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MICRODISTRIBUTION OF MACROINVERTEBRATES IN LOWLAND STREAMS

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INTRODUCTION

Lowland streams are a characteristic type of stream in the eastern and southern parts of the Netherlands as well as the adjacent parts of the Federal Republic of Germany and Belgium. Unfortunately many of these streams have been perturbed in various ways during the last half century in order to create work, to increase agricultural productivity, to lower the ground water level, to reduce inundation and to reduce bank and stream bed erosion and consequent sand transport, and to fix the freely meandering streams in a stable, often artificially lined stream bed to reduce landloss. Many of these streams bear more resemblance to long stretched stagnant ponds than to running waters because weirs and barrages have been built at regular intervals for flow reduction and water level regulation. High levels in summer enable artificial raining of farmland, and low levels in spring and winter enable discharge of the excess water that drains very rapidly from the 'improved' drainage area. These regulated streams not only differ from the natural, geomorphologically unperturbed lowland streams in the form of the stream bed, but also concerning the degree of shading by stream accompanying bank vegetation (trees and shrubs) and the heterogeneity of the environment, including current velocity, substrate composition, water depth, growth of aquatic plants and algae, as illustrated in Fig. 1.

Another highly important difference between regulated and natural lowland streams is the trophic basis of the food chain. Natural lowland streams are heterotrophic, largely depending on the input of organic particulate material from the banks (mainly leaves) as the major source of carbohydrate, protein and nutrients. Regulated lowland streams are autotrophic, with a higher primary production enabled by the reduction of flow and the removal of the light intercepting marginal vegetation.

Because of these differences between natural and regulated streams, major differences in the structure of the animal community exist. The distribution of fresh water animals is determined by a whole complex of a large number of physical, chemical and biological factors (see *e.g.* HYNES, 1970a,b; FRIBERG *et al.*, 1977) of which the current, temperature and chemical composition of the water determine the habitat tolerances and consequently the geographical distribution (macrodistribution), while substrate particle size and food supply are the more important factors responsible for the habitat preferences or the distribution of the animals within a stream (microdistribution) or within a biotope (*cf.* CUMMINS and LAUFF, 1969).

This paper presents the role of the stream bottom substrate, with emphasis on the relationships between the microdistribution of the macroinvertebrates and the composition of the substrate. Two questions were to be answered. (1). Are there relationships between macroinvertebrates and certain substrates, *i.e.* do macroinvertebrates prefer a specific grain size or sizes of the mineral substrate, possibly in combination with organic material? (2). Do they need different substrates during their aquatic development, *i.e.* is the variation of substrate composition of the stream bottom in space and time (substrate mosaic patterns) important for the occurrence and existence of the bottom dwelling macroinvertebrates?

This research was set up as a field investigation to determine microdistributional patterns

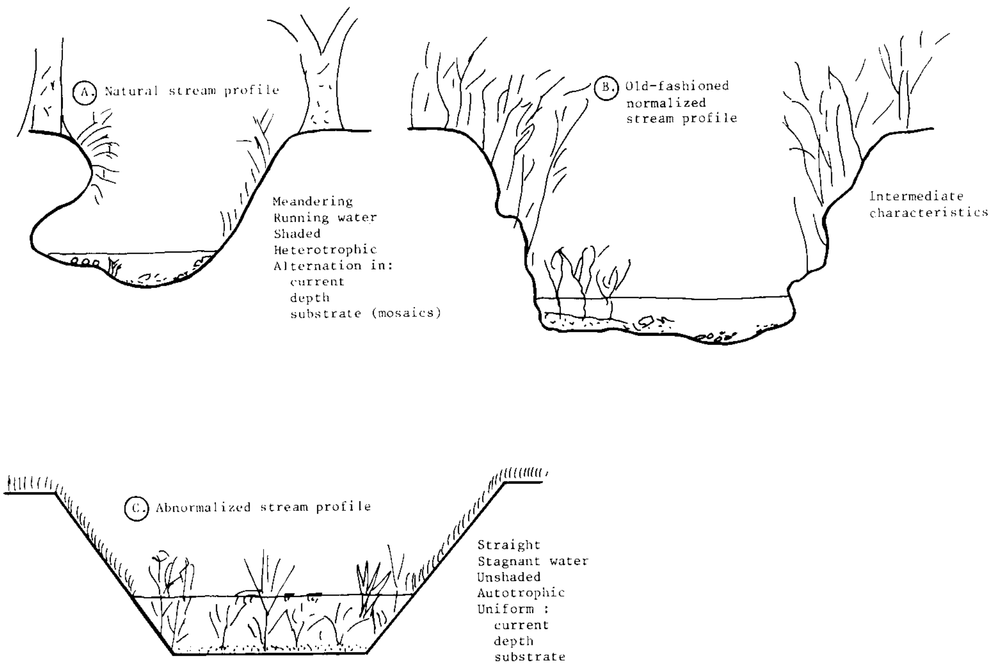

Fig. 1. Stream profiles and some of their characteristics.

of the various macroinvertebrates in two streams; a laboratory research to determine substrate preferences of a number of characteristic lowland stream species in substrate selection experiments in a laboratory stream channel and finally field experiments to determine the macroinvertebrate colonization of artificial substrates in the stream bed. Only the field investigation and laboratory experiments will be illustrated.

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STUDY AREA

Two streams in the Achterhoek were studied, *viz.* the Snijdersveerbeek and the Ratumsebeek, both described in detail by TOLKAMP and BOTH (1976) and TOLKAMP (1980). They are relatively small, unpolluted and unperturbed. The sampling stations were situated in the upper courses. The Snijdersveerbeek originates in a small valley, fed all year round by iron-rich ground water. Gravel forms a major part of the substrate, and gravel, sand and organic materials as leaves and detritus form strongly alternating mosaic substrate patterns, not only enhanced by the strong meandering of the stream bed, but also by the micro-meandering of the current within the stream bed. The Snijdersveerbeek stream bed is between 50 and 100 cm wide, with a water depth varying between 5 and 30 cm. The Ratumsebeek is a stream similar to the Snijdersveerbeek but of larger dimensions (150 -300 cm wide, water depth between 5 and 100 cm) while coarse gravel is less dominant and the substrate mosaic patterns are also of larger dimensions, each substrate type occupying larger areas. Both streams are shaded by trees and shrubs and aquatic vegetation is very scarce because of the strong shading.

METHODS

Samples of the stream bottom were taken with the mini-macrofauna shovel, which samples both substrate and macroinvertebrates at the same time on a small scale. This shovel is 10 cm wide, 10 cm high and 15 cm long and is pushed through the stream bottom at a fixed depth of 3 cm. Leaf packs and coarse detritus accumulations were sampled by hand, taking material from an area similar to that sampled by the shovel (150 cm^2). The sampler will be described in detail elsewhere (TOLKAMP, in prep.).

Samples were taken in all different substrate types as recognized by a field-classification system, by which substrates were characterized by the dominant particle sizes at the bottom surface; they include combinations of cobbles, pebbles, coarse and fine gravel, coarse and fine sand, silt/lutum with and without organic material as leaves, coarse detritus, and fine detritus. A sample was taken on each sampling occasion in each recognized substrate type. Macroinvertebrates were collected in the laboratory after which the substrate was dried and the mineral particle size composition determined by dry sieving the sample and weighing the various particle size fractions. The amount of coarse organic matter (*i.e.* that could be handeled with a pair of pincers) was also determined by drying and weighing.

The particle size composition of each sample was summarized by determining the substrate characteristic or $Q_1M_dQ_3$-index according to DOEGLAS (1968). This is an index expressing the median particle size or the second quartile of the substrate (M_d) and the heterogeneity of the substrate by the first (Q_1) and the third (Q_3) quartile. These quartile values are indicated by the negative binary logarith (phi value) of the particle size since the substrate was divided into the fractions of the Wentworth classification in which each particle size fraction is twice the preceding one. Q_1 gives the phi value at which 25 % of the substrate is coarser, Q_3 gives the phi value at which 25 % of the substrate is finer than the corresponding particle sizes. To simplify the comparison of the indices of many samples only integer phi values are used in the $Q_1M_dQ_3$-index. When the $Q_1M_dQ_3$-indices of all samples are expressed graphically in one figure (the $Q_1M_dQ_3$-graph or substrate characteristic) the substrate heterogeneity of the stream bottom becomes visible. When the distance between Q_1 and M_d and M_d and Q_3 is small, it concerns a homogeneous substrate, while for a heterogeneous substrate these distances are larger (Fig.2). Negative phi values are presented with the minus sign above them (*e.g.* $\bar{3}$).

SUBSTRATE CLASSES

On the basis of the field-classification several substrate types were distinguished at four levels, each considering the substrate composition or condition in more detail (Fig.3).

On the basis of the $Q_1M_dQ_3$-index 11 mineral substrate types were distinguished for reasons discussed by TOLKAMP (1980). Each type is characterized by one or more indices, as illustrated in Fig.2. The right hand part of the graph with M_d values larger than 3 is formed by small amounts of mineral matter as part of organic substrates. Three types of organic substrates were distinguished: leaves, coarse detritus, and leaves + coarse detritus. A sample was classified as organic when on the basis of dry weight more than 1 % (or 10 % in a second classification) of the sample consisted of organic material. Comparison of these two classification should yield information about animals preferring a combination of mineral and between 1 % and 10 % organic material. For these animals the preference for organic classes at the 1 % level must shift to the mineral classes at the 10 % level. In both classifications classes 1 - 6 consist of gravel substrates; classes 7 - 11 consist of sand substrates and classes 12 - 14 consist of detritus substrates. The coarseness of the mineral substrates decreases from class 1 up to and including 11.

The distribution of the macroinvertebrates over the different substrate types and possible preferences of these animals for certain substrate types was expressed with the index of

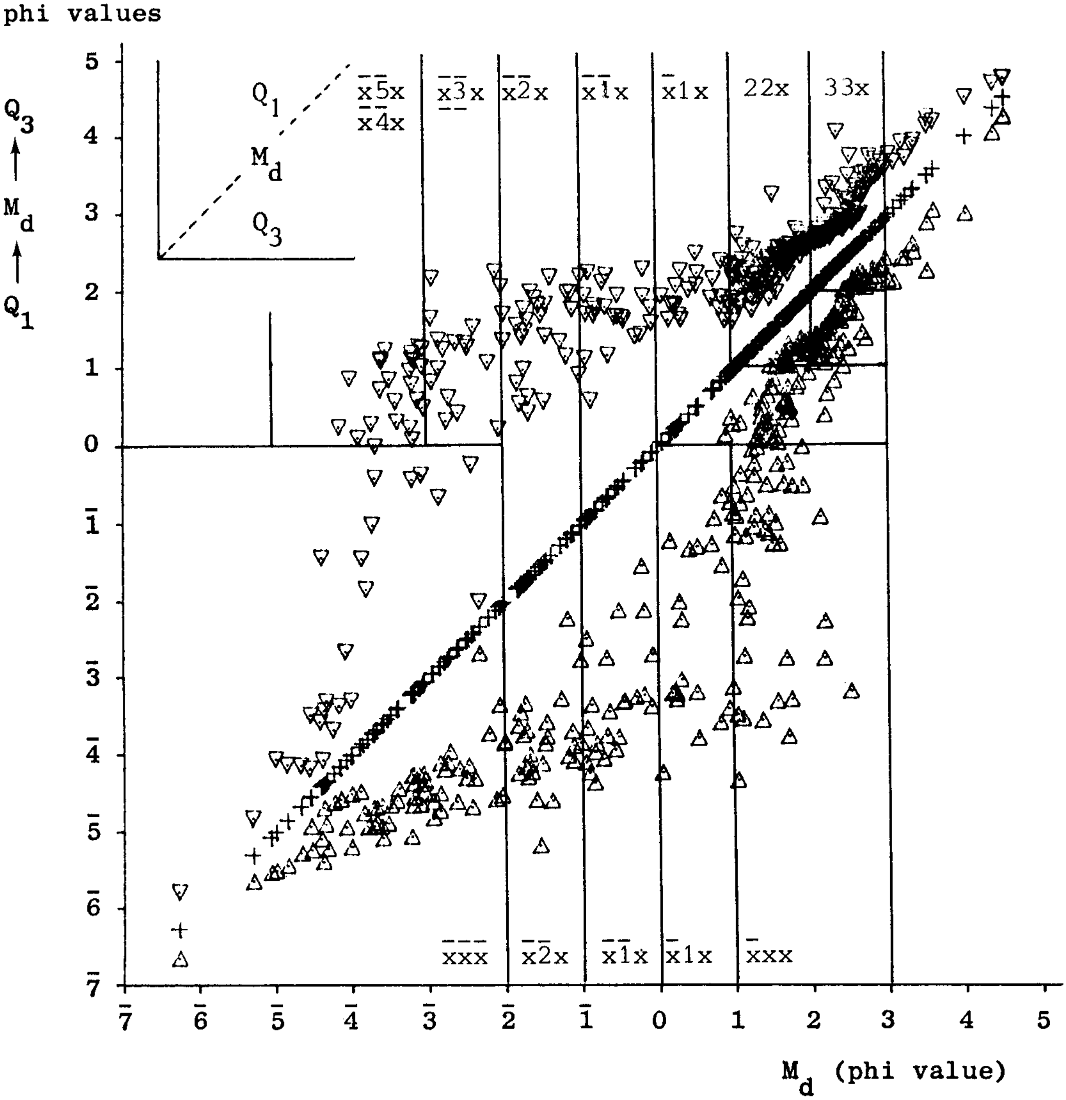


Fig. 2. $Q_1M_dQ_3$-diagram with mineral substrate classes for the mineral substrates in the Snijdersveerbeek; xxx indicates the $Q_1M_dQ_3$-index of each substrate class (see Table III).

% of organic material	$Q_1M_dQ_3$-index											detritus		
	$\overline{xxx}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD + L
1 %	−2.2	−1.9	*4.1*	1.1	*2.0*	−2.6	−0.4	−5.5	−0.2	−2.6	−0.7	*10.2*	−5.3	−3.0
10 %	−2.4	−2.4	*6.4*	*2.3*	*2.4*	−2.8	0.5	−5.5	*6.0*	*5.4*	0.9	−3.2	−5.3	−3.3

Table I. I.R. values for *Ephemera danica* (N = 436) in the grain-size classification of the substrates in the Snijdersveerbeek. Italic values indicate significant over-representation; CD = coarse detritus; L = leaves.

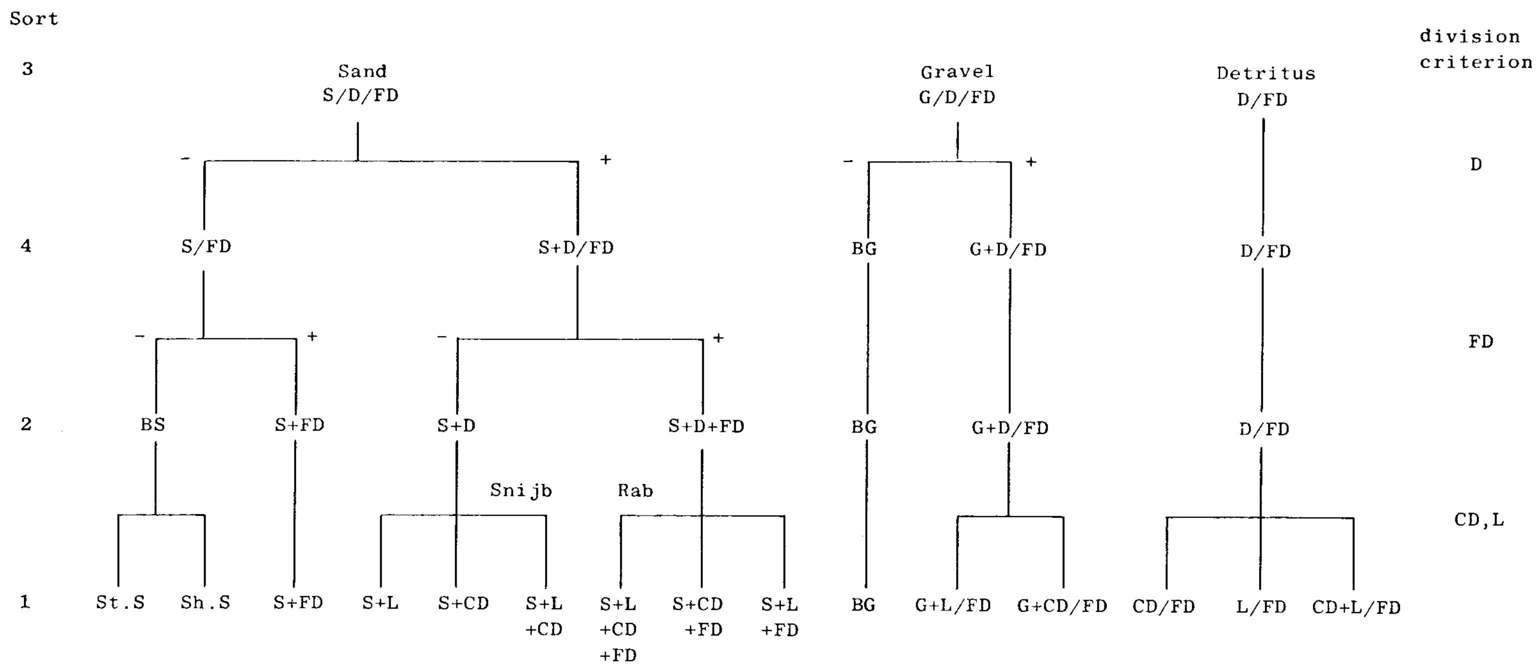


Fig.3. Substrate types based on the field-classification of the substrates at four levels (Sorts 1, 2, 4 and 3). S = sand; G = gravel; CD = coarse detritus; L = leaves; D = detritus (coarse detritus and/or leaves); FD = fine detritus; B = bare; St = stable; Sh = shifting; + = with; – = without. S + L + CD occured only in the Snijdersveerbeek (Snijb.). S + L + CD + FD occured only in the Ratumsebeek (Rab.).

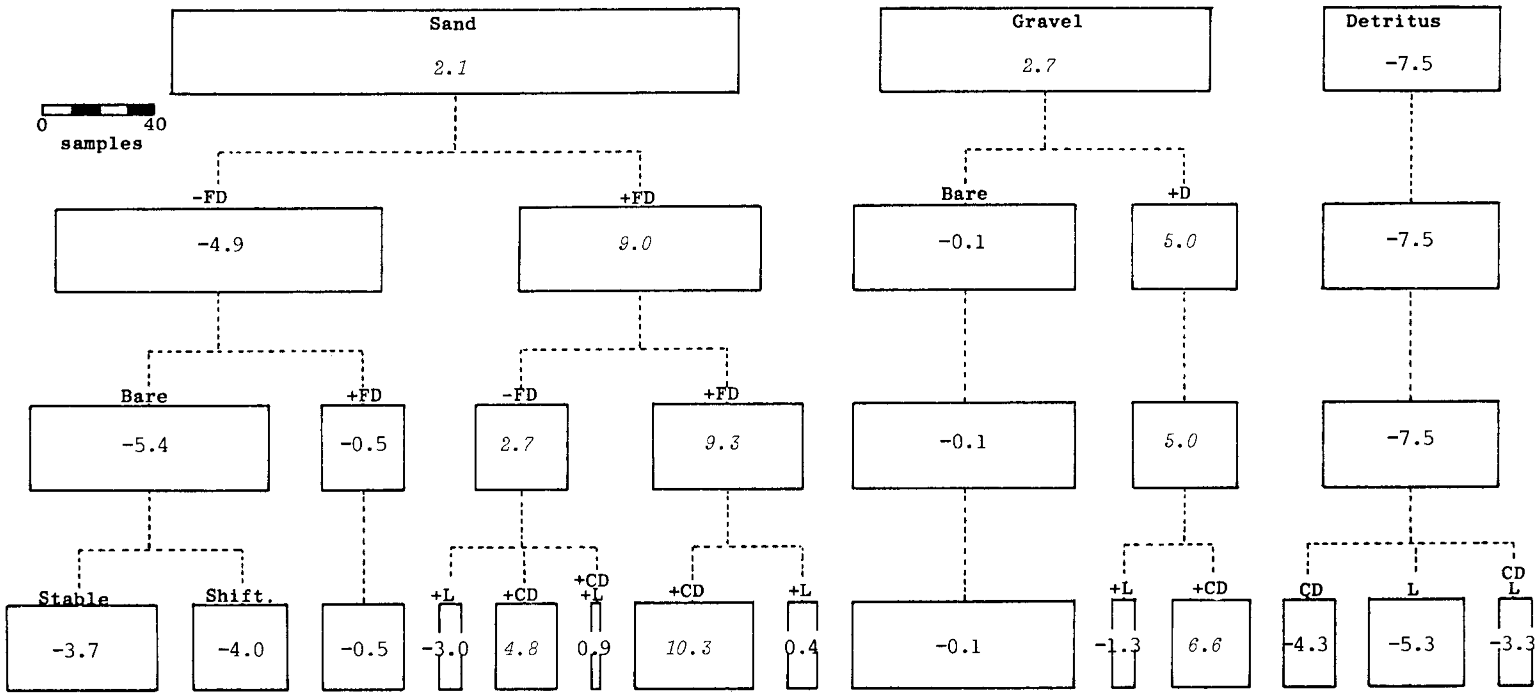


Fig.4. I.R. values for *Ephemera danica* (N = 436) in the field classification of the substrates in the Snijdersveerbeek. For explanation of symbols see Fig.3. Italic values indicate significant over-representation.

representation (I.R.) (HILDREW and TOWNSEND, 1976) and statistical significance was tested with the chi-squared test, assuming that each species should be present in equal numbers in all substrate types. The formula used was :

$$\text{I.R.} = \frac{O - E}{\sqrt{V E}}$$

where O = observed number of specimens of a species and E = expected number of specimens of this species.

Positive I.R. values indicate over-representation and negative I.R. values indicate under-representation.

The importance of the use of the four levels of classification on the basis of the characterization of substrates in the field is seen by the shifting of the preference (over-representation) of several species at different classification levels, as illustrated for *Ephemera danica*, a burrowing mayfly species characteristic for unperturbed streams (Fig.4). At the first level of classification gravel seems to be preferred, followed by sand. At the following levels, however, sand combined with coarse and fine detritus is preferred, while at the most detailed level sand + coarse detritus + fine detritus is preferred, while *Ephemera danica* is also over-represented in gravel + coarse detritus and sand + coarse detritus. These differences between a detailed and a very rough classification can be explained by the negative influence of a large number of sand samples that did not contain any *Ephemera danica* nymphs, because they reduce the expected number of nymphs in all other samples.

The function of two parallel classifications based on the particle size analysis combined with the amount of organic matter as determined by the 1 % and 10 % division of organic matter is illustrated in Table I; the preference of *Ephemera danica* shifts from coarse detritus substrates in the 1 % classification to sand + coarse detritus (containing 1 - 10 % detritus) in the 10 % classification.

	length class 1 mm	N	$Q_1M_dQ_3$-index											detritus		
			$\overline{xxx}$	$\overline{x5}x$ / $\overline{x4}x$	$\overline{x3}x$	$\overline{x2}x$	$\overline{x1}x$	$\overline{x}1x$	$\overline{x}xx$	1xx	2xx	23x	33x	CD	L	CD + L
A	1 - 5	6	−0.4	−0.7	−0.6	−0.6	−0.6	−0.6	0.5	−0.8	−0.7	−0.8	−0.5	−0.6	*6.0*	−0.5
	6 - 9	16	−0.7	1.4	−1.0	−1.0	−1.0	−1.0	0.3	−1.3	−0.3	0.1	−0.8	−0.1	*4.6*	−0.7
	10 - 15	42	0.7	1.3	−1.6	0.2	−1.0	−1.6	−1.6	−1.1	*2.5*	*2.7*	−1.3	0.7	1.1	−1.2
	16 - 20	51	−0.4	−1.6	−0.7	0.4	1.1	−1.2	0.8	−1.8	−1.1	−0.4	−0.1	*5.7*	−1.2	1.7
	21 - 30	70	−1.4	0.9	0.8	0.2	*5.3*	*3.8*	−0.1	−1.6	−1.5	−1.1	−1.7	−2.2	−0.2	−0.9
	pupae	9	−0.5	0.3	0.6	1.8	2.0	0.6	0.1	−1.0	−0.9	−1.0	−0.6	−0.8	−0.9	1.3
	total	194	−1.1	0.7	−0.9	0.4	*3.3*	0.7	−0.2	−3.6	−0.7	0.0	−2.2	1.6	*2.0*	−0.2
B	0	4	−0.3	−0.6	1.5	−0.5	1.6	−0.5	−0.6	0.6	−0.6	−0.7	−0.4	−0.5	2.7	−0.4
	1 - 3	36	−1.0	−1.7	−0.8	−1.5	−1.5	−0.8	−1.9	−1.9	−1.7	−1.1	−1.2	*18.2*	−1.3	−1.1
	4 - 7	119	−1.9	−0.3	−2.4	−2.4	−1.9	−1.9	−2.3	−3.5	−2.5	−2.7	−2.2	*28.8*	−2.1	−2.0
	8 - 11	107	1.7	*2.0*	*2.8*	−0.0	−0.2	−2.1	−1.2	−3.3	−1.9	−2.7	−1.6	*11.4*	−1.2	−1.9
	12 - 15	76	*3.3*	*3.4*	1.9	0.5	0.7	*3.5*	1.5	−2.8	−1.7	−2.7	−1.8	−0.1	−2.3	−1.6
	16 - 20	29	0.2	0.4	1.6	0.8	2.5	0.2	0.6	−0.6	−0.9	−1.9	−1.1	1.4	−1.6	−1.0
	pupae	15	−0.7	0.7	*3.2*	*3.1*	−1.0	−1.0	1.2	−0.4	−0.2	−1.3	−0.8	−1.0	−1.2	−0.7
	total	386	0.9	*2.0*	*2.0*	−0.9	−0.7	−1.1	−1.5	−5.8	−4.0	−5.3	−3.8	*27.7*	−3.6	−3.6

Table II. I.R. values for *Micropterna sequax* (A) and *Chaetopteryx* (B) per body lengthe class in mineral and organic substrates in the Snijdersveerbeek. Italic values indicate significant over-representation.

RESULTS

For all species found in one or both of the streams in numbers larger than 100 substrate preference was determined and several distributional types could be distinguished, with preferences for gravel, sand or detritus and the combination of gravel and sand with detritus, as illustrated for six species in Figs.5A-F. The chironomid larvae of *Polypedilum breviantennatum* preferred bare sand and bare gravel (Fig.5A). The caddis larvae *Lithax obscurus* (Fig.5B) preferred bare gravel and bare sand. The chironomid larvae *Brillia modesta* preferred detritus

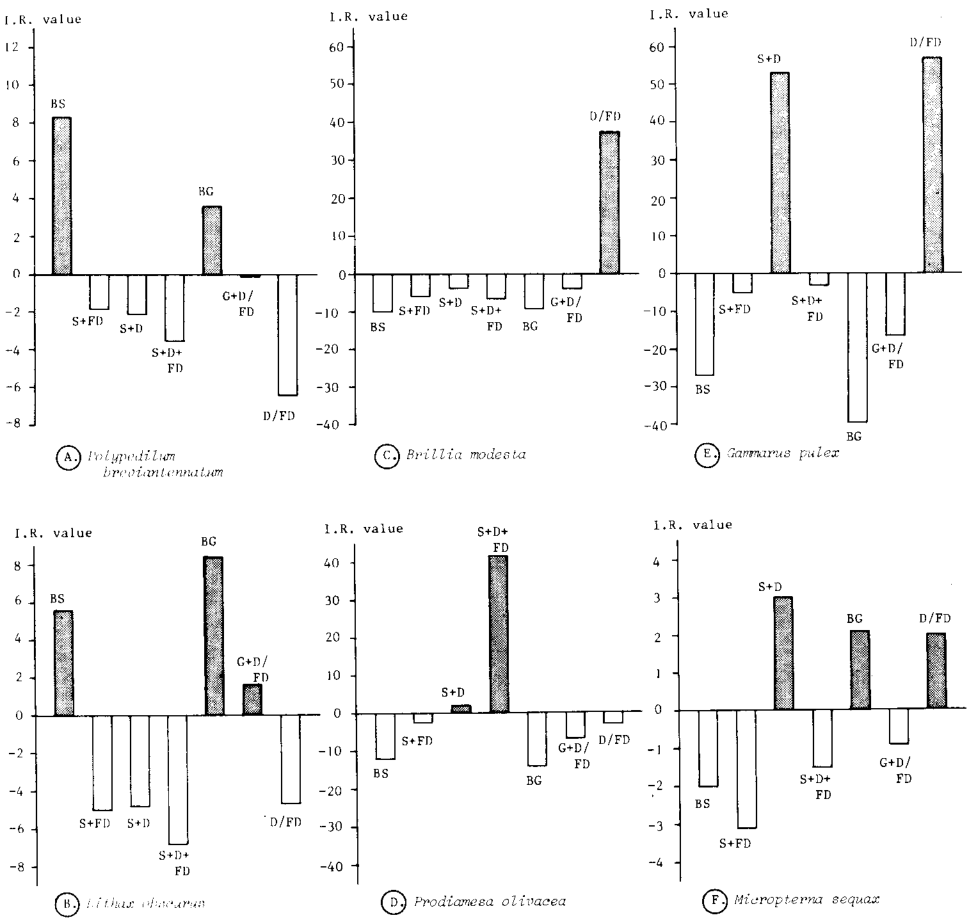


Fig. 5. I.R. values for six macroinvertebrate species in the field classification of the substrates in the Snijdersveerbeek or the Ratumsebeek. For explanation of symbols see Fig.3.

substrates (Fig.5C). The chironomid larvae *Prodiamesa olivacea* were mainly found in sand + detritus (Fig.5D), while the fresh water shrimps *Gammarus pulex* preferred purely detritus substrates or sand + detritus substrates (Fig.5E). The caddis larvae *Micropterna sequax* were mainly found in sand + detritus, purely detritus or bare gravel substrates (Fig.5F). These six species form only an illustration of the various distributional patterns encountered for the 48 taxa found in numbers large enough to justify statistical treatment. A detailed discussion of these substrate preferences, including differences in preference between different development stages of a species, is given elsewhere (TOLKAMP, 1980).

However, different instars can show a different preference as is illustrated by two caddisfly species, *Micropterna sequax* and *Chaetopteryx villosa* (Limnephilidae, subfamily Potamophylacini). Both species prefer organic substrates in early instars (leaves and leaf packs or coarse detritus) but this preference shifts to coarse mineral substrates (gravel or coarse sand) in the later instars (Table II). However, in spite of the fact that both species prefer similar substrate types in similar instars, there is no real competition for dwelling sites or food because the univoltine life cycles of these two species run parallel, which means that the similar

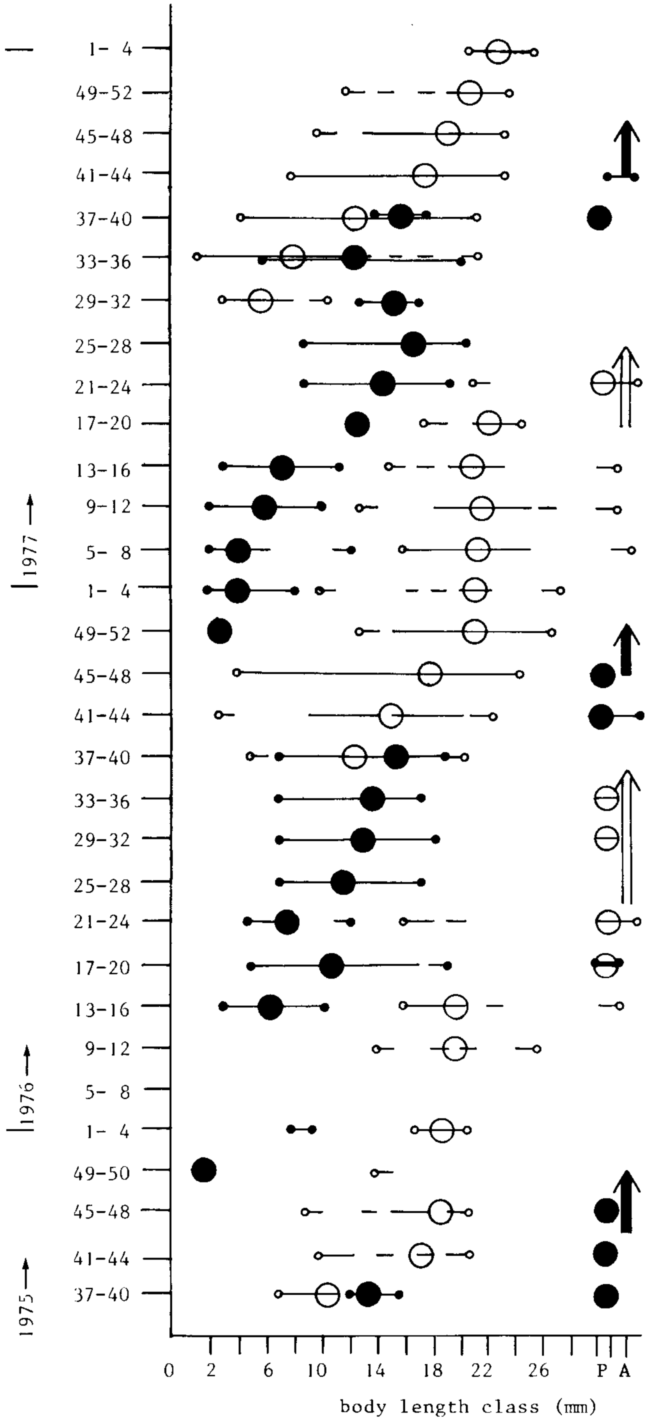


Fig.6.
Developmental cycle of *Micropterna sequax* (open circles) and *Chaetopteryx villosa* (closed circles) showing the distribution of larval body length (minima and maxima indicated with small circles), the median body length, and the presence of pupae (P) and adults (A) per period of 4 weeks.

development stages are not concurrent. *Chaetopteryx villosa* emerges in late autumn, while *Micropterna sequax* flies in spring (see Fig.6).

Another striking similarity between these two species is the changing of case building material during the larval development. *Micropterna sequax* starts with a sand case, which is replaced by an organic case by the second instar, and this case is gradually rebuilt into a sand and fine gravel case in the last instar and pupal case. *Chaetopteryx villosa* starts with an organic case which is replaced by a predominantly mineral case by the last two instars, although many larvae do not completely replace the organic matter. For both species larval development and case building materials are schematically presented in Fig.7 as a fine example of spatial and temporal ecological segregation of two caddis fly species that show similar substrate, food and habitat preferences and that build similar cases, but each at different times of the year. CUMMINS (1964) demonstrated the same in two *Pycnopsyche* species which illustrates that large taxonomical differences in palearctic and nearctic species do not necessarily result in autecological differences.

taxa no.	taxa name	substrate class													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
		$Q_1M_dQ_3$-index											detritus		
		xxx	x5x x4x	x3x	x2x	x1x	x1x	xxx	1xx	22x	23x	33x	CD	L	CD + L
18	*Eiseniella tetraedra*	*5.0*	*5.3*	*6.7*	*13.4*	*8.9*	-2.0	-3.3	-5.3	-4.4	-5.6	-2.8	-3.9	-3.5	-3.3
105	*Lithax obscurus*	*5.0*	*4.9*	*2.0*	*6.2*	1.3	*7.3*	*2.5*	-0.3	-5.4	-6.7	-4.4	-3.6	-3.5	-2.4
185	*Elmis aenea*	*13.4*	*5.9*	*2.6*	-0.9	*7.1*	-0.4	-3.4	-3.4	-3.3	-4.0	-2.4	-1.3	-1.2	-2.1
268	*Orthocladius*	-1.3	-1.6	*51.9*	*2.2*	1.8	-2.2	-8.1	-6.7	-7.2	-8.7	-5.0	0.0	-3.8	-4.7
280	*Chaetocladius*	-3.2	-4.8	-4.7	*11.6*	*14.5*	*10.5*	-4.8	-5.9	-5.1	-6.4	-3.8	-4.4	0.0	*16.1*
50	*Baetis vernus*	0.7	*18.4*	-2.7	-3.6	-1.8	1.5	-0.9	-3.5	-2.1	*4.9*	-3.2	-3.4	-4.6	-2.9
245	*Macropelopia nebulosa*	-2.5	1.1	-2.4	*2.1*	*2.6*	-2.9	*11.1*	-3.9	-4.8	*6.5*	0.8	-2.9	-5.4	-3.7
290	*Tanytarsus*	-3.3	*7.4*	-4.4	-4.1	*3.3*	-3.5	*4.0*	-5.9	-5.5	*18.7*	-1.7	-3.9	-5.3	-3.6
264	Chironomini spp. (juv.)	-1.8	-3.2	-2.7	-2.8	-2.7	-2.7	*26.1*	-2.9	-3.1	-2.4	-1.3	-2.8	-1.2	-2.0
11	Oligochaeta	-1.2	-0.0	-2.1	-3.2	-3.1	-1.5	-3.2	*3.2*	-1.3	*8.5*	*6.7*	-2.6	-3.9	*3.3*
38	Hydracarina	-1.9	-2.3	0.8	1.3	-2.4	-2.4	-1.9	*3.7*	*4.7*	1.9	-1.4	0.5	-1.3	-2.1
47	*Ephemera danica*	-2.4	-2.4	*6.4*	*2.3*	*2.1*	-2.8	0.5	-5.5	*6.0*	*5.4*	0.9	-3.2	-5.4	-3.3
109	*Sericostoma personatum*	-3.2	-0.7	*3.3*	*3.9*	1.8	1.6	*2.5*	-2.9	-1.9	1.0	-2.0	*2.8*	-4.2	-3.1
128	*Micropterna sequax*	-1.1	0.7	-0.9	0.4	*3.3*	0.7	-0.2	-3.6	-0.7	0.0	-2.2	1.6	*2.0*	-0.2
198	*Limnophila*	-2.7	*2.6*	-1.5	-0.4	*3.7*	0.8	1.9	-1.8	*2.5*	0.2	*5.2*	-2.8	-4.8	-3.3
205	*Dicranota*	-0.4	-2.0	0.5	0.1	*3.5*	0.7	1.7	-2.4	-0.5	1.9	1.4	-0.6	-2.8	-0.4
217	*Palpomyia*	-1.0	-0.5	-0.2	-0.4	-0.7	-1.2	0.8	-3.9	*3.2*	-0.9	*6.2*	*3.8*	-2.2	-1.5
241	*Ptychoptera*	-2.7	-3.5	-3.7	-3.6	-2.1	-1.6	1.5	-1.3	*8.6*	1.2	*11.6*	0.7	-3.3	-1.2
248	*Apsectrotanypus trifascip.*	-1.7	*3.6*	-2.5	-2.6	*2.0*	-2.1	-1.7	-1.7	*2.0*	*2.3*	0.4	-1.5	*2.5*	-0.8
249	*Procladius*	-2.0	-2.6	-2.0	-2.7	-1.6	-2.9	0.9	-3.5	*14.6*	*4.5*	-0.8	-2.8	-0.6	-2.2
256	*Zavrelimyia*	-1.7	-2.6	-1.4	-2.6	-1.3	-2.1	-0.8	-3.0	-0.5	*5.9*	1.7	0.7	*3.3*	*3.9*
308	*Stictochironomus*	-2.8	-3.5	-2.4	-1.3	-1.5	0.5	-1.4	*7.2*	*9.3*	*2.9*	0.8	-3.8	-4.8	-3.0
341	*Pisidium*	-2.5	-3.0	-2.7	-1.8	0.7	0.9	*6.3*	-0.6	*2.3*	0.1	*7.7*	-3.7	-2.3	-2.0
271	*Prodiamesa olivacea*	-5.2	-7.7	-6.6	-7.1	-7.3	-6.5	-7.3	-7.3	*9.2*	*21.8*	*13.7*	*6.5*	*3.3*	-5.3
311	*Polypedilum breviantennat.*	-5.8	-7.1	-6.7	-7.5	-3.4	-0.7	-0.7	0.7	*5.3*	*16.9*	*15.9*	-1.2	-6.3	-3.8
287	*Micropsectra* gr. *praecox*	-23.8	-29.8	-32.3	-29.4	-3.6	-27.2	-11.7	-33.4	-1.5	*29.5*	*30.1*	*25.8*	*88.6*	*4.5*
32	*Gammarus pulex*	-11.6	-22.3	-22.7	-20.8	-14.4	-1.2	*12.9*	-10.5	-8.6	-12.2	-7.5	*55.3*	*32.0*	*35.5*
127	*Chaetopteryx villosa*	0.9	*2.1*	*2.0*	-0.9	-0.7	-1.1	-1.5	-5.8	-4.0	-5.3	-3.8	*27.7*	-3.6	-3.6
220	*Simulium latipes*	-1.9	-1.8	-3.7	-2.4	-3.1	-0.5	-5.6	-5.6	-4.9	-6.0	-3.6	*31.9*	*10.7*	-2.9
293	*Rheotanytarsus*	-4.0	1.1	1.7	-2.2	*2.7*	-4.9	*8.4*	-7.8	-6.6	-2.1	-4.3	*18.8*	-1.3	-0.8
40	*Amphinemura standfussi*	-1.1	*4.3*	1.7	-2.1	-1.1	-2.1	-5.4	-6.4	-5.8	-6.9	-3.9	-3.0	*32.3*	-2.9
42	*Nemoura cinerea*	-2.1	-3.1	-3.1	-2.9	-2.4	-2.4	-3.5	-4.0	-3.3	-4.3	-2.2	-1.1	*31.8*	-1.0
269	*Corynoneura*	0.3	-3.9	-3.9	-3.3	-2.8	-4.6	-3.9	-5.8	-3.3	-2.8	-4.0	*14.5*	*22.5*	-0.3
272	*Brillia modesta*	-3.5	-5.5	-3.9	-5.1	-4.9	-5.1	-5.8	-6.5	-5.3	-5.6	-4.0	*10.4*	*30.7*	*16.7*
275	*Diplocladius cultriger*	-2.7	-1.0	-0.9	-3.5	-1.2	0.1	-2.2	-4.4	-3.8	-5.2	-2.6	-0.2	*18.1*	*11.7*
310	*Polypedilum laetum*	-5.7	-2.2	-4.7	-6.5	*10.0*	-8.1	*2.4*	-8.9	-9.5	-5.8	-5.6	*14.7*	*29.2*	-4.4
277	*Rheocricotopus*	-3.1	-6.3	-7.7	-5.0	-5.3	-7.3	-9.3	-10.7	-8.2	-8.6	-6.7	*8.5*	*64.3*	0.2
279	*Eukiefferiella* gr. *discol.*	-0.3	-9.9	-6.5	-7.3	-6.8	-9.4	-10.7	-12.3	-10.5	-12.4	-7.5	*31.1*	*62.6*	-2.9
190	*Helodes* larvae	-4.4	-7.6	-7.4	-5.2	-7.1	-7.5	-9.9	-10.1	-7.3	-10.9	-6.5	*54.3*	*18.4*	*18.9*
100	*Plectrocnemia conspersa*	-2.6	-4.0	-2.5	-2.9	-2.1	-2.9	-1.4	-2.8	-3.4	-3.5	1.4	*13.3*	*12.5*	1.1
155	*Agabus* larvae	-1.5	-2.8	-2.9	-2.3	-2.5	-2.5	-1.8	-3.4	0.0	1.8	-1.5	*5.9*	*10.8*	0.7
254	*Conchapelopia melanops*	-2.3	-3.8	-0.3	0.0	-1.9	-3.4	-2.6	-4.3	-1.9	-0.2	-1.2	*16.1*	*2.2*	*5.8*
318	Chironomini pupae spp.	-1.8	-1.2	-2.7	-1.6	0.5	-1.7	-1.6	-3.7	-2.2	-1.2	-0.9	*14.3*	*5.3*	-2.0

Table III. I.R. values for the 43 most-abundant taxa (more than 100 specimens) in the Snijdersveerbeek in the substrate classification based on the $Q_1M_dQ_3$-index with the 10 % detritus level (see text). Italic values indicate significant over-representation; Boxes indicate groups of taxa with similar over-representation.

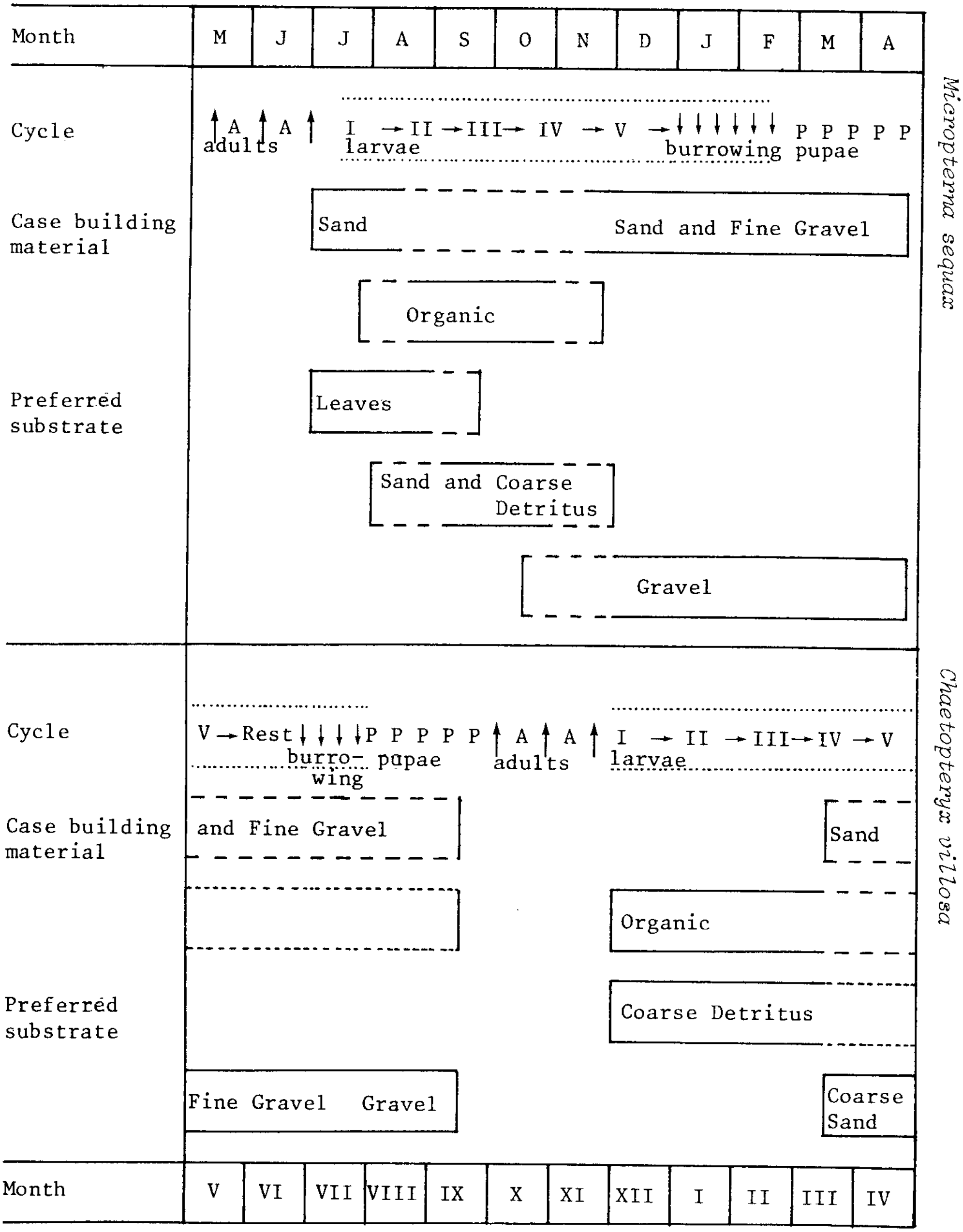


Fig. 7. Seasonal variations in the use of case-building materials and substrate preference of the limnephilid caddisflies *Micropterna sequax* and *Chaetopteryx villosa*.

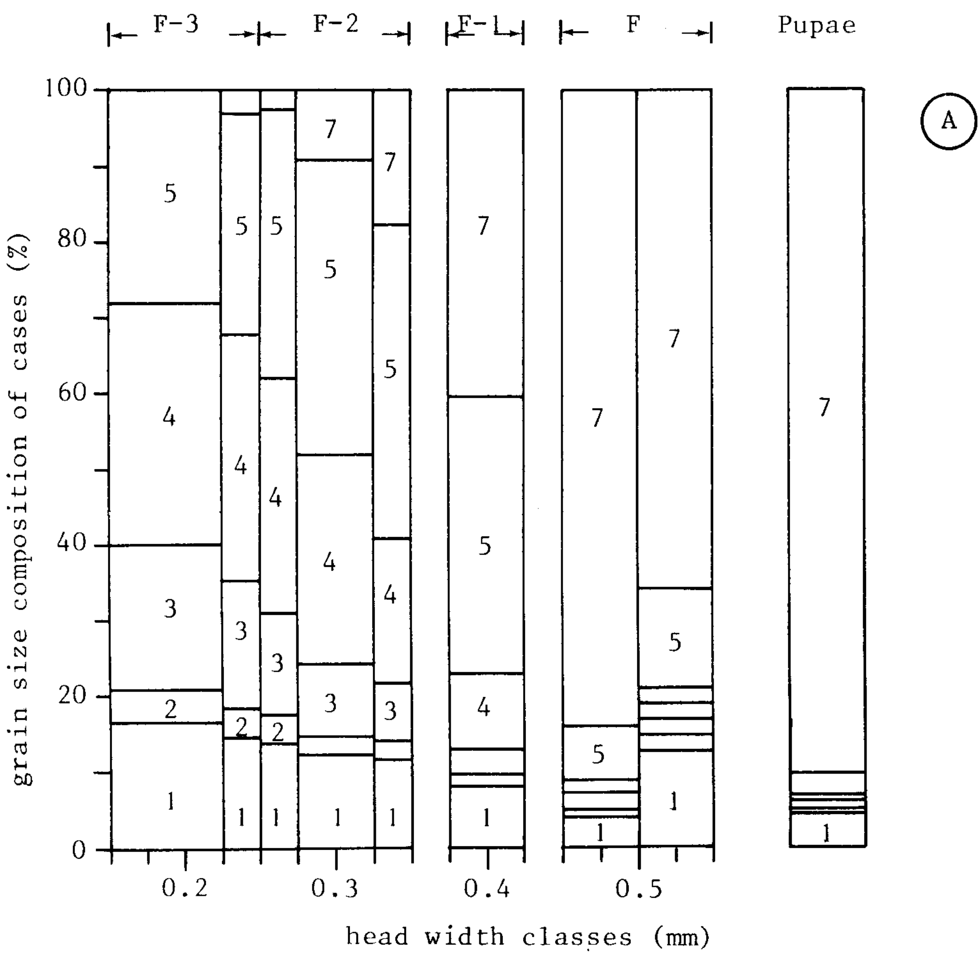
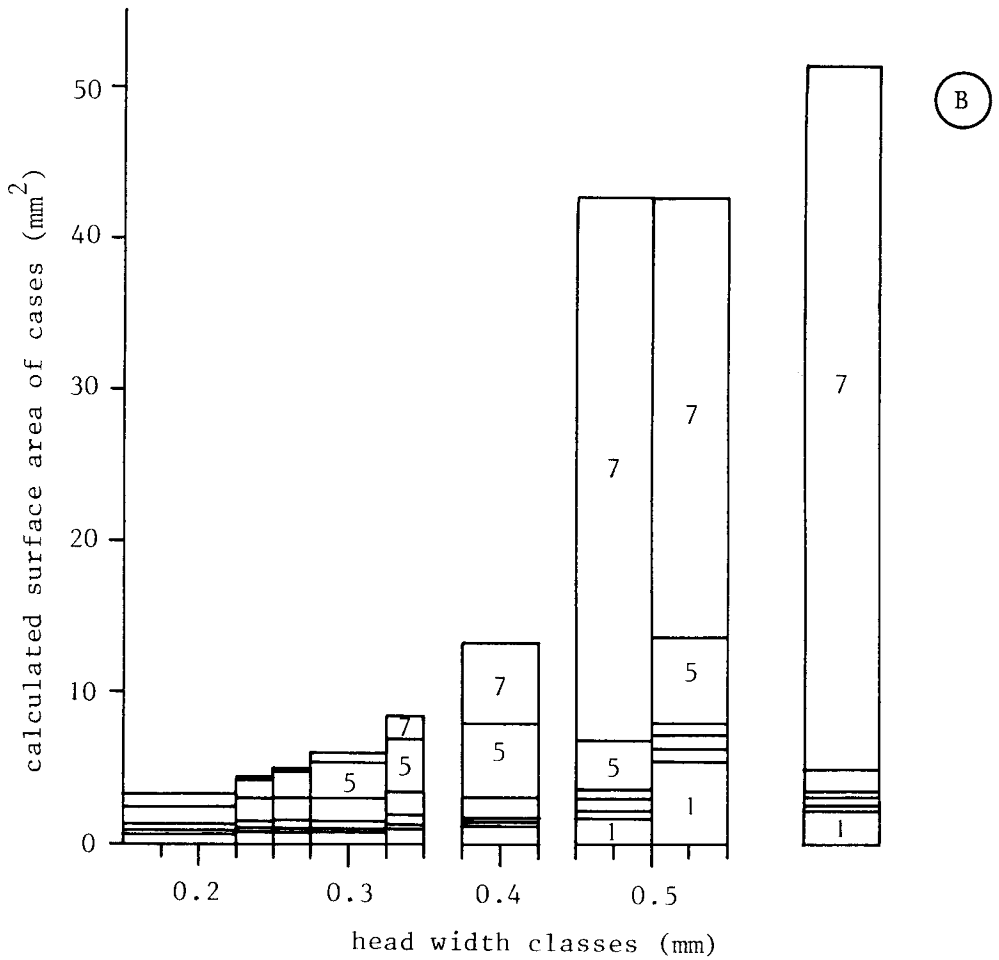


Fig. 8. Grain-size composition of natural cases of *Agapetus fuscipes.* A. percentage distribution of grain-size fractions. B. cumulative surface area of grain-size fractions. 1 = 0.105 – 0.210 mm; 2 = 0.210 – 0.250 mm; 3 = 0.250 – 0.350 mm; 4 = 0.350 – 0.500 mm; 5 = 0.500 – 0.850 mm; 6 = 0.850 – 1.0 mm; 7 = 1.0 – 2.0 mm.

Differences in the use of case building material by caddis larvae were also observed for *Potamophylax luctuosus*, of which the last instar builds a completely mineral case that replaces a case of round discs of beech-leaves similar to that of *Glyphotaelius pellucides.* Other species always build a mineral case with differences in grain size composition for the different instars, as illustrated by *Agapetus fuscipes* (Fig.8; see also VERDONSCHOT, 1977). As the larvae of *Agapetus fuscipes* grow, they build larger cases by using increasing particle sizes. Other species, like *Sericostoma personatum*, use the same grain size throughout their development (see VERDONSCHOT, 1977; TOLKAMP, 1980).

In order to find species with similar substrate preferences, the abundant species found in the two streams were grouped by a cluster analysis using the unweighted pair-group method with arithmetic averages (SNEATH and SOKAL, 1973) on the basis of the (average) I.R. values for each group of species. This resulted for the Snijdersveerbeek in three main groups of species with preference for gravel, sand and detritus, respectively, and in a few small groups of



species preferring a combination of these main substrate types. The groups of species with similar substrate preferences are outlined in Table III, where the I.R. values are given for each substrate class distinguished on the basis of the $Q_1M_dQ_3$-index for the substrates. In the Ratumsebeek a similar result was obtained.

Analysis of the microdistribution of the various species clearly demonstrates that substrate preference of species is strongly linked with their feeding habits and food preferences, as illustrated by the distribution of the four functional trophic groups on the 7 main substrate types distinguished in the field (Table IV). Predators are quite evenly distributed over the different substrate types. They are predominantly present in sand with coarse detritus and fine detritus, but they are also over-represented in all other substrate types except for the two bare mineral substrates. Scrapers and grazers feeding on periphyton prefer gravel and bare sand substrates (*e.g. Lithax obscurus, Agapetus fuscipes,* Elminthidae and *Pisidium*). Species feeding mainly on coarse detritus and leaves (shredders, *e.g.* many Limnephilidae larvae) are predominantly found in detritus or mineral substrates combined with (mixed and/or covered) organic material. Filter feeding species (*e.g. Simulium*) or deposit feeding species (*e.g. Ephemera danica*) and fine detritus collectors (*e.g. Micropsectra praecox*) dwell preferably in mineral substrates that are combined with detritus.

trophic group	substrate class and substrate type						
	1 BS	2 S + FD	3 S + D	4 S + D + FD	5 BG	6 G + D/FD	7 D/FD
predators	−11.8	*4.5*	*3.5*	*12.9*	−10.3	*4.3*	*4.8*
scrapers and grazers	*3.3*	− 3.0	− 6.9	− 7.8	*11.1*	*5.9*	− 6.7
shredders without *G.pulex*	−17.5	−11.8	− 4.4	−14.2	− 6.2	− 0.6	*52.2*
Gammarus pulex	−27.2	− 4.6	*52.6*	− 3.0	−39.5	−16.5	*56.9*
collectors without *M.* gr. *praecox*	−32.4	− 7.1	*4.6*	*5.0*	−21.0	*13.9*	*47.7*
Micropsectra gr. *praecox*	−55.6	*20.3*	−11.5	*74.6*	−63.0	− 2.8	*64.7*
total	−36.1	− 9.3	1.5	1.3	−20.5	*14.2*	*58.7*

Table IV. I.R. values for the trophic groups in the Snijdersveerbeek in seven substrate types based on a field classification of the substrates.
Italic values indicate significant over-representation.

LABORATORY EXPERIMENTS

The validity of the conclusions based on the collected field data was tested in the laboratory for several species. Substrate selection experiments were carried out in an artificial stream, offering the animals a number of particle sizes in various spatial arrangements. Substrate selection was usually determined after two hours. The preference of a species for one or more particle sizes in the experiments was compared with that found for certain substrate types in the field. For all species tested experimentally the preference for certain particle sizes (which in fact formed an unrealistic substrate because the grains were all of about the same size) could be related to the preference for complex substrates consisting of a mixture of various particle sizes.

Detailed results on substrate selection experiments for several caddisfly species are given and discussed elsewhere (TOLKAMP, 1980). To illustrate the method of comparison an example is given for the mayfly *Ephemera danica* in Fig.9, where the particle sizes preferred in the experiments are shaded and the substrate composition preferred in the field is presented unshaded in the $Q_1M_dQ_3$-diagram. In the field these nymphs are mainly found in gravel substrates consisting of x$\overline{3}$x, x$\overline{2}$x and x$\overline{1}$x (median particle size 1-8 mm; first quartile 16 -32 mm = $\overline{5}$) and sand substrates consisting of 22x and 23x (median particle size 0.125 -0.500 mm). In the experiments, the nymphs prefer the particles corresponding to the median particle sizes of the field substrates (M_d = $\overline{3}$, $\overline{2}$, $\overline{1}$ and 2) with additionally preference for 16 -32 mm particles, corresponding to the preferred Q_1 present in gravel substrates.

For the other species tested the conclusions based on the analysis of the field data were also confirmed by the experimental results. This means for these species that the over-representation found in the field is really a preference for the substrate or more in general for the habitat. Preference based on the active choise of 'optimal' conditions by the animals. Often preference will not be aimed at the substrate composition or the particle size itself, but at (the combination of) other factors prevailing in that particular habitat, and perhaps one should speak of habitat preference rather than of substrate preference, especially when only field data are available and the substrate is in fact used as a descriptor of the habitat. Current, food and oxygen conditions are all strongly related to the substrate conditions and the substrate is therefore an outstanding parameter to describe a habitat. Not only because it catches the eye and is easier to describe or measure, but also because it usually reflects the conditions prevailing in the period before sampling.

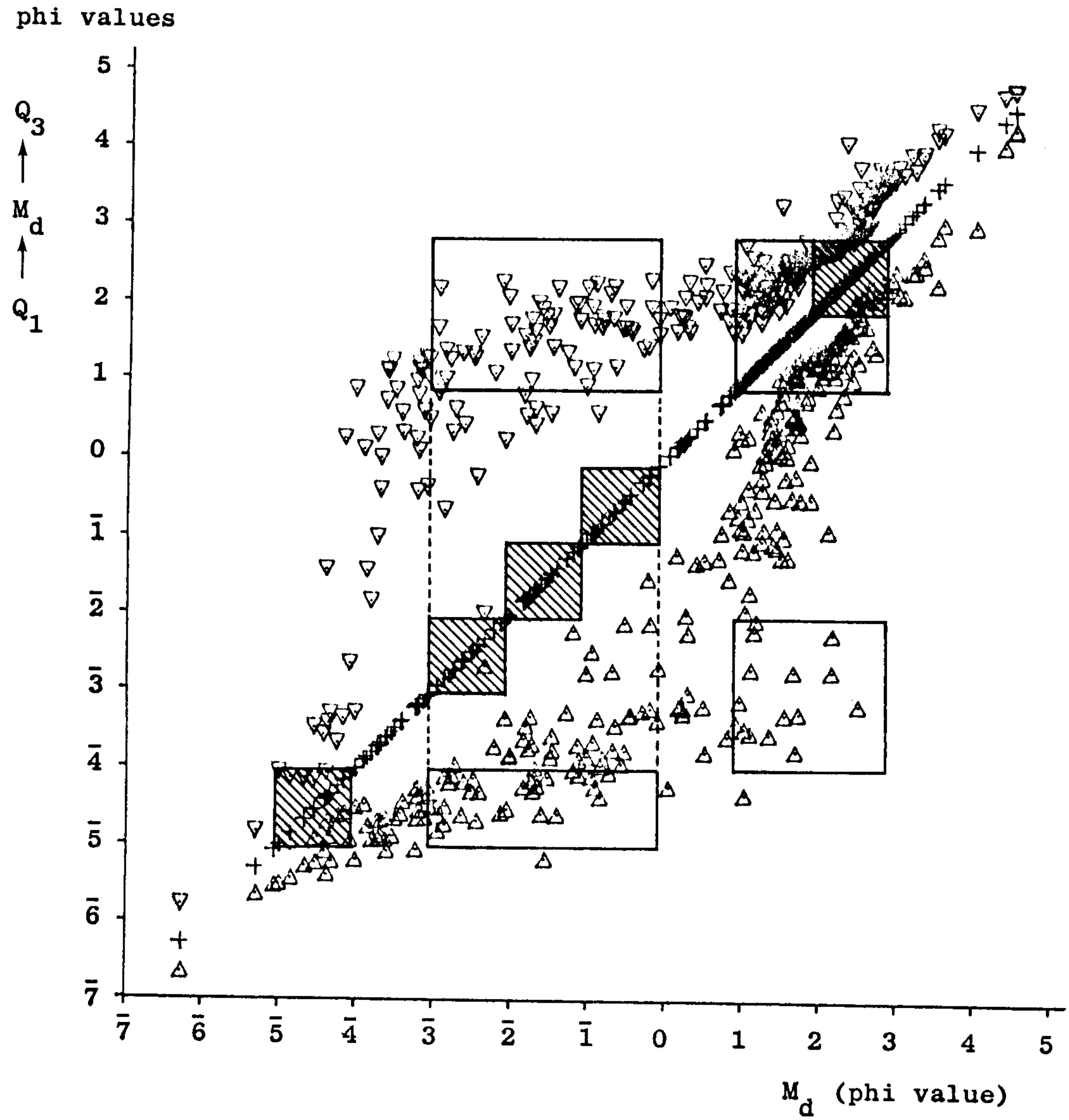


Fig. 9 Comparison of substrate preference in the field (unshaded) with particle size selection in laboratory experiments (shaded) for the burrowing mayfly *Ephemera danica.*

SUMMARY

Most benthic macroinvertebrate species are related to substrates types. Three main groups of species can be distinguished, each consisting of species with a similar preference for coarse mineral substrate (gravel), fine mineral substrate (sand) and organic material (leaves and/or coarse detritus), respectively. The particle size of the mineral component of the substrate, as well as the amount and the nature of the organic detritus, and the various combinations of both components, influence the microdistribution of most of the investigated species. Factors related to the substrate (*e.g.* oxygen and current conditions and food availability) are also important.

Several macroinvertebrate species prefer more than one substrate type, at the same time or consecutively, to be able to maintain themselves in a lowland stream. Preference for several substrate types is often seasonally determined or dependent on the development stage of the species.

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