche guttifer	8	− 4.6	+ 2.7, − 4.6	− 5	+ 3, − 6
Sialis vagans	7	+ 0.3**	+ 5.2, − 2.4	− 2**	+ 5, − 4
Ephemera simulans	22	− 2.1	+ 2.7, − 4.3	− 3	+ 3, − 5
Pycnopsyche lepida	12	− 2.1	− 1.6, − 3.1	− 3	− 3, − 4
Helisoma anceps	6	− 2.9	+ 2.7, − 4.3	− 5	+ 3, − 6

*Data from Limnology class, 1961, Department of Zoology, University of Michigan.
**Average given since each sample contained one larva.

Adults of *S. crenata* showed a significant selection for the three largest particle sizes and a non-significant (no significant bias due to tray arrangement) tendency to move upstream in the full-tray experiments. The upstream movement was indicated by increased recoveries from the fines in the coarse downstream tray arrangement (Table IV; Fig. 3). When recoveries from non-silted half-trays are compared with those from the full-trays there is no significant difference.
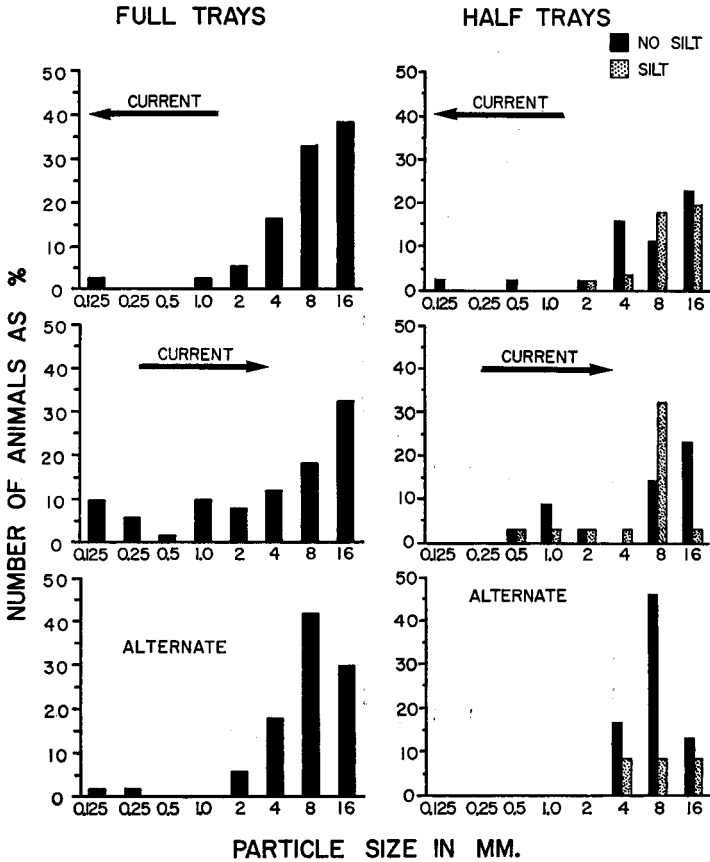

Fig. 3. Substrate particle size selection by *Stenelmis crenata* adults.

No significant selection for silted or non-silted substrates was found when results of half-tray experiments were analyzed. However, recoveries from non-silted half-trays were equal to or greater than recoveries from the silted portions in all but 4 and 8 mm gravels. In both graded series, the silted half of the 8 mm substrate was

161

selected but non-silted 4 mm particles were favored only in the coarse downstream tray arrangement.

These experiments indicate that *S. crenata* adults select a coarse substrate, that light silting causes a slight but non-significant avoidance reaction, and that the beetles tend to move against the current.

The Mdø and peak ø values for field samples containing the most *S. crenata* adults were in the fine and coarse gravel ranges respectively (Table V). The ranges of the Mdø and peak ø values for the field samples containing the beetles were quite narrow, all samples falling within the gravel-pebble range. Although the experimental and field results agree quite well, due to the small number of samples, the field data can only be regarded as preliminary.

Tipula caloptera LOEW. Larvae of the cranefly *T. caloptera* are
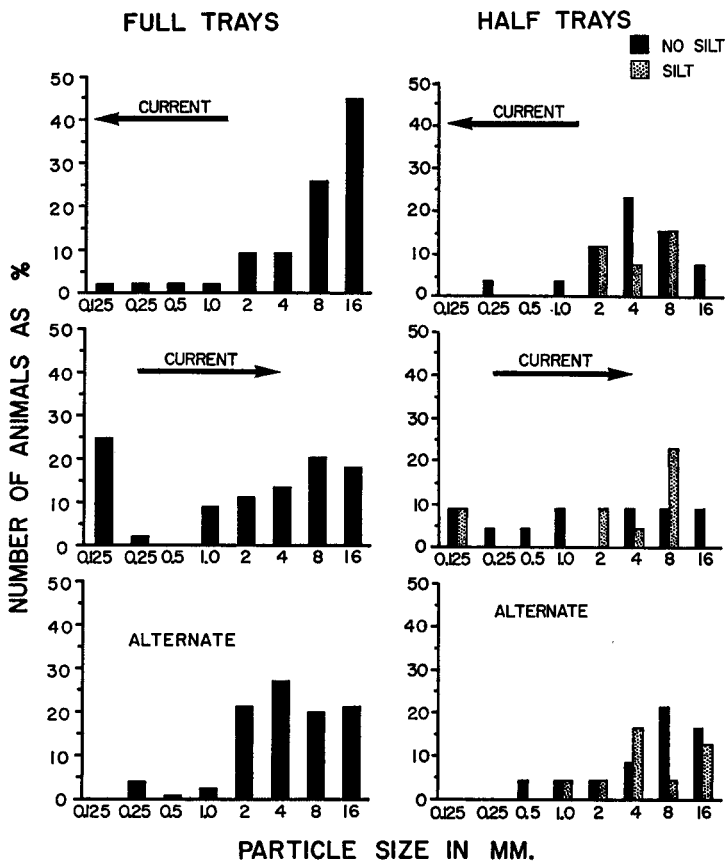
Fig. 4. Substrate particle size selection by *Tipula caloptera* larvae.

reportedly found in both slow and fast moving streams in and on silt as well as gravel substrates (ALEXANDER, 1920; JOHANNSEN, 1934). Gut analyses, using the technique of MECOM and CUMMINS (1964), of larvae from Fleming Creek indicate that they feed primarily on diatoms and vascular plant detritus.

In general, *T. caloptera* larvae selected the 2 mm and coarser particle sizes during the full-tray experiments (Table IV; Fig. 4). Definite bias due to tray arrangement (p < .01) reflects the strong tendency of the larvae to move with the current. This is especially evident from the large recoveries of larvae from the 1/8 and 4 mm (alternate series) substrates when these occupied the terminal downstream position.

There is no significant difference in particle sizes selected when the recoveries from non-silted half-trays and full-trays are compared. However, the results of the coarse upstream trials did differ (Table IV; p < .05 > .01), especially with regard to a reduced selection of the 16 mm pebbles. A comparison of the recoveries from non-silted and silted half-trays reveals that the presence of a skim of silt made no difference in the suitability of a substrate for *T. caloptera* larvae. Most *T. caloptera* larvae were able to burrow into all particle sizes, although some animals recovered from 1/2, 1/4 and 1/8 mm substrates had remained on the surface. Larvae burrowed into the substrate were visible by the spiracular disc and extended gills that remained exposed at the surface.

Only five of the field samples contained *T. caloptera* larvae. Mdø and peak ø values for the sample containing the most larvae were in the fine and coarse gravel ranges respectively (Table V). These values were the same as those for *H. borealis* and *S. crenata*. However, the range of Mdø and peak ø values was extremely wide. One field sample had an Mdø and peak ø in the silts while for another sample they were both in the pebble size class.

In summary, the larvae of *T. caloptera*, found in the riffle areas of Fleming Creek, select coarse particle sizes but show a wide tolerance for finer sediments, including silt, and tend to move with the current. It seems most likely that the larvae are actually distributed in microhabitats of finer sediments and organic material that develop between and behind coarse substrate particles.

Slow-water Species

Caenis latipennis BANKS (= *forcipatra* McDUNNOUGH). Nymphs of the mayfly genus *Caenis* are generally described as bottom sprawlers inhabiting slow water, pond-like situations where they are found among silt and organic debris (NEEDHAM et al., 1935; PENNAK,

1953; LEONARD, 1962; LEONARD & LEONARD, 1962). *C. latipennis*, BANKS thought to be a pond species in some cases (BURKS, 1953), is especially abundant in the slow water, silt covered sections of Fleming Creek where they feed on diatoms and detritus (MILKMAN, 1961).

The nymphs of *C. latipennis* showed a general selection for the 1 mm and coarser particles and an avoidance of the 1/2 mm and finer sediments. The somewhat weak selection of the coarse substrates coupled with a general tendency to move upstream actually erased the statistical significance found in the coarse downstream tray arrangement; the coarsest upstream particle size, 1 mm sand, was favored (Table IV; Fig. 5). The upstream movement of nymphs was demonstrated statistically as a definite bias due to tray arrangement (p < .01).

There is no statistically significant difference in the trend of
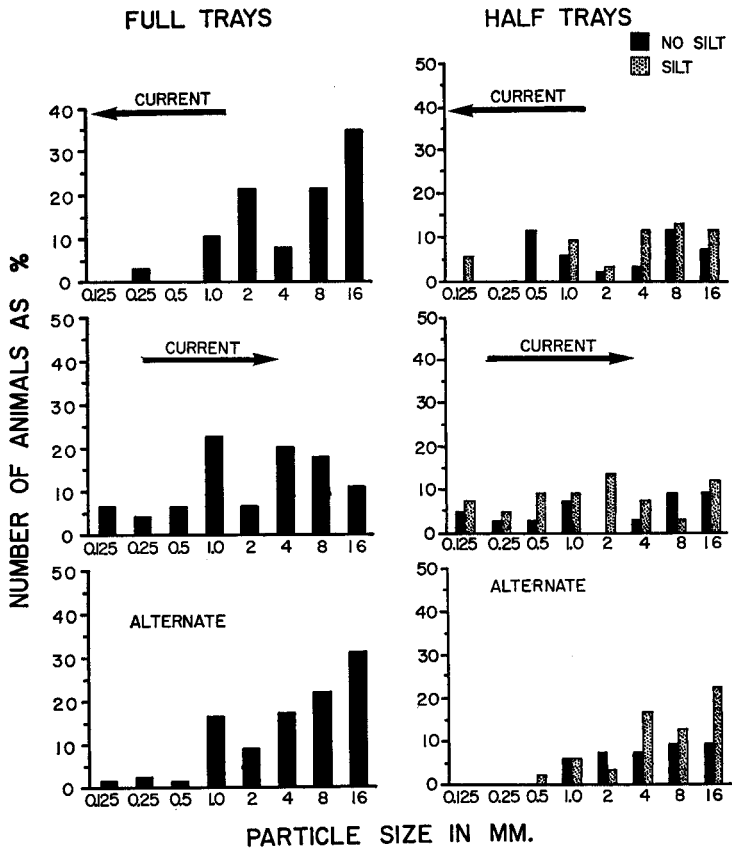
Fig. 5. Substrate particle size selection by *Caenis latipennis* nymphs.

164

selection when the full-tray and non-silted half-tray results are compared (Table IV). In 17 out of 21 cases, more *C. latipennis* nymphs were recovered from the silted half-trays than from non-silted half-trays. The instances of greater selection (1/2 mm, coarse upstream; 8 mm coarse downstream) and equal selection (1 mm, alternate) for the non-silted substrates did not represent a consistent trend (Fig. 5). Nevertheless, only in the coarse downstream tray arrangement did the difference in selection approach the 1% level when tested statistically (Table IV).

The above results indicate that *C. latipennis* nymphs select very coarse sand and larger particle size classes but that a skim of silt tends to increase the suitability of any given sediment and that nymphs showed a tendency to move upstream. Field samples also indicate a general association with coarse particle sizes as evidenced by Mdø and peak ø values, for the sample containing the most nymphs, and the coarse limits of Mdø and peak ø values (Table V); all these lie in the gravel-pebble-cobble range. At least a tolerance of, if not a selection for, silt is indicated by the lower limits of Mdø and peak ø values which are both in the silts.

Thus, experimental and field data suggest that *C. latipennis* nymphs are distributed in the intersticies of coarse sediments and among the periphytal cover of large particles where a skim of silt tends to collect.

Pycnopsyche guttifer (WALKER). Larvae of the caddisfly *P. guttifer* are climbers and sprawlers inhabiting slow water areas of Fleming Creek. They are especially abundant at the stream margin among organic debris and higher aquatic plants where they feed primarily on plant detritus along with some living plant tissues. During the latter part of the terminal larval instar, *P. guttifer* individuals fasten their cases to large submerged objects at the stream margin, such as cobbles, pebbles, and branches, and remain inactive for a good portion of the late summer and early fall. When such larvae are removed from their attachment sites, they move about and soon fasten their cases to other submerged objects (CUMMINS, 1961, 1964).

Non-feeding, terminal instar larvae showed an overwhelming selection for the 16 mm pebbles (Table IV; Fig. 6). There may have been a slight tendency to move upstream, but no bias due to tray arrangement was detected ($p > .20$). No significant difference was demonstrated between the results obtained in the full trays and those obtained in the non-silted half-trays (Table IV). Also, no significant difference between the recoveries from silted and non-silted half-trays was observed, although significance at the 5% level

(p < .05 > .01) was encountered in the coarse upstream tray arrangement in which the silt covered 16 mm pebbles were not favored over the silted particle sizes. The non-silted 16 mm sediment was favored in all three tray arrangements. In five of eight recoveries from 8 mm and smaller particles, the silted portions were selected.
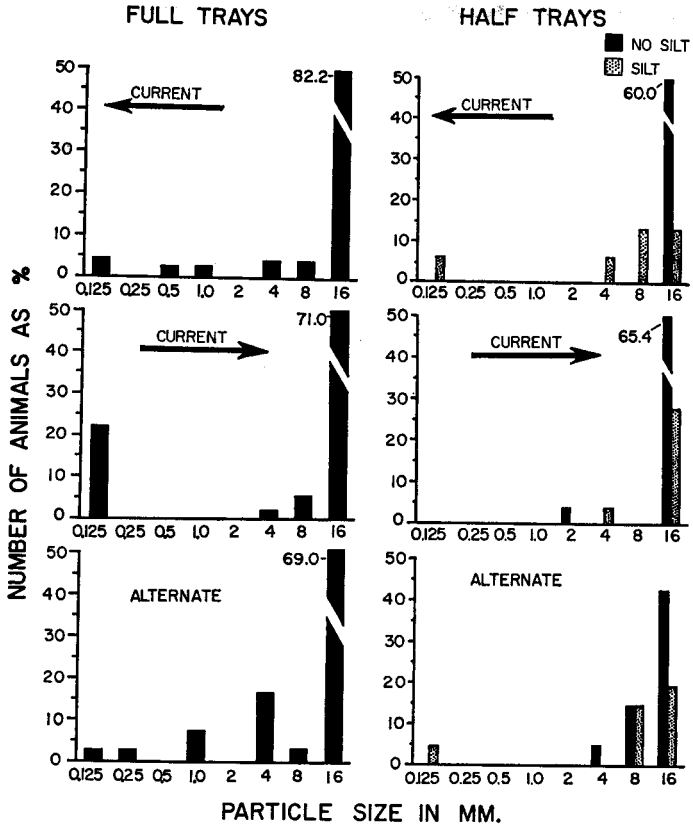

Fig. 6. Substrate particle size selection by *Pycnopsyche guttifer* larvae.

In all experiments, only larvae in the 16 mm sediment tray had fastened their cases to the substrate. It is possible that a skim of silt served as a cue associated with the proper general habitat type in which attachment sites are located, as evidenced by the greater selection of the silted portion of 8 mm and finer sediments. However, the actual attachment was more readily achieved on non-silted, coarse 16 mm pebbles. It is interesting that *P. guttifer* larvae did not select the sides of the trough or the end screens for attachment and the response was independent of light conditions since experiments in the dark did not change the pattern of selection. Apparently

166

phototaxis and climbing per se are not involved in the substrate selection. Additional experiments, in which a tray of stripped and washed *Salix* sticks of uniform size was added to an alternate tray series (as the terminal upstream or downstream tray or at the center of the series), resulted in an 80 to 90% selection of the stick-filled tray. The remainder of the larvae were recovered from the 16 mm sediment tray (CUMMINS, 1961, 1964).

The field sample containing the most *P. guttifer* larvae had Mdø and peak ø values in the pebble size class. The upper and lower limits of Mdø and peak ø values were fine sand and pebbles, and fine sand and cobbles, respectively. Although these phi values indicate the general coarse nature of the sediments, silt percentages for the samples containing *P. guttifer* larvae were comparatively high – ranging from about 2 to 13% by weight (CUMMINS, 1961, 1964).

There is little doubt that non-feeding, terminal instar *P. guttifer* larvae select coarse substrate particles or submerged sticks and branches for attachment. It may be that silt is an important surface cue in maintaining the larvae in the general slow water, stream-margin type of habitat.

Sialis vagans Ross.   Larvae of *S. vagans* are active predators which inhabit slow-water areas where they are usually abundant in the detritus and on vascular hydrophytes (ROSS, 1935; PENNAK, 1953; EDMONDSON, 1959).

Laboratory experiments with *S. vagans* larvae showed a selection that centered about the 4 mm particle size, ranging from 2 mm to 16 mm sediments, in the two graded series. The pattern of selection was somewhat different in the alternate series in which the 16 mm and 8 mm sediments were favored (Table IV; Fig. 7). The difference between alternate and graded series results was sufficient that a very significant bias due to tray arrangement was found (p > .01). There was no significant difference between the full-tray and non-silted half-tray recoveries (Table IV). *S. vagans* larvae showed a wide range of tolerance for silt as evidenced by a lack of statistical significance when recoveries from silted and non-silted trays are compared (Table IV). However, in 17 out of 22 cases more larvae were recovered in the non-silted half-trays (Fig. 7). This avoidance of silted substrates was particularly noticeable in the 2 mm and finer particle sizes of the coarse downstream and alternate tray arrangements.

Average Mdø and peak ø values have been given for the field samples since each of seven samples contained one *S. vagans* larva (Table V). The mean Mdø was in the very coarse sand range and the mean peak ø value in the gravel size class. Limits of the range of
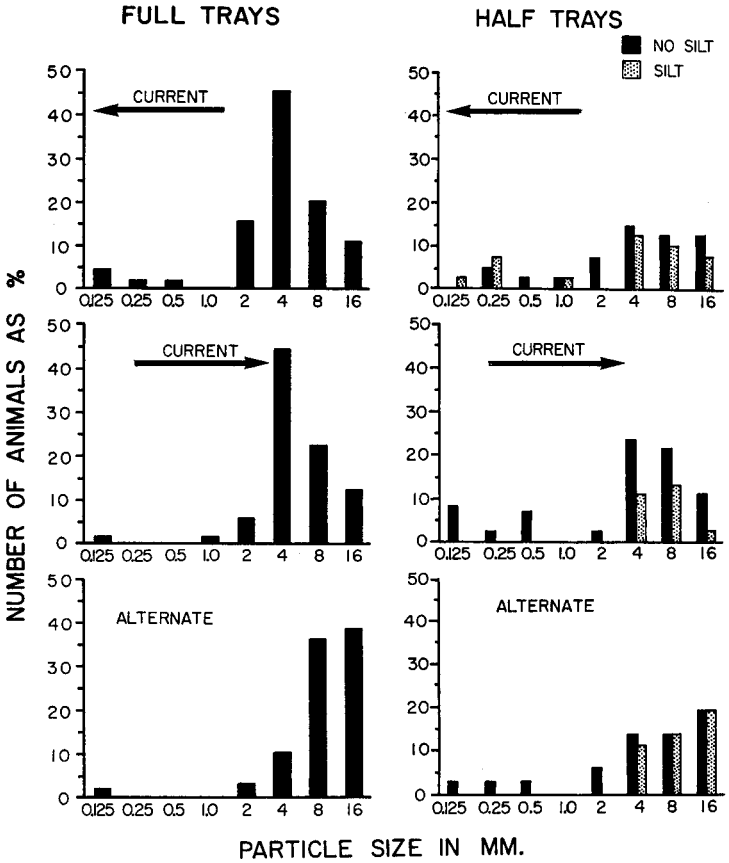
Fig. 7. Substrate particle size selection by *Sialis vagans* nymphs.

Mdø and peak ø values were silt and gravel, and silt and pebbles, respectively.

Thus, *S. vagans* larvae select particle sizes primarily in the gravel range but show a wide tolerance of silting and exhibit no particular current orientation. Such a pattern of substrate selection might be expected of slow-water organism limited to the margins of streams rather than extensive pool-like stretches. Certainly the distribution of prey species imposes strict limits on the microhabitat selection of *S. vagans* larvae in the field, and their distribution with respect to particle size probably reflects the general tolerances of such food organisms.

Intermediate Habitat Species

Ephemera simulans WALKER. The nymphs of *E. simulans* are generally described as burrowers found in sand or gravel, bottom regions of lakes and streams where they feed primarily upon detritus and diatoms (NEEDHAM, 1918; NEEDHAM et al., 1935; BURKS, 1953; PENNAK, 1953; ERIKSEN, 1961; LEONARD, 1962; LEONARD & LEONARD, 1962; CUMMINS et al., 1966, 1968; COFFMAN, 1967).

E. simulans nymphs demonstrated no significant substrate selection in the full-tray experiments but showed a tendency to favor very coarse sand and gravel (Table IV; Fig. 8). Definite bias due to tray arrangement undoubtedly reflects the large selection of the terminal downstream tray (1/8 mm) in the coarse upstream tray arrangement. This tendency to move downstream was not born out in the other two tray arrangements.
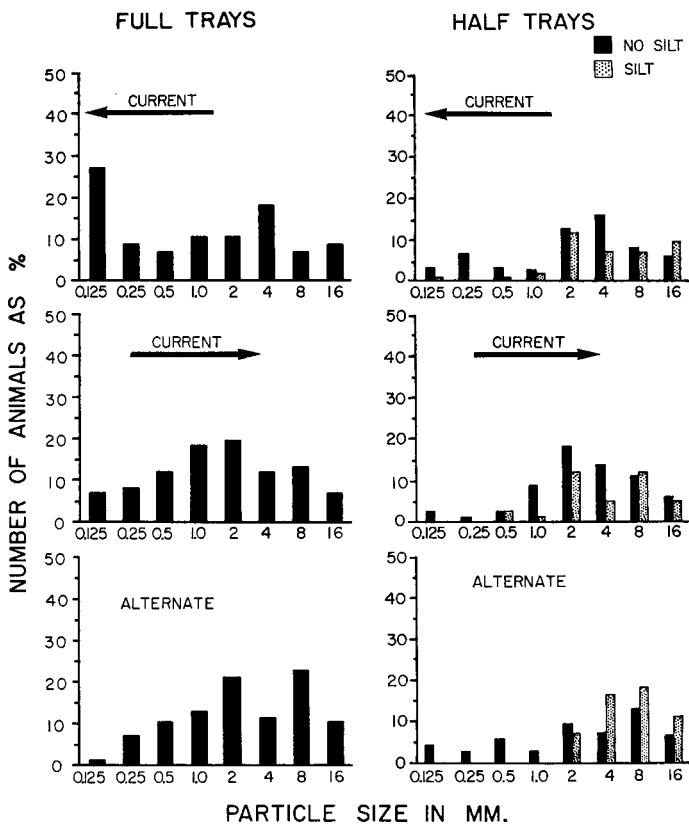

Fig. 8. Substrate particle size selection by *Ephemera simulans* nymphs.

169

The full-tray and non-silted half-tray recoveries are significantly different when results of the two graded series are compared (Table IV) but the trends of recovery in the alternate series are quite similar. The presence of silt altered the way in which nymphs reacted to the non-silted portions of the substrate particle sizes in the two graded series but not in the alternate series in which silt selection constituted a fairly consistent trend. There was no significant difference between the silted and non-silted half-tray results in the two graded series, but the trends of selection were significantly different in the alternate series. On the basis of all the half-tray experiments, selection for the non-silted and silted sections was about equal in the 4 mm and coarser particles. However, the non-silted portions of the 2 mm and finer substrates were favored in all but one instance (equal selection of 1/2 mm).

Mdø and peak ø values for the field sample containing the most *E. simulans* nymphs were in the gravel size class. The fine and coarse limits for both Mdø and peak ø values were in the fine sand and pebble ranges respectively (Table V).

In summary, field and laboratory data indicate that *E. simulans* nymphs favor sand and gravel substrates, but no statistically significant size selection was demonstrated experimentally. There was a general avoidance of a silt covering over fine sediments but silting made no difference in the burrowing suitability of coarse substrates. Thus, even though *E. simulans* can be described generally as a gravel insect of intermediate stream habitats, it is apparent that the exact limits of microdistribution are set by other parameters. The nature and abundance of detrital food substances are undoubtedly of importance and ERIKSEN (1961, 1963a, 1963b, 1964a, 1964b, 1966) has shown that localized variations in oxygen concentration are also of significance.

Pycnopsyche lepida (HAGEN).   Larvae of the caddisfly *Pycnopsyche lepida* show a changing pattern of habitat selection associated with maturation. Early instar larvae are found in slow-water regions along the margins of Fleming Creek. Terminal instar larvae are found on gravel substrates in regions of intermediate current velocity. The larvae spend the latter portion of the terminal instar in an inactive, non-feeding state burrowed into gravel sediments (CUMMINS, 1961, 1964).

Non-feeding, burrowing, terminal instar larvae showed a significant selection for the 2 mm to 16 mm particle size range (Table IV; Fig. 9). There may have been a slight tendency for the larvae to move into the current and to select the terminal portion of the experimental area but no statistically significant bias due to tray arrange-
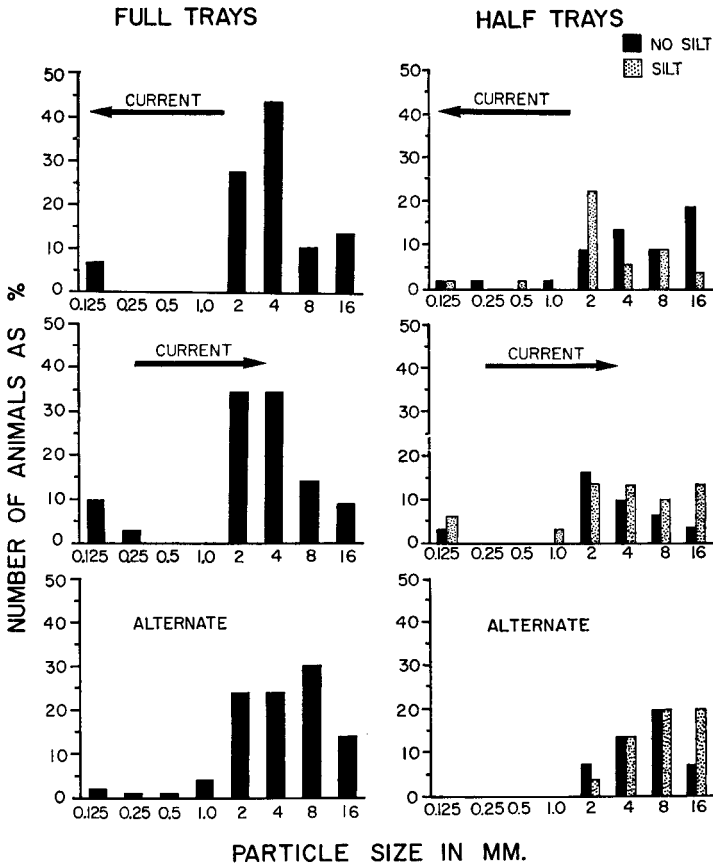
Fig. 9. Substrate particle size selection by *Pycnopsyche lepida* larvae.

ment was found (p > .20). No significant difference was demonstrated between results obtained in full-trays and those recorded for non-silted half-trays (Table IV). Also, there was no significant difference between larval recoveries from silted and non-silted half-trays, although significance at the 5% level (p < .05 > .01) was encountered in the coarse upstream tray arrangement. The difference, however, was not due to any particular trend cf selection for silted or non-silted sediments associated with increasing or decreasing particle size (Fig. 9). *P. lepida* larvae showed a significant difference (p < .01) between trials in complete darkness (covered trough) and normal photoperiod experiments in the same tray arrangement. Burrowing was inhibited in the dark and 70% of the larvae were recovered on the surface of the 1/8 mm sediment (CUMMINS, 1961, 1964).

171

The Mdø and peak ø values determined for field samples containing burrowing *P. lepida* larvae are all within the range of sediment sizes selected by individuals in substrate experiments; i.e., ø—1 to ø—4 in the gravel and fine pebble range (Table V). It seems apparent that in nature, terminal instar *P. lepida* larvae select burrowing sites on the basis of sediment particle size (CUMMINS, 1961, 1964).

Helisoma anceps MENKE.   Species of freshwater snails in the genus *Helisoma* are found in a wide variety of aquatic habitats. Although the majority of species occur in quiet waters, there are a number of species which can be found in lotic environments (BAKER, 1928; GOODRICH, 1932; PENNAK, 1953). In Fleming Creek, *H. anceps* occurs on a wide range of substrates, but appears to be most abundant on gravel where it feeds on periphytic algae and detritus.

Although *H. anceps* individuals selected the 8 mm and 16 mm particle sizes in the coarse upstream arrangement of the full-trays, a
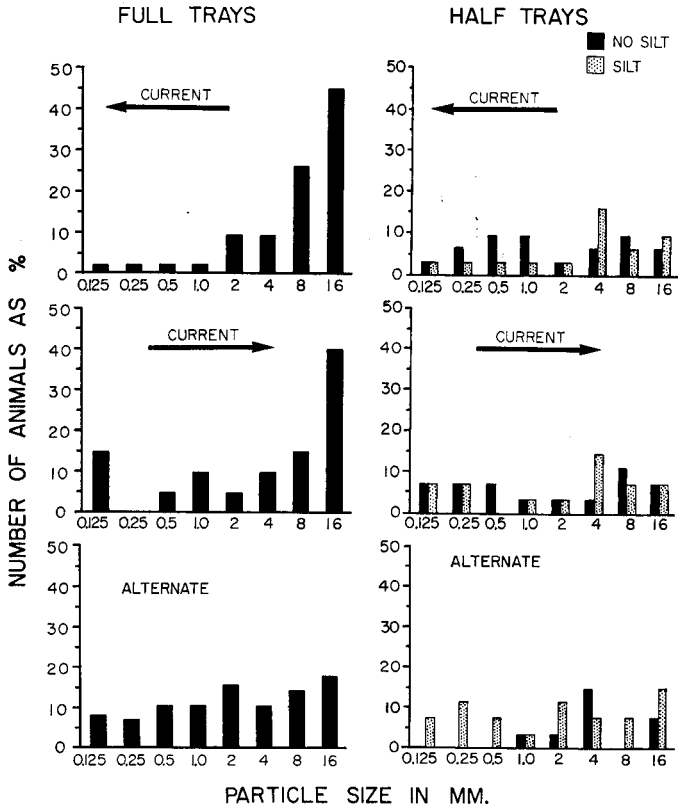

Fig. 10. Substrate particle size selection by *Helisoma anceps.*

172

definite bias due to tray arrangement was detected (p < .01). There was a tendency for the animals to move into the current in the two graded series and significant selection was eliminated when the trays were arranged in alternate series (Table IV; Fig. 10). When the two graded series were tested under conditions of no current, the distribution patterns were similar to those obtained in the alternate series.

There is no significant difference in the recoveries from full-trays and non-silted half-trays, of the coarse downstream and alternate tray arrangements. However, the significant selection of 8 mm and 16 mm particles observed in the full-tray coarse upstream trials was not observed in the non-silted portions of the substrates of the half-tray, coarse upstream experiments. Hence the two sets of results are significantly different (p < .01). The addition of silt to one half of each sediment size eliminated what had appeared to be selection peaks in the two graded series of full-tray experiments. There was no significant difference in the selection for silted and non-silted portions of the substrates in either of the graded series, although, in the alternate series, there was a greater overall selection for silted substrates, especially in the finer sediments.

A very large range of Mdø and peak ø values was obtained for field samples containing *H. anceps*; from fine sand to fine pebbles and from fine sand to cobbles, respectively.

. Both laboratory information and field data demonstrated that a wide range of sediment particle sizes are suitable for *H. anceps*. Although there may be a tendency to select silted areas, microdistribution is undoubtedly related to substrate particle size only in a secondary way. It seems most probable that the substrate requirements or associations of food materials are responsible for any observed relationship between *H. anceps'* microdistribution and sediment character.

General conclusions

Some general relationships between a species of benthic stream macroinvertebrate and its environment have been summarized in Fig. 11. The diagram is arranged so as to emphasize the importance of four general environmental influences determining a given microdistribution pattern. Although benthic stream animals probably respond to all four major categories of environmental influence simultaneously, the evidence presented in this paper suggests that some species respond to a hierarchial arrangement of such parameters. Whereas current, temperature or concentration of a chemical factor may limit the general ranges of habitat tolerance (macrodistribution), it seems that substrate particle size or food supply
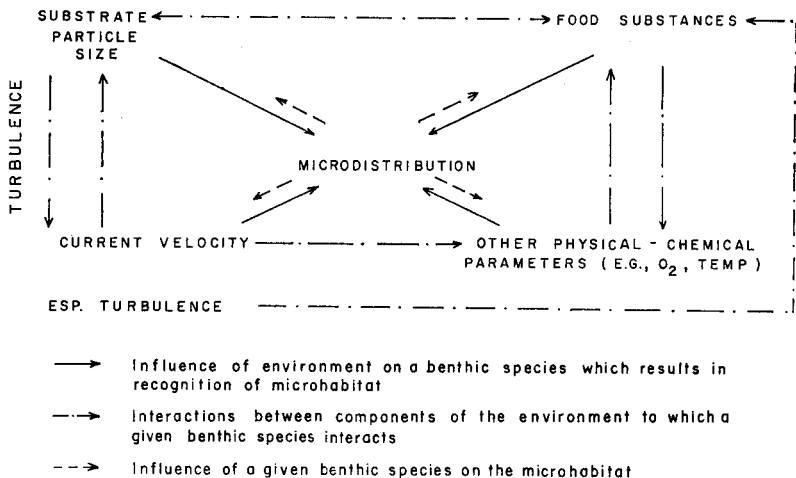
173

SUBSTRATE PARTICLE SIZE

TURBULENCE

CURRENT VELOCITY

MICRODISTRIBUTION

FOOD SUBSTANCES

OTHER PHYSICAL - CHEMICAL PARAMETERS (E.G., O_2 , TEMP)

ESP. TURBULENCE

⟶ Influence of environment on a benthic species which results in recognition of microhabitat

—·—➤ Interactions between components of the environment to which a given benthic species interacts

— —➤ Influence of a given benthic species on the microhabitat

Fig. 11. General relationships between environmental parameters and the microdistribution of a species of benthic stream macroinvertebrate (see text for further explanation).

probably exert primary microdistributional influences. In fact, in many cases, substrate particle size may serve as a common denominator in benthic stream ecology (CUMMINS, 1962, 1964, 1966). The important distinction may be the difference between "tolerance" and "preference" ranges. For example, for a given species of stream macro-invertebrate the "tolerance" and "preference" limits with regard to current velocity may be the same, whereas the substrate preference limits may be considerably narrower than the ranges that a species can tolerate, at least for short periods of time. Thus the degree of discrepancy between tolerance and preference would determine the hierarchial position of an environmental parameter; the greater the discrepancy the more critical the parameter. The above relationships have been depicted graphically in Fig. 12.

The present investigation illustrates the feasibility of utilizing integrated field studies and laboratory experiments to evaluate the importance of various environmental parameters in determining the microdistribution patterns of benthic stream macroinvertebrates. The primary importance, and in some cases possible secondary importance, of substrate type, have been demonstrated for a number of species in the present study. Given the geographical range of a given species, an established primary relationship between substrate type and microdistribution pattern can be of critical importanceoah establishing index species in water quality studies.
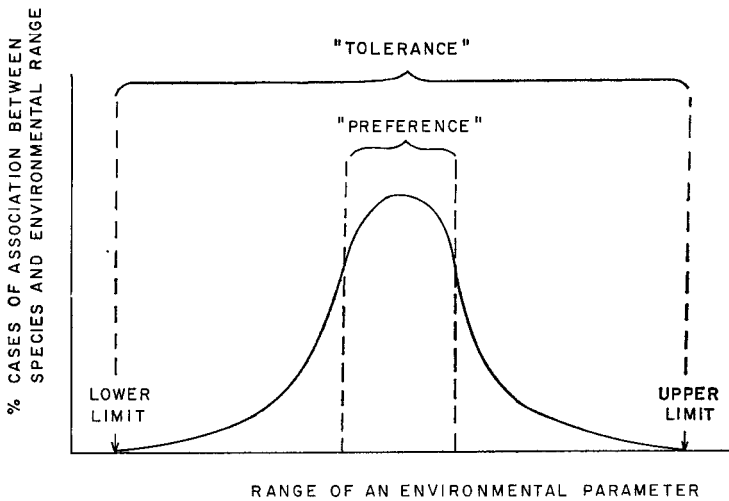
174

Fig. 12. Hypothetical example showing % of cases in which a given species is found associated with a particular range of an environmental parameter to which the species responds, and remains alive (see text for further explanation).

SUMMARY

Substrate microhabitat preferences of ten species of benthic macro-invertebrates were investigated in a laboratory flowing water system and compared with preliminary field data. Eight particle size categories of both silted and non-silted substrates were tested in the laboratory.

The correspondence between field and laboratory data indicated primary microhabitat selection on the basis of substrate particle size by the stonefly *Perlesta placida*, the riffle beetle *Stenelmis crenata* and the caddisflies *Pycnopsyche guttifer* and *P. lepida*. Broad substrate responses in the laboratory and lack of correspondence with field data indicated a secondary importance of substrate particle size in microhabitat selection by the pulmonate snail *Helisoma anceps*, the caddisfly *Helicopsyche borealis*, the cranefly *Tipula caloptera*, the alderfly *Sialis vagans* and the mayflies *Caenis latipennis* and *Ephemera simulans*.

Silting had minor effects on substrate selection patterns in all species tested except *Caenis latipennis* and *Perlesta placida* in which it enhanced selection for the intersticies of coarse sediments.

175

ZUSAMMENFASSUNG

Die Vorliebe für Substratarten mit Rücksicht auf die Substratpartikelgrösse von zehn Arten im Benthos lebender Wirbelloser wurde in einer Labor-Fliesswasseranlage untersucht und mit vorläufigen Feldergebnissen verglichen. Acht Anordnungen von Substratpartikelgrössen, sowohl verschlammt als auch nicht verschlammt, wurden im Labor untersucht.

Die Entsprechung zwischen Feld- und Laborergebnissen zeigte dass die Wahl des Lebensraumes in erster Linie durch die Substratpartikelgrösse bestimmt wurde für die Steinfliege *Perlesta placida*, den Hakenkäfer *Stenelmis crenata* und die Köcherfliegen *Pycnopsyche gutiffer* und *P. lepida*. Die breite Streuwirkung des Substrates im Labor und der Mangel an Übereinstimmung mit den Feldergebnissen zeigte, dass die Substratpartikelgrösse in der Wahl des Lebensraumes eine untergeordnete Rolle spielte bei der Lungenschnecke *Helisoma anceps*, der Köcherfliege *Helicopsyche borealis*, der Schnake *Tipula caloptera*, der Schlammfliege *Sialis vagans* und den Eintagsfliegen *Caenis latipennis* and *Ephemera simulans*.

Die Verschlammung hatte geringen Effekt auf die Auswahl des Substrates bei allen untersuchten Arten mit Ausnahme von *Caenis latipennis* und *Perlesta placida*. In diesen Fällen verstärkte sich die Besiedlung wegen der Zwischenräume in dem groben Sediment.

REFERENCES

ADAMS, C. C. - 1901 - Baseleveling and its faunal significance (with illustrations from southeastern U.S.). *Am. Nat.*, 35: 839−852.
ALBRECHT, M. L. - 1953 - Die Plane und andere Flamingbäche. *Z. Fisch.*, 1: 389−476.
ALEXANDER, C. P. - 1920 - The crane-flies of New York. Part III. Biology and phylogeny. *Memoir Cornell Univ. Agric. Exper. Sta.*, 38: 695−1133.
ARNETT, R. H. - 1960 - The beetles of the United States. Catholic Univ. Press, Wash., D. C. 1112 pp.
BADER, R. G. - 1954 - The role of organic matter in determining the distribution of pelecypods in marine sediments. *J. Mar. Res.*, 13: 32−47.
BAKER, F. C. - 1928 - The freshwater Mollusca of Wisconsin. Part I. Gastropoda. *Bull. Wisc. Geol. Surv.*, 70: 1−507.
BESTY, L. D. & HOOPER, F. F. - 1958 - Benthic associations of Sugarloaf Lake. *Pap. Mich. Acad. Sci., Arts, Lett.*, 43: 89−106.
BETTEN, C. - 1934 - The caddisflies or Trichoptera of New York State. *Bull. N. Y. State Mus.*, 292: 1−576.
BOVBJERG, R. V. - 1959 - Density and dispersal in laboratory crayfish populations. *Ecology*, 40: 504−506.
BOVBJERG, R. V. - 1964 - Dispersal of aquatic animals relative to density. *Verh. Int. Ver. Limnol.*, 15: 879−884.
BREWER, J. W. & GLEASON, G. R. - 1964 - A modification of the Dendy principle for stream bottom sampling. Paper presented 12th Annual Meeting Midwest Benthological Soc., Franz Theodore Stone Lab., Ohio State Univ. Put-in-Bay, Ohio April 1−3.
BRINKHURST, R. O. - 1967 - The distribution and abundance of aquatic oligochaetes in Saginaw Bay, Lake Huron, *Limnol. Oceanogr.*, 12: 137−143.
BUCHANAN, J. B. - 1963 - The bottom fauna communities and their sediment relationships off the coast of Northumberland. *Oikos*, 14: 154−175.
BURKS, B. D. - 1953 - The mayflies, or Ephemeroptera, of Illinois. *Bull. Ill. Nat. Hist. Surv.*, 26: 1−216.
CIANFICCONI, F. & RIATTI, M. - 1957 - Impiego di pietre artificiali per l'analisi quantitative delle colonizzazioni faunistiche dei fondi potamici. *Boll. Pesca Piscic. Idrobiol.*, 22: 299−335.
CLAASSEN, P. W. - 1931 - Plecoptera nymphs of America (north of Mexico). Thomas Say Foundation. 199 pp.
CLARK, R. B. & HADERLIE, E. C. - 1960 - The distribution of *Nephthys cirrosa* and *N. hombergi* on the southwestern coasts of England and Wales. *J. Adnim. Ecol.*, 29: 117−147.
COFFMAN, W. P. - 1967 - Community structure and trophic relations in a small woodland stream, Linesville Creek, Crawford County, Pennsylvania. Unpubl. Ph. D. Dissertation, Univ. Pittsburgh, Vol. I 376 pp. Vol. II 573 pp.
CORBELLA, DELLA CROCE, C. N. & RAVARA, O. - 1956 - Plancton, bentose chimismo delle acque e dei sedimenti in un lago profundo (lago Maggiore). *M m. Ital. Idrobiol.*, 9: 125−262.
CORBETT, D.ᵉ M. - 1955 - Stream-gaging procedure. A manual describing methods and practices of the Geological Survey. *U. S. Geol. Surv. Water Supply Paper*, 888: 1−245.
CRAWFORD, G. L. - 1937 - Notes on the distribution of burrowing Isopoda and Amphipoda in various soils on the sea bottom near Plymouth. *J. Mar. Biol. Assoc. U. K.*, 21: 631−646.

CUMMINS, K. W. - 1961 - The micro-distribution of the caddisfly larvae *Pycnopsyche lepida* (HAGEN) and *Pycnopsyche guttifer* (WALKER) in a restricted portion of a small Michigan stream. Unpubl. Ph.D. Dissertation, Univ. Mich., 158 pp.

CUMMINS, K. W. - 1962 - An evaluation of some techniques for the collection and analysis of benthic samples with a special emphasis on lotic waters. *Amer. Midl. Nat.*, 67: 477—504.

CUMMINS, K. W. - 1964 - Factors limiting the micro-distribution of larvae of the caddisflies *Pycnopsyche lepida* (HAGEN) and *Pycnopsyche guttifer* (WALKER) in a Michigan stream. *Ecol. Monogr.*, 34: 271—295.

CUMMINS, K. W. - 1966 - A review and future problems in benthic ecology. Pp. 2—51 *In:* CUMMINS, K. W., TRYON, C. A. & HARTMAN, R. T. (eds.). Organism-substrate relationships in streams. Spec. Publ. Pymatuning Laboratory of Ecology, Univ. Pittsburgh. 4: 145 pp.

CUMMINS, K. W., COFFMAN, W. P. & ROFF, P. A. - 1966 - Trophic relationships in a small woodland stream. *Verh. Int. Ver. Limnol.*, 16: 627—638.

CUMMINS, K. W., COFFMAN, W. P., WYCHECK, J. C. & ROFF, P. A. - 1968 - The ecology of a woodland stream. I. Species composition, standing crop and ingestion food web of the fall riffle community. In manuscript.

DENDY, J. S. - 1963 - Sampling benthos to estimate productivity. Paper presented 11th Annual Meeting Midwest Benthological Soc., Middle Tennessee State College, Murfreesboro, Tenn. April 18—19.

DILLON, E. S. & DILLON, L. S. - 1961 - A manual of the common beetles of eastern North America. 884 pp.

DRISCOLL, E. G. - 1967 - Attached epifauna-substrate relations. *Limnol. Oceanogr.*, 12: 633—641.

EDMONDSON, W. T. (ed.) - 1959 - Freshwater biology. John Wiley & Sons, N. Y. 1248 pp.

ELLIS, M. M. - 1936 - Erosion silt as a factor in aquatic environments. *Ecology*, 17: 29—42.

ERIKSEN, C. H. - 1960 - The oviposition of *Enallagma exsulans* (Odonata: Agrionidae). *Am. Amer. Ent. Soc.*, 53: 439.

ERIKSEN, C. H. - 1961 - Respiration and substrate as factors influencing the distribution of the burrowing mayflies *Ephemera simulans* and *Hexagenia limbata*. Unpubl. Ph.D. Dissertation. Univ. Michigan. 113 pp.

ERIKSEN, C. H. - 1963a - Respiratory regulation in *Ephemera simulans* (WALKER) and *Hexagenia limbata* (SERVILLE) (Ephemeroptera). *J. Exp. Biol.* 40: 433—467.

ERIKSEN, C. H. - 1963b - The relation of oxygen consumption to substrate particle size in two burrowing mayflies. *J. Exp. Biol.*, 40: 447—453.

ERIKSEN, C. H. - 1964a - Evidence of a spring rise in metabolic rate in the burrowing mayfly *Ephemera simulans* WALKER. *Hydrobiologia*, 23: 506—510.

ERIKSEN, C. H. - 1964b - The influence of respiration and substrate upon the distribution of burrowing mayfly naiads. *Verh. Int. Ver. Limnol.*, 15: 903—911.

ERIKSEN, C. H. - 1966 - Benthic invertebrates and some substrate-current-oxygen interrelationships. Pp. 93—115 *In:* CUMMINS, K. W., TRYON, C. A. & HARTMAN, R. T. (eds.). Organism-substrate relationships in streams. Spec. Publ. Pymatuning Laboratory of Ecology, Univ. Pittsburgh, 4, 145 pp.

FRISON, T. H. - 1935 - The stone flies, or Plecoptera, of Illinois. *Bull. Ill. Nat. Hist. Surv.*, 20: 281—471.

FRISON, T. H. - 1942 - Studies of North American Plecoptera (with special

reference to the fauna of Illinois). *Bull. Ill. Nat. Hist. Surv.*, 22: 235—355.

GOODRICH, C. - 1932 - The mollusca of Michigan. Univ. Mich. Press, Ann Arbor, 120 pp.

HARDEN, P. H. & MICKEL, C. E. - 1952 - The stoneflies of Minnesota (Plecoptera). *Tech. Bull. Minn. Agri. Exper. Sta.*, 201: 1—84.

HENSEN, E. B. - 1954 - The profundal bottom fauna of Cayuga Lake. Unpbl. Ph.D. Dissertation, Cornell Univ., 109 pp.

HENSEN, E. B. - 1962 - Bottom organisms of the Straits of Macinac region. Publ. Great Lakes Res. Div., Inst. Sci. Tech., Univ. Mich.

HOLME, N. A. - 1949 - The fauna of sand and mud banks near the mouth of the Exe estuary. *J. Mar. Biol. Assoc. U. K.*, 28: 189—237.

HOLME, N. A. - 1954 - The ecology of British species of *Ensis. J. Mar. Biol. Assoc. U. K.*, 33: 145—172.

HUNT, B. P. - 1953 - The life history and economic importance of a burrowing mayfly, *Hexagenia limbata*, in southern Michigan Lakes. Mich. Dept. Cons., *Inst. Fish Res. Bull.*, 4: 1—151.

HUNT, J. S. - 1930 - Bottom as a factor in animal distribution in small streams. *J. Tenn. Acad. Sci.*, 5: 11—18.

JOHANSEN, O. A. - 1934 - Aquatic Diptera. Part I. Nemocera, exclusive of the Chironomidae and Ceratopogonidae. *Memoir Cornell Univ. Agri. Exper. Sta.*, 164: 1—71.

JOHNSON, M. G. & MATHESON, D. H. - 1968 - Macroinvertebrate communities of the sediments of Hamilton Bay and adjacent Lake Ontario. *Limnol. Oceanogr.*, 13: 99—111.

JONES, N. S. - 1950 - Marine Bottom Communities. *Biol. Rev.*, 25: 283—313.

KAMLER, E. & RIEDEL, W. - 1960 - A method for quantitative study of the bottom fauna of Tatra streams. *Polskie Arch. Hydrobiologii*, 21: 95—105.

KRECKER, F. H. & LANCASTER, L. Y. - 1933 - Bottom shore fauna of western Lake Erie: a population study to a depth of six feet. *Ecology*, 14: 79—93.

LAUFF, G. H. & CUMMINS, K. W. - 1964 - A model stream for studies in lotic ecology. *Ecology*, 45: 188—190.

LAUFF, G. H., CUMMINS, K. W., ERIKSEN, C. H. & PARKER, M. - 1961a - A method for sorting bottom fauna samples by elutriation. *Limnol. Oceanogr.*, 6: 462—466.

LAUFF, G. H., CUMMINS, K. W., MARZOLF, G. R. & ERIKSEN, C. H. - 1961b - The distribution of the flora and fauna of Fleming Creek. *Mimeo Rept., Univ. Mich.*, 12 pp.

LAUFF, G. H., HENSEN, E. B., AYERS, J. C., CHANDLER, D. C. & POWERS, C. F. - 1961c - The bottom sediments of the Straits of Macinac region. Publ. Great Lakes Res. Div., *Inst. Sci. Tech., Univ. Mich.*, 6: 1—69.

LEONARD, J. W. - 1962 - Environmental requirements of Ephemeroptera. Pp. 110—117 *in:* TARZWELL, C. M. (ed.). Third seminar in biological problems in water pollution. *U.S.P.H.S. Publ.* No. 999-WP-25, 424 pp.

LINDUSKA, J. P. - 1942 - Bottom types as a factor influencing the local distribution of mayfly nymphs. *Can. Ent.*, 74: 26—30.

LLOYD, J. T. - 1921 - The biology of North American caddis-fly larvae. Bull. Lloyd Lib., *Ent. Ser.*, I, 21: 1—124.

LOOSANOFF, V. L., MILLER, W. S. & SMITH, P. B. - 1951 - Growth and settling of larvae of *Venus mercenaria* in relation to temperature. *J. Mar. Res.*, 10: 59—81.

LYMAN, F. E. - 1956 - Environmental factors affecting distribution of mayfly nymphs in Douglas Lake, Michigan. *Ecology*, 37: 568—576.

MARZOLF, G. R. - 1962 - Substrate relations of the burrowing amphipod

Pontoporeia affinis LINDSTROM. Unpubl. Ph.D. Dissertation, Univ. Mich., 92 pp.

MARZOLF, G. R. - 1966 - Trophic and distributional relationships of detrital-bacterial feeding benthic organisms. Pp. 131—135 *in:* CUMMINS, K. W., TRYON, C. A., HARTMAN, R. T. (eds.). Organisms-substrate relationships in streams, Spec. Publ. Pymatuning Laboratory of Ecology, Univ. Pittsburgh, 4: 145 pp.

MECOM, J. O. & CUMMINS, K. W. - 1964 - A preliminary study of the trophic relationships of the larvae of *Brachycentrus americanus* (BANKS) (Trichoptera: Brachycentridae). *Trans. Amer. Microscop. Soc.*, 83 :233—243.

MILKMAN, MRS. E. KINGENER - 1961 - The distribution of nymphs of *Caenis latipennis* BANKS in Fleming Creek. Dept. Zool., *Univ. Mich. Mimeo. Rept.*, 5 pp.

MILNE, D. J. - 1943 - The distribution and life histories of the caddisflies of Waskesin Lake, Saskatchewan. *Can. Ent.*, 75: 191—198.

MOON, H. P. - 1939 - Aspect of the ecology of aquatic insects. *Trans. Brit. Ent. Soc.*, 9: 39-49.

MOON, H. P. - 1940 - An investigation of the movements of fresh-water invertebrate faunas. *J. anim. Ecol.*, 9: 77-83.

NEEDHAM, J. G. - 1920 - Burrowing mayflies of our larger lakes and streams. *Bull. U. S. Bur. Fish.*, 36: 269—292.

NEEDHAM, J. G., TRAVER, J. R. & HSU Y.-C. - 1935 - The biology of mayflies. Comstock Publ. Co., Ithaca, N. Y., 759 pp.

PARKER, R. H. - 1956 - Macroinvertebrate assemblages as indicators of sedimentary environment in the eastern Mississippi delta region. *Bull. Amer. Assoc. Petrol. Geol.*, 40: 295—376.

PENNAK, R. W. - 1953 - Fresh-water invertebrates of the United States. Ronald Press, N. Y., 769 pp.

PENNAK, R. W. & VAN GERPEN - 1947 - Bottom fauna production and physical. nature of the substrate in northern Colorado trout streams. *Ecology*, 28: 42—48.

PERVICAL, E. & WHITEHEAD, H. - 1929 - A quantitative study of the fauna of some types of stream bed. *J. Ecol.*, 17: 283—314.

POMERAT, C. M. & NEISS, C. M. - The influence of the texture and composition of surface on the attachment of sedimentary marine organisms. *Biol. Bull.*, 91: 57—65.

PRATT, D. M. - 1953 - Abundance and growth of *Venus mercenaria* and *Callocardia morrhuana* in relation to the character of bottom sediments. *J. Mar. Res.*, 12: 60—74.

RAWSON, D. S. - 1941 - Soils as a primary influence in the biological productivity of lakes. *Trans. Can. Conserv. Assoc.*, 1941: 78—87.

ROSS, H. H. - 1937 - Studies of Nearctic aquatic insects. I. Nearctic alder flies of the genus *Sialis* (Magaloptera, Sialidae). *Bull. Ill. Nat. Hist. Surv.*, 21: 57—78.

ROSS, H. H. - 1944 - The caddisflies, or Trichoptera, of Illinois. *Bull. Ill. Nat. Hist. Surv.*, 23: 1—326.

SANDERS, H. L. - 1956 - Oceanography of Long Island Sound, 1952—1954. X. Biology of Marine bottom communities. *Bull. Bingham Oceanogr. Coll.*, 15: 345—414.

SANDERS, H. L. - 1960 - Benthic studies in Buzzards Bay. Ill. The structure of the soft-bottom community. *Limnol. Oceanogr.*, 5: 138—153.

SANDERS, H. L., GOUDSMIT, E. M., MILLS, E. L. & HAMPSON, G. E. - 1962 - A study of the intertidal fauna of Barnstable Harbor, Massachusetts. *Limnol. Oceanogr.*, 7: 63—79.

SANDERS, H. L. - 1958 - Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnol. Oceanogr.*, 3: 245—258.

SCOTT, D. - 1958 - Ecological studies on the Trichoptera of the River Dean, Cheshire. *Arch. Hydrobiol.*, 54: 340—392.

SCOTT, D. & RUSHFORTH - 1959 - Cover on river bottoms. *Nature*, 183: 836—837.

SCOTT, D. - 1966 - The substrate cover-fraction concept in benthic ecology. *In:* CUMMINS, K. W., TRYON, C. A. & HARTMAN, R. T. (eds.). Organism-substrate relationships in streams. Publ. Pymatuning Laboratory of Ecology, Univ. Pittsburg, 4: 145 pp.

SHELFORD, V. E. - 1914 - An experimental study of the behavior agreement among animals of an animal community. *Biol. Bull.*, 26: 294—315.

SUBLETTE, J. E. - 1957 - The ecology of the macroscopic bottom fauna in Lake Texoma (Denison Reservoir), Oklahoma and Texas. *Am. Midl. Nat.*, 57: 371—402.

SUBLETTE, J. E. - 1958 - The physico-chemical features and bottom fauna of Chaplin's Lake, Natchioches Parish, Louisiana, 20: 85—94.

SWAN, E. F. - 1952 - The growth of the clam *Mya arenaria* as affected by the substratum. *Ecology*, 33: 530—534.

TEST, F. H. - 1945 - Substrate and movements of the marine gastroped *Acmaea asmi*. *Amer. Midl. Nat.*, 33: 791—793.

THROUP, J. - 1966 - Substrate type and its value as a basis for the determination of bottom fauna communities in running waters. Pp. 59—86. *In:* CUMMINS, K. W., TRYON, C. A. & HARTMAN, R. T. (eds.). Organism-substrate relationships in streams. Spec. Publ. Pymatuning Lab. Ecol., Univ. Pittsburgh, 4: 145 pp.

VORHIES, C. T. - 1909 - Studies on the Trichoptera of Wisconsin. *Trans. Wisc. Acad. Sci.*, 16: 647—738.

WENE, G. - 1940 - The soil as an ecological factor in the abundance of aquatic chironomid larvae. *Ohio J. Sci.*, 40: 193—199.

WENE, G. & WICKLIFF, E. L. - 1940 - Modification of stream bottom and its effects on the insect fauna. *Can. Ent.*, 72: 131—135.

WENTWORTH, C. K. - 1922 - A scale of grade and class terms for classic sediments. *J. Geol.*, 30: 377—392.

WIESER, W. - 1956 - Factors influencing the choice of substratum in *Cumella vulgaris* HART (Crustacea, Cumasea). *Limnol. Oceanogr.*, 1: 275—285.

WIESER, W. - 1957a - Archiannelids from the intertidal of Puget Sound. *Trans. Amer. Microscop. Soc.*, 76: 275—285.

WISER, W. - 1957b - *Gastroptricha macrodasvoidea* from the intertidal of Puget Sound. *Trans. Amer. Microscop. Soc.*, 76: 372—381.

WISER, W. - 1959 - The effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. *Limnol. Oceanogr.*, 4: 181—194.

WISER, W. - 1960a - Benthic studies in Buzzards Bay. II. The meiofauna. *Limnol. Oceanogr.*, 5: 121—137.

WISER, W. - 1960b - Populationsdichte und Vertikalverteilung der Meiofauna mariner Böden. *Int. Revue ges. Hydrobiol.*, 45: 487—492.

WILLIAMS, A. B. - 1958 - Substrates as a factor in shrimp distribution. *Limnol. Oceanogr.*, 3: 283—290.

WILSON, D. P. - 1955 - The role of micro-organisms in the settlement of Ophelia bicornis Savigny. *J. Mar. Biol. Assoc. U. K.*, 34: 531—543.

WILSON, D. P. - 1958 - Some problems in larval ecology related to the localized distribution of bottom animals. Pp. 87—103. *In:* BUZZATI-TRAVERSO, A. A. (ed.). Perspectives in Marine biology. Univ. Cl. Press, Berkeley, 621 pp.