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Substrate size selection by stream invertebrates and the influence of sand

Abstract—A field experiment showed that benthic invertebrates in running water exhibit preferences for different substrate particle sizes. Maximum numbers and biomass occurred on medium gravel (24.2-mm mean diam), whereas diversity was greatest on large gravel (40.8 mm). Individual species fell into four groups: upper, medium, and lower size preference, and no preference. The addition of a limited quantity of sand to medium gravel affected only a few species.

Studies of the relationship between aquatic invertebrates and the substrates they live in have been made in marine, freshwater lentic, and freshwater lotic environments, in that order. A large proportion of the running water reports have described the importance of substrate type in determining invertebrate distributions (Cummins and Lauff 1969). Such descriptive works have been useful in laying a foundation for more applied studies. Unfortunately, the latter appear to be slow in coming.

Mundie (1974) tried to apply the principles of natural stream rearing of salmon fry to high density populations in a seminatural channel by alternating high-velocity food-producing areas (riffles) with low-velocity habitat (pools). Although these fish were to be fed mainly artificial foods, aquatic invertebrates from the riffles were considered an important supplement which would also promote the acquisition of natural feeding behavior. Since the channel was to be entirely man-made, size and composition of the riffles could be adjusted to maximize benthic production. We here examine the responses of benthic invertebrates to substrate sizes within the range that could be practically used in such a channel.

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The experiment was done in a flow-control rearing channel similar to that proposed by Mundie (1974). The channel, 400 m long by 4.5 m wide and operated at a discharge of 0.42 $m^3 \cdot s^{-1}$, was constructed alongside the Big Qualicum River on the east side of Vancouver Island, British Columbia. The physical characteristics of this river were described by Lister and Walker (1966). It is low in nutrients and has an alkalinity of 30 ppm $CaCO_3$. The features designed into the channel stress uniformity of conditions, so that certain natural stream properties, such as edge effect, have been virtually eliminated.

Eight wooden troughs each measuring 210 × 22 cm were laid side by side across the lower end of the rearing channel. Three sizes of gravel were used (11.5-, 24.2-, and 40.8-mm mean diameter), each placed separately into two troughs, chosen at random, to a depth of 15 cm. The current flowing through the troughs was adjusted to about 45 $cm \cdot s^{-1}$ by vertical slats at the upstream end. Because the surrounding soil had a high sand content and would probably enter the channel through rain action, we decided to use the two remaining troughs to study the effect of sand on benthos. An amount calculated to be what might realistically enter the channel riffles over a set period (4 liters) was added to 24.2-mm-diameter gravel in these two troughs. The substrates were left to be colonized for 28 days during October–November 1976, the contents of each trough then thoroughly disturbed, and the organisms and sediment collected in a 50-μm mesh net attached to the downstream end.

Formalin-preserved (5%) material from each trough was subsampled into five equal units (Mundie 1971*a*)—three for counting and identification and two for dry weight (110°C for 24 h, i.e. to constant weight). Each unit contained about 600

Table 1. Significant relationships between major taxa and substrate size (S—small, M—medium, L—large) ($P < 0.05$); 1st, 2nd, and 3rd choices are indicated.

	S	M	L	Size preference
Baetis sp. A	2	1	1	upper
Prosimulium sp.	2	1	1	range
Paracamptus ?reggiae	1	1	2	lower
Brachyptera sp.	1	1	2	range
Micropsectra/ Tanytarsus spp.	1*	1	2*	
Thienemanniella sp. B	1	1	2	
Nematoda	2	1	3	medium
Nais variabilis	2	1	3	range
Chaetogaster diaphanus	2	1	2	
Rheotanytarsus sp.	3	1	2	
Phaenopsectra/ Polypedilum spp.	2	1	3	
Thienemanniella sp. C	2*	1*	2	
Eukiefferiella sp. C	2	1	2	
Eukiefferiella sp. A	1	1	1	none
Eukiefferiella sp. B	1	1	1	
Baetis parvus	1	1	1	

* $P < 0.10$.

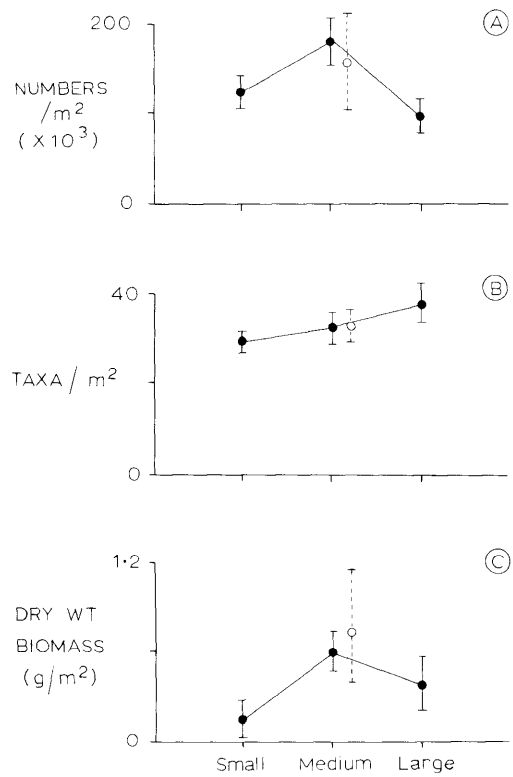

Fig. 1. Response of benthos to different substrate sizes. A—Numbers of animals; B—number of taxa; C—dry weight biomass (●—mean of six subsamples within 95% confidence limits; ○—medium gravel and sand).

animals; once the animals had been removed, three from each set were dried and their residual organic matter was measured by a high temperature (550°C for 24 h) weight reduction method.

Mean grain size and heterogeneity of grain size were calculated according to Schwoerbel (1961) and porosity from Pollard's (1955) formula.

Figure 1 shows the standing crop of invertebrates on the different substrates after 28 days of colonization. The means and their 95% confidence limits have been calculated from the six subsamples taken from each pair of replicate troughs according to Student's t-distribution for small samples (Sokal and Rohlf 1969). The medium-sized gravel supported the greatest numbers of animals (mean = $180{,}314 \cdot m^{-2}$), followed by small ($124{,}291 \cdot m^{-2}$) and large gravel ($98{,}922 \cdot m^{-2}$) (Fig. 1A), although the difference between these last two values was not significant ($P < 0.10 > 0.05$). The greatest diversity of animals (Fig. 1B) occurred in the large gravel troughs (mean = 37.2 taxa); there was no significant difference between the number of taxa in the medium and small gravel. Dry weight biomass was greatest in the medium gravel (Fig. 1C), and the large gravel supported a greater biomass than the small. In terms of these three parameters, there was no difference between the animals found in the medium gravel and the medium gravel plus sand.

Table 1 presents the substrate size preference of the most common animals (about half the fauna) based on the numbers present; first, second, and third choices are shown. The differences in the numbers present between choices are significant at $P < 0.05$. Four groups are apparent: the mayfly *Baetis* sp. A and the blackfly *Prosimulium* sp. preferred the medium and large gravel equally over small. Small and medium were preferred equally over large by the harpacticoid *Paracamptus ?reggiae* (M. S. Wilson), the

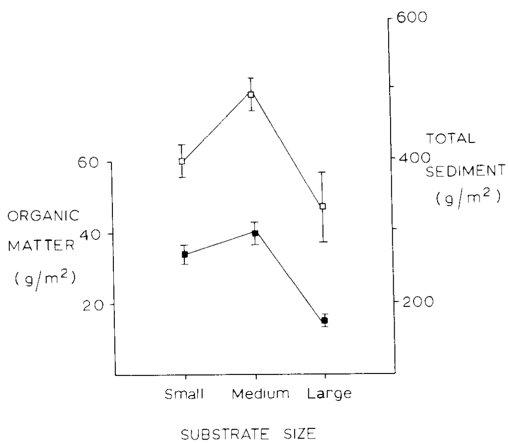

Fig. 2. Amounts of organic matter (■) and total sediment (□) collected by the different-sized substrates (means of six subsamples within 95% confidence limits).

stonefly *Brachyptera* sp., and the chironomid genera *Micropsectra*, *Tanytarsus*, and *Thienemanniella* sp. B. Medium gravel was selected by nematodes, the oligochaetes *Chaetogaster diaphanus* (Gruithuisen) and *Nais variabilis* Piguet, and by five chironomid genera. Only three species (two of the chironomid genus *Eukiefferiella* and the mayfly *Baetis parvus* Dodds) showed no substrate preference.

Comparison of the troughs containing medium gravel and medium gravel plus sand showed that only 6 of the 18 major taxa were significantly affected. Numbers of the chironomids *Phaenopsectra*, *Polypedilum*, and *Eukiefferiella* sp. A, together with nematodes, were depressed by the addition of sand, while there was almost a doubling of the numbers of *Prosimulium* in the sand troughs. The reason for this last response is unclear.

The medium gravel trapped the most organic matter and total sediment, followed by small and then large gravel (Fig. 2). Mean values suggest that the organic content of the sediment collected by the small gravel may have been slightly higher than that of the medium and large sizes.

Physical characteristics of the substrates are given in Table 2. Heterogeneity of grain size was greater in the small gravel than in large and medium, and porosity was greatest in medium followed by small and then large

Table 2. Characteristics of the three substrate sizes (S—small, M—medium, L—large).

	S	M	L
Mean particle size (mm)	11.5	24.2	40.8
Heterogeneity	3.21	1.29	1.90
Porosity	0.348	0.383	0.338

So far as maximizing benthic standing crop is concerned, the medium-sized substrate supported the greatest numbers and biomass, with 8 of the 18 major taxa showing a definite preference for, or an increased survival on, this type. Greatest diversity occurred, however, in the large gravel. Of the taxa preferring the medium gravel, five were chironomids (an important element in the diet of young salmonids: Mundie 1971*b*), two were oligochaetes (not generally considered important, although trout may eat them: Aarefjord et al. 1973), and the rest were free-living nematodes which, although sometimes found in fish stomachs (Williams unpublished), are probably unimportant in the diet. Two species of chironomid and a mayfly showed no substrate size preference and so may be expected to occur in medium gravel at sufficient densities to be exploited by fry.

This whole notion of substrate preference is interesting. Cummins and Lauff (1969) underlined the difference between "tolerance" and "preference" ranges. They argued that for current velocity, the tolerance and preference limits for a particular species may well be the same. On the other hand, substrate preference limits can be considerably less than the tolerance range. The results of our experiment clearly support this idea. The partitioning of species in this way as a result of particle size selection has important consequences for microdistributional studies.

There is a reasonably good correlation between porosity and the amount of sediment (including organic matter) collected by each substrate type. This is perhaps not surprising as it probably reflects the amount of interstitial space available for debris retention. The greatest abundance of organic matter in the medium gravel may account for the greatest standing crop of invertebrates there, but there was a greater biomass in the large than in the small gravel even though the amount of organic matter was greater in the latter. The number of taxa was also greatest in the large gravel, but this may be due to the use of this size as a site for attachment by certain of the rarer species which filter food particles out of the water column, e.g. *Simulium* sp. and *Hydropsyche* sp. Alternatively, there may simply have been more advantage in terms of shelter or space in the interstices of the large gravel.

In our experiments we dealt only with relatively uniform gravel mixtures. It is reasonable to suppose that more extensive tests with more combinations of substrate sizes would increase benthic standing crop even further. It is apparent even from this study that maximization of invertebrates for use as food for salmonid fry in the type of seminatural rearing channel proposed by Mundie (1974) could be attained by the selection of a suitable substrate.

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