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Factors affecting microdistribution of stream benthic insects

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The microdistribution of stream insects in relation to current velocity, substratum particle size, silt, and detritus was studied in field experiments utilizing substratum-filled trays. 31% more organisms occurred in trays placed in a riffle than in those placed in a pool. In both riffle and pool the amount of colonization for most taxa was least on the smallest substratum sizes studied (0.5–0.7 cm diam.), was greater on the 1.0–2.0 cm size, reached a maximum on the 2.5–3.5 cm size, and was markedly reduced on the largest substratum size (4.5 × 7.0 cm). The reduction of current velocity alone accounted for reductions in the numbers of four or five species, while the addition of a light coating of silt (< 1 mm deep) significantly reduced the numbers of only three species. The 1.0–2.0 cm substratum trays consistently contained more small-sized (<3.95 mm) detritus particles than did the trays filled with the largest sized substratum. When the amount of these particles was similar in both sizes of substrata, the preference previously shown by the insects for the small substratum did not hold. Thus, insects may colonize small (1.0–3.5 cm) substrata primarily because these serve as a better food collecting device than do larger (or smaller) substrata, and manipulation of the substratum may alter the productivity of a stream through an influence on its detritus storage capability. The substratum-detritus interaction was the overriding influence on insect microdistribution under the conditions of this study and current velocity and a light deposition of silt play only secondary roles. A general model was formulated to show the interaction of biotic and abiotic factors which influence the microdistribution of stream insects.

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Микрораспределение речных насекомых в зависимости от скорости течения, величины частиц субстрата, мощности осадка и детрита исследовалось в полевых опытах с помощью лотков, заполненных субстратом. В лотках, помещенных в протоки, оказалось на 31% больше организмов, чем в лотках в заводях. В обоих типах участков количество насекомых из всех групп было наименьшим в тонких субстратах с частицами 0,5–0,7 см в диаметре, увеличивалось на субстратах с диаметром частиц 1,0–2,0 см, достигало максимума в субстратах с диаметром частиц 2,5–3,5 см, и затем существенно снижалось в самых грубых субстратах с частицами 4,5–7,0 см в диаметре. Снижение скорости течения само по себе ведет к снижению численности 4 или 5 видов, в то время как добавление тонкого слоя осадка (<1 см толщиной) существенно снижает численность только трех видов. Лотки с субстратом из 1,0–2,0 см частиц содержали как правило более мелкие (<3,95 см) частички детрита, чем лотки с более грубым субстратом. Если количество мелких частиц было одинаковым на разных субстратах, преферендум, ранее отмеченный у насекомых для тонких субстратов, не наблюдается. Таким образом, насекомые могут заселить тонкие субстраты (диаметр частиц 1,0–3,5 см) прежде всего потому, что они могут служить лучшей пищей, чем грубые субстраты, и изменение субстрата может изменить продуктивность реки через воздействие на аккумуляцию детрита. Взаимодействие между субстратом и детритом оказывает наиболее сильное воздействие на микрораспределение насекомых в данных условиях, в то время как скорость течения и распределение осадка играют второстепенную роль. Создана общая модель, демонстрирующая взаимодействие абиотических и биотических факторов, влияющих на распределение речных насекомых.

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1. Introduction

Habitat selection by benthic stream insects depends upon the interaction of numerous physical and biotic factors. An organism may respond to these factors in a preferential manner and optimum conditions may be different for each species and even for different life stages of the same species. Investigation of this area of stream ecology is complicated by the difficulty of separating the effects of competing variables. The present study reports on a series of field experiments designed to investigate the interaction of distributional parameters at the microhabitat level. Many factors which affect distribution of stream insects exert their influence over a wide area and usually can be ignored or controlled when microhabitat is dealt with. For example, temperature, water chemistry, and dissolved oxygen may be considered to operate in a homogeneous manner over localized areas of a stream and attention therefore may be directed to the heterogenous conditions within a small area of stream bottom. Here certain factors, most notably current velocity, substratum conditions, and detritus distribution (Reice 1974), are quite varied, and it is with these factors that the present study is concerned. This work is an extension of studies begun by Minshall and Minshall (1977) and incorporates the use of additional substratum sizes and exploration of the effects of silt and detritus. The experimental design permitted determination of whether there exists a hierarchial pattern of factors affecting distribution.

2. Methods and materials

2.1. The study area

All experiments were conducted in a 20-m stretch on Mink Creek at the northern boundary of Caribou National Forest, Idaho (elevation 1700 m), about 500 m downstream from the site described by Minshall and Minshall (1977). The study area was a natural riffle, which was manipulated at times to provide pool conditions. Mean width of the study area was 5 m and mean depth was 20 cm. Free-water velocity ranged from a minimum of 35 cm s^{-1} in December to a maximum of 104 cm s^{-1} in late April. The water was alkaline (182–232 mg l^{-1} as $CaCO_3$), slightly basic (pH 8.0–8.6), and (during spring runoff) turbid (0–61 JTU) (Minshall and Minshall unpubl.).

2.2 Substratum-filled trays

Wooden trays (inside dimensions 25 cm × 25 cm × 5 cm deep) were filled with stones of uniform size to assure a homogeneous substratum. All particles were obtained from Mink Creek and passed through a series of screens to sort out the proper sizes.

Each tray was positioned in the stream with its upper surface flush with the stream bottom. After a colonization period the trays were transferred to a large tub of water where the stones were cleaned of all material and removed. The contents of the tub were then concentrated by passing them through a 0.49 mm sieve (Tyler size 30). The material in the sieve was preserved in the field to 5% formalin and later hand sorted by the same individual. All experiments were conducted using the substratum-filled trays.

Care was exercised to insure that similar conditions of depth and solar radiation existed for all trays. Water velocity was measured with a small Ott C-1 current meter at three depths (water surface, mid-depth, 5 cm above substratum) over each tray when it was placed in the stream and again at the termination of the experiment.

Although organism densities have been standardized to organisms m^{-2} in the Results, the Student's t-Test and the Analysis of Variance were applied to the original densities in the artificial substratum (625 cm^2) using a log + 1 transformation (Elliott 1971).

2.3. Microhabitat measurements

Current velocity

The limitations of standard current meters are evident when one attempts to measure turbulent microcurrents and alternating surges of water. Besides being too large to be manipulated within the substratum, they respond to a composite of many vectors of water flow. An alternating surge of water may have a cancelling effect on a current meter but an additive effect on an organism.

In this study these difficulties were overcome by using the rate of dissolution of sodium chloride tablets as an index to the rate of exchange of water molecules over a submerged surface (McConnell and Sigler 1959). Tablets were immersed for 2 min and current velocities of 2–20 cm s^{-1} were measured.

To determine current velocity within the substratum a plastic vial was attached to the bottom of each box to

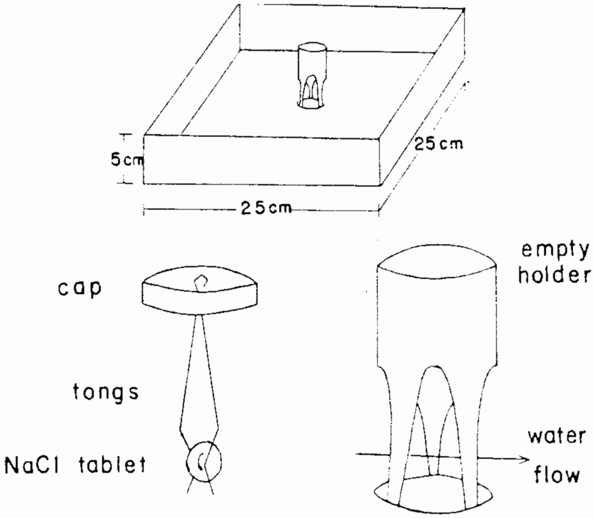

Fig. 1. Substratum box modified with NaCl current meter and the NaCl tablet holder

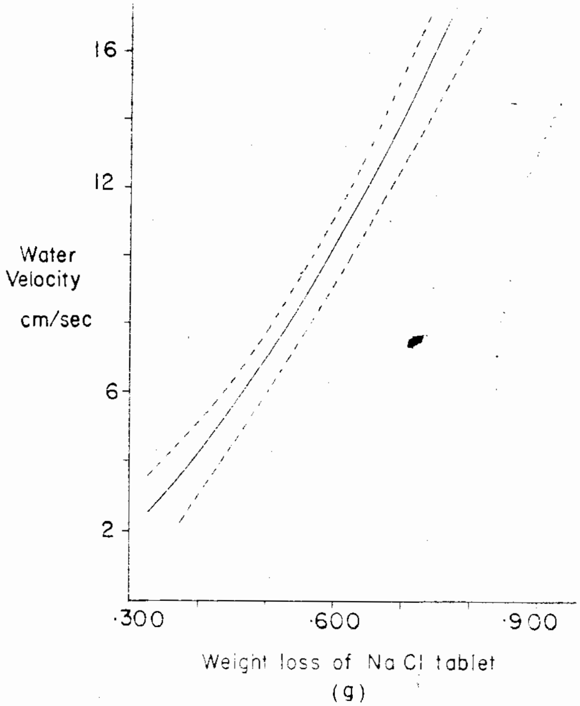

Fig. 2. Relation of sodium chloride tablet weight loss to water velocity using a 2 minute immersion period. The least squares regression line is bracketed by lines enclosing the prediction interval at 95% confidence.

hold the salt tablet (Fig. 1). Sections of the vial were cut out leaving three thin legs which supported the upper portion of the vial without hindering water flow through it. The box was filled with stones, completely surrounding the tablet holder. A pre-weighed tablet was inserted into a pair of tongs attached to the cap of the holder. The tablet was positioned in the holder so as to be streamlined in the direction of the main current. The apparatus was raised during some of the trials to measure water velocity throughout the substratum and at the substratum surface. The mean weight loss of four tablets after immersion was taken as one measurement. Each NaCl tablet was weighed to the nearest 10^{-4} g. After immersion the tablets were allowed to dry 24 h at room temperature before being reweighed.

A conversion graph to relate NaCl weight loss to current velocity (Fig. 2) was developed by passing water through a glass tube at various current velocities and determining NaCl dissolution. Ten trials at ten different water velocities were made at 15°C which was ± 1°C of the stream temperatures during the field trials.

Detritus

All detritus larger than 0.49 mm was collected from the substratum trays, separated from any mineral matter, and passed through a series of Tyler sieves to produce two size classes (0.5 mm– 3.95 mm, >3.95 mm). The material was then dried at 60°C for 24 h and weighed. In addition, the detritus from Group I (six trays) of Experiment II was burned at 550°C for 1 h, cooled in a chemical desiccator for 1 h, and reweighed to determine ash-free dry weight. The ratio of ash-free dry weight to dry weight was consistent for all samples: therefore, dry weights alone were used to compare detritus amounts with organism abundance.

Temperature and oxygen

On several occasions measurements were taken at different depths and within the intersticies of the substratum boxes. Negligible differences were found during any one experiment and it was concluded that neither temperature nor oxygen was important in influencing the microdistribution of the organisms.

3. The experimental program

Experiment I. Effects of variations in substratum size and current velocity

Methods

The first experiment was designed to offer a wide range of substratum sizes and widely different current velocity conditions for colonization. Four particle size categories were used. Size A consisted of stones with a diameter of 0.5–0.7 cm. Size B contained stones with diameters of 1.0–2.0 cm and size C diameters of 2.5–3.5 cm. Size D stones, which tended to be more irregular, averaged 4.5 cm in cross section and did not exceed 7.[illegible] cm in length. Size C overlapped the "small" – substratum size class (2.6 cm dia.) used by Minshall and Minshall (1977), while size D was smaller than their "large" – substratum category (6.2 cm dia.).

One set of four trays was placed in a non-turbulent area with a mean freewater velocity of less than 15 cm s^{-1}. A second set was positioned in a riffle area with a mean free-water velocity of 80 cm s^{-1}. Other environmental factors are given in Tab. 1. The colonization period was 30 d.

Tab. 1. Environmental conditions of Experiment I.

		Pool	Riffle
Temperature	Day 1	2°C	2°C
	Day 30	5°C	5°C
Mean depth to substratum	Day 1	9 cm	6 cm
	Day 30	24 cm	11 cm
Mean current velocity			
Water surface	Day 30	20.9 cm s^{-1}	98.0 cm s^{-1}
Mid depth	Day 1	[illegible].0 cm s^{-1}	40.0 cm s^{-1}
	Day 30	15.6 cm s^{-1}	96.5 cm s^{-1}
5 cm from substratum	Day 30	9.4 cm s^{-1}	28.0 cm s^{-1}
Dissolved oxygen	Free water	11.9 mg l^{-1}	11.9 mg l^{-1}
	Within substratum	10.8 mg l^{-1}	–

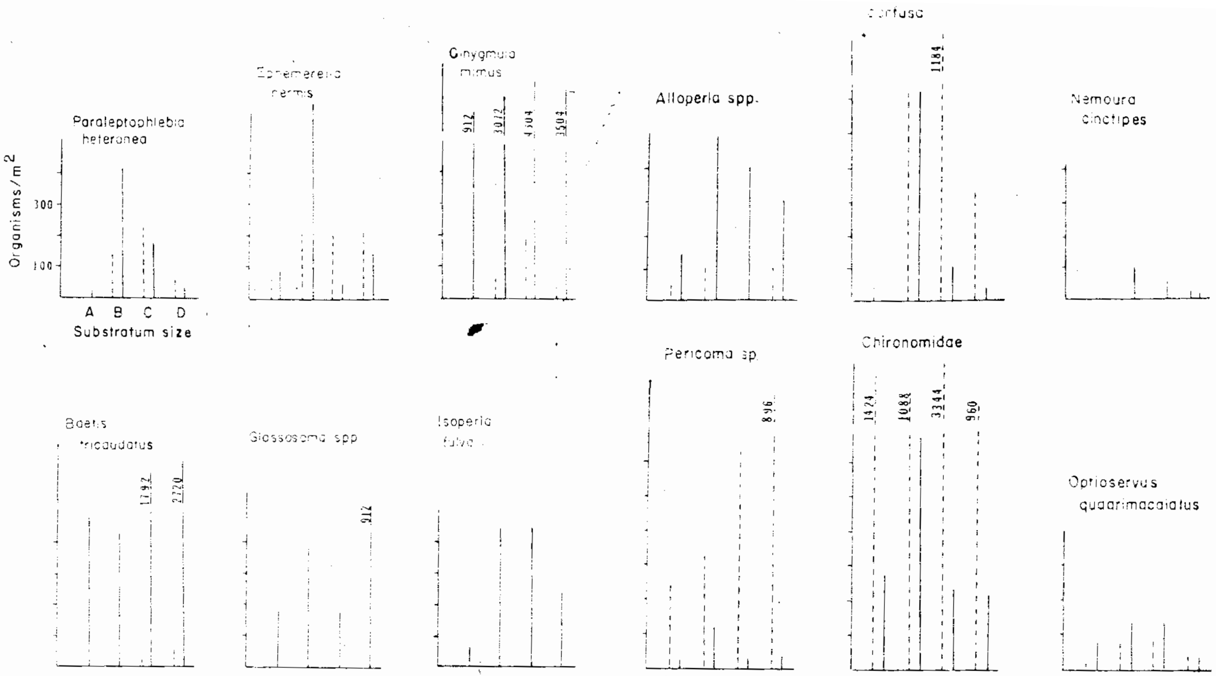

Fig. 3. Distribution of the major species of insects over the two current velocities and four substrata of Experiment I. The solid line represents the riffle and the broken line represents the pool.

Results

The results of this experiment indicate two main points (Fig. 3 and Tab. 2).

1. Thirty-one percent more organisms occurred in the riffle than in the pool.
2. The distribution of insects over the range of particle sizes was similar for both current conditions, i.e., the amount of colonization of the majority of species was least on the smallest substratum particle size A, was greater on B, reached a maximum on size C, and was markedly reduced on the largest substratum size D. Minshall and Minshall (1977) also found the greatest abundance on their equivalent of size C stones.

Sixteen insect taxa colonized the substrata in sufficient numbers to present a distributional pattern (Tab. 2 and Fig. 3). Three taxa (Chironomidae, *Capnia*, *Pericoma*) were most abundant in the pool substrata, nine in the riffle substrata (three occurring only in the riffle), and four (*Ephemerella inermis*, *Pteronarcys californica*, *Paraleptophlebia heteronea*, *Optioservus quadrimaculatus* larvae) fairly evenly distributed between the two. In the pool no species was most abundant in the smallest substratum size (A or B); nine species showed the greatest abundance in size C and four in the largest particle size D. In the riffle no species was most abundant in size A; nine species were most abundant in size B, four in size C, and three in size D.

Four species of mayflies occurred with regularity

Tab. 2. Total insect fauna of Experiment I and individual values for taxa not shown in Fig. 3. X̄ column represents mean number of organisms for the four substratum sizes.

	Pool (organisms m⁻²) Substratum particle size (cm)						Riffle (organisms m⁻²) Substratum particle size (cm)					
	0.5–0.7 A	1–2 B	2.5–3.5 C	4.5 × 7 D	X̄	% Total	0.5–0.7 A	1–2 B	2.5–3.5 C	4.5 × 7 D	X̄	% Total
Total of all organisms collected	1840	2624	6032	2640	3284		2196	7584	8204	8340	6581	
Ameletus oregonensis (Ephemeroptera)	0	16	16	0	8	17	0	80	80	0	40	83
Pteronarcys californica (Plecoptera)	0	0	32	16	12	43	0	0	16	48	16	57
Ephemerella grandis (Ephemeroptera)	0	0	0	16	4	5	0	16	192	64	68	95
Simulium spp. (Diptera)	0	0	0	0	0	0	0	0	16	48	16	100

(Fig. 3) *Cinygmula mimus* and *Baetis tricaudatus* heavily colonized the riffle substrata. *Cinygmula* was most abundant in size C while *Baetis* was concentrated in the two largest substrata. *Paraleptophlebia heteronea* was more evenly distributed over the two current conditions and was concentrated in the two middle sized substrata. *Ephemerella inermis* was fairly evenly distributed between the pool and riffle, with the majority of organisms inhabiting the size B substratum.

The most abundant Plecoptera was *Capnia confusa* (Fig. 3) which heavily colonized the pool area and was concentrated in substrata sizes B and C in the pool and B in the riffle. *Pteronarcys californica* (Tab. 2) was fairly evenly divided between the pool and riffle and did not appear in the two smallest particle sizes under either current condition. *Isoperla fulva* (Fig. 3) was collected only from the riffle substrates and was concentrated in the two middle-sized substrata. *Alloperla* spp. exhibited the same pattern as *I. fulva* in the riffle but it was found in small numbers in the pool area as well. *Nemoura cinctipes* colonized in only small numbers but seemed to concentrate in the fast current area.

The only abundant caddisfly, *Glossosoma* spp., (Fig. 3) occurred in the riffle but was never taken in the pool. It was most abundant in the largest-sized substratum but was common in the three other substrata. The Chironomidae concentrated in the pool, the majority in size C substratum; but they were also well represented in the riffle, where each substratum contained over 200 m^{-2}. *Pericoma* spp. heavily colonized the pool area and was found in increasing numbers as the substratum size increased. *Optioservus quadrimaculatus* occurred in both current conditions in low numbers, with a small majority in the riffle area (Fig. 3). It concentrated in the two middle-sized substrata.

Discussion

Experiment I shows that a slow current per se does not necessarily inhibit colonization. When a more suitable substratum was presented, populations of Ephemeroptera and Plecoptera reached over 3000 m^{-2} where they had been rare or absent before. Most studies which have shown fast current conditions to be essential for the occurrence of organisms have investigated insects with highly specialized food gathering apparatus, e.g., some Trichoptera (Philipson 1955, Edington 1968) or Simuliidae (Phillipson 1956). This experiment indicates that microdistribution of some insects is only indirectly influenced by current velocity. Current velocity does, however, directly influence substratum particle size.

The most productive particle sizes of this experiment were in the intermediate range of 1–3.5 cm diameter. This contrasts with results of several studies (Needham 1927, Tarzwell 1936, Pennak and Van Gerpen 1947, Sprules 1947, Bell 1969, Barber and Kevern 1973) which indicate increased population abundance correlated with increasing substratum particle size, and it confirms and extends the findings of Minshall and Minshall (1977).

The influence of size, shape, and texture of the substratum on benthic invertebrates has been little investigated although all three appear to exert an important influence on distribution (Minshall and Minshall 1977). Most studies of this parameter lack control of other interacting variables. Early studies (Percival and Whitehead 1929, Linduska 1942) showed differences in species diversity in areas of different substrata but did not control or separate out the influence of current velocity or substratum shape and texture. In an attempt to standardize the substratum some investigators have filled containers with different types of material and allowed them to become colonized (Moon 1938, 1940, Wene and Wickliff 1940, Minshall and Minshall 1977). In the study by Wene and Wickliff, increasing stone size was related to increasing numbers of organisms, and in one pool area which had previously yielded only Chironomidae the provision of stony substratum permitted colonization by a large number of Trichoptera, Plecoptera, and Ephemeroptera. The latter observation was confirmed by Minshall and Minshall (1977) as well as by the present study. Cummins and Lauff (1969) performed laboratory experiments with different sized substratum particles and a constant current. Many insects showed a definite preference for certain particle sizes.

Results of this experiment suggested general patterns of distribution in response to the influence of current and substratum and were used to determine where emphasis would be placed in designing further tests. Two substratum particle sizes were selected for use in the remaining tests, sizes B and D. These are hereafter referred to as "small" and "large" substratum particle sizes.

Experiment II. Interaction of current, substratum, silt and detritus

Methods

This experiment was designed to examine the maintenance of a particular habitat type by organisms under altered environmental conditions of current and silt. It was assumed that factors which discourage initial colonization of an area will cause emigration when imposed on a previously suitable habitat. If emigration does not occur, it is assumed that the newly imposed factors do not discourage organism habitation. Since the substrata were manipulated for just three days before the end of the experiment, it is unlikely that any increased colonization resulted.

Three identical groups (I, II, III) of substratum types were prepared, each group with three trays of small substratum and three of large substratum. All eighteen trays were placed in a riffle area (Fig. 4) and allowed to be colonized for 30 d. Four trays in each group were equipped with the apparatus for measuring within substratum current velocity with NaCl tablets. The current

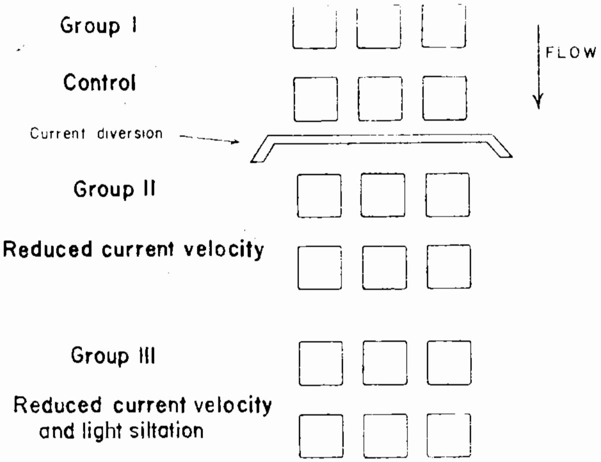

Fig. 4. Placement of the substratum trays in Experiment II. The current diversion was erected on the 30 th day and remained in place for 3 days. Each group contains three large and three small substratum trays.

regime of these trays was measured before and after reduction of current.

Many workers have emphasized the importance of the current factor in relation to organism distribution (e.g., Scott 1958, Ambühl 1959, Edington 1968, Chutter 1969) but evidence has been lacking on the absolute current ranges within the substratum which influence organism distribution. This study attempted to overcome the problem of relating open water current velocity to that in the substratum.

After 30 d a current diversion device was placed around Groups II and III, and a light coating of silt (<1 mm deep) was placed on the trays of Group III. This produced a situation where Group I possessed normal current-substratum conditions. Group II possessed reduced current and normal substratum conditions, and Group III possessed reduced current and a light coating of silt.

The trays remained in this condition for 72 h. This period was sufficient for organisms to move out if conditions were unfavorable yet short enough so silt would not accumulate appreciably. An Analysis of Variance (Woolf 1968) was conducted to determine if (1) substratum particle size influenced distribution and (2) reduction of current velocity or reduction of current plus light siltation had an adverse effect on habitat maintenance by the organisms or no effect at all. The two substratum sizes served as blocks while current and silt variations were considered treatments. Dunnett's procedure (Steel and Torrie 1960) was used to determine which treatments were significantly different from the control.

Results

Current velocities: In the fast current (Group I) the mean free-water velocity 3 cm above the substratum

sizes of substrata the mean current velocity dropped to 12 cm s^{-1}. The velocity was further reduced to between 3–6 cm s^{-1} at 3-cm distance within both substrata. But the current within the small substratum was somewhat lower than that within the large substratum. The decrease in current within the small substratum was rapid, reaching a minimum in the first cm. The reduction was more gradual within the large substratum.

The pattern of current reduction was similar for the slow current (Group II, after current diversion) (Fig. 5). Here the current response within both substrata was similar. Manipulation of the current to produce pool conditions brought about a fivefold decrease in free-water current over the large substratum, accompanied by a threefold decrease at the substratum surface and a twofold decrease within the substratum. The fivefold decrease in free-water velocity over the small substrata was accompanied by a threefold decrease at the substratum surface and an additional threefold decrease within the substratum.

Detritus: All detritus was collected from each substratum tray and sorted into two size classes (0.05–3.95 mm, >3.95 mm) (Tab. 3). The smaller class consisted mostly of leaf fragments, which represent more nearly the potential food for the insects than do fragments in the >3.95-mm class which were primarily sticks and twigs. The small substratum consistently contained

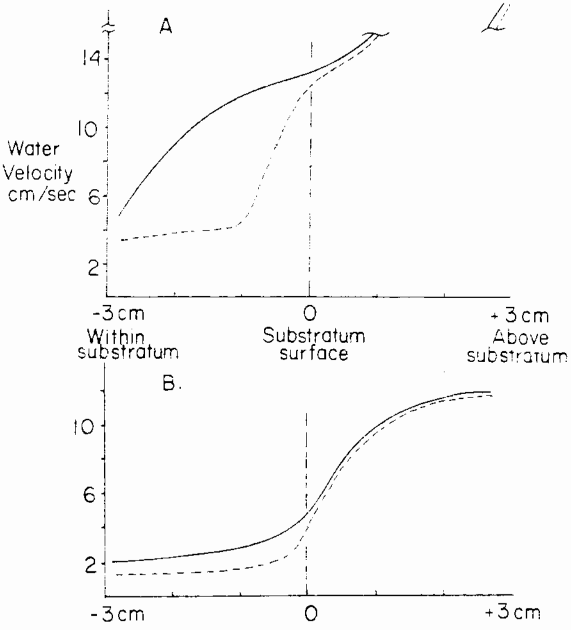

Fig. 5. Current regime within large and small substratum boxes in normal (A) and reduced (B) current conditions of Experiment II as measured by the NaCl technique. The solid line indicates large substratum; the broken line indicates small substratum.

Substratum	Detritus size class 0.05–3.95 cm g m^{-2}	 % of Total	 >3.95 cm g m^{-2}	 % of Total	Total g m^{-2}
Group I (normal flow and silt)					
Large substratum size	33.0	36	53.3	64	86.3
Small substratum size	81.5	80	20.2	20	101.7
Group II (reduced flow, normal silt)					
Large substratum size	84.7	41	122.0	59	206.7
Small substratum size	133.2	90	16.5	10	149.7
Group III (reduced flow, silt added)					
Large substratum size	103.4	44	133.8	56	237.2
Small substratum size	118.1	75	19.1	25	137.9

more small-sized (<3.95 mm) detritus particles than did the large substratum and vice versa.

Biota: The six trays of Group I served as a control (no manipulation was performed). Reduction of the mean number of organisms in Group II as compared to Group I was considered to be due to a lessening of current velocity from a mean of 48 cm s^{-1} to a mean of 11 cm s^{-1} (mid-water depth). Reduction of the mean number of insects in Group III as compared to Group I (Analysis of Variance Test) was considered to be due to current reduction and a light coating of silt. Differences between the mean numbers of insects in Group II and those in Group III were considered due to the effect of silt alone.

The most notable feature of this experiment is that insects colonized the small substratum in greater numbers than the large substratum (Tab. 4). The preference of seven taxa for smaller particle sizes was significant to the 0.05 level. Colonization of the two substratum types was about equal for three species: none of the organisms concentrated in the large substratum.

The reduction of current velocity alone affected six taxa significantly: *Paraleptophlebia heteronea*, *Baetis tricaudatus*, Chironomidae, *Optioservus quadrimaculatus* (A), *Arcynopteryx parallela*, and *Alloperla* spp. Seven taxa were significantly affected by addition of silt: Chironomidae, *Paraleptophlebia heteronea*, *Ephemerella grandis*, *Optioservus quadrimaculatus* (A) and (L), *Arcynopteryx parallela*, and *Alloperla* spp. The Chironomidae was the only taxon to show a significant increase in numbers during the experiment.

Discussion

The fact that the within-substratum current regime (Fig. 5) showed a gradual reduction within large substratum trays but an immediate steep decline in the small substratum, indicates the existence of a wider range of current conditions in the large substratum. If an insect possessed a very narrow tolerance range for current and was sensitive to velocity changes, his best opportunity for a suitable habitat would be the large substratum. However, colonization was greatest in the smallest substratum, which offered the least variable and slowest current condition. In addition, Experiment I showed that every organism which appeared in the riffle (except *Glossosoma* spp. and *Isoperla fulva*) was common in the very slow current conditions of the pool.

It appears that most of these organisms will function normally in a very slow current velocity under certain conditions (e.g., rubble substratum, no silt, high oxygen content), although definite current preferences are apparent. When the current in Experiment II was reduced to 2–3 cm s^{-1}, six of eleven species emigrated in significant numbers (Tab. 4). For the majority of insects in this experiment only a minimum current velocity (about 2 cm s^{-1}) was required for them to function normally. Two exceptions should be mentioned. *B. tricaudatus* was found in greatest numbers throughout the study in the fastest current conditions. Ambühl (1959), in a laboratory experiment which offered progressively increasing current velocities, found species of *Baetis* to occur at the highest velocities (near 18 cm s^{-1}). This is probably due to *Baetis*' greater oxygen requirements (i.e., greater than that of any other insect in Ambühls' study). The distribution of *Glossosoma* in this study is similar to that reported by Scott (1958) where the insect showed a sharp decrease in numbers at currents of 20 cm s^{-1} (free-water velocity). This was attributed to deposited silt which interfered with feeding. It is possible that the same condition occurred during this study (Experiment I).

It has been amply demonstrated (see Cordone and Kelley 1961) that an excess of silt will smother the biotope and drastically reduce the numbers of Plecoptera, Ephemeroptera, and Coleoptera. In this study the presence of a light coating of silt (<1 mm deep) had a variable effect on species composition. This supports evidence of other investigators (Ellis 1936, Hamilton 1961, Cummins and Lauff 1969) who reached the conclusion that a light coating of silt may have either a

Tab. 4. Insect fauna of Experiment II. Those insects significantly (P < 0.05, Analysis of Variance) more abundant in the small substratum are indicated by an (*) in column one. Those insects significantly affected by reduction in current or silt addition are indicated by (*) in the appropriate column. Each value is the mean of three trays expressed as organisms m^{-2}.

		Small substratum			Large substratum		
	Small substratum preference	Group I normal current	Group II reduced current	Group III reduced current and silt	Group I normal current	Group II reduced current	Group III reduced current and silt
Chironomidae	*	4304	4176	3120	1274	2064*	1760*
Paraleptophlebia heteronea	*	3520	1916*	1296*	1840	890*	688*
Ephemerella grandis	*	2208	1906	1056*	1088	1168	624*
Optioservus quadrimaculatus (A)	*	1488	922	192*	288	64*	16*
Baetis tricaudatus		1152	656*	672	928	160	384
Optioservus quadrimaculatus (L)	*	768	972	480	352	480	224*
Arcynopteryx parallela	*	512	576	240*	336	208*	240
Alloperla spp.	*	416	192*	160*	154	112	96*
Ameletus oregonensis		256	366	272	228	336	272
Cinygmula mimus		260	208	160	234	197	176
Pteronarcys californica		80	96	48	112	80	16

positive or negative effect on distribution but does not seriously reduce insect populations.

The concentration of insects in the smaller particle size may be explained several ways. The first is the substratum particle size itself influenced insect behavior. A bed of stones continually in motion could either destroy the organisms by grinding and crushing or at least discourage colonization. This type habitat would also limit algal growth and the accumulation of detritus. However, all substrata were stable in this study and this cannot be considered important.

The substratum particle also serves as a "coverfactor" (Scott 1966) and provides a surface area on which the organisms exist. Determining surface area available within any particular tray is difficult because of surface irregularities; however in an equal volume, smaller particle sizes offer greater surface area for colonization. If surface area were important, colonization should be progressively greater through a series of progressively smaller substratum sizes until the surface becomes too small or the material too unstable for the animals to occupy. However, Experiment I suggests that this is not the case. In both pool and riffle, the majority of species were more abundant in size C (2.5–3.5 cm) substrata than in substrata with particles either larger or smaller than that. Likewise, Minshall and Minshall (1977) found that the increase in numbers of only a few taxa was associated with an increase in surface area.

Another possibility to explain insect distribution relative to substratum is that particle size may influence subsurface current velocity. This factor has been investigated in this study, and it has been concluded that alteration of current within the substratum cannot explain the large differences in insect distribution.

A more plausible explanation of the effect of substratum particle size on microdistribution is that certain substratum conditions are more efficient at collecting food (detritus), which is then "sought out" by the insects. The importance of detritus as an energy sourc for invertebrates of a stream ecosystem is well documented (Nelson and Scott 1962, Chapman and Demory 1963, Minshall 1967, Fisher and Likens 1973, Cummin et al. 1973). Egglishaw (1964) has shown a strong positive correlation between the amount of plant detritu and the distribution of many stream insects. However little is known of the effect of different detrital mixture or sizes of detrital particles on organism distribution The present study not only supports Egglishaw's findings, but proceeds further in an attempt to explain the physical factors that determine the distribution of detritus in a stream.

Substratum-detritus relationship: It was found tha large sized detritus (>3.95 mm), primarily sticks an pieces of wood, predominated in the large substratu sizes, and small detrital particles (<3.95), primarily lea fragments and soft bark, predominated in the small substratum particle size (Tab. 3). The small size detrita class more closely represents food available to the insects than does the large size detritus since detritivore consume primarily the soft mesophyll portion of th leaves (e.g., Wallace et al. 1970). There were no whol leaves or mats of allochthonous material on the strea bottom in the study area. The current velocity was to great and any such material was either shredded o swept away. Down to a certain point the smaller substrata contain more interstices where the small lea fragments can be caught and accumulate. The large spaces within the large substrata allow greater wate velocity and less chance for the detritus to settle out This suggests that more insects are colonizing the smaller (1.0–2.0 cm) substrata primarily because the substratum particles serve as a better food collecting device. A final experiment was designed to differentiate the effects of substratum particle size and detritus particle size on insect distribution

Experiment III. The effect of detritus versus the effect of substratum particle size

Methods

In normal conditions (Tab. 3) the boxes of large substratum contained proportionally more large (>3.95 mm) detrital particles and the small substratum trays contained proportionally more small (<3.95 mm) particle sizes. In this test the conditions were reversed. Three trays of small and three of large substrata were prepared. Interspersed in each box of small substrata were approximately 10 g of detritus in the size range of 4–8 mm. Interspersed in each box of large substrata were approximately 10 g of detritus in the size range 0.5–4 mm. This detritus was collected from Mink Creek and returned to the laboratory for sorting and weighing. Excess water was removed but the detritus was never completely dried, a precaution against destroying any microflora which might be an important constituent of the insects' diet. To prevent the added detritus from being washed away, each tray was covered by an empty inverted tray before it was placed in the stream. After a minute the inverted tray was removed and very little of the added detritus floated out.

A compromise 7-d colonization period was chosen to allow enough time for organisms to become established and yet prevent the normal detrital distribution from becoming re-established. The detritus from each tray was collected, sorted, and reweighed at the end of the experiment. A Group Comparison t-Test (Woolf 1968) was conducted to determine if the composition of the detritus or substratum size had an effect on insect distribution.

Results

Apparently the natural deposition of detritus during the 7-d test period altered the prepared composition. At the termination of the experiment the amount of small detritus particles (<3.95 mm) was similar for all trays (Tab. 5). Therefore, the only variable affecting colonization was substratum particle size.

Most taxa appeared to colonize both the large and small substrata at a similar rate (Tab. 5). However, to realistically evaluate distribution in this experiment a taxon was arbitrarily disregarded if it did not colonize either substratum condition with a mean greater than 100 individuals m^{-2}. Seven taxa met this criterion, but only for *Ephemerella grandis* did the difference between the mean numbers of organisms in the small and large substrata exceed 15% of the total. Distribution differences between the two sizes of substrata were not significant ($P < 0.05$, Group Comparison t-Test) for any species.

Tab. 5. (A) Total organisms and (B) detritus from the substratum trays at the termination of Experiment III, expressed as organisms m^{-2} and g m^{-2}, respectively. Each value is the mean of three trays and is given with its standard deviation.

A. Organism	Small substratum		Large substratum	
	X̄	± S.D.	X̄	± S.D.
Chironomidae	432	219	405	264
Ephemerella grandis	427	161	253	120
Paraleoptophlebia heteronea	176	32	133	81
Ameletus oregonensis	155	88	123	18
Pericoma sp.	128	100	139	109
Optioservus quadrimaculatus larvae	112	58	112	32
Isoperla fulva	112	28	85	9
Alloperla spp.	80	16	53	40
Nemoura cinctipes	53	46	11	18
Baetis tricaudatus	37	40	43	33
Ephemerella inermis	32	24	27	24
Pteronarcys californica	27	9	64	55
B.				
Detritus size class				
0.5 mm–3.95 mm	126	29	119	29
≥ 4 mm	59	22	28	11

Conclusion

The results suggest that the insects were colonizing in response to amounts of detritus. It is therefore concluded that detritus is of primary importance to insect [illegible] but it is the [illegible] of substratum particle size which determines the distribution of the detritus.

4. General theory of microdistribution

Sufficient information was acquired during this investigation to permit the development of a general therory to explain insect microdistribution in Mink Creek (Fig. 6). This model probably is also applicable to other streams in which most of the potential food for benthic insects is allochthonous detritus and a moderate-to-fast current velocity is present to prevent the detritus from settling and accumulating on the substratum surface. The broad arrows of Fig. 6 indicate the most important relationships affecting organism microdistribution, but other factors may modify this pattern. Heavy siltation drastically reduces organism populations but light siltation has a differential effect depending upon the species.

As shown in Fig. 6, current velocity interacts with all other distributional factors. It sorts and separates the substratum particles, deposits or carries away silt, transports and shreds leaf detritus, and is necessary for organism respiration. The substratum particles act as detritus collectors. Small particle sizes tend to accumulate large amounts of the small detrital particles, which are primarily leaf fractions. This type of detritus does not accumulate in the larger-size substrata, where the interstices are larger and current velocity is higher. Here twigs and sticks predominate. Benthic insects concentrate where the food is most abundant (small substratum) and the number of organisms should be directly related to the composition of the stream bottom. It is

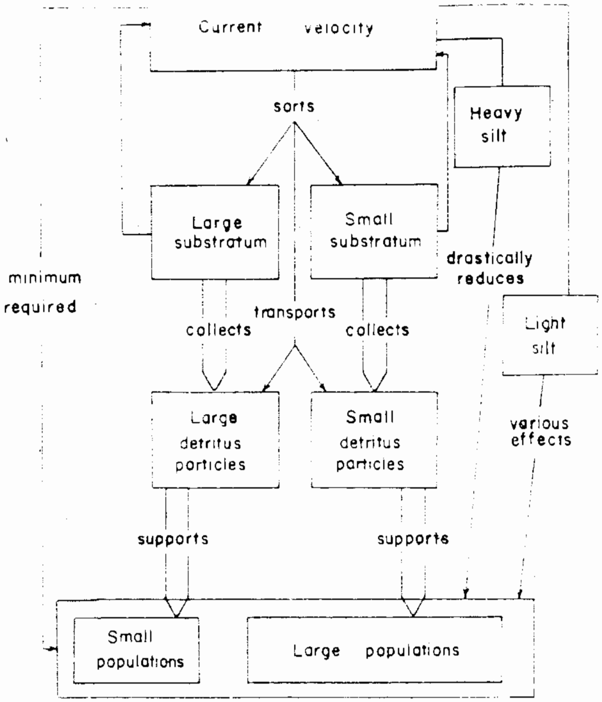

Fig. 6. General model of biotic and abiotic interrelationships influencing the microdistribution of benthic stream insects. Relative importance is indicated by the width of the arrows.

also probable that the greater current modifying effect of the smaller substratum is important to many species.

Substratum is increasingly being used in attempts to classify streams into community types (see Thorup 1966). The present study suggests that in some situations substratum may be used to estimate or to enhance the productivity of sections of streams; however, further analysis is necessary to strengthen this idea.

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