Harry H. Tolkamp

Organism-substrate relationships in lowland streams

Proefschrift
ter verkrijging van de graad van
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op gezag van de rector magnificus,
dr. H.C. van der Plas,
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Abstract

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A field and laboratory study on the microdistribution of bottom dwelling macroinvertebrates to investigate the role of the stream substrate in the development and preservation of the macroinvertebrate communities in natural, undisturbed lowland streams is described. Field data on bottom substrates and fauna were collected between 1975 and 1978 from two Dutch lowland streams. Substrates were characterized by the nature and the amount of organic detritus and the mineral particle sizes: in a field classification on the basis of the visually dominant particle sizes; in a grain-size classification on the basis of exact particle-size analysis in the laboratory. Substrate preference for 84 macroinvertebrate species was demonstrated using the Index of Representation.

Substrate-selection experiments were conducted in a laboratory stream for three Trichoptera species (*Micropterna sequax, Chaetopteryx villosa* and *Sericostoma personatum*) and one Ephemeroptera species (*Ephemera danica*). An experiment on the colonization of artificial substrates in the field was also conducted.

From the field data, several faunal groups could be distinguished, each group made up of species with similar substrate preferences. Detailed data on the microdistribution in relation to substrate particle size are given for 26 species, which represent the various taxonomical units that compose the faunal groups: Trichoptera (5 species), Ephemeroptera (1 species), Plecoptera (1 species), Coleoptera (3 species), Amphipoda (1 species), Diptera (15 species, among which 13 species of Chironomidae). The microdistribution is discussed in relation to case-building behaviour, life cycle and food preferences. For several species substrate preferences may be different for different development stages or in different seasons.

It is concluded that most species show distinct preferences for a specific substrate. The small scale spatial variation in substrate composition of the stream bed is essential for the existence of many lowland stream macroinvertebrate species.

Free descriptors: substrate preference, microdistribution, benthos, macroinvertebrates, particle size, detritus, organic matter, habitat preference, environmental factors, lowland stream, laboratory stream

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Woord vooraf

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Curriculum vitae

Harry Hendrik Tolkamp werd geboren op 3 september 1952 te Aalten te midden van de toen nog grotendeels natuurlijke beken. Hij volgde in Aalten het kleuter-, basis- en voortgezet onderwijs en bracht veel van zijn vrije tijd door in de bossen en de beken in de omgeving. Na het behalen van het einddiploma HBS-B, begon hij in 1969 met de studie in de Milieuhygiëne (N42) aan de Landbouwhogeschool te Wageningen, waar hij in 1972 het kandidaats- en in 1975 het doctoraalexamen aflegde. Voor het doctoraal examen werd het onderzoek vooral gericht op het waterkwaliteitsbeheer: Natuurbeheer-Hydrobiologie bij Prof.Dr. M.F. Mörzer Bruyns o.l.v. Drs.J.J.P. Gardeniers; Waterzuivering bij Prof.P.G. Fohr o.l.v. Ir.J.G. den Blanken, T.H. Delft, Afd. Gezondheidstechniek; Microbiologie bij Prof.E.G. Mulder o.l.v. W.L. van Veen (†).

Na het doctoraal examen was hij werkzaam als wetenschappelijk ambtenaar bij de Vakgroep Natuurbeheer van de Landbouwhogeschool tot december 1975, vervolgens als wetenschappelijk assistent bij dezelfde Vakgroep voor het verrichten van voorliggend onderzoek en van juni 1979 tot januari 1980 wederom als wetenschappelijk ambtenaar. Sindsdien is hij werkzaam als hydrobioloog bij het Waterschap Zuiveringschap Limburg te Roermond.

Contents

Outline of substate classification

Abbreviations used in the field classification of substrate types

S = Sand
G = Gravel
CD = Coarse Detritus
L = Leaves
D = Detritus = CD + L

FD = Fine Detritus
St = Stable
Sh = Shifting
B = Bare
CD/FD = CD with or without FD

Names, phi values and phi indices of grain-size fractions

Fraction (mm)	Phi value ($-\log_2$ fraction)	Phi index	Name of fraction
128 - 256	-7	$\bar{8}$	cobbles
64 - 128	-6	$\bar{7}$	cobbles
32 - 64	-5	$\bar{6}$	large pebbles
16 - 32	-4	$\bar{5}$	small pebbles
8 - 16	-3	$\bar{4}$	coarse gravel
4 - 8	-2	$\bar{3}$	medium gravel
2 - 4	-1	$\bar{2}$	fine gravel
1 - 2	0	$\bar{1}$	very coarse sand
0.500 - 1	1	1	coarse sand
0.250 - 0.500	2	2	medium sand
0.125 - 0.250	3	3	fine sand
0.050† - 0.125	4	4	very fine sand
0 - 0.050†	5-10	0	silt and lutum

† : 0.050 mm is used instead of 0.0625 mm

$Q_1M_dQ_3$ index describes the grain-size composition of a substrate by giving the first (Q_1), second (median)(M_d) and third (Q_3) quartiles expressed in integer phi values (phi indices).

1 Introduction

1.1 GENERAL

Lowland streams, with a strongly fluctuating discharge, water level, current velocity, bottom composition and vegetation pattern, are a characteristic type of stream for the Netherlands. A large number of benthic macroinvertebrate species are restricted to this type of environment and form the characteristic animal community of the natural lowland stream.

Since the 1930s most lowland streams in the Netherlands have been regulated in connection with land reclamation schemes or programmes aimed at the improvememt of stream hydrology to increase drainage and in the more recent decades also to lower the groundwater level in vast areas. This implies the reduction of inundation, peak flow, erosion and sediment transport. To this end meanders are cut off, bends are straightened, the stream bed is deepened and widened, the slope of the banks is standardized to a 1:2 or 1:3 profile, bank vegetation is removed and paths are constructed for grass mowers; weirs and barrages are placed at regular intervals to reduce sediment transport and retain a minimum water level in summer for irrigation purposes. Banks are often reinforced with concrete, nylon matting or wood and sometimes the whole stream bed is reinforced with concrete blocks. Several terms are in use to describe these kind of physical perturbations. Hereafter the term regulation will be used, to save the term channelization for streams and rivers that have been regulated with the purpose of facilitating transport by boat.

Regulation strongly affects the physical characteristics of the stream system, and investigations in the Achterhoek (Gardeniers & Tolkamp, 1976) and elsewhere in the Netherlands (Heijdeman & van 't Oever, 1976; Peters & Leijten, 1977; de Graaff, 1979) demonstrate that the animal community living in regulated streams is quite different from that living in unperturbed, natural lowland streams, a feature frequently reported in other countries for other stream types as well (e.g. Wene & Wickliff, 1940; Engelhardt, 1951; Stuart, 1959; Einsele, 1960; Rouyer, 1975). The typical fauna present in natural lowland streams is often practically absent from streams that have been regulated. Only in streams regulated in the old fashioned way, where maintenance has been neglected since the major regulation works, may the fauna of the natural stream be able to stay or re-establish itself in places where conditions are returning to the original state. In such semi-regulated streams the fauna may consist of a mixture of pond- and stream-dwelling species. In most regulated streams, however, the species composition resembles that of canals, ditches and ponds. This can be attributed to the changes the physical environment has undergone. Levelling down the spatial and temporal variation in current velocity will result in more uniform substrate patterns, while the absence of bank vegetation (trees and shrubs) which would shade the water, results in higher water temperatures and the development of macrophytes or even microphytes when current velocity is low enough. Less allochthonous material will enter the stream system and algae and aquatic plants will replace leaves as the trophic basis of the community. The stream system changes from heterotrophic to autotrophic (Cummins et al., 1973).

Consequently, major changes in community structure will result. For each animal species it is essential that environmental factors are present in the right extent within reach of the animal. Comparing natural and regulated lowland streams, and noting the differences in species composition of the communities present, the impression becomes stronger that the environmental demands of species characteristic for unperturbed lowland streams are so specific that they can only be met in very distinct places within the stream. Apparently these species can only find the optimal combination of physical parameters in a stream with much variation, with the right extent or range of each factor important for their existence (e.g. substrate particle size, current velocity, food, oxygen supply).

Many investigations have been carried out in Dutch lowland streams during the last two decades, mainly concerning the description of the stream fauna and the effects of pollution (e.g. Mur Atzema, 1962; Gardeniers, 1966; Moller Pillot, 1971; Higler, 1972; Tolkamp, 1975a; Gardeniers & Tolkamp, 1976). These investigations on the physical and chemical quality of the streams as related to the macroinvertebrates have led to a reasonably complete picture of the geographical distribution of the benthic macroinvertebrates in Dutch lowland streams and of the differences between natural and regulated streams in the sense of the composition of the animal community. The differences in species composition have even been used as an instrument to measure the degree of regulation of a lowland stream (Tolkamp & Gardeniers, 1977).

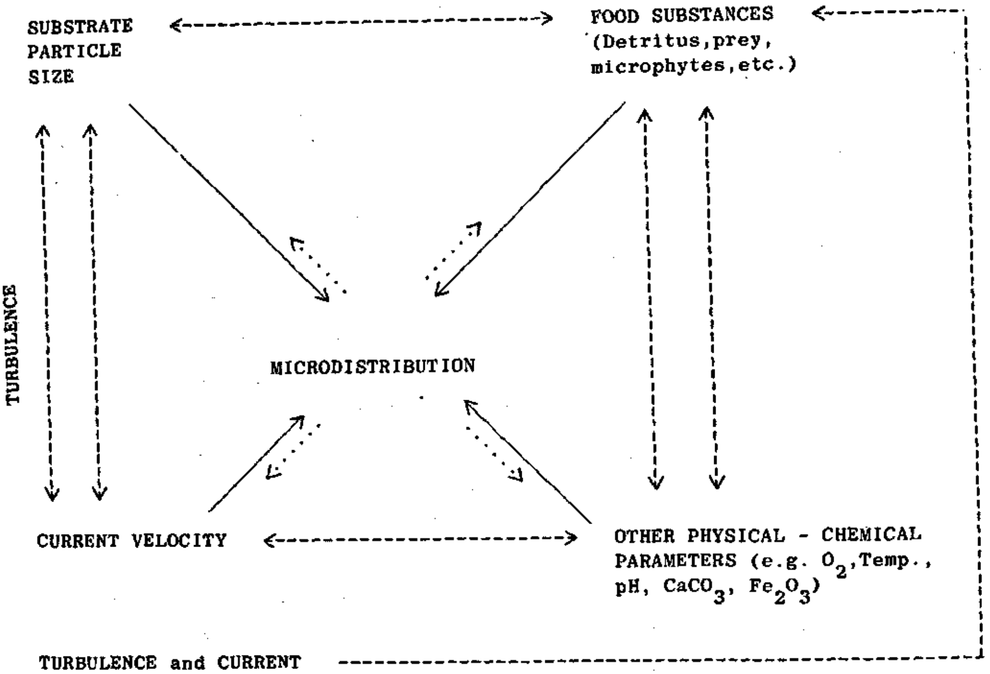
However, current velocity is only one of the parameters that may change after regulation and no detailed information is available on the specific reasons for the differences in animal communities between natural and regulated streams. Current velocity is of course one of the reasons, but the distribution of freshwater animals is also determined by a whole complex of a large number of physical, chemical and biological factors (Wesenberg-Lund, 1943; Engelhardt, 1951; Albrecht, 1953; Macan, 1961, 1962; Cummins, 1966; Thorup, 1966; Cummins & Lauff, 1969; Hynes, 1970a, b; Meadows & Campbell, 1972; Macan, 1974; Décamps et al, 1975; Friberg et al, 1977). Schmitz (1954) followed Thienemann (1912) in the conception that current velocity and temperature are the primary factors influencing the development of running-water zoocoenoses. Whitehead (1935) concluded that the nature of the stream bed is of great importance as a factor determining the nature of the fauna, either directly (providing shelter, suitable attachment sites) or indirectly (providing food, influencing the nature of plant growth, giving suitable oxygen conditions).

The stream bottom is the product of two sources that provide the basic components: mineral and organic allochthonous material supplied by water and air, and mineral and organic autochthonous material present in the stream bed, originating from geomorphological conditions. Under the influence of the discharge regime and the form of the stream channel, interacting in two major counter processes, erosion and sedimentation, the basic components are arranged in substrate patterns with characteristic properties concerning composition (particle size and nature of mineral and organic matter), structure (spatial variations-vertical and horizontal, stability, packing, porosity) and dynamics (temporal changes in structure). Because of the sorting activity of the current, the structure of the stream bottom is inseparably interwoven with the variation of the current (velocity, regime, turbulence) (Schmitz, 1961; Scherer, 1965), resulting in a constantly varying (in space and time) mosaic pattern of substrate types, each with different environmental conditions. Grain-size composition may vary at very short distances and influence, for example, the oxygen content of the interstitial water, the amount of trapped organic detritus, the growth of periphyton and the number of crevices.

Cummins & Lauff (1969) presented a diagram showing the four major categories of environmental parameters (Fig. 1). They emphasized that current, temperature and concentration of chemical factors may limit the range of habitat tolerances (macrodistribution) and that substrate particle size or food supply are probably the main microdistributional factors. Although several additional physical factors influencing distribution are often mentioned, these are mostly directly related to one of the main factors: flow regime, drought, spates, illumination, suspended solids, proximity of suitable habitats (Sprules, 1947; Hynes, 1970a). Biotic factors as competition and predation (Macan, 1962), oviposition and drift habits (Macan, 1961; Hynes, 1970a) are also related to the main factors food, current and substrate.

Ulfstrand (1967) stressed the point that the most important factor linked with substrate is the provision of food in the form of allochthonous and autochthonous matter and prey animals. This agrees with the view of Cummins (1975), who stated that food will undoubtedly be the ultimate determinant of macroinvertebrate distribution and abundance in non-perturbed running waters. But he added that when food conditions are favourable, other factors, as sediment particle size, current, competition for space or predation will determine the microdistribution within a given section of a stream. Moreover, food is part of the substrate for algal feeders (grazers, scrapers) as well as detritus feeders (shredders, consumers) and the presence and abundance of food substances is influenced by, for example, the particle size (accumulation of detritus (Rabeni & Minshall, 1977)), sediment transport (scouring off attached algae), light conditions and current (distribution of detritus, growth of hydrophytes, bringing food to filter feeders). The preference of prey organisms for certain substrate or food types will influence the distribution of their predators (Ulfstand et al., 1971; Hildrew & Townsend, 1976).

For the very reason that the substrate is the resultant of and strongly inter-



------> : Interactions between environmental parameters to which a given benthic species interacts
———> : Influence of the environment on a benthic species which results in recognition of the habitat
......> : Influence of a given benthic species on the habitat

Fig. 1. General relationship between environmental parameters and the microdistribution of benthic stream macroinvertebrates (after Cummins & Lauff, 1969).

linked with a number of physical factors and is of great ecological importance for macroinvertebrates, it is an outstanding parameter for the study of macroinvertebrate microdistribition. Because the substrate composition, structure and dynamics are the first to change under the influence of alterations in current velocity and discharge regime following stream regulation, they may prove to be the major reasons for the differences in species composition between natural and regulated lowland streams.

1.2 PURPOSE OF THE INVESTIGATION

The purpose of the investigation was to gain insight into the role the substrate plays in the development and preservation of the macroinvertebrate communities in natural, undisturbed lowland streams. Testing and quantification of the relationships between temporal and spatial environmental factors as measured by substrate characteristics and the composition of animal communities will increase the knowledge of the autecology of some typical lowland stream species and will make it possible to indicate some of the critical conditions that distinguish natural lowland streams from other watercourses.

As a basis for preservation and management of these streams this knowledge is indispensable and it will contribute to the quantification of the limiting conditions concerning stream dimensions, profile, meandering, bank vegetation, weir level, current speed, maintenance, effluent discharge, recreation and bank protection. There is an urgent need for this kind of information since the demands made from the hydrological point of view are often contradictory to the wish to preserve the Dutch lowland stream as a unique type of environment.

1.3 HYPOTHESES

It has been shown by numerous authors that distinct differences occur in the species composition found in different substrate types (e.g. Pennak & van Gerpen, 1947; Thorup, 1966; Mackay, 1969; Mackay & Kalff, 1969; Ward, 1975; Cummins, 1975). Many authors used the substrate merely to describe the various habitats they encountered and were not trying to establish differences in the faunal composition of the substrate types, but described the stream fauna itself and where to find it (e.g. Thienemann, 1912; Behning, 1928; Beyer, 1932; Geijskes, 1935; Sprules, 1947). More recently, studies directly relating species distribution and substrate composition have become numerous and many references were given by Cummins (1966), Thorup (1966) and Hynes (1970a, b).

Although a species may show a distinct preference for a certain substrate type, other features prevailing in the same place or in the neighbourhood may cause the animals to tolerate less-preferred substrates. Cummins & Lauff (1969) demonstrated this for the stonefly *Perlesta placida*, in substrate-selection experiments. Various authors have shown for several species that different instars may prefer or demand different substrate grain sizes or compositions (e.g. Scott, 1958; Hanna, 1961; Cummins, 1964; Schwoerbel, 1967; Mackay, 1969; Elliot, 1971; Harman, 1972; Otto, 1976). Rees (1972) found a significant relationship between the body length of *Gammarus pseudolimnaeus* (Amphipoda) and the substrate particle size in laboratory experiments, and Wesenberg-Lund (1943) already gave examples of several caddis fly species that use different house-building materials during their development. Mackay (1977) demonstrated that *Pycnopsyche scabripennis* (Trichoptera) pupae burrow in other substrates than the larvae prefer. Thus many benthic-stream-dwelling macroinvertebrates may need several substrate types to complete their life cycle.

These observations formed the basis for the following hypothesis:
The demands of many benthic lowland stream macroinvertebrate species of the substrate are of such a nature that they can only be met in a non-regulated lowland stream with its typical substrate composition and pattern.

Two working hypotheses were formulated to test this hypothesis:

- Many benthic lowland stream macroinvertebrate species show distinct preferences for a specific substrate composition.
- For many of these species the small-scale spatial variation in substrate composition of the stream bed is essential for their existence.

1.4 RESEARCH APPROACH

Testing of the working hypotheses was performed in three steps:

- Determination of the microdistributional patterns of the macroinvertebrates in two natural, undisturbed lowland streams (field investigation).
- Determination of substrate preferences of a number of characteristic lowland streams species in substrate-selection experiments in a laboratory stream channel (laboratory experiments).
- Determination of the macroinvertebrate colonization of artificial substrates in the stream bed (field experiments).

This approach was chosen because the interpretation of data from field research only leads to correlations between animal distribution and certain environmental parameters. Experiments in the laboratory or the field, or both, are necessary to provide data that can be used to test the conclusions derived from the field research.

2 Description of the streams

The investigation was carried out in two natural, unperturbed, unpolluted lowland streams: the Snijdersveerbeek (Snijb) and the Ratumsebeek (Rab). Both streams are situated in the eastern part of the Achterhoek in the province of Gelderland, where natural streams are still present (Fig. 2). In both streams the investigation was restricted to a section of 1500 metres.

2.1 THE SNIJDERSVEERBEEK (FIGS. 3 AND 4)

Only the first 1500 m of the Snijdersveerbeek is in a natural state. The downstream part has been regulated and contains only stagnant water or no water at all for the largest part of the year. The stream originates at the western border of the

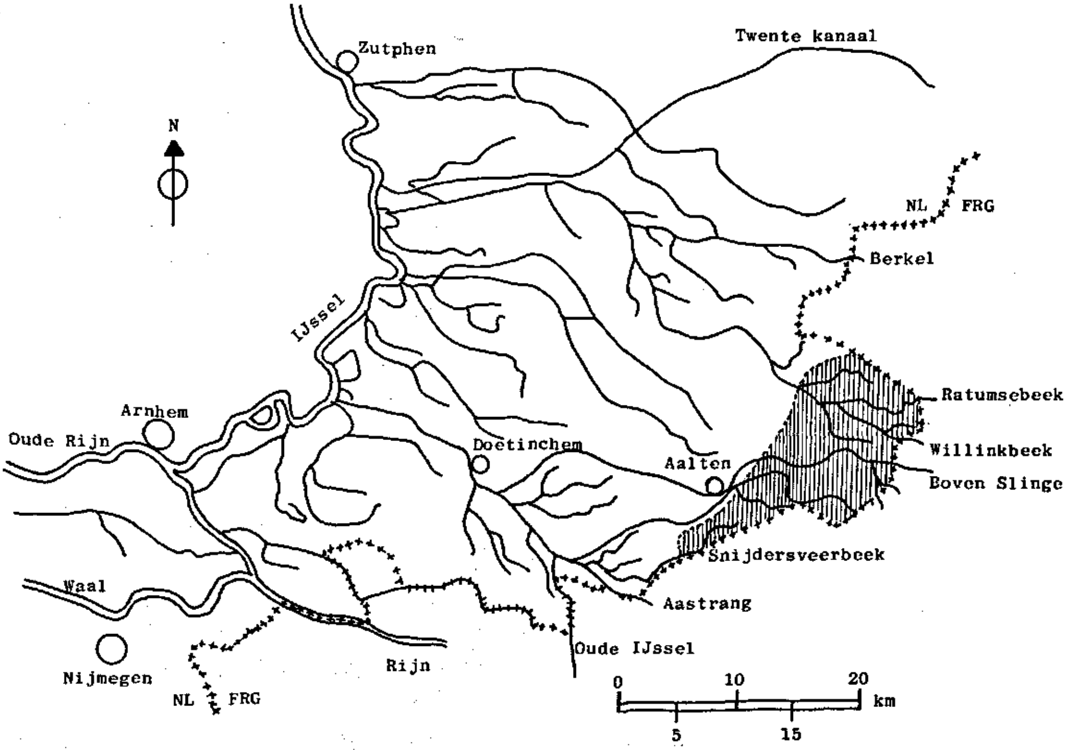


Fig. 2. Streams in the Achterhoek. The shaded area indicates the area where natural, unpolluted streams still exist (modified after Gardeniers & Tolkamp, 1976).

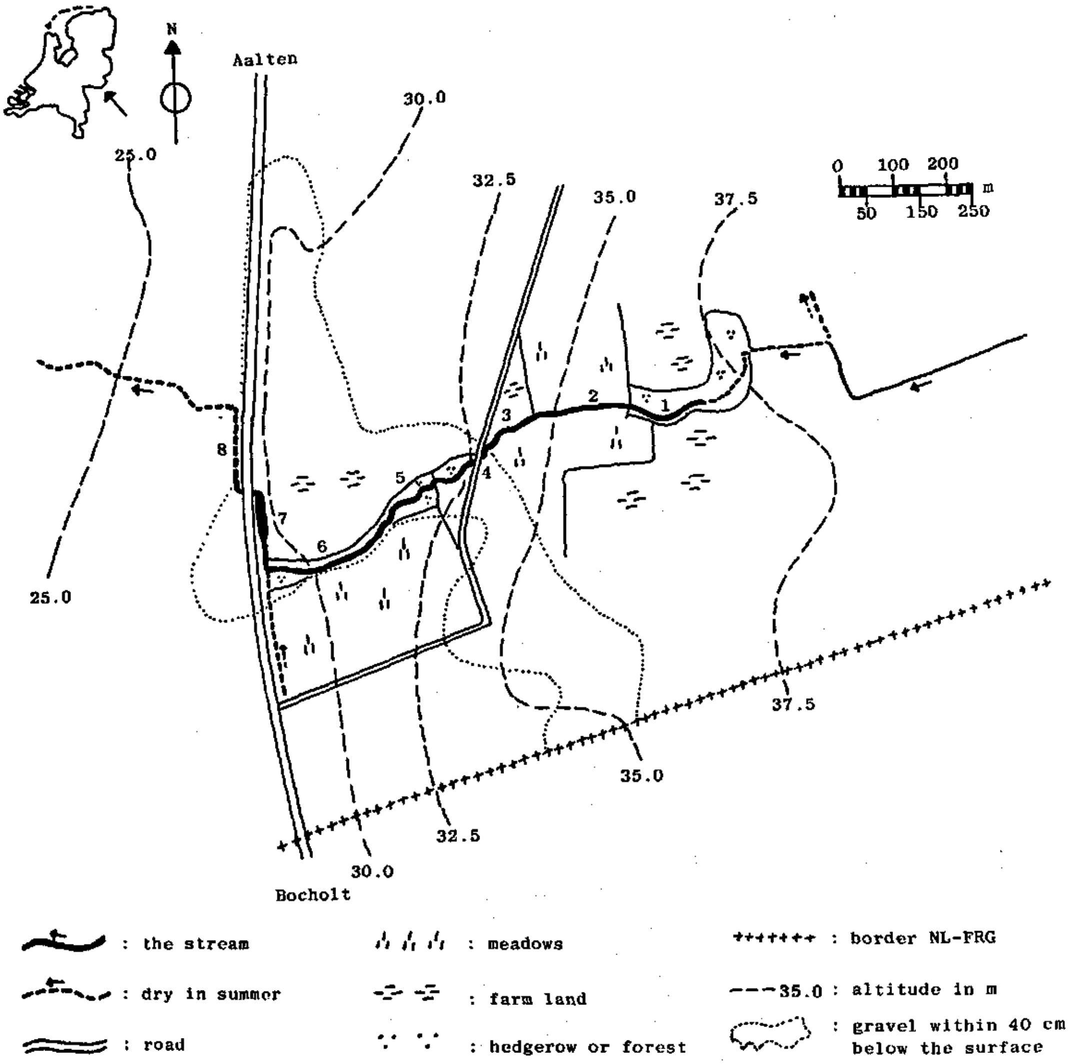


Fig. 3. The Snijdersveerbeek, showing Sections 1-8.

'tertiary plateau' in a small valley approximately 3 m below the level of the surrounding area. It runs in a westerly direction over the slope of the plateau and reaches, after passing the relatively steep edge of the plateau, the flat area called 'Pleistocene basin'. This basin is filled with coarse sands to a great depth, which gives rise to the intermittent character of the downstream part of the stream.

The upper part of the stream is fed by iron-rich groundwater, which continuously seeps into the stream through the bed and banks. Even in the extremely dry summer of 1976 this did not stop. The continuous seepage is connected with the specific geomorphological and hydro-geological characteristics of the area: coarse sediments (wind-blown sands and Middle Pleistocene fluviatile sand and gravel) are situated on

Fig. 4. Sampling site in Section 6 of the Snijdersveerbeek.

heavy clay (teriary 'old' clay), which gives rise to a groundwater supply to the Snijdersveerbeek from a fairly large catchment area. The groundwater runs over the clay through the coarse fluviatile sands and gravel. Where the stream bed reaches the groundwater level, seepage occurs (Kloosterhuis, 1968). This happens in the first 500 m of the stream (Fig. 3, Sections 1-4).

During the winter, the water in the stream partly originates from a more upstream part, to the east of the valley. This part was regulated in 1975 and peak discharges are diverted by a ditch running in northerly direction, reducing the peak flow in the actual stream. The small amount of water still permitted to flow through the stream is determined by the difference in size and level of the culverts connecting the upstream and downstream watercourses. In summer, the water of the regulated section does not reach the investigation part of the stream.

After a preliminary investigation (Tolkamp, 1975b; Both, 1976), eight sections were distinguished in the Snijb (Fig. 3), each characterized by degree of meandering, bank vegetation, stream profile and substrate composition (Table 1). The width of the stream bed varied between 0.4 m and 1.0 m with some pools up to 2.0 m wide. Water depth varied from 2 cm to 30 cm, with an average in summer of 2-10 cm and in winter 15-20 cm. The combination of a continuous and rather constant discharge with a strong slope (5 m/km) resulted in a steady current all year round. The average current speed was 5-10 cm/s in summer. In winter it increased to 20-30 cm/s, with occasional

Table 1. Physical characteristics of the eight sections in the Snijdersveerbeek and the upstream section of the Ratumsebeek.

	Snijdersveerbeek sections								Ratumsebeek
	1	2	3	4	5	6	7	8	1
Length/m	150	200	100	50	200	200	200	150	1500
Depth/cm	0-20	5-20	10-30	5-30	10-30	5-25	80-110	0-30	0-100
Width/cm	40-60	40-60	50-100	60-100	40-80	60-100	165-200	40-80	150-300
Meandering	strong	not	strong	little	strong	little	none	none	strong
Shade	trees	herbs	trees herbs	trees	trees	trees	none	herbs	trees
Substrate	S;L; FD;CD	S;G; Veg (CD)	S+G; FD;CD; Veg	G+S; Co; Veg	S;L; FD;CD	G;S; Co;L; FD;CD	S;FD	G;S; Co; Veg	G;S; Co;L; FD;CD

S=Sand ; G=Gravel ; Co=Cobbles and Pebbles ; L=Leaves ; CD=Coarse Detritus ; FD=Fine Detritus ; Veg=Vegetation

higher speeds after heavy rainfall. The temperature regime was similar to that of the Ratumsebeek. Measurements were carried out monthly. Minimum temperatures in winter were about 2°C, while summer temperatures varied between 13°C and 16°C.

The stream is shaded by trees, brushwood, high growing herbs or high and steep banks, except for occasional short stretches in the four upstream sections where the bank vegetation or the banks had been damaged by cattle and man. In these unshaded places, aquatic vegetation occurred in small mosaic patterns, mainly consisting of *Veronica beccabunga, Mentha aquatica, Myosotis palustris* and in Section 2 also *Glyceria fluitans*. Especially the steep banks were covered with liver mosses, among them *Marchantia polymorpha*.

Substrate varied with current velocity and geological conditions. The presence of gravel was clearly linked with the occurrence of fluviatile Rhine deposits. However, only in the Sections 4, 6 and 8 did gravel form a major part of the substrate. Here it occurred over the whole width of the stream bed, while it surfaced only incidentally in the Sections 2, 3 and 5. Gravel substrates were mostly situated on or mixed with sand. Only in the Sections 6 and 8 did clay or loamy sand form the base for gravel or sand substrates. In all sections except Section 7, leaves and organic detritus formed a major part of the substrate - accumulated near the banks, in pools, against obstacles projecting from the bed in riffles or trapped in vegetation. Large quantities were also found to be mixed with the mineral substrate.

Section 7 was not included in the routine sampling programme because this part of the stream functioned as a sand collection basin, which was redimensioned in 1976. The width and depth of the stream channel were enlarged to such an extent (and the trees alongside cut) that in summer retention and evaporation were higher than the water supply from upstream. This caused the desiccation of Section 8 in the summers following June 1976.

2.2 THE RATUMSEBEEK (FIGS. 5 AND 6)

This stream is fed by a large number of regulated, and mostly man-made small tributaries, mainly situated in Germany, draining some 1200 ha. In the Netherlands, it drains an area of approximately 2200 ha in a rather narrow drainage area where the stream is fed by a small number of short tributaries. To prevent inundations, peak discharges are diverted into a smal concrete-lined canal some 6 km downstream of the investigated section. The investigated section of the stream (Fig. 5), the first 1500 m after the German border, is strongly meandering in an oak-beech forest. The stream has been left free to find its own way, producing all degrees of meandering, although undermined trees that would obstruct the flow of the water are removed by the local waterboard or (concerned) farmers.

Normally the stream flows all year round. However, in the summer of 1976 the downstream part dried out completely and in the investigated section only some pools remained with an occasional trickle from one to the other. This period lasted only for a few weeks, and the planned sampling programme was postponed until the following January (1977). The slope of the stream is rather constant in this section (1.5

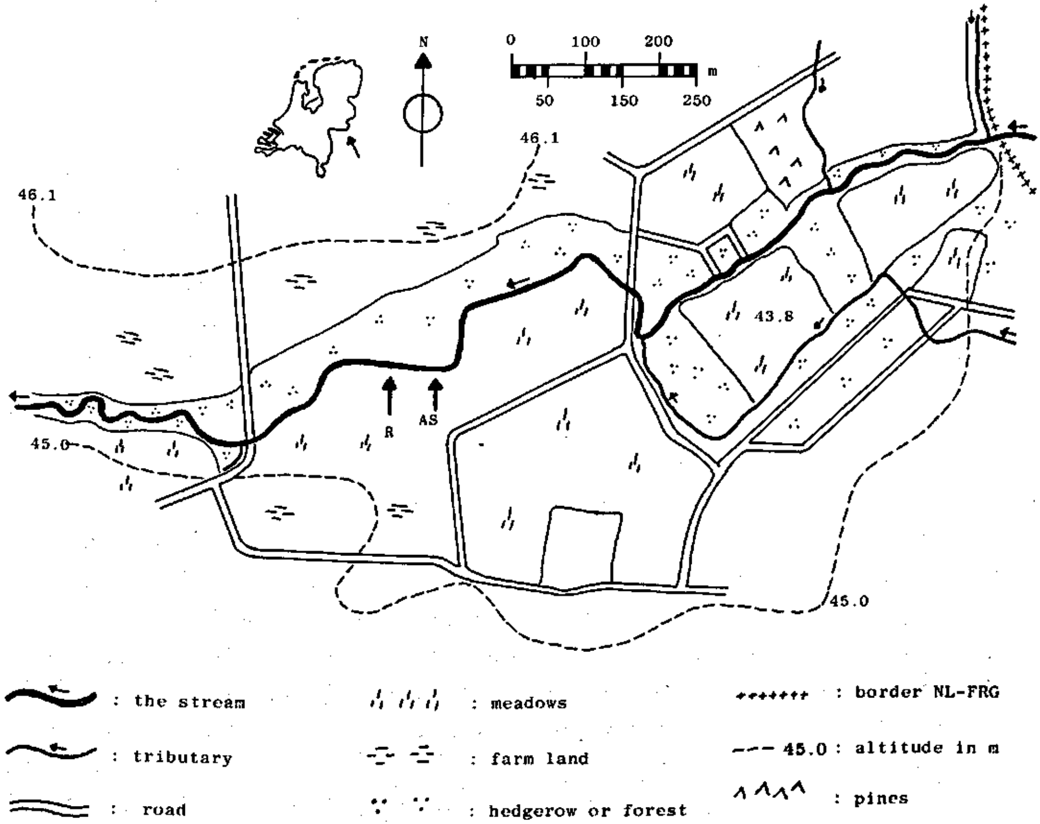


Fig. 5. Upstream section of the Ratumsebeek. The arrows indicate the routine sampling site (R) and the site where artificial substrates (AS) were placed.

Fig. 6. Sampling site in the upstream section of the Ratumsebeek.

m/km). Current velocity varied in summer from very low in pools to 10-15 cm/s at riffles. In winter, pool-riffle differences were less pronounced and the current was 30-40 cm/s on the average, with peaks up to 100 cm/s after heavy rainfall.

The width of the stream bed varied from 1.5 m to 3.0 m. Depth ranged from 0-40 cm in summer to 30-100 cm in winter. Temperature varied between 0° C and 5° C in winter, although ice was practically never formed. In summer, temperature rose to 12-16°C, with occasional peaks of 19°C. For comparison, these data have been included in Table 1.

In the investigated section the stream bed cuts rather deep through the landscape, in some places 2 m or more below the surface level. A strongly varied range of geological deposits reach the surface in the stream bed (Bosch, 1967; Kramer, 1972). From the German border to some 2.5 km downstream lias deposits emerge, especially in the outer bends. In this area, where the stream meanders between the high farmlands, local moraine covers the lias deposits. In some places this boulder clay is compressed to a very hard layer. Claystone banks are also present, formed through compression of clay and sand under pressure in the lias period. Over a distance of about 1 km oligocene clay reaches the surface in some places as well. In the investigated section of the stream, the substrate consists for approximately 40% of gravel and stones embedded in or on top of sand or clay. Iron concretions, resembling rough gravel particles form an important part of the mineral substrate.

The stream bed consists of a number of pools and riffles. Upstream and downstream of the hard banks (claystone), the slope of the stream bed is less strong and sedimentation takes place. Here the stream is deeper and the substrate consists of sand and mud (fine detritus mixed with sand), together with large amounts of leaves and coarse detritus. On the hard banks the slope is steeper and erosion takes place. Here the bottom consists of coarse sand, fine and coarse gravel, iron concretions, claystone, clay and pebbles. By the alternation of pools and riffles, the water runs stepwise downstream.

Leaves and organic detritus form an important substrate in this stream. This material is constantly blown into the stream from the banks and can be found in various forms of degradation all year round. In autumn and winter the input of fresh leaf material is greatest, while the amount gradually decreases through spring and summer. Sometimes large accumulations of leaves form dams in the stream, leading to considerable level differences. In this way a riffle can be temporarily transformed into a pool, although this did not happen at the sites sampled in 1977.

In general, substrate composition fluctuated markedly during the year. As an illustration, the surface views of the sampling site in the Ratumsebeek have been presented for each season in Fig. 7. In this section of the Ratumsebeek, which is completely shaded, no aquatic vegetation grew.

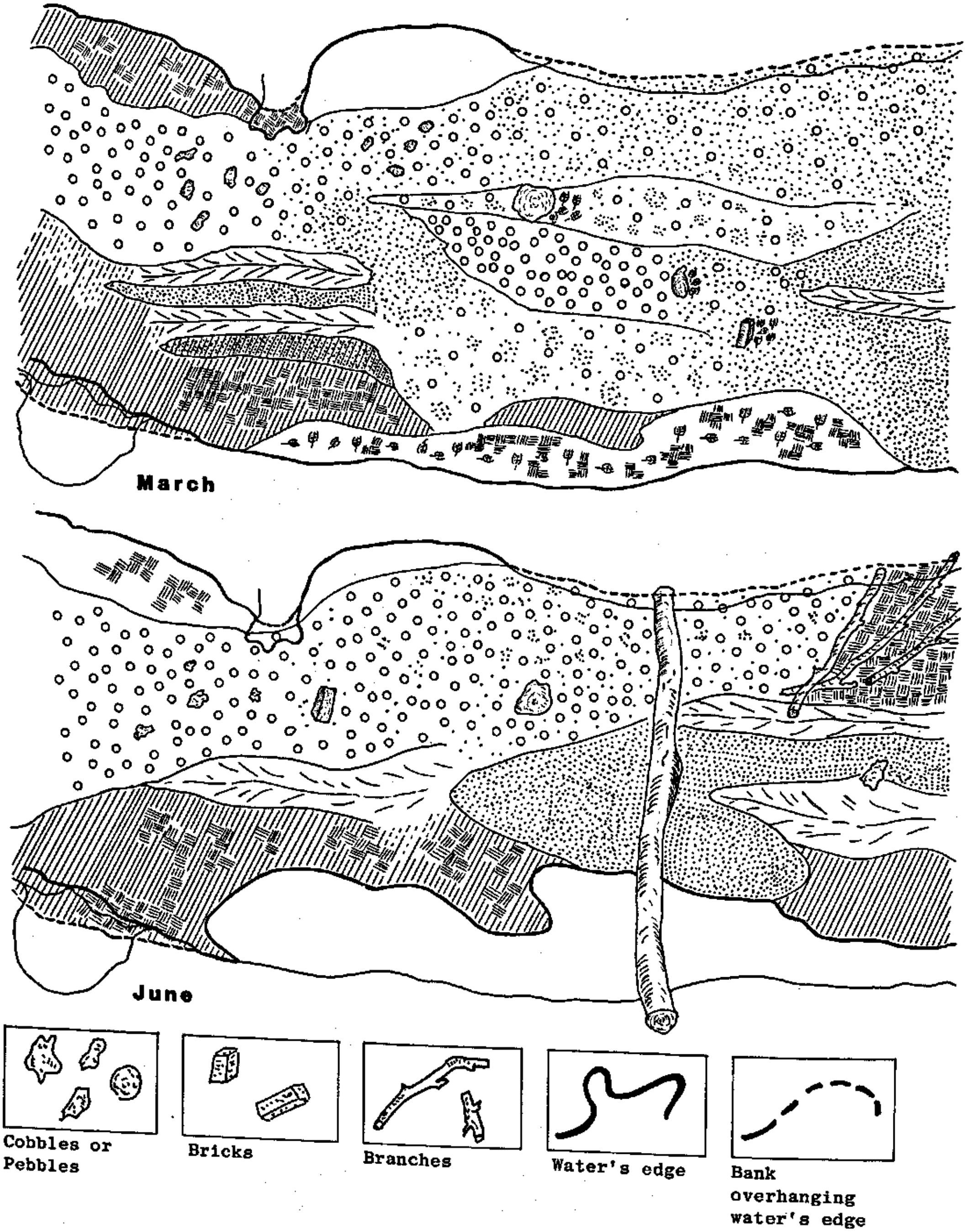
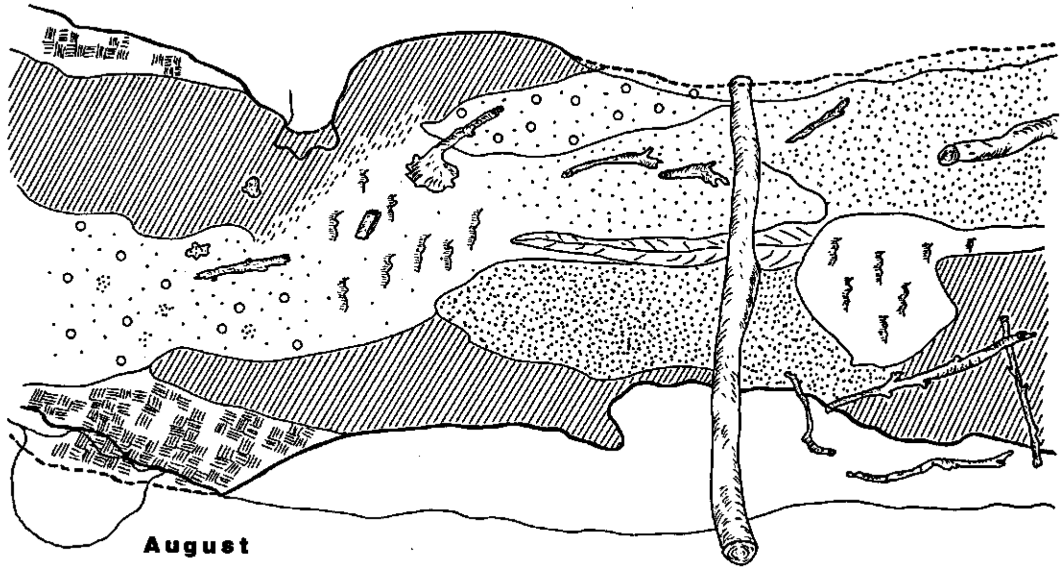
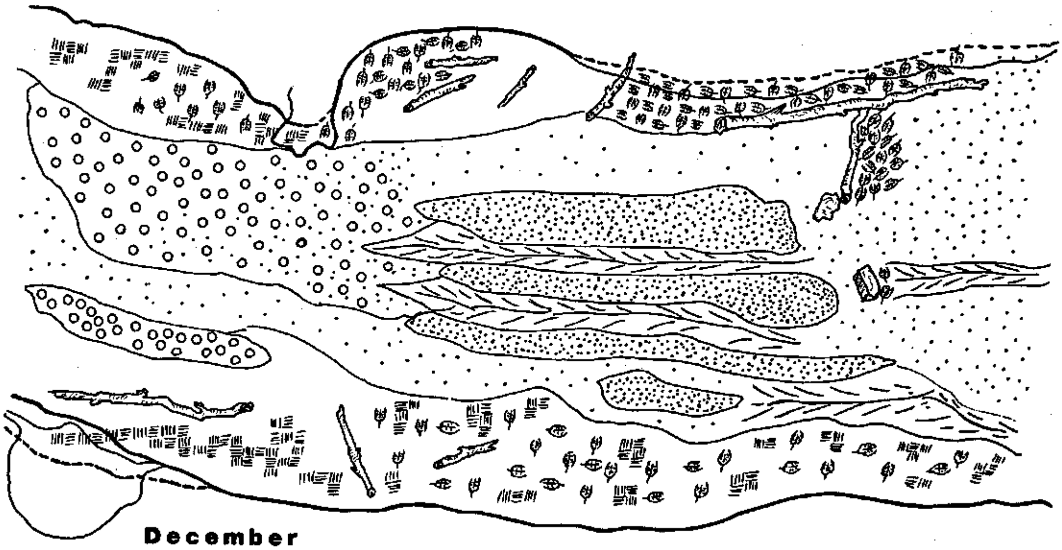
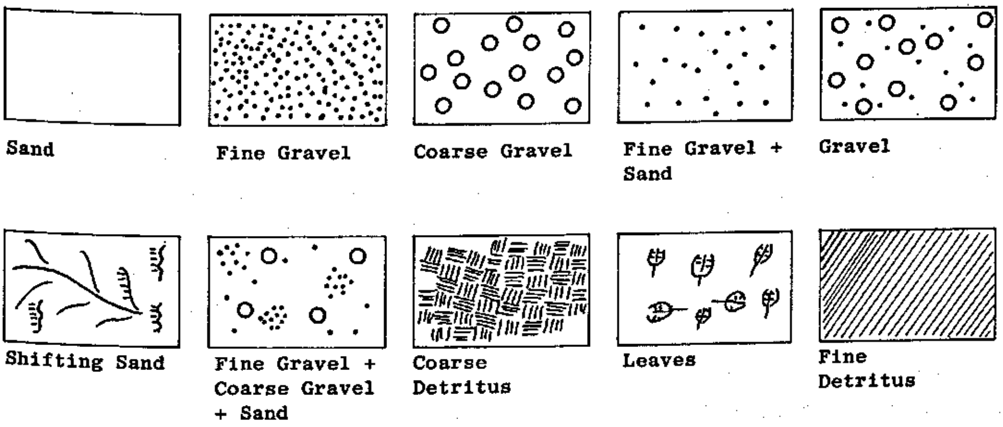


Fig. 7. Substrate mosaic structure of the stream bed at the Ratumsebeek sampling site for each season of 1977.


August


December



3 Methods

3.1 FIELD PROCEDURE

3.1.1 *Selection of sampling sites*

A representative sampling site of approximately 5 m length was chosen in each section on the basis of the substrate composition and variation. In the Sections 4, 5 and 6 in the Snijb and the one section in the Rab, the same site was used on all sampling dates. This gives an impression of the temporal substrate variation and any related changes in macroinvertebrate distribution.

After the selection of a sampling site (always working in upstream direction) a sketch was made of the stream bed (Fig. 7) and the stream profile. The position of the various substrate types and the exposition of the substrates to the current was thus indicated. All dimensions were measured without stepping into the stream. Places inaccessible from the banks were measured after completing the sampling programme. In each sketch the exact position of the samples was indicated and numbered. Samples were taken from all substrate types present at a chosen site. Before actually taking the samples, the site was observed for a while and bottom fauna visible on the substrate surface recorded.

3.1.2 *Sampling dates*

In the Snijdersveerbeek, sampling was carried out monthly from September 1975 to September 1976 and once every two or three weeks from September 1976 to April 1977. Emphasis was placed on the four downstream sections; the three upstream sections were only sampled incidentally. From Table 2, which gives the seasonal number of samples in each section, it is clear that the number of samples in Section 8 decreased after June 1976. This was caused by the desiccation of the stream bed from July to November 1976 as a result of the enlargement of the sand-collecting section upstream in June 1976 and the fact that the summer of 1976 was extremely dry.

Compared to other sections, Section 5 showed less substrate variation, which is the reason for the smaller number of samples taken there; no samples were taken in April 1976. After September 1976, the sampling frequency was increased, as mentioned above, resulting in a larger number of samples in autumn and winter than in spring and summer. Of the spring samples, equal numbers were taken in 1976 and 1977. Only the summer samples were almost all taken in 1976, except for the first samples from

Table 2. Number of samples taken in the Snijdersveerbeek and the Ratumsebeek by season.

Season	Weeks	Snijdersveerbeek sections								Ratumsebeek sections				
		1	2	3	4	5	6	8	Total	1	4	5	8	Total
Winter	51-52 1-11	5	8	1	32	18	39	21	124	41	-	-	-	41
Spring	12-24	2	3	2	20	8	22	20	77	34	-	-	-	34
Summer	25-37	2	-	8	18	17	22	18	85	63	7	4	6	80
Autumn	38-50	5	5	16	26	14	23	7	96	40	-	-	-	40
Total		14	16	27	96	57	106	66	382	178	7	4	6	195

1975 in Week 37, the last week in summer.

In the Ratumsebeek, samples were taken every two or three weeks from January 1977 to January 1978. Sampling dates are summarized per season in Table 2. Samples taken in this stream in July 1976, before the stream dried up, were also included. The more downstream Sections 4, 5 and 8 were not sampled on a routine basis in 1977 but the available data clearly indicate that the substrate and fauna of these sections resemble those of the upstream section studied in 1977.

3.1.3 Field classification of substrates

Substrates on a sampling site were characterized by the dominant-particle size at the surface of the stream bed. Mostly this concerned combinations of several particle sizes together with several types of organic detritus in different quantities. Nine mineral substrate components were distinguished: Cobbles (Co), Pebbles (P), Coarse Gravel (CG), Fine Gravel (FG), Gravel (G, a mixture of CG and FG), Coarse Sand (CS), Fine Sand (FS), Sand (S, a mixture of CS and FS) and Silt/Lutum (not abbreviated). Although no grain-size measurements were carried out in the field, the differences between the components roughly correspond with the limits given in Table 3, combining two fractions at a time, starting with very fine sand and proceeding upward from 0.05 mm.

Practically every combination of these components was found in the two investigated streams. Most samples consisted of a combination of two or more of these components, which together formed a substrate type. This was noted by mentioning the dominant component first, followed by the less abundant components, e.g. FG+CG on FS with P. This means that the substrate mainly consisted of Fine Gravel mixed with (less) Coarse Gravel situated on a base of Fine Sand with an occasional Pebble in the substrate. Mineral substrates not combined with organic material were indicated as Bare, i.e. Bare Sand (BS) or Bare Gravel (BG). Unstable or shifting sand substrates were noted as Shifting Sand (Sh.S), while compact, stable sand substrates were noted as Stable Sand (St.S).

Organic detritus was distinguished in three types and a number of combinations of these:

- Leaves (L): accumulations or layers of intact or only partly disintegrated leaves, predominantly of allochthonous origin.
- Coarse Detritus (CD): smaller pieces of leaves, leaf skeletons, sticks, fruits (acorns, beech nuts), bark, bud scales (beech), seed capsules, remains of higher plants, etc.
- Fine Detritus (FD): very fine organic material, already very disintegrated (e.g. macroinvertebrate excrements). Often amorphous, brown in colour and finer than 0.05 mm.

Organic substrates were also designated according to the ratio between the combining types with the dominant type named first. When CD and L occurred in equal amounts or at the most a ratio of 2 : 1, the substrate was named CD+L (Coarse Detritus and Leaves). When one of these types was more abundant, the substrate was named after the dominant type and the ratio between the types was noted. In the following CD+L or CD or L will sometimes be referred to as Detritus (D) (e.g. Fig. 12). One has to bear in mind that this does not include the Fine Detritus fraction.

Fine Detritus was noted, stating whether there was much or little. The impression obtained during the actual sampling about the packing and stability of the substrate (shifting or stable) and the composition of the underlying, but from the surface invisible, substrate was also processed in the field classification, including data on the ratios of the underlying substrate types.

3.1.4 Sampling method

Since substrate heterogeneity is very marked in both streams, with a strong alternation of substrate types, resulting in small-scale mosaic patterns, a small-scale sampler was necessary for the collection of substrate and fauna. These must be collected together in one sample since it is often impossible to take a separate substrate sample in a certain type because of its restricted area. In streams with more uniform and larger substrate types separate substrate and fauna samples may work satisfactory (e.g. Edwards, 1975; Petran, 1977), but it often proved to be impossible in the Dutch small lowland streams.

A shovel sampler was devised, fit to sample at the same time both substrate and macroinvertebrates on a small scale. This sampler, called a micro-macrofauna shovel (Fig. 8), is made of stainless steel. It is 10 cm wide, 10 cm high and 15 cm long. On the top and at the rear are openings and these are screened with 0.5 mm nylon gauze. A removable handle-bar is attached to the rear. On the sides, adjustable wings are attached, preventing the shovel from digging too deep into the stream bed and making it possible to operate with a standard sampling depth. This depth was fixed at 3 cm in the present investigation. The wings ski over the substrate on both sides of the shovel.

The shovel is pushed into the substrate at an angle of approximately 30 - 45°C and tilted backwards, bringing it horizontal as soon as the desired depth is reached.

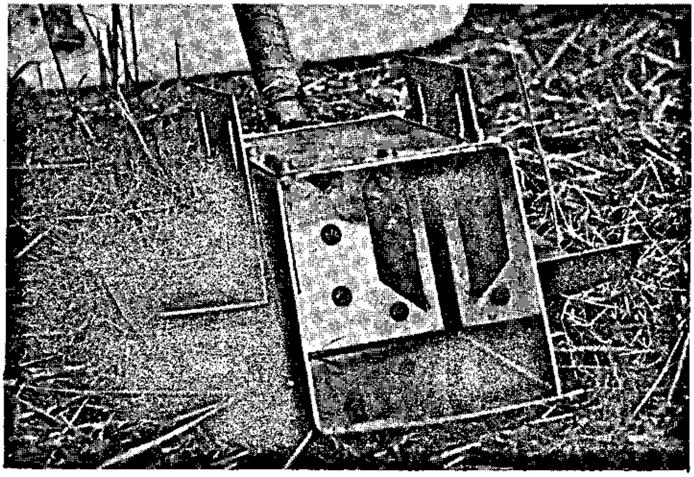


Fig. 8. The micro-macrofauna shovel.

At that moment the wings are resting on the stream bottom. In the same movement the shovel is pushed forward through the substrate over a distance of 15 cm and brought above the water surface after tilting it further backwards. The sample is transferred into a bucket or jar by means of a large, wide-mouthed funnel. Remaining substrate and animals are rinsed out with water. A more detailed description of the micro-macrofauna shovel, its construction and sampling efficiency is to be published (Tolkamp, to be published).

Samples were always taken in an upstream direction. On each date at least four stream sections of the Snijdersveerbeek were sampled, which yielded 15-25 samples. In the Ratumsebeek, only one section was sampled. An average of 6 samples was taken on each occasion. The number of samples always depended on the number of visible substrate types. The samples were transported to the laboratory as quickly as possible and stored at 2-4°C (3-4 hours after taking the first sample). In a few exceptions the samples were conserved with 10 % (V/V) formaldehyde and stored to be sorted later.

Preliminary research (Both, 1976) showed that it is not practical to use the shovel sampler in leaf packs or coarse detritus accumulations, because it will push these substrates ahead of the sampler, or part of the underlying mineral matter will be included in the organic sample. Since this would make the interpretation of the data too complex, the organic substrates and the underlying mineral matter were sampled separately. The organic material was sampled by hand, by pushing the leaves or coarse detritus into the shovel or bringing it directly into a small bucket; the underlying mineral matter was sampled afterwards with the shovel. The amount of organic material sampled by hand was taken from an area comparable to that sampled by the shovel (150 cm^2), but if the organic layer was too thin an additional area was included to reach a more or less constant volume of detritus (approx. 750 ml in a locse packing).

3.1.5 *Additional collections*

A number of animals were hand-picked from stones, branches, aquatic vegetation or any other substrate after taking the routine samples. These animals were collected in order to check whether species dwelling on substrates not sampled with the shovel or by hand might have been missed. The body-length measurements of the animals collected this way were used in addition to the data from the routine samples to construct life-history patterns (especially for the Trichoptera).

3.2 LABORATORY PROCEDURE

3.2.1 *Sample sorting*

As soon as the samples arrived in the laboratory, the sorting procedure was started. This was completed within 24 hours, mostly on the same day. No significant mortality was observed during transportation and storage, except for occasional *Baetis* nymphs. These nymphs are easily injured in the process of transportation. All macroinvertebrates visible with the naked eye were hand-picked from the samples and stored in 80 % (V/V) ethanol. Collecting the animals was facilitated by dividing the sample into some fractions with the aid of a number of sieves. From each of these fractions, the organic material that could be handled with a pair of pincers was removed after careful inspection for macroinvertebrates, which were picked off. Of the mineral material, the pebbles and cobbles were scrutinized individually. The finer fractions were gently stirred in water, after which the animals and detritus in suspension were decanted through a 0.5 mm sieve. This process was repeated until no more animals appeared in the sieve, followed by searching the mineral matter in small portions for remaining animals (strongly clinging or heavy species, e.g. Elminthidae, Gastropoda, case builders).

During this process all the water was retained. As soon as most animals had been removed, the silt and lutum fraction was brought into suspension in this water, poured through a 0.050 m sieve and collected in 1000 ml cylinders. The animals that had slipped through the 0.5 mm sieve were picked off the 0.050 mm sieve. This process was repeated several times to remove the largest portions of the silt and clay fraction. This should be done before dry sieving the coarser fractions (Cummins, 1962) since these fine particles tend to cling to the coarser ones in dry conditions and are easily missed.

3.2.2 *Substrate analysis*

The particle sizes of the organic detritus were not determined. The nature and the composition of the organic material was recorded (sticks, fruits, leaves, leaf species, etc.) during sample sorting, in addition to the field recordings. After drying at 105°C for 24 hours the organic material was weighed to the nearest 0.1 g.

A boiling water-bath was used to evaporate most of the water, after which the mineral substrate coarser than 0.050 mm was dried at 105°C. After cooling to room temperature the substrate was divided into the fractions of the Wentworth scale (Wentworth, 1922; Cummins, 1962; Hynes, 1970a) (Table 3). The Wentworth classification was used because it is possible to convert the geometric particle-size classification, in which each particle-size fraction is twice the preceding one, into an arithmetic one with equal class intervals by using the phi scale, i.e. negative binary log of the particle size in mm. A set of seven, copper-wired, square-mesh sieves (1/20, 1/8, 1/4, 1/2, 1, 2 and 4 mm) was used to separate the finer fractions. At the start of the investigation a 1/16 (0.0625) mm mesh sieve was not available, so a 1/20 (0.050) mm mesh sieve was used. This deviates from the Wentworth classification, but since the silt-lutum fraction was always very small (mostly less than 2%) it was considered unnecessary to change to a 1/16 mm mesh sieve. A mesh of 1/20 (0.050) mm is the limit used in more recent grain-size classifications to separate silt-lutum from very very fine sand (De Bakker & Schelling, 1966).

The sample was sieved on a Ro-Tap Testing Sieve Shaker (Tyler Company, Cleveland, Ohio, USA). This shaker moves the sieve set in a horizontal, elliptical movement. After completing one ellipse a hammer strikes the top of the set, causing a continuous redistribution of the material on the sieves. The standard sieving time was 15 minutes per sample, unless the sieves clogged, in which case smaller portions were used. Substrates coarser than 4 mm were hand-sieved (8 mm and 16 mm sieves with a circular mesh), while larger particles were measured individually with a rule (the largest diameter of the smallest projection). The contents of each sieve or otherwise determined fractions were weighed to the nearest 0.1 g.

Whenever a reference is made to a certain grain-size fraction, the fraction is

Table 3. Grain-size fractions and their definition following the Wentworth classification (after Cummins,1962 and Doeglas,1968).

Fraction (mm)	Phi value (-log$_2$ fraction)	Sieve mesh (mm)	Phi index of fraction(Doeglas)	Name of fraction
128-256	-7	rule	$\bar{8}$	cobbles
64-128	-6	rule	$\bar{7}$	cobbles
32- 64	-5	rule	$\bar{6}$	large pebbles
16- 32	-4	16(round)	$\bar{5}$	small pebbles
8- 16	-3	8(round)	$\bar{4}$	coarse gravel
4- 8	-2	4(square)	$\bar{3}$	medium gravel
2- 4	-1	2(square)	$\bar{2}$	fine gravel
1- 2	0	1(square)	$\bar{1}$	very coarse sand
0.500- 1	1	0.500(square)	1	coarse sand
0.250-0.500	2	0.250(square)	2	medium sand
0.125-0.250	3	0.125(square)	3	fine sand
0.050†0.125	4	0.050(square)	4	very fine sand
0-0.050†	5-10	pipette	0	silt and lutum

†:used instead of 0.0625 mm

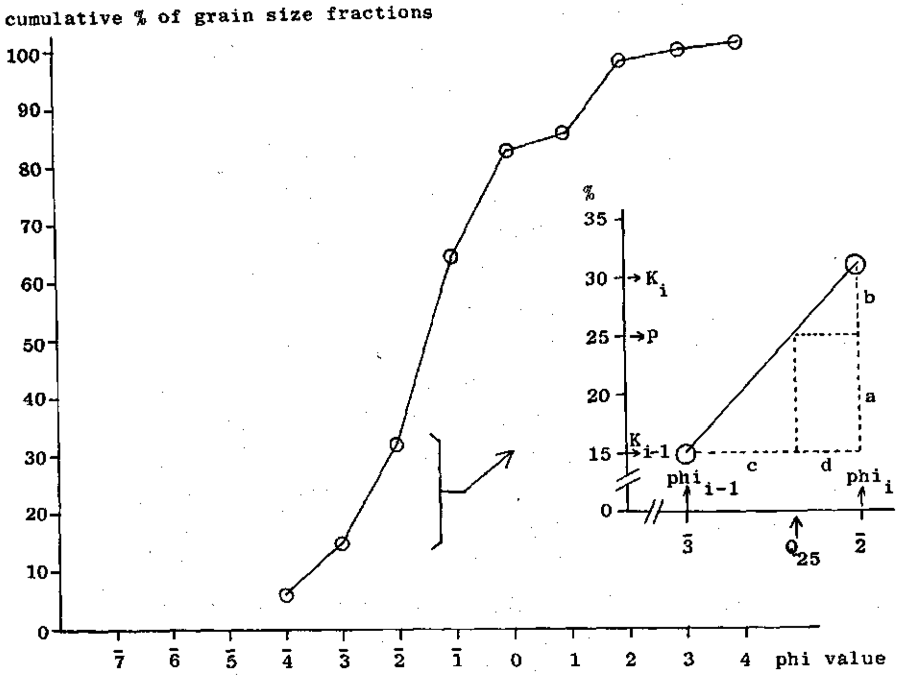


Fig. 9. Example of cumulative distribution of grain-size fractions in a sample expressed as a percentage against the -log$_2$ of the particle size in mm (phi value). The inset illustrates the calculation of a quartile index by linear interpolation of the cumulative percentages at the nearest integer phi value, following the formula $a/(a+b) = c/(c+d)$; $|c+d| = 1$.

referred to by the lower limit, which corresponds with the sieve mesh that retained the fraction (e.g. the 2-4 mm fraction is referred to as the 2 mm fraction). Sometimes the corresponding phi unit will be used, e.g. phi = $\bar{1}$ for the 2-4 mm fraction. It should be noted that the negative sign of phi units is placed above the figure.

The fraction finer than 0.050 mm in the cylinders was determined with the pipette method. The cylinders were filled up to the 1000-ml line, after which the contents were resuspended by shaking vigorously. A sample of 20.00 ml was taken from the centre of the column with a vacuum-operated, standard pipette. This sample was dried and weighed. After conversion to 1000 ml the results of all cylinders used per sample were added to those for the silt-lutum fraction obtained in the dry-sieving procedure.

The fraction weights were converted to percentages of the total mineral weight. With the aid of the cumulative percentages, the first quartile (Q_{25} or Q_1), the median (Q_{50} or M_d) and the third quartile (Q_{75} or Q_3) were calculated with the following formula, derived from the cumulative sediment curve where the particle sizes are expressed in phi values (- log$_2$ of the particle size in mm) (Fig. 9):

$$Q_p = phi_{i-1} + \frac{p - K_{i-1}}{K_i - K_{i-1}} \quad , \text{ where}$$

p = 25, 50 or 75 for Q_{25}, Q_{50} or Q_{75} (used as Q_1, M_d, Q_3 when rounded off), respectively

K_i = cumulative percentage of the particle size where the 25 %, 50 % or 75 % limit, respectively, is exceeded

K_{i-1} = cumulative percentage of the particle size before the 25 %, 50 % or 75 % limit, respectively, is exceeded.

These quartile values can also be derived from the cumulative sediment curve (Morgans, 1956), but this is less accurate and more time consuming.

The $Q_1M_dQ_3$ index (Doeglas, 1968) was calculated with these quartile values. In this index the phi value 0 is reserved for the finest clay fraction, instead of the value 10, and all phi values larger than zero are substituted by the next highest integer value (Table 3). This means that, according to this system, the fraction index (the substituting phi value) for the particle sizes coarser than 1-2 mm is calculated by taking the negative binary log of the upper limit of the fractions, but for the fractions finer than 1 mm this is done with the lower limit. In fact, a positive fraction index is rounded off to the next highest positive integer value and a negative fraction index to the next lowest negative integer value, e.g. Q_{25} = -2.15 becomes Q_1 = -3 or $\bar{3}$ and Q_{50} = 2.15 becomes M_d = 3.

3.2.3 Macrofauna analysis

The lower limit of the smallest macroinvertebrates collected was determined by two factors: they had to be visible to the naked eye and it should be possible to handle them with a pair of pincers. In general, animals with a body length smaller than 1 mm were not collected. Whenever very small midge larvae were observed, their small tubes on the bottom of the sorting pan being clearly visible, it was recorded. In most cases the larvae themselves were not visible to the naked eye, and their numbers were not included in the final results. Identification of these very small larvae showed them to belong to the Tanytarsini, mainly *Micropsectra* gr. *praecox*. First instars of many faunal groups are missed by this method of sorting. However to include these instars as well would make it necessary to examine all samples under a stereomicroscope or a large magnifying glass. This is very time consuming and the large number of samples did not permit this.

Animals were collected quantitatively from the samples. Only in samples with hundreds of (juvenile) *Gammarus* or Chironomidae larvae, were these abundant species counted, after removal of all other species and a representative part of the abundant species. To this end, the remaining sample was split into 4 - 10 equal portions. After identification of all animals in a sample, the counted numbers were added to the collected numbers of the species concerned. If it concerned more species (e.g. Chironomidae), the ratio found in the collected numbers was supposed to be present in the not-collected part as well and it was used as a measure to divide the counted numbers over the species.

In counting tube-building Chironomidae, the ratio between empty and inhabited tubes was taken into account. Empty cases of caddis and dead molluscs were collected as well, but they are not included in the results. Sometimes half specimens of *Ephemera danica* (Ephemeroptera) and *Micropterna sequax* (Trichoptera) were found. They probably had been cut in two by the shovel. These half specimens were considered to be whole.

The collected macroinvertebrates were killed and preserved in 80 % (V/V) ethanol which was renewed after some days and again after identification of the material. Tricladida were identified alive and were not preserved.

Identification was carried out with the most recent keys and descriptions available (the keys used are listed in a separate literature list). Identifications carried out with keys that proved to be out of date were redone with the latest key (e.g. *Sericostoma personatum* and *Notidobia ciliaris* (Trichoptera) larvae identified with the keys of Ulmer (1909), Hickin (1976) and Lepneva (1964) were checked with the key of Wallace (1977), which showed that it concerned only one species: *Sericostoma personatum*.

As shown in Table 4, the level of identification was not the same for all taxa. This level mainly depended on the availability of keys, but it also proved impossible to identify certain juvenile specimens, especially of the Chironomidae and the Trichoptera. When there was doubt, identifications were checked by several Dutch specialists (Simuliidae, drs. J.J.P. Gardeniers; Chironomidae, dr. H.K.M. Moller Pillot; Trichoptera, dr. L.W.G. Higler; Coleoptera, drs. J. Cuppen). Larval and pupal identifications of several species of Trichoptera, Ephemeroptera and Plecoptera were checked on the adults by rearing them in the laboratory: *Potamophylax luctuosus*, *Micropterna sequax*, *Chaetopteryx villosa*, *Sericostoma personatum*, *Agapetus fuscipes*, *Lithax obscurus* (Trich.), *Ephemera danica*, *Habrophlebia fusca* (Ephem.), *Nemoura cinerea*, *Amphinemura standfussi* (Plec.).

For the majority of the species (Table 4), body length of all specimens was measured in 1 mm size classes. Although measurements of head capsule width is often the most accurate way to determine the instar, this method was not employed because it is very time consuming. Besides, the objective was not the construction of the life history of these species but the determination of possible differences in substrate preferences between smaller and larger (younger and older) specimens. Body length is certainly accurate enough to make this distinction.

Body length was measured using the stereomicroscope with millimetre graph paper under the petri dish containing the animals. The distance between the anterior edge of the head and the posterior edge of the abdomen was measured, excluding antennae and caudal appendages as cerci or breathing tubes. The length of contracted specimen (e.g. Plecoptera) was determined after bringing the animal back into its 'normal' position. Curved animals (*Gammarus*) were measured in a standard position, with an average body curve. This reduced the absolute body length by approximately 25%, giving a maximum body length for *Gammarus pulex* of 18 mm; keys state 24 mm for the largest males.

Table 4. Identification level for macroinvertebrates and indication of body length measurements.

Macroinvertebrates	Body length measurement	Identification level			
		Order	Family	Genus	Species/group
Tricladida					x
Oligochaeta		x	x^1		x^2
Hirudinea					x
Amphipoda	x				x
Isopoda					x
Hydracarina		x			
Plecoptera	x				x
Ephemeroptera	x			x^3	x
Odonata					x
Heteroptera					x
Trichoptera	x			x^4	x
Coleoptera	x^5			(x)	x
Diptera			x^6	x	x
Chironomidae	x		x^6	x	x
Tipulidae	x			x	
Dixidae	x				x
Ptychopteridae	x			x	
Simuliidae	x				x
Psychodidae	x			x^1	
Ceratopogonidae	x			x	
Culicidae	x				x
Stratiomyiidae	x			x	
Empididae	x			x	
Tabanidae	x		x	x^1	
Dolichopodidae	x			x	
Tetanoceridae	x		x	x^1	
Ephydridae	x			x	
Mollusca				x	x
Bivalvia				x	
Gastropoda					x

1:Only the higher level was used for results; 2: *Eiseniella tetraedra* and *Stylaria lacustris*; 3: Baetidae; 4: Juveniles; 5: Only larvae; 6: Pupae

Of five Trichoptera species, head width, head length, case width and case length were measured in addition to body length. An ocular micrometer (10:100) in the stereomicroscope was used. The measurements were performed in classes of 0.025 mm.

3.3 LABORATORY EXPERIMENTS

3.3.1 *Artifical stream channel experiments*

3.3.1.1 The stream

Substrate-selection experiments were performed in an artificial stream channel. The design followed that of Lauff & Cummins (1964) and Feldmeth (1970). The channel was constructed of Perspex, 42 cm wide, 200 cm long and 30 cm high (Fig. 10). Water

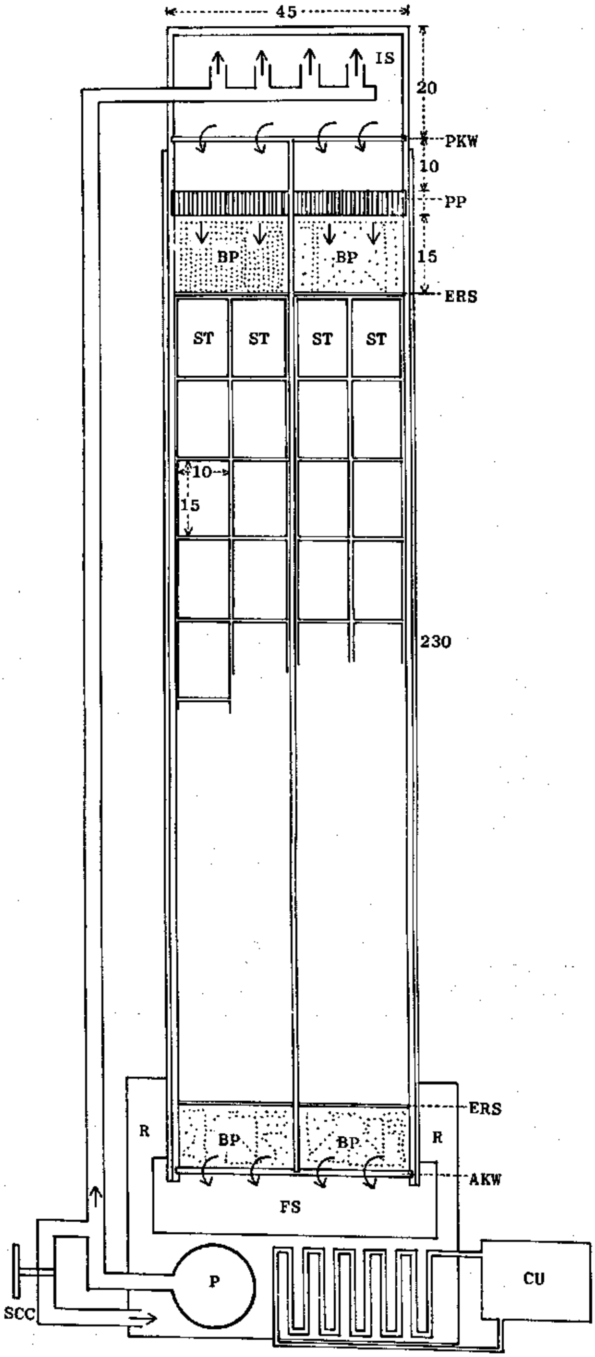


Fig. 10. Plan view of the artificial stream (measurements in cm). IS = inlet section; PKW = permanent knife weir (h = 18 cm); PP = pipe plate (diam.= 4 cm; h = 18 cm); BP = buffer plate; ST = substrate trays (h = 3 cm); AKW = adjustable knife weir (h = 0-18 cm); CU = cooling unit; R = reservoir (150 l); P = pump; FS = filter section; ERS = end retaining screen (mesh = 0.5 mm); SCC = short cut circuit; stream height = 30 cm; stream width = 45 cm ; stream length = 230 cm.

was circulated from a cooling reservoir with an immersion pump (maximum capacity 300 l/min) that released it in a small reservoir in the stream. From here it flowed over a knife weir and through a 4-cm-thick tube plate (consisting of pipes of 4 mm inner diameter) before entering the experimental area in a laminar flow. At the end of the channel the water flowed over a second knife weir and through a filter back into the cooling reservoir. The water was cooled by passing it through a silver-coated copper spiral filled with Freon, which was circulated by a compressor. All experiments were conducted at a temperature of 11°C, the minimum temperature that could be reached with a water depth of 10 cm and current speed of 10 cm/s (the maximum speed used). Water depth was regulated by the height of the downstream weir. Current velocity could be regulated by returning more or less of the pump flow directly back into the reservoir. Tap water was used in all experiments because it was of excellent quality.

After each experiment, and at least twice a week, the water was changed. Substrates were introduced in 40 trays, each 10 cm x 15 cm x 3 cm, in 4 parallel rows. It was possible to divide the channel in two parallel channels with the aid of a Perspex partition: two rows of trays in each channel. Removable screens (1.3 mm mesh) could divide the stream into sections of a minimum of 2 and maximum of 40 trays per section. Upstream and downstream of the experimental area a Perspex plate was laid as a buffer between the experimental area and the end retaining screens. The surface of these plates was level with the surface of the filled substrate trays and roughened by a monolayer of 1-2 mm sand grains glued to the plate.

Illumination of the stream followed the outside light pattern, during the day supplemented with time-switch-operated fluorescent daylight lamps.

3.3.1.2 Substrates tested

Substrates used in the experiments were obtained by storing all samples from the Snijdersveerbeek by grain size after substrate analysis. In experiments all grain sizes ranging from 0.050 to 32 mm were used, together with leaf packs and coarse detritus. Substrates were arranged in graded series within each experimental section in a number of standard positions according to the model presented in Fig. 11. A test on the influence of the substrate-tray arrangements showed that for species tested there was no significant difference in substrate selection connected with the arrangement, apart from the influence of the current velocity.

3.3.1.3 Experimental design

All experiments were replicated, partly at the same time in 2 or 4 parallel series. The final number of experiments varied from species to species. Substrate selection was assesssed after a fixed period, which was determined experimentally for each species. For most species the substrate selection showed no significant differences after 2, 4, 6, 8, 12 or 24 hours, which meant that all observations could be made a.

screen V screen IV screen III screen II screen I screen

V		IV		III		II		I	
		125	2	2	125	125	2	2	125
		250	4	4	250	250	4	4	250
		500	8	8	500	500	8	8	500
		1	16	16	1	1	16	16	1

b.

II		I	
125	16	16	125
250	8	8	250
500	4	4	500
1	2	2	1

c.

II		I	
1	500	250	125
2	4	8	16
125	250	500	1
16	8	4	2

d.

	V		IV		III		II		I	
A	2	16	④	②	⑧	①	4	2	8	1
	8	4	①	③	②	④	1	8	2	4
B	8	2	125	250	500	1	1	500	250	125
	16	4	16	8	4	2	2	4	8	16
	V		IV + III				II + I			

Fig. 11. The most common substrate tray arrangements. Each grain-size fraction is indicated by the lower limit of the fraction in µm or mm (125 = 0.125 - 0.250 mm; 2 = 2 - 4 mm). Water runs from right to left. Arrangements a-c : Sections I and II have opposite arrangements regarding upstream or downstream placement of the fine and coarse substrates. Sections III and IV are replicates of Sections I and II, respectively. Section V is alternately a replicate of Sections I and II, rearranged after each experiment. Arrangement d : Two parallel streams: 4 trays per Sections IA and IIA in opposite arrangements. IIIA and IVA are also opposite arrangements and comparable with IA and IIA, except for the leaf packs (circled) placed on top of the mineral substrate. VA and VB are opposite arrangements. IB+IIB and IIIB+IVB are opposite and can be compared with Sections I and II in Arrangements a-c. The grain sizes may be different in some experiments but this arrangement model was kept: 0.125 - 16 mm becomes 0.250 - 32 mm in the same sequence from fine to coarse fractions.

after 2 hours. However, animals were left regularly in the experimental area for 24 hours to have a check on the selection period. Species like case-building Trichoptera that can be handled with a pair of pincers were introduced in the experimental area by placing them on top of each substrate tray in densities of 2 or 4 animals per tray, although densities of 3, 5, 6 or 8 specimen per tray were used as well. This will be indicated for each experiment in the results.

After the set selection period, the positions of the animals were recorded and the animals collected by picking them off the surface after lightly stirring the substrate *in situ*. More vulnerable species, like *Ephemera danica*, were introduced by placing them on the filled trays in a small petri dish and letting the nymphs swim away of their own volition. For these animals particle-size selection was determined by removing the trays from the stream and carefully bringing the contents in a larger tray with water of the same temperature. The same retrieving process was used for species difficult to trace *in situ*, e.g. small larvae of *Sericostoma personatum*.

3.3.1.4 Species tested

Experiments were conducted with several instars of four Trichoptera species and one Ephemeroptera species. Table 5 summarizes the species and instars, including possible differences in case-building material used by the caddis larvae.

3.3.1.5 The influence of current velocity on substrate selection

The effect of current velocity on the substrate selection was tested for current velocities of 10 cm/s and 5 cm/s for all species in sections with 8 trays, with identical particle sizes in the 4 upstream and downstream trays. Experiments were conducted with several particle-size combinations and selection periods. For species that showed no significant differences in substrate selection between upstream and down-

Table 5. Species, instars and case building material in substrate-selection experiments.

Species	Instar	Length/mm	Case-building material
Micropterna sequax	F	> 15	mineral (F ; F-1)
	F-1	10-15	organic (leaves/detritus) (F-2 ; F-1 ; F)
	F-2	6-10	1/2 mineral- 1/2 organic (F-2 ; F-1 ; F)
			1/2 pupal (mineral, one end enlarged
Chaetopteryx villosa	F	> 10	mineral
			organic
			1/3 mineral- 2/3 organic
			1/2 mineral- 1/2 organic
			1/2 pupal (mineral,one end enlarged)
Sericostoma personatum	F	11-14	mineral
	F-1	8-11	mineral
	F-2	7-10	mineral
	F-3	6-7	mineral
Ephemera danica		15-20	
		15-25	
		20-25	

stream trays or end retaining screens, the current speed was maintained at 10 cm/s in all experiments.

3.3.2 Rearing channel

A small rearing channel similar to the laboratory stream described by Higler (1975) was used to acclimatize animals to laboratory conditions and to keep them in stock for experiments in the artificial stream described in Section 3.3. Water temperatures followed the temperature fluctuations of the Ratumsebeek with approximately one week delay. The stream was driven by four small pumps giving an average current velocity of 1-10 cm/s, depending on water depth and obstacles placed in the stream. Nylon-mesh screens divided the channel in sections to keep the different species apart, and screens on top prevented emerging adults from escaping. Substrate in all sections consisted of a 3 cm thick mixture of sand and gravel, with additional stones and sticks. Fresh leaves and detritus collected from the Ratumsebeek were supplied as food and additional substrate. Illumination followed the outside light pattern.

Several species of Trichoptera, Ephemeroptera and Plecoptera (see Subsection 3.2.3) were reared successfully to adults. Some species even mated although only *Sericostoma personatum* produced eggs in the stream (these hatched later).

3.3.3 Experiments with Trichoptera

Case-building macroinvertebrates often use materials from the stream bed for their cases. Trichoptera form the major group of animals that use mineral and/or organic material to build their cases. Other groups are tube-building Chironomidae and case-building Lepidoptera. The (grain-size) composition of the cases might at least partly reflect the substrate composition of their habitat. The presence or absence of certain grain sizes or organic substrates might be a factor determining the presence or absence of certain case-building species in a habitat or stream.

Cases of five species of Trichoptera were analysed on their grain-size composition. With four species, case building experiments were carried out, offering several grain sizes and organic materials as building materials, while the latter also functioned as food. Additional experiments were performed in which only sub-optimal materials were offered.

3.3.3.1 Case-building experiments

Experiments on the case-building behaviour of four species of Trichoptera were conducted in temperature and photo-period controlled climate cells. Day length followed the natural pattern and temperature was held at $14^{o}C \pm 1^{o}C$. Experiments with *Micropterna sequax*, *Agapetus fuscipes* and *Lithax obscurus* were performed in petri dishes filled with water. For building experiments with *Sericostoma personatum*, 250

Table 6. Grain-size fractions used in case-building experiments with Trichoptera.

Grain-size fractions (mm)	Colour	Fraction name
0.050 - 0.125	not coloured	very fine sand
0.125 - 0.250	red	fine sand
0.250 - 0.500	white quartz sand	medium sand
0.500 - 1.0	green	coarse sand
1.0 - 2.0	blue	very coarse sand
2.0 - 4.0	not coloured	fine gravel

ml glass beakers were two-thirds filled with water and aerated with compressed air blown in through pasteur pipettes. This produced a stream of fine air bubbles and created constant water movement. All water used was brought in from the Ratumsebeek. Food was supplied in the form of leaves and coarse detritus, collected in the Ratumsebeek and rinsed in tap water. In order to facilitate the recognition of the grain sizes used by the animals, all fractions (ranging from very fine sand to fine gravel) were coloured differently with waterproof Edding^R ink. This proved to be non-toxic to the caddis larvae (*M. sequax* larvae were kept for 14 days on coloured substrates and showed no reduction in activity) and the ink does not alter the surface structure of the grains. The grain size fractions used are listed in Table 6.

For each experiment, some or all grain sizes were provided together with a few fresh and old beech leaves. Larvae (each in its own dish or beaker) were introduced without their cases or with only the front half of the cases removed, after having been adapted to the experimental conditions for a few days. They were left in the experimental cells until they had completed the building of their final case. This was mostly reached within 7 days after completing an emergency case that was build within 2-3 days after introduction into the experimental area. After each building experiment, the number of grains in each size fraction used in each case was counted and the relative proportion of each size fraction in the total case surface was calculated. The method used for this calculation will be described in detail by Tolkamp & Verdonschot (to be published).

3.3.3.2 Grain size analysis of natural Trichoptera cases

To compare the grain-size selection in the case-building experiments with the composition of the natural cases the latter were analysed for their grain-size composition. After measuring case length and case width, together with larval body length, head width and head length, cases of which less than approximately 5% of the surface consisted of organic material were combined in classes of 10 or more for each larval instar. When enough material was available classes within each instar were distinguished on the basis of larval head width. Cases with more than 5% organic material were treated separately.

Grain-size analysis was carried out after dissolving the organic material and salivary secretion by boiling the cases in 30% (V/V) H_2O_2 for 24 hours, followed by treating the remaining material with 1 N HCL and rinsing with water. After drying in a stove at 110°C, 13 grain-size fractions were determined by hand sieving, using as many sieves as available (diameter 10 cm) with openings of: 0 - 0.050 - 0.105 - 0.150 - 0.210 - 0.250 - 0.350 - 0.500 - 0.850 - 1.0 - 2.0 - 4.0 - 8.0 - 16.0 mm. Each fraction was weighed and its relative proportion to the total mineral case weigth was calculated. Its relative proportion to the surface area of the case was calculated with the aid of experimentally determined factors (see Tolkamp & Verdonschot, to be published).

3.4 FIELD EXPERIMENTS

In order to check in the field the selection by the macroinvertebrates of the grain-size of the substrate several methods were used for the introduction of artificial substrates in the natural environment.

3.4.1 Artificial substrate trays

Since no experience with the use of artificial substrate samplers was available in the Netherlands, a study was started on the use of wire baskets filled with small pebbles (16-32 mm) or large pebbles (32-64 mm) in the Snijdersveerbeek. The results of this study will be published elsewhere (Tolkamp & Verdonschot, to be published). Wire baskets are only fit for relatively coarse substrates, since finer materials need to be introduced in closed containers, e.g. plastic or tin cans (Khalaf, 1975).

For the experiments described in this subsection two sizes of shallow plastic trays were used. These trays measured 13.25 cm length x 8 cm width x 3 cm depth and 18.25 cm length x 12.25 cm width x 3.5 cm depth, giving contents of 318 cm^3 and 782 cm^3, respectively. The small trays were filled with approx. 600 g of substrate and the large trays with approx. 1300 g; all trays were filled to the brim. All experiments were carried out in April and May 1978 in a section of the Ratumsebeek with a more-or-less uniform gravel-sand substrate, uniform flow over the total width of the stream bed and a water depth of 5-10 cm. Trays were placed in the stream bed in rows of three, spaced 50 cm in width and length from neighbouring trays.

Initially, for each collection date 6 small trays of each grain size were used with 1 large tray, except for the 8-16 mm grain size, for wich 4 large trays were used for the first set of experiments. Later on, only 2 large trays were used for each grain size, the amount of available substrate and time to work up all samples being the restricting factors. Small trays were used as well in the later experiments, but all were lost during one period, being removed from the stream by persons unknown.

The trays were dug into the stream bottom so that they were level with it. The substrate from the stream bed was smoothed over the edges of the trays and what was

Table 7. Number of substrate trays for each grain size and period of colonization in the Ratumsebeek.

Period of colonization	Number of trays by grain size (mm)								
	0.125	0.250	0.500	1.0	2.0	4.0	8.0	16	32
4	.	6 S	.	.	.	6 S	6 S 3 L	.	.
6	.	6 S	.	.	.	6 S	.	.	.
10	.	6 S 1 L	.	.	.	6 S 1 L	6 S 1 L	.	.
12	.	.	2 L	2 L	2 L	2 L	2 L	2 L	.
14	.	.	.	2 L	2 L	2 L	2 L	2 L	2 L
28	2 L	2 L	2 L	2 L	2 L	2 L	2 L	2 L	2 L

S= small tray ; L= large tray ; . = no trays

left was distributed on the bed downstream of the experimental section. Trays were retrieved after different periods, ranging from 4 days to 4 weeks (Table 7). Animals were sorted in the laboratory, organic matter was picked out, dried and weighed and the grain-size composition of the mineral substrate in the trays was determined to establish the amount and nature of lost and gained substrate. Only on two occasions were the tray contents washed out, in which case the sample was omitted.

3.4.2 Artificial substrates introduced without trays

Dug-in trays filled with substrate can only be colonized from above. Horizontal migration through the stream bed or vertical migration from below is prevented by the trays, sides and bottoms. Moreover, the trays themselves may act as an attachment site for clinging and sucking animals (e.g. snails and leeches) and they are gradually colonized by diatoms, bacteria and fungi, trapping fine detritus in their turn, providing food and foothold for many macroinvertebrates.

In order to exclude these possibly disturbing influences, several grain sizes were introduced into the stream bed with no casing around them. Channels 3 cm deep, 15 cm wide and 75 cm long were dug in the stream bottom and filled with dried substrate; one grain size in each channel, eight channels, in two rows of four.

The upstream row contained grain sizes of 0.250, 8.0, 4.0 and 0.500 mm and the downstream row grain sizes of 1.0, 16, 2.0 and 0.125 mm; the coarsest grain sizes in the middle of the stream, the finest on the edges. After one month, 3 samples were taken from each grain size with the micro-macrofauna shovel. The samples were sorted in the laboratory and the substrate analysed following the normal procedures. These experiments were carried out in November-December 1978 in the same section of the Ratumsebeek as where the substrate trays were introduced.

3.4.3 Litter bags

Leaves form an important substrate for several species of macroinvertebrates and the breakdown rate and colonization of several leaf species are quite well documented. A study was undertaken in the Ratumsebeek on the breakdown rates and colonization by macroinvertebrates of alder (A), oak (Q), beech (F) and poplar (P) leaves during different incubation periods. A detailed description of this study will be published by Tolkamp & Knol (to be published).

3.5 DATA PROCESSING

3.5.1 Data storage

All field data were processed with the aid of the computer of the Agricultural University of Wageningen. Sampling dates were transformed to year and week numbers. Field classification of the substrates was binary coded by the presence/absence of the seven main grain-size classes mentioned in subsection 3.1.3 (the smallest and largest particle sizes were not used) and the presence/absence of the three detritus classes. The substrate stability was recorded as stable or shifting. Weights of particle-size fractions were rounded off to the nearest gram, since this hardly influences the percentages of each fraction or the quartile values calculated later. Animals were coded by numbers (Appendix 1). Length classes were indicated by the upper limit of the class (i.e. 1-2 mm = 2), with a separate code for pupae (99) and adults (98).

Data were stored in two data files for each stream. The first file with the data of the sample (stream, section, sample number, year, week, fraction weights, field classification, number of species/taxa, number of specimens). The second file with the data concerning the species and the number of specimens in each length class, together with the sample code. Mistakes made in the process of filling in the punch lists were partly checked by comparing the number of specimens and species as counted by hand (in the sample file) and by the computer (from the species file). After these and other checks, to econimize the programs, the sample file was extended with the $Q_1M_dQ_3$ index and a binary file for the presence/absence of each species.
With the aid of several programs, developed in close cooperation with the Computer Centre of the Agricultural University, various parameters were calculated, e.g. longitudinal distribution of species in the Snijb, distribution of different development stages in time and place, Index of Representation (I.R.) values for several classifications, percentage occurrence in different substrate types and Whittaker's Index of Association.

3.5.2 *Statistical methods*

Statistical methods used for testing significance of certain (calculated) data are excellently described in several textbooks. The better part of the methods used in this thesis can be found in Elliot (1977b).

Distribution of taxa over different substrate types was expressed as the Index of Representation (I.R.) (Hildrew & Townsend, 1976) (Table 8) and statistical significance was tested with the chi-squared test. Calculation of the I.R. values is based on the null hypothesis (H_0) that a species occurs in all substrate types in equal densities. H_0 is accepted when the difference between observed and expected densities is not enough to yield chi-squared values above the 5% level. H_0 is rejected when chi-squared values are higher than the 5% level in a chi-squared distribution table (e.g. Lindgren & McElrath, 1970, Table II).

When H_0 is rejected, this is an indication of under or over representation in one or more of the substrate types. Positive I.R. values indicate over representation and negative values indicate under representation. However, differences in I.R. values were only considered to be significant when the values deviated 2 or more from zero. Only values outside this range (-2 to +2) were considered to be indicative for aversion or preference, respectively, for certain substrate types. An example of the calculation of the I.R. values and chi-squares is given in Table 8.

Whittaker's (1952) Index of Association was used to calculate the degree of comparibility between substrate types on the basis of species composition. This index is calculated by summarizing the minimum percentages of occurrence of each species in a set of two samples or substrate types:

$$W = \sum_{n=1}^{S} \min\,(a_i,\ b_i),$$

where a_i and b_i are the percentages of occurrence of the i^{th} species in the samples A and B, and S is the number of species occurring in both samples.

Table 8. Example for the calculation of the Index of Representation (I.R.).

	Substrate type			Total
	I	II	III	
Number of samples	20	15	15	50
O = observed number of species i	120	30	0	150
E = expected number of species i	60	45	45	150
I.R. value	7.75	-2.24	-6.71	χ^2 = 110.00

$$\text{I.R.} = (O - E)/\sqrt{E} \quad \text{and} \quad \chi^2 = \sum_{n=1}^{p} (O - E)^2/\,E$$

where E = the total number of species i multiplied by the proportion of the samples in a substrate type in the total set of samples.with p substrate types.

Cluster analyses were carried out with the Clustan 1C program written by Wishart (1975) that is present in the library files of the Computer Centre. I.R. values were used as raw data for several linkage methods to distinguish groups of species with similar preferences or aversions for certain substrate types. Since other methods tested did not lead to other conclusions, the method used for presenting the results is Ward's method of hierarchical linkage using the error sum of squares.

4 Results

4.1 DATA

4.1.1 Field classification of substrate types

For statistical treatment the multitude of possible combinations of the individual substrate characteristics had to be restricted to a maximum of 14 substrate classes. This means that some types distinguished in the field were combined later in order to obtain substrate classes containing enough samples to allow statistical treatment.

Four classification levels were used, with 3 (Sort 3), 5 (Sort 4), 7 (Sort 2) and 14 (Sort 1) substrate classes (Fig. 12), respectively. Appendix 2 gives the number of samples in each substrate class for the Snijdersveerbeek and Appendix 3 those for the Ratumsebeek.

On the first level (Sort 3) samples with mineral substrate were distinguished from samples consisting mainly of organic matter (coarse detritus and/or leaves). Samples classified as organic always contained less than 150 g mineral material and the average dry weight of the organic matter was 21 g per sample. Mineral samples always contained less than 8 g detritus and an average of 900 g mineral substrate.

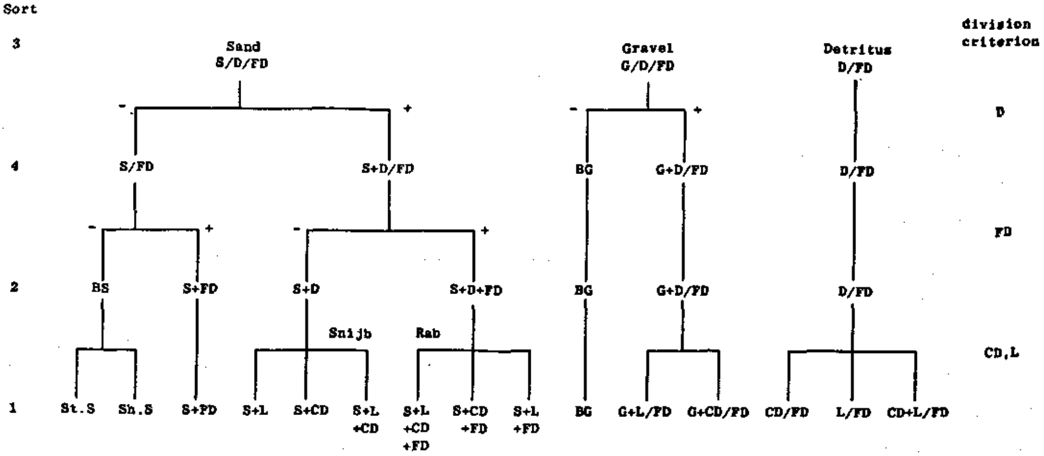


Fig. 12. Substrate types based on the field classification of the substrates at four levels (Sorts 1, 2, 4, 3). S= Sand; G= Gravel; CD= Coarse Detritus; L= Leaves; D= Coarse Detritus and/or Leaves; FD= Fine Detritus; B= Bare; St= Stable; Sh = Shifting; + = with; - = without; / = with or without. S+L+CD occurred only in the Snijdersveerbeek (Snijb). S+L+CD+FD occurred only in the Ratumsebeek (Rab).

Mineral samples were distinguished in Sand and Gravel on the basis of the dominant grain sizes (Subsection 3.1.3). However, to obtain a more objective means to separate sand and gravel substrates, the median particle size determined after dry sieving was used as well. Samples with a negative median phi value ($M_d < 0$, i.e. 50% or more coarser than 1 mm) were reckoned among gravel and samples with a positive median phi value ($M_d > 0$, i.e. 50% or more finer than 1 mm) among sand.

This classification can easily be obtained in the field as well, using a standard comparison system. This is a method to be recommended for future studies, but it was not used in this study because the author learned of it too late. Figure 13 gives the quartile percentage of the samples classified with this method as Gravel or sand. Very little overlap occurs between the first (Q_1) and the third (Q_3) quartile values of Gravel and Sand. The two peaks in each quartile illustrate the correctness of the choice for a median particle size of 1 mm ($M_d = 0$) as the boundary. Comparison of this division with the field code showed that the presence of a relatively small proportion of coarse particles is easily over-estimated because the coarse material is more abundant at the surface of the substrate than deeper in the bottom. These samples were often coded as FG+S, which should have been S+FG. However, such differences are very difficult to quantify in a classification system, emphasizing the need for a parameter to distinguish these substrates.

On the second classification level (Sort 4), the two mineral classes were further divided on the basis of the presence of Coarse Detritus and/or Leaves into Sand or Gravel with or without Coarse Detritus and/or Leaves. Together with the purely organic substrate class of the first level this gives five substrate classes for this classification level.

On the third level (Sort 2), the mineral classes were further divided into classes with and without Fine Detritus, giving seven classes in total, since Gravel substrates combined with Coarse Detritus without Fine Detritus did not occur.

On the fourth level (Sort 1), all classes with detritus were divided into classes with or without Leaves, Coarse Detritus or a combination of both. This is the first level where the organic class is divided. On any of the first three levels a more detailed classification of the detritus samples was not possible since some classes would have contained too few samples.

For the mineral substrates some theoretically possible classes had to be combined to obtain classes large enough to justify statistical treatment. In order to include all species except incidental ones it is necessary to combine at least six samples in each substrate class (Tolkamp, to be published). However, one substrate class in the Snijdersveerbeek (S+L+CD) contained only 3 samples. This class was maintained anyway because it would have obscured preferences of some species for S+L or S+CD, although one should bear in mind that possible over-representation in this three-sample class must be considered critically. In the Ratumsebeek, several classes contained less than six samples, which means that comparison of the results of the two streams should be made on a less detailed level.

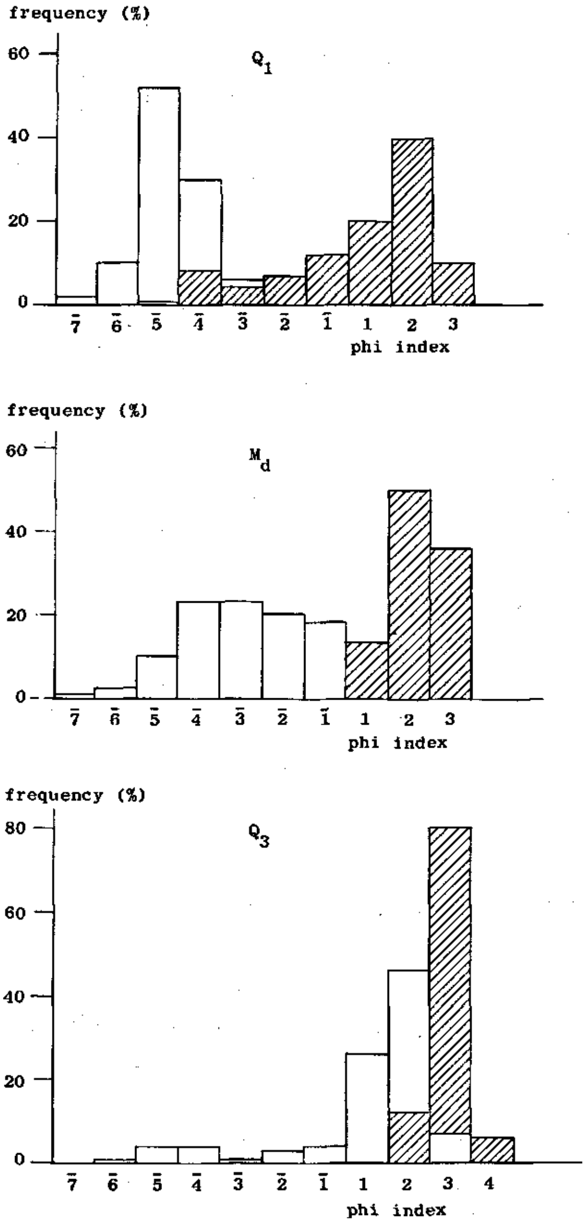


Fig. 13. Frequency distribution of the first (Q_1) quartile , second (median)(M_d) quartile and third (Q_3) quartile over all samples in both streams. Unshaded = Gravel substrates; Shaded = Sand substrates.

Because of the use of the median particle size (phi value) to distinguish Gravel and Sand, the field classifications Fine Sand, Coarse Sand, Fine Gravel and Coarse Gravel, Large and Small Pebbles were not used in the classification presented above. This information will be used again when referring to the preferences of the individual species and when comparing with literature data on the microdistribution of these species.

Silt and lutum substrates only occurred sporadically and were not included in this research. Mud substrates occurred regularly, but these were normally accounted for in the classes S+CD+FD or S+FD. Mostly it concerned a thick suspension of fine sand, coloured brown by the Fine Detritus. Only occasionally were these substrates black and anaerobe, but then no animals were present and the samples were not included in the programme.

Substrates only occurring incidentally (e.g. branches, tree trunks, bricks, kettles, plastic bags, beer tins, aquatic vegetation) were not included in the classification because they could not be sampled with a comparable method. Reference to the presence of certain species on these substrate will be made when discussing the microdistribution of the species involved.

4.1.2 Grain-size classification in the laboratory

4.1.2.1 Substrate composition

The substrate composition of each sample was expressed as the $Q_1M_dQ_3$ index according to Doeglas (1968) (Subsection 3.2.2). The exact 25%, 50% and 75% quartiles are presented in Fig. 14 as the $Q_1M_dQ_3$ graph or substrate-characteristic of the stream for the Snijdersveerbeek, and in Fig. 15 for the Ratumsebeek. The graphs should be read from bottom to top as M_d values are in a 45 degree angle between abcissa and ordinate, while Q_1 and Q_3 are plotted below and above the M_d value, respectively, of the sample. This means Q_1 and Q_3 should be read from the ordinate (y axis), while M_d can be read from both axes.

It is quite obvious that both graphs are similar and that the only difference between the two streams consists of fewer data in the Ratumsebeek, especially on the coarse (left hand) side. It can be concluded from this observation that the two streams can function as each others twin concerning the mineral-substrate composition. To check the reliability of the $Q_1M_dQ_3$ graph as being representative for the substrate composition of the stream, a separate set of 64 samples was taken in the Snijdersveerbeek (covering all sections with 6 (Section 7), 8 (Sections 1, 2 and 3), 10 (Section 5) or 12 (Sections 4 and 6) samples). The resulting $Q_1M_dQ_3$ graph (not presented) fitted exactly over the graph of Fig. 14. It again illustrated the abundance of fine, more-or-less uniform substrates ($M_d > 1$) and the scarceness of coarse substrates, which were found incidentally in the Ratumsebeek and more-or-less restricted to Stations 6 and 8 in the Snijdersveerbeek (the latter was dry at the time of the check). For both graphs it is clear that the largest number of samples was taken in homogeneous, fine substrates, while the other samples are composed of a heterogeneous mixture of coarse and fine particles. Homogeneous coarse substrates were very scarce.

To separate Gravel from Sand samples and Sand from Silt samples Doeglas (1968) drew horizontal lines through phi = $\bar{1}$ and phi = 4, respectively. This is the accepted distinction between Sand and Gravel (Cummins, 1962), where substrates with a median

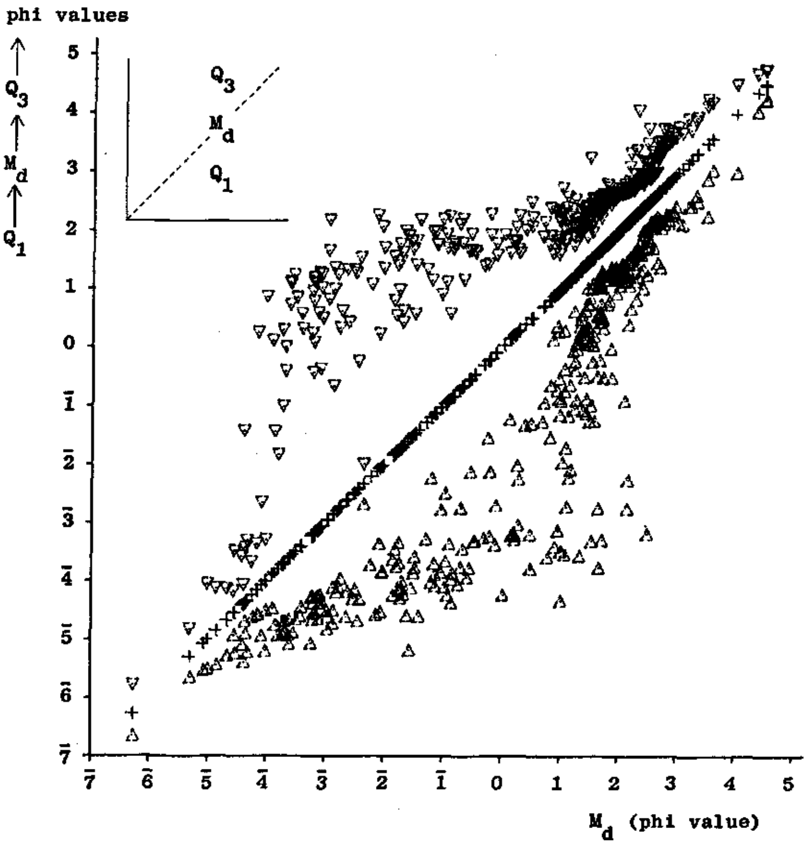


Fig. 14. $Q_1M_dQ_3$ graph for the mineral substrate of the Snijdersveerbeek. The graph should be read from bottom to top because Q_1 and Q_3 are plotted below and above the M_d value, respectively, which is plotted in a 45 degree angle between abcis and ordinate.

particle size larger than 2-4 mm are classified as Gravel. However, the $Q_1M_dQ_3$ graphs illustrate that especially the Sand substrates cover a wide range of grain sizes. The composition of the Sand substrate varies from very well sorted (e.g. 222) to poorly sorted (e.g. $\bar{1}23$) to very poorly sorted (e.g. $\bar{3}12$). Thus the well-sorted sandy substrates can be denominated as pure Sand, while the poorly sorted ones are a combination of Gravel and Sand, with Sand dominating.

4.1.2.2 Substrate types

To distinguish substrate types on the basis of the grain-size analysis and the amount of organic detritus it is necessary to have a reproducible measure. To find such a measure several ratio's between mineral and organic matter were tested. To this end samples with less than 1, 2, 4, 6, 8 or 10% Coarse Detritus and/or Leaves were considered mineral samples. Comparing the classifications with each other, these

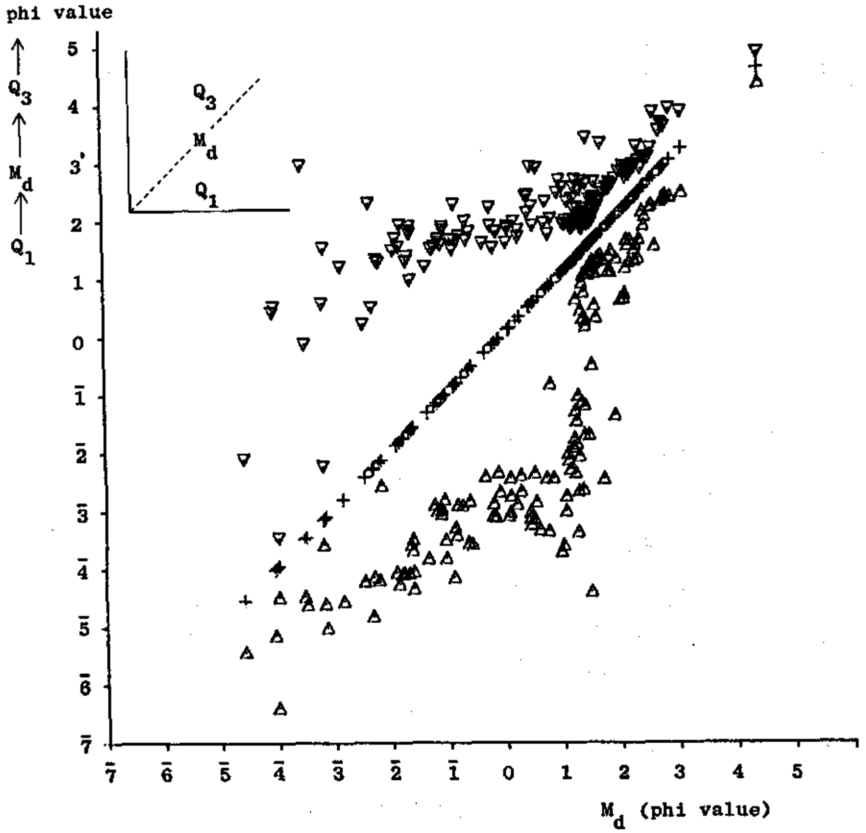


Fig. 15. $Q_1M_dQ_3$ graph for the mineral substrate of the Ratumsebeek. The graph should be read from bottom to top because Q_1 and Q_3 are plotted below and above the M_d value, respectively, which is plotted in a 45 degree angle between abcis and ordinate.

ratio's showed that 2, 4, 6 and 8% added little information to the 1% and 10% division and that this concerned only a limited number of samples. The latter two percentages were maintained, expecting that comparison of the two classifications would yield information about animals preferring a combination of mineral and between 1 and 10% organic material. For animals preferring between 1 and 10% organic material, the preference for organic classes at the 1% level must shift to the 'mineral' classes at the 10% level.

After this separation of the organic samples, the mineral samples were classified in several classifications on the basis of the phi index of the first quartile (Q_1 :Sort 5), the median (M_d : Sort 6) and the third quartile (Q_3 : Sort 7) using the rounded-off quartile values (Doeglas, 1968). Together with the three detritus classes (CD/FD;L/FD;CD+L/FD) this gives 13 classes for Q_1 ($\bar{7}$ to 3), M_d ($\bar{7}$ to 3) and Q_3 ($\bar{6}$ to 4) in the Snijdersveerbeek. Appendix 4 gives the number of samples in each class. In the Ratumsebeek less samples in coarse substrates were taken and 13 classes for Q_1

($\bar{7}$ to 3), 11 for M_d ($\bar{5}$ to 3) and only eight for Q_3 ($\bar{1}$ to 4) could be seen, including the three detritus classes. Appendix 5 presents the number of samples per class.

Several classes in Sort 5 to 7 contained only a few samples. These classes were not combined further since preferences of species with a relatively low abundance but a specific substrate selection could be masked on a less-detailed level by the combination with other, not preferred classes. However, apparent over-representation in these small classes should be considered critically before drawing conclusions regarding preferences.

Finally, a classification was made on the basis of a combination of the three quartiles to include substrate complexity. Arranged from coarse to fine mineral substrates 77 different $Q_1M_dQ_3$ indices were combined in several mineral classes in Sort 8, also using the 1% and 10% organic matter division in the same three organic classes (Appendices 4 and 5).

In Fig. 16 these substrate classes are indicated in the $Q_1M_dQ_3$ graph, while the

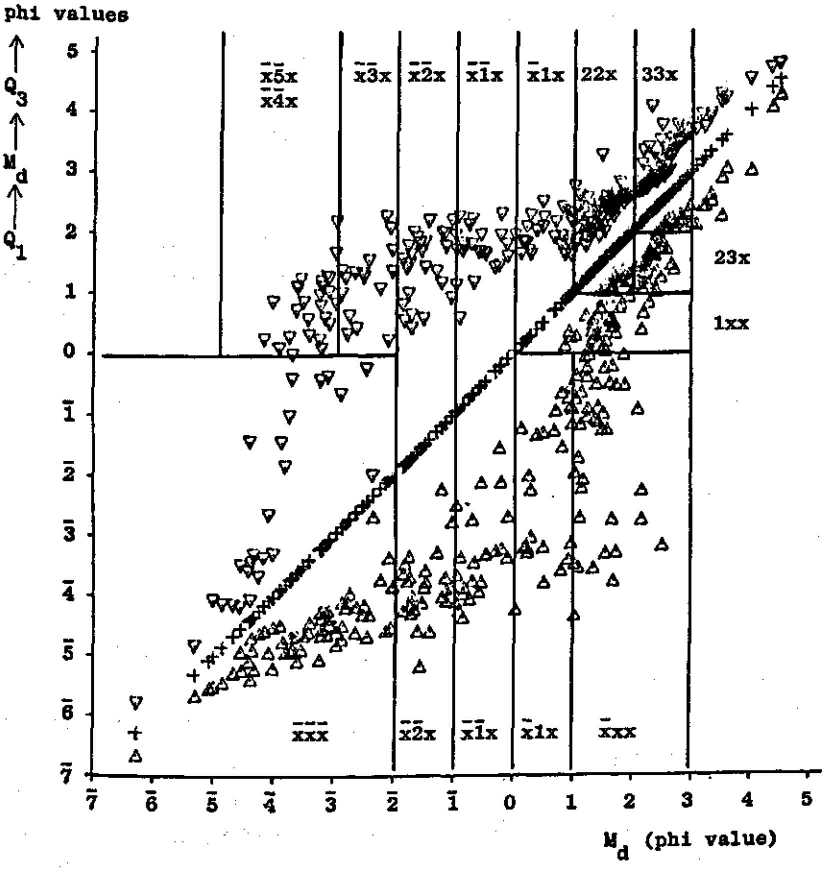


Fig. 16. Substrate classes in Sort 8 projected on the $Q_1M_dQ_3$ graph of the Snijdersveerbeek. xxx indicates the $Q_1M_dQ_3$ index of each substrate class (cf. Appendices 4 and 5).

$Q_1M_dQ_3$ indices for these classes are given in Appendices 4 and 5. However, when more than one Q_1, M_d or Q_3 index occurred in a substrate class in Sort 8, the indices were replaced by an x. One should bear in mind that this x does not mean that all values can be filled in. Only the phi indices occurring in the $Q_1M_dQ_3$ graph and corresponding with the other two quartiles are valid.

Classes 1 and 2 in Sort 8 are the coarsest substrates, characterized by the median (M_d smaller than $\bar{3}$) and first quartile (Q_1 negative and positive for class 1 and 2, respectively). In xxx code this is presented as $\bar{x}\bar{x}\bar{x}$ and $\bar{x}\bar{5}x$ + $\bar{x}\bar{4}x$. In class 2, in fact $\bar{x}\bar{x}x$ should be used, but the one sample that had an M_d index smaller than $\bar{5}$ was a sample consisting of a cobble plus a little bit of sand as part of a detritus substrate.

Classes 3 to 6 are characterized by the median particle size of $\bar{3}$, $\bar{2}$, $\bar{1}$ and 1, combined with all possible negative Q_1 and positive Q_3 indices ($\bar{x}\bar{3}x$, $\bar{x}\bar{2}x$, $\bar{x}\bar{1}x$, $\bar{x}1x$, respectively). Classes 7 and 8 are characterized by a median particle size between 1 and 3. Class 7 has a negative Q_1 ($\bar{x}xx$) while class 8 has a Q_1 between 0 and 1 (1xx). In class 9, Q_1 and M_d phi values are between 1 and 2 (22x). Class 10 contains the 23x substrates. Class 11 contains the 33x substrates.

The right-hand part of the graph with M_d values larger than 3 is formed by the small amounts of mineral matter present in organic substrates and is therefore part of the classes 12 - 14. Comparison of the detritus classes in the field classification with the detritus classes in the grain-size classification using the 10% organic detritus level showed that this concerned the same samples in the Ratumsebeek. This confirms the correctness of the choice of the 10% level. In the Snijdersveerbeek, only small differences were present, especially concerning the Coarse Detritus samples.

Further reference to the 1% and 10% detritus classification will be made by adding 1% and 10%, respectively, to the classification number, e.g. Sort 6, 10% or Sort 8, 1%.

4.1.3 Discussion

4.1.3.1 The use of the Index of Representation compared to other statistical methods

To check the method used to determine substrate preference, i.e. the reliability of the Index of Representation (I.R.) as a tool to assess differences between the animal numbers on different substrates, several methods were studied and used incidentally for comparison of the outcome. Cummins & Lauff (1969) used the probability values of the one-sample Kolmogorov-Smirnof (K-S) test (De Jonge, 1963) for evaluating the results of their experiments in a laboratory stream. This test can also be used on field data, but it is rather time consuming and although it gives the probability values indicating the significance of differences between substrate types, it does not indicate the relative differences in substrate preference, which must be calculated or assessed in another way. Cummins & Lauff (1969) do this graphically, but using their method no information was obtained that contradicted the probability values obtained with the calculation of the chi-squared value, which makes the use of the K-S test rather superfluous. Application of the analysis of variance (Elliot, 1977, p.108) to the frequencies of a species within the substrate classes in a Sort did not give any supplementary information either.

All these methods for the calculation of levels of significance and probability values indicate the same tendency: for most species differences between substrate classes exist at a highly significant level, all indicating a distribution of the negative binomial contagious type.

4.1.3.2 The importance of the joint use of 1% and 10% detritus classifications

Comparing the number of samples in the 1% and 10% detritus classifications (Sort 5-8) in Appendices 4 and 5 shows that in the Snijb 68 samples change from the 3 detritus substrates to the mineral substrates. This happens to 33 samples in the Ratumsebeek. Appendix 6 illustrates which kind of mineral material is combined with 1-10% organic detritus and it is apparent that in both streams this mainly concerns substrates with $Q_1 = 2$, $M_d = 3$ or 2 and $Q_3 = 3$. Only a very small number of samples in coarser substrates contain 1-10% organic detritus (CD). Thus as a general conclusion it can be stated that a preference shift from detritus to mineral substrates or vice versa concerned:

- that they have a preference for mineral substrates combined with 1-10% organic detritus, especially substrates which are well sorted with $Q_1 = 2$ or more.
- that they have a preference for mineral substrates with less than 1% organic detritus; or for organic substrates with more than 10% organic detritus, which concerns only two species in the Ratumsebeek, *Amphinemura standfussi* and *Procladius*, both showing preference for CD and $Q_3 = 4$ in the 1% classification, but for L and CD in the 10% classification.

Only *Gammarus pulex*, *Micropsectra* gr. *praecox* and *Apsectrotanypus trifascipennis* show a shift from CD to substrates with a negative Q_1 (which concerns 16 samples in total), together with a shift to the substrates with $Q_1 \geq 2$. All other species that show differences between the 1% and 10% detritus classifications shift to substrates with $Q_1 = 2$ or 3, $M_d = 2$ or 3 and $Q_3 = 3$. This concerns the following taxa in the Snijdersveerbeek: Oligochaeta, Hydracarina, *Palpomyia*, *Stictochironomus*, *Polypedilum breviantennatum*, *Macropelopia nebulosa* and *Tanytarsus*. In the Ratumsebeek it concerns: Hydracarina, *Amphinemura standfussi*, *Nemoura cinerea*, *Procladius*, *Prodiamesa olivacea*, *Epoicocladius flavens* and *Paratendipes*. Only taxa with more than 100 specimens in one of the streams in the total species list are mentioned.

4.1.3.3 The influence of animal abundance on the Index of Representation

Working with the Index of Representation the question arose whether differences in abundance of a species between seasons or instars would influence the overall substrate preferences measured with the index. *Ephemera danica* was selected as test organism since this mayfly is much more abundant in its earlier instars (like most invertebrates) and also because high densities of rather small individuals were only found in late summer and early autumn.

From Appendix 7 it can be seen that in the Ratumsebeek high densities of *Ephemera danica* are more or less restricted to animals in their first year (< 10 mm) which were especially found in October. Three-hundred and ten of the total of 482 individuals were found in 11 samples, while the remaining 172 animals occurred in 62 samples. Two-hundred and thirty three of these 310 specimens were present in 8 samples in S+D+FD, 46 in 2 samples in S+FD and 31 in 1 sample in BS, illustrating the clear preference of these small nymphs for S+D+FD and S+FD. The sample in BS (no. 142) presented an extra difficulty since the substrate, consisting of Shifting Sand with Fine Detritus, was classified as Sh.S in Sort 2, although the presence of FD was probably more important for *E.danica*. The sample could also have been classified as S+FD.

In the Snijdersveerbeek, never more than 20 individuals of *E.danica* occurred in a sample, yet 183 animals occurred in 13 samples, all but one taken in Section 6. One-hundred and fifty of these 183 were present in 7 samples (Appendix 8). Calculation of the I.R. values for *E.danica* in Sort 2 for both streams, excluding samples containing 10 or more specimens, showed that the highest preference for S+D+FD is maintained in both streams (see Tables 9 and 10). In the Ratumsebeek, however, the small over-representation in S+FD is replaced by one for S+D and BG. In the Snijdersveerbeek, the preference for both G+D and S+D decreases and is replaced by one for BG. This shows that the shift only concerns the secondary preferences in both streams. The high density samples included, the secondary preference is linked with the occurrence of high numbers of smaller specimens in a few samples and low numbers of larger specimens in many samples. Without these high density samples, the secondary preference is linked with low numbers of small and large specimens in a large number of samples.

High densities of (especially) small *Ephemera danica* nymphs do influence the distributional pattern as measured by the Index of Representation. However, no change in the favourite substrate was seen and the only conclusion left from this excercise is that small nymphs tend to occur in higher densities than larger specimens, mainly in the most preferred substrate (S+D+FD) in both streams and to a smaller extent in other substrate types.

Table 9. Numbers of samples and specimens of *Ephemera danica* in the Snijdersveerbeek and the I.R. values before (left) and after (right) exclusion of samples containing more than 10 specimens (high density samples) in Sort 2.

	Substrate type													
	BS		S+FD		S+D		S+D+FD		BG		G+D		D	
Number of samples	87	86	29	28	33	30	53	49	80	79	37	34	63	63
Body length/mm														
0							1	1	1	1	1	1		
0- 5	3	2	7	6	8	1	27	18	10	10	30	7	2	2
5-10	12	9	8	3	12	1	31	13	35	29	21	8	6	6
10-15	21	16	14	8	27	4	48	41	32	31	20	5		
15-20	8	7	1	1	5	1	12	3	8	5	1	1		
20-27	2	1			2	1	4	2	4	4	4	4		
Total	46	35	30	18	54	8	133	78	90	80	75	26	8	8
I.R. value	-5.4	-3.1	-0.5	-0.3	*2.7*	-2.8	*9.3*	*7.7*	-0.1	*3.5*	*5.0*	0.6	-7.5	-5.4

Italic values indicate significant over-representation

Table 10. Numbers of samples and specimens of *Ephemera danica* in the Ratumsebeek and the I.R. values before (left) and after (right) exclusion of samples containing more than 10 specimens (high density samples) in Sort 2.

	Substrate type													
	BS		S+FD		S+D		S+D+FD		BG		G+D		D	
Number of samples	49	47	13	12	9	9	36	28	31	31	10	10	47	47
Body length/mm														
0- 5	50	5	8	4	1	1	126	8	1	1	1	1	4	4
5-10	14	13	20	3	20	20	103	16	20	20	3	3	6	6
10-15	6	6	9	1	5	5	16	10	5	5	6	6		
15-20	8	8	5	4	11	11	14	10	11	11	2	2	1	1
20-27	2	2	1	-	5	5	39	21	5	5			1	1
sub-imago													1	1
Total	80	34	43	12	16	16	298	65	42	42	12	12	13	13
I.R. value	-4.1	-2.2	1.6	-0.2	-1.5	*2.1*	*21.3*	*6.5*	-4.3	1.6	-2.7	0.5	-9.8	-5.2

Italic values indicate significant over-representation

4.1.4 *Grouping of substrate types based on species composition*

Substrates were compared on the basis of the faunal composition of all samples in each substrate type (class) in Sort 8, 10% using Whittaker's Index of Association (see Subsection 3.5.2). A dendrogram was drawn using the Unpaired Pair-Group method using arithmetic averages (UPGMA) (Sneath & Sokol, 1973), presented for the two

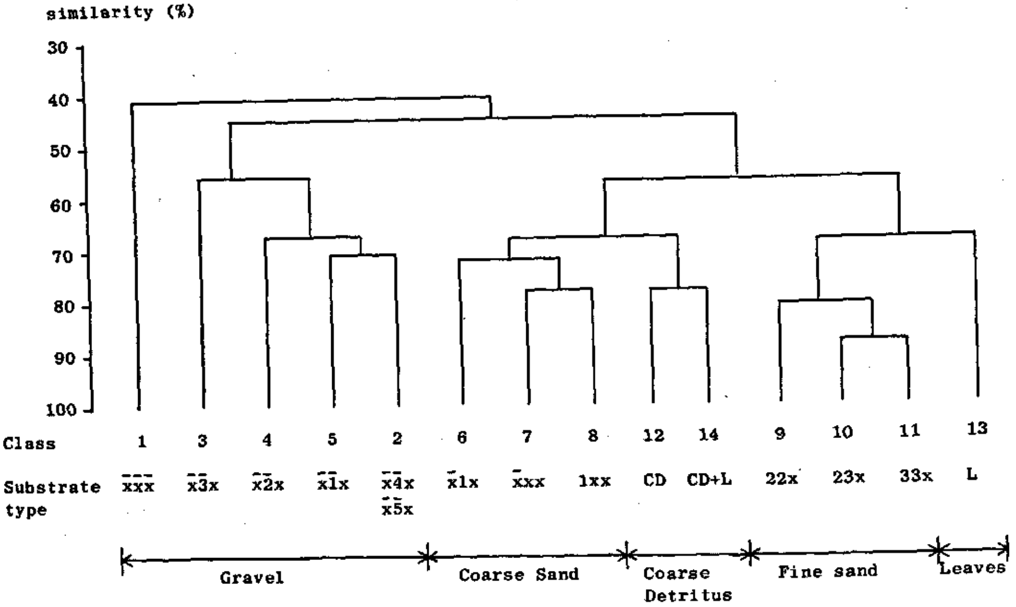


Fig. 17. Dendrogram representing the grouping of substrate types by group averaging in Sort 8,10% in the Snijdersveerbeek, based on Whittaker's Index of Association.

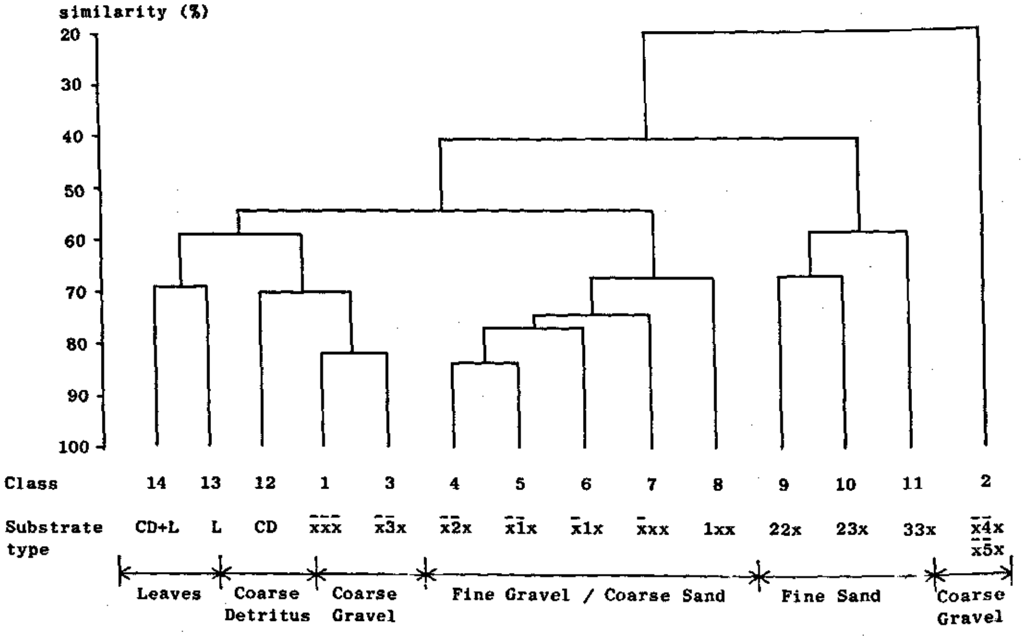


Fig. 18. Dendrogram representing the grouping of substrate types by group averaging in Sort 8,10% in the Ratumsebeek, based on Whittaker's Index of Association.

streams in Figures 17 and 18, respectively. Both figures show that substrates linked by similar faunal compositions are also similar in grain-size composition.

In the Snijdersveerbeek, coarse substrates (Classes 1-5) are least alike, indicating large differences in faunal composition. Leaf substrate (Class 13) is more similar to Fine Sand substrates (Classes 9-11) than Coarse Detritus substrates (Classes 12 and 14). Coarse Detritus substrates have the highest affinity to Coarse Sand substrates (Classes 6-8). However, in the Ratumsebeek a similar grouping occurred with slight differences, which are probably due to the low number of samples in some substrate types (Classes 1, 2, 3, 11, 12, 14) (cf. Appendix 5)

Although the information that can be extracted from this kind of grouping is of restricted significance, it does provide a way of distinguishing main groups of substrates on the basis of animal composition rather than physical parameters. For a similarity of approx. 70% as criterion, an arbitrarily chosen figure, in Fig. 17 for the Snijdersveerbeek only nine of the 14 original substrate types remain, five of which are Gravel substrates. Apparently there are differences between Coarse Sand ($Q_1 \leq 1$) and Fine Sand ($Q_1 \geq 2$) and between Leaves and Coarse Detritus, but not so much within Fine Sand and Coarse Sand substrates.

In the Ratumsebeek (Fig. 18) a more refined distinction within Fine Sand classes is necessary, since 22x, 23x and 33x emerge as separate clusters, while these are combined in one cluster in the Snijdersveerbeek. Also distinction between Coarse and Fine Gravel is needed, as well as the separation of Leaves from other Detritus substrates.

4.1.5 Grouping of species based on substrate preferences

Several methods of grouping (clustering) were applied in order to find taxa with similar substrate preferences. Based on the seven substrate classes in the field classification of Sort 2, seven faunal groups could be distinguished by manually rearranging the sequence of the species on the basis of the I.R. values. These groups are characterized by the main preference(s) of the taxa involved for Gravel (I), Sand (III), Detritus (VII), Gravel Sand (II), Gravel/Detritus (VI), Sand/Detritus (V) and Gravel/ Sand/Detritus (IV). In using Sort 2, emphasis is put on the sand substrates (4 classes). Since sand is the most abundant substrate in both streams, this does represent the actual situation quite well.

Appendix 9 gives the I.R. values for the taxa found with more than 20 specimens or in more than 10 samples in one of the two streams. This concerned 84 taxa, of which 80 occurred in the Snijb and 74 in the Rab. I.R. values indicating over-representation have been printed in italics and these were outlined per group of species within which preferences of the individual species are similar. The number of samples and the number of specimens in each of the streams are also given in Appendix 9. For the taxa showing no significant over-representation on the basis of the chi-squared test, not the I.R. values but the actual numbers have been presented. These taxa are indicated with an arrow after the number of specimens.

Within each faunal group, the taxa have been arranged taxonomically as in Appendix 1. Each taxon was placed in a group on the basis of the Snijdersveerbeek data, except for the taxa not occurring in this stream or present in lower numbers than in the Ratumsebeek (e.g. *Limnephilus lunatus*). This grouping emphasizes the importance of Coarse Detritus and Fine Detritus for the microdistribution of several species in 'mineral' substrates. *Gammarus pulex* is classified to the S/D group because of its over-representation in D and S+D substrates in the Snijdersveerbeek. In the Ratumsebeek the over-representation occurs only in Detritus substrates, indicating the importance of detritus for *Gammarus*.

Most taxa/species with a preference for 'mineral' substrates beside detritus substrates have preferences for Sand or Gravel combined with detritus (S+D, S+D+FD, G+D/FD), again indicating the importance of detritus. On the other hand other taxa seem to avoid detritus substrates and occur mainly in Bare Sand or Bare Gravel, like *Lithax obscurus* and *Pisidium*.

The field classification gives a reasonably reliable picture of the influence of the nature and amount (roughly) of the organic material in a substrate type (especially on the most detailed level, Sort 1 with 14 classes). Sort 1 is only presented in Section 4.2 for some selected species. However, to gain insight in the possible master factor(s) determining the substrate preferences, more objective criteria are needed. Bias due to errors made in the field (only the surface of the substrate is visible) must be minimal. This was already reduced by taking the median value zero as the division between Sand and Gravel, but still the total particle-size variation of the substrates is hardly included in the field classification.

With the aid of Ward's (1963) method of hierarchical linkage, using the error sum of squares, incorporated in the Clustan 1C program (Wishart, 1975), taxa occurring with more than 20 specimens were grouped on the basis of the I.R. values in the grain-size classification of Sorts 6 and 8 (10%) and the field classification of Sort 2. Comparison of the results of these groupings showed that the general trend is the same for all classifications but that differences do occur. Sneath & Sokol (1973, p. 204) already discussed the fact that Ward's method may divide dense clusters in an unacceptable manner. In the material of this investigation the division of the clusters was not unacceptable, but it did happen that some points in a certain cluster were nearer the centroid of another cluster than to the centroid of their own cluster. This especially concerned the taxa with very low or very high numbers of specimens giving rather deviatiant I.R. values. However, other linkage methods did not show more acceptable groupings and Ward's method was retained, but only as a means of grouping taxa with similar preferences to create a starting point for the presentation.

Sort 8, 10% was selected to represent all Sorts 5-8, because it includes the total particle-size variation of the substrate. It is a more integrated method than Sort 5-7. The 10% limit for the organic matter was chosen because it gives a well defined distinction between organic and mineral substrates, enabling comparisons with

Sort 1-4. It was necessary to distinguish at least 14 clusters to gain insight into the factors causing the grouping.

Initially, all taxa occurring with more than 20 specimens were used for the grouping. This concerned 72 taxa in the Snijdersveerbeek and 51 in the Ratumsebeek. The results are presented in dendrograms (Appendices 10 and 11). In these dendrograms letter codes for Gravel (G), Sand (S) and Detritus (D) have been inserted afterwards on the basis of analysis of the main over-representation of the species within each cluster.

After careful analysis of the basic data used for the clustering (the I.R. values of each species) it became clear that most species were grouped together on the basis of corresponding positive I.R. values (over-representation or preference) but that some of the species occurring in very low numbers were classified on the basis of similar negative or close-to-zero I.R. values, thus influencing the ultimate average I.R. values. In order to reduce the influence of these less abundant taxa, the basis for the following chapters was laid by using only the taxa occurring with 100 or more specimens in total. This reduced the list to 48 taxa, 43 of which occurred in the Snijb in this abundance and 26 in the Rab. As illustrated with the average I.R. values for each cluster (Tables 11 and 12), three main groups can be distinguished, consisting of clusters composed of species with preference for Gravel substrates (Classes 1-6 in Sort 8, 10%), Sand substrates (Classes 7-11) and Organic substrates (Classes 12-14).

Comparison of the two dendrograms (Figs. 19 and 20) illustrating the grouping of the species on the basis of these average I.R. values in the two streams shows that species belonging to one of the two main detritus clusters in the Snijdersveerbeek (Fig. 19, Cluster 6+7+4 and 3+8+12+14) are also grouped in one of the four main detritus clusters in the Ratumsebeek (Fig. 20, Cluster 14, 3+6+11+9, 4+13 and 2).

The species in the Sand and Gravel clusters in the Ratumsebeek (Fig. 20, Clusters 1+12+5+10 and Clusters 7+8, respectively) also occur in these clusters in the Snijdersveerbeek (Fig. 19, Cluster 11+1+9+5 resp. 2+13+10). Only two species show a difference between the streams in their main grouping: *Baetis vernus* (Taxa no. 50) and *Micropterna sequax* (taxa no. 128). Both species are grouped with the Sand species in the Snijdersveerbeek (Fig. 19) and with the Detritus species in the Ratumsebeek (Fig. 20). Considering the I.R. values for these species in the substrate types in Sort 8, 10% (Appendices 12 and 13), it can be seen that *Baetis* occurred in Gravel and Sand in the Snijb (Appendix 12) but in Detritus and Gravel in the Rab (Appendix 13), suggesting that Gravel might be the more important substrate for *Baetis vernus*.

M. sequax is grouped with the species preferring Sand substrates in the Snijb, although it is over-represented in Gravel and Detritus substrates (Appendix 12). In the Rab it showed preference in Detritus substrates (Appendix 13), indicating Detritus as the favourite substrate type.

In Appendices 12 and 13, the I.R. values for all more abundant taxa are presented and the I.R. values indicating over-representation have been outlined in the same way

Table 11. The average positive I.R. values for each cluster in Sort 8,10% for the Snijdersveerbeek.

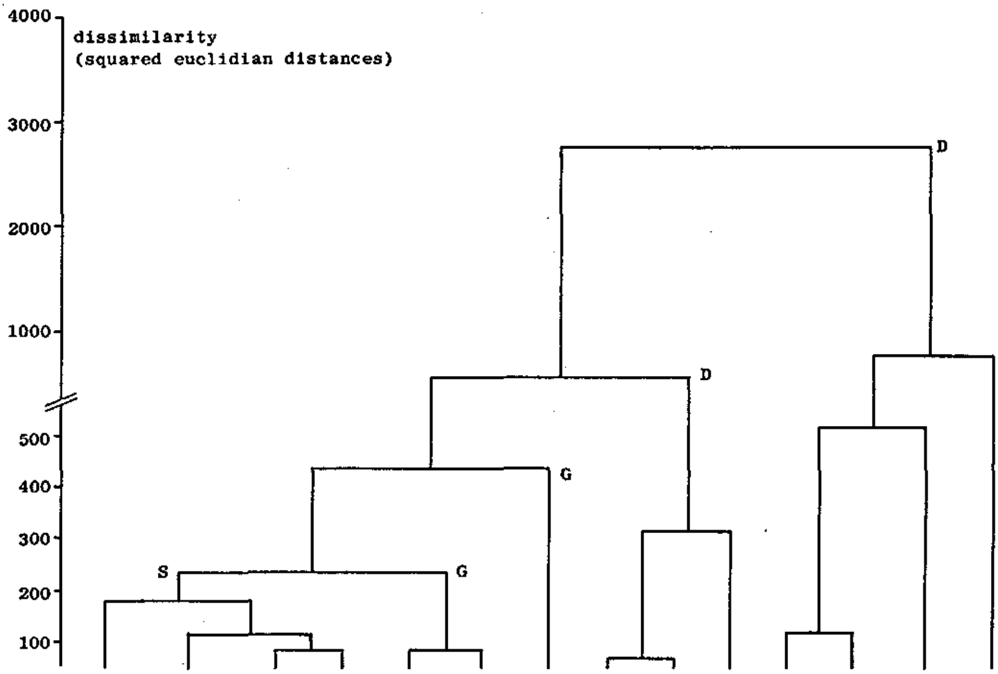
Cluster no.	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	Gravel						Sand					Detritus		
	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
2	7.8	5.4	3.8	6.2	5.7	1.6								
10			51.9	2.2	1.8									
13				11.6	14.5	10.5								16.1
5		9.0			1.4		4.7			10.0				
9							26.1							
1					0.3		0.5		3.4	2.5	2.6			
11									7.2	19.4	14.8	2.7		
14										29.5	30.1	25.8	88.6	4.5
3							12.9					55.3	32.0	35.5
7		0.4	0.0				0.5					26.1	1.9	
4												5.9	27.4	3.3
12												19.8	63.4	
8												54.3	18.4	18.9
6												12.4	7.7	1.4

See Fig. 19 for taxa in each cluster.
Boxes indicate groups of taxa with similar substrate preferences.

the clusters in the Tables 11 and 12 were outlined. The taxa are arranged in the same sequence as the clusters in Tables 11 and 12. For some species (*Habrophlebia fusca*, taxa no. 48; *Agapetus fuscipes*, taxa no. 103; *Limnius volckmari*, taxa no. 186; *Epoicocladius flavens*, taxa no. 283; *Paratendipes*, taxa no. 302) comparison between the two streams is not possible, because these species occurred in too small numbers in the Snijb. The same applies for 22 other taxa not abundant enough or absent in the Rab.

Gravel substrates (Classes 1-6 in Sort 8, 10% in Appendices 12 and 13) are preferred by, for example, the caddis flies *Lithax obscurus* and *Agapetus fuscipes*, the riffle beetles *Elmis aenea* and *Limnius volckmari* and the midge larvae *Orthocladius* sp. and *Chaetocladius* sp. The latter species is also over-represented in Detritus substrates (Class 14). Sand (Classes 7-11 in Sort 8, 10% in Appendices 12 and 13) as the preferred substrate is only inhabited by a few species, e.g. the midges *Prodiamesa olivacea, Polypedilum breviantennatum. Procladius* sp. and *Stictochironomus* sp., the Diptera *Ptychoptera* and *Palpomyia*, water mites (Hydracarina), Oligochaeta and the mollusc *Pisidium*.

Many of the species clustered to the Sand group show over-representation in Sand substrates. However, their preference may in fact be for a Gravel or Detritus substrate, e.g. the caddis flies *Sericostoma personatum* and *Micropterna sequax*, which seem to prefer Gravel and Detritus substrates in the Snijb. (Appendix 12). In the Rab



Cluster no.	11	1	9	5	2	13	10	6	7	4	3	8	12	14
Taxa no.	271 311	11 217 38 241 47 248 109 249 128 256 198 308 205 341	264	50 245 290	18 105 185	280	168	100 155 254 318	127 220 293	40 42 269 272 275 310	32	190	277 279	287

Fig. 19. Dendrogram representing the grouping of the 43 most abundant taxa (100 specimens or more) in the Snijdersveerbeek in Sort 8,10%, based on the similarity of I.R. values. Cluster numbers correspond with those in Table 11. Taxa numbers refer to the numbers in Appendices 1 and 12. The letters S (Sand), G (Gravel) and D (Detritus) indicate the main preferences of the taxa in the clusters below. They were added after analysis of the basic data in Appendix 12.

M.sequax prefers Detritus substrates (Appendix 13).

From the I.R. values of each individual species it becomes clear that in both streams Cluster 1 contains many species that are over-represented in both Sand and Gravel substrates, but that they are clustered in the Sand group on the basis of the average I.R. values (Tables 11 and 12). Working with averages small differences soon disappear, and because positive as well as negative I.R. values occur in Gravel substrates, the average approaches zero. Before drawing any conlusions on the basis of the average values, one should reconsider the original data. Species preferring both Sand and Gravel substrates are e.g. the mayfly *Ephemera danica* and the Diptera *Limnophila* sp. and *Dicranota* sp. Comparison of the data from the Snijb (Appendix 12) with that from the Rab (Appendix 13) shows that species preferring Sand and Gravel

Table 12. The average positive I.R. values for each cluster in Sort 8,10% for the Ratumsebeek.

Cluster no.	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	Gravel						Sand					Detritus		
	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
7		9.9	1.3	0.4	10.8	10.2								
8	6.0	1.5	4.0	5.6	10.3	2.3	0.9					1.8		
10				0.8	0.2		3.8	0.4	6.1					
5						1.3	12.2			6.6	10.9			
1							0.4		3.5	12.1				2.3
12									17.3	5.3	6.0			
6	0.6		4.1		0.2								9.6	
4		17.3											53.7	
3								1.2				0.6	17.4	11.3
9								0.8				17.6	14.6	1.2
14	1.6									0.9	2.3	65.0		26.9
2	3.2											160.5	49.2	22.6
11												0.7	26.1	
13													53.2	13.4

See Fig. 20 for taxa in each cluster.
Boxes indicate groups of taxa with similar substrate preferences.

substrates in the Snijb are also clustered together in the Rab (Cluster 1 in both streams). In the Rab, the preference for Gravel is much less pronounced, however. These phenomena will be discussed in detail when dealing with the individual species (Section 4.2).

Detritus substrates (Classes 12-14 in Sort 8, 10% in Appendices 12 and 13) are preferred by the largest group of species, e.g. the fresh water shrimp *Gammarus pulex*, two stonefly species, *Nemoura cinerea* and *Amphinemura standfussi*, the caddis fly *Chaetopteryx villosa*, the net spinning caddis *Plectrocnemia conspersa*, the beetle larva *Helodes* sp. and many Chironomidae, e.g. *Brillia modesta, Eukiefferiella* gr. *discoloripes* and *Diplocladius cultriger*. Separate groups are formed by some individual species, such as *Micropsectra* gr. *praecox*. This Tanytarsini is strongly over-represented in Fine Sand and Detritus substrates in the Snijb, while it prefers Detritus substrates in the Rab.

Nemoura cinerea obviously prefers Detritus substrates in both streams, as mentioned before, but in the Rab, Gravel is also favoured, a phenomenon seen in the Snijb for *Amphinemura standfussi*. *Baetis vernus, Macropelopia nebulosa* and *Tanytarsus* sp. are over-represented in Gravel and Sand substrates in the Snijb (Appendix 12). *Baetis* prefers Gravel in the Snijb. In the Rab it prefers Detritus substrates, but it is also over-represented on Gravel (Appendix 13). *Macropelopia nebulosa* and *Tanytarsus* sp. are fairly evenly distributed over the substrate types in Sort 8, 10%,

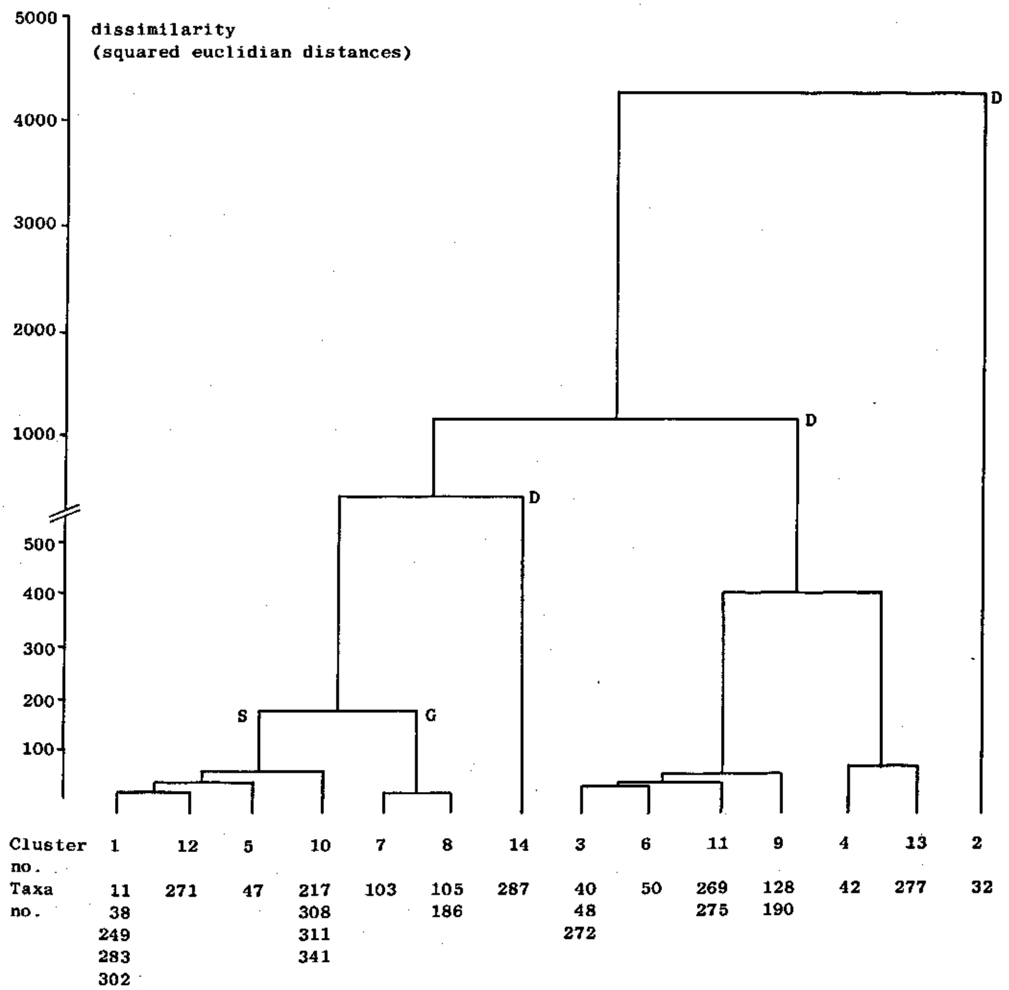


Fig. 20. Dendrogram representing the grouping of the 26 most abundant taxa (100 specimens or more) in the Ratumsebeek in Sort 8,10%, based on the similarity of I.R. values. Cluster numbers correspond with those in Table 12. Taxa numbers refer to the numbers in Appendices 1 and 13. The letters S (Sand), G (Gravel) and D (Detritus) indicate the main preferences of the taxa in the clusters below. They were added after analysis of the basic data in Appendix 13.

although the former prefers Coarse Gravel (Class 7) and the latter Fine Sand (Class 10).

These and other differences in species preferences between the two streams will be discussed in detail in Section 4.2., where 26 of the 48 taxa presented in Appendices 12 and 13, are dealt with. Comparison of the main groups of species having similar substrate preferences in the grain-size classification in the laboratory in Sort 8, 10% (Appendices 12 and 13) with these groups in the field classification in Sort 2 (Appendix 9) leads to the conclusion that main preferences can be adequately described on the basis of the field classification. However, detailed data on the microdistribution can only be obtained with the aid of a thorough grain-size classification, including the amount of combined organic detritus.

4.1.6 Numbers of species and specimens in different substrate types

Some general conclusions can be drawn when considering numbers of species in each taxonomical unit (Table 13), together with their average abundance (Table 14). From both tables Chironomidae emerge as the most abundant group in number of species as well as in number of specimens, but distinct differences in abundance in the various substrate types are present. Detritus substrates are inhabited by the largest numbers of animals, predominantly composed of Tanytarsini (*M.* gr. *praecox*), *Gammarus pulex* (included in Others), Orthocladiinae (several species) and Coleoptera (*Helodes* larvae). Then follow S+D+FD, S+D and S+FD in this sequence, where Tanytarsini (*M.* gr. *praecox*), *G. pulex*, Chironomini and Orthocladiinae predominate. G+D/FD comes next with Tanytarsini, Orthocladiinae and *G.pulex*. Finally the bare mineral substrates BS and BG show the smallest population densities. In BS, Tanytarsini and *G.pulex* are still rather dominant, but in BG the numbers of specimens are fairly equally distributed over the various taxonomic groups. Chironomini occur in equally high numbers in Sand substrates combined with Detritus, while Orthocladiinae are more abundant in Gravel substrates with Detritus and Pure Detritus substrates. Tanypodinae and Tanytarsini are least present in BS and BG. Diptera are rather evenly distributed while Coleoptera are abundant in Gravel and Detritus substrates. Considering the number of species found in each substrate type, the differences between most groups are minimal. Only Coleoptera and Trichoptera occur with more species in Gravel, Detritus and Bare Sand substrates. However, since the number of samples is different for the various substrate classes, absolute comparison is not possible, although major changes are not likely.

Table 13. Number of species for the main taxonomical groups in the substrates distinguished in Sort 2 in the Snijdersveerbeek.

	BS	S+FD	S+D	S+D+FD	BG	G+D/FD	D/FD
Chironomini	13	14	18	21	19	18	17
Orthocladiinae	10	9	13	13	14	12	15
Tanypodinae	4	4	5	6	5	5	6
Tanytarsini	4	5	5	6	8	7	6
Other Diptera	13	8	10	13	16	13	14
Coleoptera	15	7	5	6	18	18	16
Ephemeroptera	2	2	2	2	2	2	2
Plecoptera	2	1	2	1	2	2	2
Trichoptera	17	5	8	10	14	16	18
Mollusca	1	2	3	1	3	3	2
Oligochaeta	2	1	2	3	2	2	2
Others	7	7	4	6	7	6	6
Total	86	60	72	82	102	97	100
Number of samples	87	29	33	53	80	37	63

Although these differences in animal numbers in the 7 substrate types in Sort 2 are illustrated for the Snijdersveerbeek in Table 14, comparison of the total number of animals per substrate class through I.R. values leads to the same conclusions and the same sequence of abundances in both streams (cf. Tables 77 and 78). Of course the height of the I.R. value cannot be taken as a precise measure, but the general trend is significant. The number of animals is lower when the I.R. value is lower (more negative).

In a study of a small woodland stream in Canada, Mackay (1969) distinguished Sand, Gravel, Stones, Leaves and Leaf-Detritus as substrate types and she found that the diversity and the number of animals increased from sand, through gravel and stones to leaves and detritus. She also demonstrated that although leaf and detritus substrates were richest in species and numbers they are predominantly inhabited by Diptera and that gravel and stony substrates house more Plecoptera, Ephemeroptera, Trichoptera and Coleoptera. In general, differences in numbers of species and numbers of animals follow the same trend, showing an increase from sand through gravel to detritus (Pennak & van Gerpen, 1947; Ward, 1975; Walton, Reice & Andrews, 1977). However, this is not always in the same sequence, especially in streams where stony substrates are scarce or coarse substrates always consist of a mixture of stones, gravel, sand and detritus, forming very complex substrates. In these streams one may find another sequence or differences in the sequence between the number of animals and their biomass (Mackay & Kalff, 1969).

In lowland streams, substrates are also very complex, consisting predominantly of sand and detritus, occasionally mixed with gravel and/or pebbles. Although no estimations of animal biomass were made, the numbers of animals increase from Bare Sand and Bare Gravel through Sand with Detritus to Leaves and Detritus substrates. The reasons for the occurrence of exceptionally low numbers of animals on gravel substrates, compared to many foreign streams, is probably that the bare gravel substrates are mostly situated in the most unstable zones of the stream bed, while the

Table 14. Average number of specimens in 10 samples in the substrates distinguished in Sort 2 in the Snijdersveerbeek.

	BS	S+FD	S+D	S+D+FD	BG	G+D/FD	D/FD
Chironomini	65	140	136	126	41	56	125
Orthocladiinae	15	28	125	138	63	302	466
Tanypodinae	2	48	28	63	6	49	32
Tanytarsini	114	831	428	1315	39	542	1144
Other Diptera	37	57	48	52	38	31	72
Coleoptera	7	5	20	11	28	61	154
Ephemeroptera	10	15	33	26	26	24	1
Plecoptera	2	-	2	-	17	4	61
Trichoptera	37	16	46	21	57	56	74
Mollusca	11	14	4	6	4	3	3
Oligochaeta	10	17	24	18	32	25	5
Others	144	252	792	276	55	152	693
Total	455	1424	1686	2052	407	1304	2820

area consisting of this kind of substrate is relatively small and sand and silt transport (scouring) high.

Cordone & Kelley (1961) reviewed some of the older papers on the differences in production and standing crop of sand compared to mud, detritus, gravel, rubble and vegetation. Sand appeared to be lowest in production and standing crop, while rubble together with organically enriched mud showed the highest production. These findings are confirmed by a large number of more recent papers (Maitland, 1964; Mackay, 1969; Pennak, 1971; Nuttall, 1972; Ward, 1975; Russev, 1977; Petran, 1977; Resh, 1977). Chutter (1969a) discussed the effect of sand and silt transport on macroinvertebrates and concluded that they cause considerable changes in the fauna. Increases in the amount of silt and sand increase the instability of the river bed, which adversely affects the fauna (Mackay & Kalff, 1969).

4.1.7 Field experiments

4.1.7.1 Trays filled with artificial substrate

For statistical analysis of the number of animals and the species caught in each substrate tray and comparison of the colonization of the grain sizes, only the data of the 14 and 28 days colonization period can be used. In table 15, the I.R. values for the more abundant taxa after 14 days are given. Tabel 16 gives these data after 28 days. This concerned 7 and 10 species, respectively, with 5 of them abundant after both periods; *G.pulex*, *M.* gr. *praecox*, *C.melanops*, *E.octoculata* and *H.fusca*. Only *E.octoculata* show a distinct difference between the two periods, which is not very surprising since these leeches were mostly found on the inside of the trays itself and not on the substrate. The leeches were also abundantly present on the outside of the trays, but these were discarded. *Habrophlebia fusca* showed preference for the coarser particle sizes after both periods. *Gammarus pulex* also displayed a clear preference for coarse grain sizes, while *Conchapelopia melanops* preferred 4 and 2 mm grain sizes after both periods. *M.* gr. *praecox* was significantly abundant in 8 and 4

Table 15. Number of specimens (N) and I.R. values for the most abundant species in substrate trays after 14 days of colonization in the Ratumsebeek.

	N	Particle size (lower limit)/mm				
		32	16	8	4	2
Gammarus pulex	2034	*3.6*	*9.7*	-1.2	0.1	-12.2
Habrophlebia fusca	183	*2.9*	*2.2*	1.1	-0.4	-5.7
Baetis vernus	89	-3.0	-2.3	-3.7	*7.2*	1.9
Amphinemura standfussi	130	-2.9	-0.2	0.2	*6.1*	-3.1
Erpobdella octoculata	15	-1.2	-1.7	0.6	1.7	0.6
Conchapelopia melanops	97	-4.2	-4.0	-4.0	*6.3*	*5.8*
Micropsectra gr. *praecox*	15	0.6	0.6	0.0	0.0	0.0

Italic values indicate significant over-representation

Table 16. Number of specimens (N) and I.R. values for the most abundant species in substrate trays after 28 days of colonization in the Ratumsebeek.

	N	Particle size (lower limit)/mm								
		32	16	8	4	2	1	0.5	0.25	0.125
Gammarus pulex	5230	*6.0*	*23.6*	*48.9*	*33.3*	-16.3	-24.0	-24.0	-23.7	-23.8
Micropsectra gr. *praecox*	136	-3.6	-0.0	*3.8*	*8.7*	1.5	-0.0	-3.4	-3.6	-3.4
Prodiamesa olivacea	108	-3.5	-2.6	1.7	*13.6*	0.0	-2.3	-2.3	-2.9	-1.7
Macropelopia nebulosa	53	-2.4	-2.4	-2.4	*7.5*	*3.8*	0.8	-0.4	-1.6	-1.2
Chaetopteryx villosa	42	*6.2*	0.6	-2.2	0.2	-1.2	-1.2	-2.2	0.2	-0.3
Erpobdella octoculata	27	*3.5*	0.6	0.6	0.0	-1.2	0.0	0.0	-1.7	-1.7
Dicranota sp.	26	-1.7	-1.1	-1.7	-1.7	-1.7	1.2	*5.4*	*3.0*	-1.7
Conchapelopia melanops	23	-1.6	-1.6	-0.4	*2.2*	*5.9*	-0.4	-1.0	-1.6	-1.6
Polypedilum brevianten.	23	-1.6	-1.6	0.3	0.9	*2.2*	0.3	-1.6	-1.6	*2.8*
Habrophlebia fusca	18	1.4	-0.7	*3.5*	*2.8*	-1.4	-1.4	-1.4	-1.4	-1.4

Italic values indicate significant over-representation

mm substrates after 28 days, although showed no preference after 14 days.

Comparing these data with the distribution shown in Appendix 13 for the natural substrates of the stream as determined with the shovel samples, agreement is seen for some species and disagreement for others. It will be demonstrated in Subsection 4.2.2 that this phenomenon can at least partly be explained by the absence of organic matter, especially the absence of detritus in the four finer substrates, which collect less drifting detritus than the coarser particle sizes. These four substrates are probably best comparable to unstable sand substrates, which are not rich enough in fine and coarse detritus to support large populations of animals with a preference for these grain sizes under natural conditions, when more organic material is present in combination with these particle sizes. Moreover, the trays were all exposed to the same current velocity, which may also cause artificial results.

4.4.2 Particle sizes introduced without trays

Only one experiment of this nature was performed. Unfortunately a spate occurred during the experimental period, washing the finer substrates away and covering the coarser ones with much fine material. Although the substrates were sampled after the set period, analysis of the grain sizes of the samples showed that a considerable change in particle-size composition had taken place. The populations of the substrates showed much more resemblance to that of the mineral substrates in the stream than any of the substrate trays, but the experiment was considered unsuccessful because the basic conditions had changed too much. However, the impression persisted that experiments of this kind should be given priority over those with experimental trays.

4.2 ORGANISM-SUBSTRATE RELATIONSHIPS

4.2.1 Outline of presentation

Several species apparently display a similar distributional pattern, differing from that of other species or groups of species. (Subsections 4.1.4 and 4.1.5). To test the hypotheses stated in Section 1.3 it is not necessary to deal in detail with all the species listed in Appendices 9, 12 and 13. Therefore a selection of species, representative for the various distributional patterns will be discussed in detail to illustrate the different substrate preferences. Emphasis will be put on the taxa found in numbers large enough to justify statistical treatment, especially those with more than 100 specimens present in the total series of samples in one of the streams (Subsection 4.1.5). This concerned 48 taxa and from these taxa representatives for each distributional pattern were chosen on the basis of criteria aimed at finding species within each taxonomic unit (family or sub-family) that demonstrate the different mechanisms (either direct, such as burrowing, clinging, hiding, building, or indirect, such as oxygen content, current velocity, light intensity or food conditions) resulting in substrate selection.

Not all species/taxa were treated with the same degree of detail because of lack of sufficient background data or because they were only identified to a low taxonomic level. Except for a few species - those more numerous in the Ratumsebeek or restricted to that stream - the data from the Snijdersveerbeek will be used as a starting point. This concerns more samples and yields more statistically valid results. The data from the Ratumsebeek will function as a check on the validity of those results in a stream of larger dimensions. Attempts will be made to explain possible differences in substrate preferences of (groups of) species between the two streams.

In the following chapters, which deal with the 26 selected taxa, the analysis of the results of the field study (microdistribution) will be emphasized. When available the subsection on microdistribution will be preceded by data on the life cycle and followed by data on case-building and substrate-selection experiments. Thus the following subsections can be expected: life cycle, microdistribution, case-building and substrate-selection experiments. For some species an introduction on identification or population density will be given first.

Life cycle Animal growth in the two streams studied is presented in a histogram, summarizing body length in 1-mm classes as percentage per four week periods (e.g. Fig. 21). In these histograms the data of both streams are presented together. Up to 1977, this concerns Snijdersveerbeek data only, and after Week 15 in 1977 Ratumsebeek data only. In the first 15 weeks of 1977 data from both streams were pooled, but not before comparison of the body-length distribution over the length classes in the two streams had shown that there were no significant differences in body-length composition of the two populations. The data on animal growth will be compared with data from the literature on the life cycle of the species concerned, or related species.

Microdistribution I.R. values for the substrate types of the four levels of field classification (Sort 1 - 4) will be presented in a dendrogram-like table (e.g. Table 26) comparable to Fig. 12, where the names of the substrate types are given. At the top of these tables the substrate types in Sort 3 are indicated, Sand (S), Gravel (G) and Detritus (D), while at the bottom of each table the types in Sort 1 are abbreviated (see Outline of substrate classification, page after contents): Stable (St) Sand, Shifting (Sh) Sand, Sand + Fine Detritus (FD), Sand + Leaves (L), Sand + Coarse Detritus (CD), Bare (B) Gravel, or other combinations using the same abbreviations. These tables can be compared to Appendix 2 or 3, where the numbers of samples in each substrate type are given.

I.R. values for the substrate types in the grain-size classification in the laboratory are presented for both levels of organic detritus (1% and 10%; see Subsection 4.1.2.2) in Sort 5 - 8 (e.g. Tables 37 and 38). When no differences in substrate preference between these two levels were observed, only the 10% level is presented (e.g Tables 19 and 20). For several taxa, a table is included giving the I.R. values for different animal length classes in Sort 8, 10% (e.g. Table 21A), and the I.R. values per season (e.g. Table 21B). Week numbers corresponding with the seasons can be found in Table 2.

A discussion of these results will follow in the light of data from the literature on life cycle, food habits and habitat preferences.

Case building For the case-building Trichoptera, data on the grain-size composition of the natural case (e.g. Fig. 22) will be presented. When applicable, data on case-building experiments will be discussed only briefly, because these will be published in full detail on a later date (Tolkamp & Verdonschot, to be published). The grain-size composition (or mineral and organic composition) of these cases will be compared with the grain-size and organic composition of the preferred substrate types.

Substrate-selection experiments For the species subjected to substrate-selection experiments in the laboratory stream (see Subsection 3.3.1.4), the results of these experiments will be given in histograms (e.g. Fig. 25) and compared with the results obtained in the field. In these figures the grain-size fractions are indicated by the lower limit of the fractions. Grain sizes smaller than 1 mm are expressed in micrometre sizes, larger grains are expressed in millimetre sizes (e.g. 125 stands for the 0.125 - 0.250 mm fraction; 2 stands for the 2 - 4 mm fraction).

For some species, the selection of grain-size fractions in field experiments will be discussed, comparing the results with those of the field study and data from the literature when available.

4.2.2 *Autecological data for selected species*

4.2.2.1 Lithax obscurus (Hagen) (Trichoptera: Goeridae)

Life cycle The life cycle of *Lithax obscurus* in both the Snijdersveerbeek and the Ratumsebeek is summarized in Fig. 21. Data from 1977 are mainly from the Rab and earlier data are mainly from the Snijb. In both streams pupae are present from the beginning of December to August/September, with a peak in April/May, which agrees with the May/June flight period as reported by Beyer (1932) and Tobias (1967). However, the extended presence of pupae to the end of summer points to a longer flight period. Illies (1952) found that *Lithax niger* emerged from early April till the end of May, and also from early July to mid-August. Since adults were not collected systematically, but only incidentally in both streams, these emergence data can only be compared on the basis of the pupae.

The F-2 (2.2 - 4.5 mm body length), F-1 (3.4 - 6.7 mm) and F (4.8 - 9.5 mm) instar larvae occur all year round, with a peak in August for the F-2 and F-1 instars and in November/December for the F (final) instar. *Lithax* overwinters mainly in the final instar or as a pupa, but partly also in earlier instars. However, these are only the most pronounced points in the life cycle, which is strongly dispersed over the whole year because of the long flight period and dispersed egg hatching. Another reason might be that larvae that hatch early in the year grow faster than larvae that hatch late in autumn, because of more favourable food conditions (periphyton, fine detritus).

Microdistribution This member of the Goeridae family occurred in both streams mainly in coarse substrates (BG, St.S and G+CD, Tables 17 and 18), although over-representation is also seen on CD in the Rab. This over-representation is probably caused by food scarcity, since *Lithax* was only found in CD in summer, when the amount of detritus in the middle of the stream (where most of the coarse substrates occur) is low. This is also true of periphyton production, because of the heavy shading of the stream bed by the bank vegetation. *Lithax* is a caddis, with feeding habits quite similar to various Limnephilidae species and the Glossosomatidae (Grenier et al. 1969), feeding on detritus and diatoms. As Castro (1975) and Douglas (1958) showed for *Agapetus fuscipes*, the consumption of each food type varies with its relative abundance.

The over-representation in St.S in Sort 1 is present in both streams, but in the Rab it is not seen in any of the less-detailed classifications. Here the preference for St.S is obscured in Sorts 4 and 2 by Sh.S and S+FD, two not-preferred substrate types. This illustrates the importance of a detailed classification. It also emphasizes the fact that it may be very important to distinguish bare substrates from substrates mixed with detritus, and that the nature and amount of detritus is very important.

From the grain-size classifications in both streams (Tables 19 and 20) it is

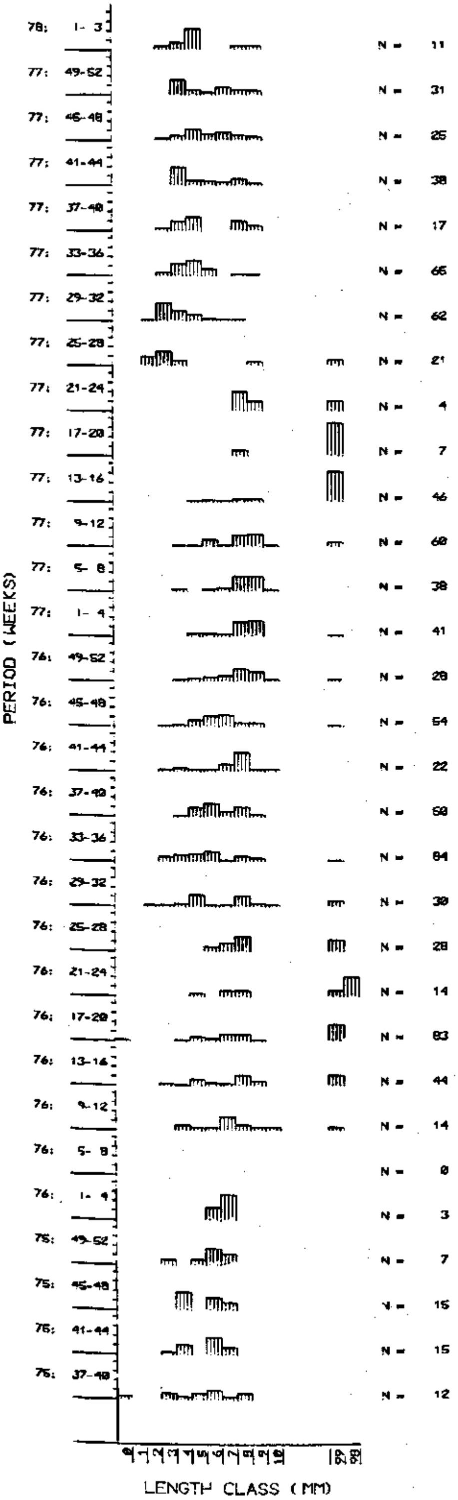


Fig. 21. Life cycle histograms of *Lithax obscurus* showing the distribution (%) of larval body length, pupae (99) and adults (98) per four-week period.

Table 17. I.R. values for *Lithax obscurus* (N = 451) in the field classification of the substrates in the Snijdersveerbeek.

Sort	Sand								Gravel			Detritus		
3	-3.7								*8.2*			-4.7		
4	*2.3*			-8.3					*8.9*	1.6		-4.7		
2	*5.6*		-5.0	-4.8			-6.8		*8.9*	1.6		-4.7		
1	*8.1*	-1.3	-5.0	-1.5	-4.5	-1.4	-6.6	-1.9	*8.9*	-0.2	1.9	-2.7	-3.3	-1.9
	St	Sh	FD	L	CD	CD+L	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

Table 18. I.R. values for *Lithax obscurus* (N = 218) in the field classification of the substrates in the Ratumsebeek.

Sort	Sand								Gravel			Detritus		
3	-6.1								*9.0*			0.8		
4	-2.2			-6.8					*8.4*	*3.5*		0.8		
2	-0.5		-3.8	-3.2		-6.0			*8.4*	*3.5*		0.8		
1	*2.9*	-4.3	-3.8	-1.1	-3.0	-1.3	-5.5	-2.1	*8.4*	-1.1	*4.1*	*5.7*	-1.0	-0.7
	St	Sh	FD	L	CD	CD+L +FD	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

Table 19. I.R. values for *Lithax obscurus* (N = 451) in the grain-size classification of the substrates in the Snijdersveerbeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,10%	*9.0*	1.7	*3.0*	*7.4*	*2.5*	0.6	*8.0*	-0.3	-8.6	-4.4	-	-3.6	-3.5	-2.4
Sort 6,10%	*9.0*	-1.1	-0.3	*7.1*	1.9	*6.2*	1.3	*6.6*	-1.3	-7.9	-	-3.6	-3.5	-2.4
Sort 7,10%	-	*9.0*	-0.8	-0.8	0.8	*5.7*	-1.2	*7.5*	*4.4*	-3.2	-2.3	-3.6	-3.5	-2.4
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,10%	*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

Italic values indicate significant over-representation

Table 20. I.R. values for *Lithax obscurus* (N = 218) in the grain-size classification of the substrates in the Ratumsebeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,10%	-1.1	1.9	*3.4*	-0.6	*11.0*	-2.6	-1.5	-3.4	-7.0	-1.9	-	*5.7*	-1.0	-0.7
Sort 6,10%	-	-	-1.1	*3.1*	*2.1*	*6.2*	*5.9*	*2.6*	-6.5	-4.6	-	*5.7*	-1.0	-0.7
Sort 7,10%	-	-	-	-	-	-	*4.6*	-1.5	*5.6*	-6.6	-1.1	*5.7*	-1.0	-0.7
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,10%	*4.6*	0.3	*2.1*	*6.2*	*5.9*	*2.6*	-2.1	-3.4	-5.9	-2.8	-1.9	*5.7*	-1.0	-0.7

Italic values indicate significant over-representation

Table 21. I.R. values for *Lithax obscurus* per length class (A) and season (B) in the Snijdersveerbeek in Sort 8,10%.

Length class and Season	N	Substrate class and $Q_1M_dQ_3$ index													
		1 $\bar{x}\bar{x}\bar{x}$	2 $\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	3 $\bar{x}\bar{3}x$	4 $\bar{x}\bar{2}x$	5 $\bar{x}\bar{1}x$	6 $\bar{x}1x$	7 $\bar{x}xx$	8 1xx	9 22x	10 23x	11 33x	12 CD	13 L	14 CD+L
A 0	3	-0.3	3.5	-0.4	-0.4	-0.4	-0.4	1.3	-0.6	-0.5	-0.6	-0.4	-0.5	-0.5	-0.3
1 - 3	18	-0.7	-0.4	0.8	*7.2*	-1.0	-0.1	0.1	-1.4	-1.2	0.6	-0.9	-1.1	-1.3	-0.8
4 - 5	94	0.2	-0.7	0.9	*3.6*	0.1	*7.7*	*2.1*	0.1	-2.8	-3.0	-2.0	-1.3	-2.6	-1.2
6 - 10	283	*2.8*	*2.3*	*2.0*	*3.8*	1.7	*5.6*	*2.6*	0.4	-4.2	-5.8	-3.4	-2.6	-1.6	-1.8
99 - 98	53	*8.5*	*9.3*	-0.2	0.3	0.5	-1.8	-1.9	-1.0	-1.6	-2.5	-1.5	-1.9	-2.2	-0.6
Total	451	*5.0*	*4.9*	*2.0*	*6.2*	1.3	*7.3*	*2.5*	-0.3	-5.4	-6.7	-4.4	-3.5	-3.5	-2.4
B Spring	113	*7.8*	*7.9*	0.3	-0.1	*3.6*	0.5	-0.0	-2.8	-2.3	-2.7	-1.2	-2.8	-2.8	-1.2
Summer	143	-1.4	-1.4	-0.2	*4.7*	-0.7	*6.7*	*2.9*	-1.6	-1.8	-5.0	-2.9	-1.3	-	-
Autumn	106	*7.5*	-2.1	1.5	*4.0*	0.1	0.5	0.1	*4.2*	-3.0	-3.4	-1.8	-2.3	-0.9	-1.5
Winter	89	-1.1	*4.0*	1.5	0.7	-0.3	*4.1*	1.3	-0.0	-2.9	-2.7	-2.2	-0.0	0.9	-0.9

Italic values indicate significant over-representation

clear that *Lithax* prefers substrates with a large proportion of the fraction coarser than 1-2 mm (Coarse Sand, $Q_1 \leq \bar{1}$). A presentation of the distributional pattern per length class in the Snijdersveerbeek (Table 21A) in Sort 8, 10% shows that the smallest specimens (1-3 mm) are mainly found on $\bar{x}\bar{2}x$, which mainly concerns samples with $Q_3 = \bar{5}$ or $\bar{4}$ (cf. Fig. 16). Analysis of the preference of these small larvae in Sort 5, 10% (not presented) showed that they prefer $Q_1 = \bar{4}$.

Pupae are present on the two coarsest substrate types (coarser than $\bar{x}\bar{4}x$, especially $Q_1 = \bar{7}$, $\bar{6}$ and $\bar{5}$; $M_d = \bar{7}$ and $\bar{4}$, based on length class preference in Sort 5, 10% and Sort 6, 10% not presented).

The other length classes are found on the total range of substrate types with $Q_1 < \bar{1}$ and $M_d < 1$. This means that *Lithax obscurus* occurs mainly on coarse to very coarse substrate in spring and autumn (pupae and early instars, respectively) and can be found on all other substrates for the rest of the year, as confirmed by Table 21B.

In the Ratumsebeek a similar preference of the small larvae (1-3 mm) for $\bar{x}\bar{2}x$ was observed, but they shared this with $\bar{x}\bar{x}\bar{x}$. The larger larvae occurred in all substrates coarser than $\bar{x}1x$. Pupae were only found incidentally in shovel samples from the Rab, but were very numerous on stones, claystone banks and branches, especially those protruding above the water surface near the banks. This could be observed clearly after a strong fall of the water level, bringing many attached pupae above the water surface, although this did not hinder the emergence, which followed within a few days.

The above data agree with the conclusions of Beyer (1932) and Geijskes (1935) that the Goeridae belong to the typical stone fauna. They are characteristic for unpolluted, natural streams with a moderate to fast current, although the several genera select different current speeds for their optimal habitat (Scott, 1958; Nielsen, 1942). This is reflected in the size of the ballast stones on the sides of the case, which increase from *Lithax* through *Silo* to *Goera* (Wesenberg-Lund, 1943; Webster & Webster, 1943; Grenier et al., 1969).

Case building *Lithax obscurus* builds a case of mineral material. The case is at least 6-7 mm long and about 3 mm wide in the final instar (Grenier et al, 1969), although Ulmer (1909) and Lepneva (1964) reported a length of 9-10 mm, which agrees with our measurements. The case is slightly curved and the rear opening is closed by a membrane with an excentric circular opening. This membrane is always covered with some small sand grains, which is a taxonomic characteristic for the genus *Lithax* within the Goeridae.

The case 'grows' spasmodically, whereby the larva enlarges the case, probably just before a moult. This is clearly visible from the lighter colour of the newly-added front, which is still free from attached diatoms in the beginning. The case consists of sand grains and is well camouflaged (Lepneva, 1964).

The different instars show a different preference, which shifts from small to larger grains with increase in larval size (Fig. 22). The F-3 instar uses mainly 0.105 - 0.500 mm grains and this preference is replaced by one for 0.250 - 2 mm in the final instar. In the final instar cases the 1 - 2 mm grains are mainly used for ballast stones on the lateral sides of the case and as cap stones for the pupal case.

Comparing the grain-size preferences of *L.obscurus* for case building with the grain sizes present in the substrates in its preferred substrate type in the streams shows that they will be able to find the sizes needed in all substrate types showing over-representation, even in the coarsest types since this is always situated on top of finer material. Lack of suitable grains for case building will not occur in the preferred substrates, but it may be one of the reasons for the under-representation

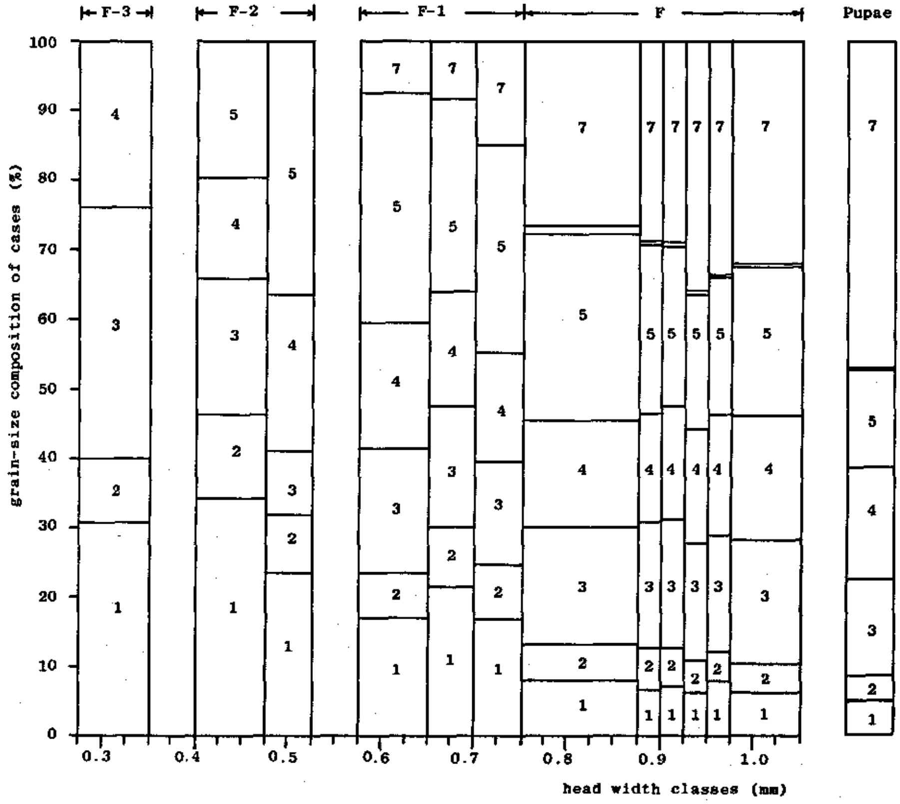


Fig. 22. Distribution (%) of grain-size fractions in natural cases of *Lithax obscurus*. 1 = 0.105 - 0.210 mm; 2 = 0.210 - 0.250 mm; 3 = 0.250 - 0.350 mm; 4 = 0.350 - 0.500 mm; 5 = 0.500 - 0.850 mm; 6 = 0.850 - 1.0 mm; 7 = 1.0 - 2.0 mm.

of *L.obscurus* in the finer substrates. However, in substrates with $M_d > 1$ still enough of the suitable grains will be available, and yet L.obscurus occurs here only sporadically. This suggests that other factors than house-building material play a more important role in determining its distribution, e.g. current velocity or availability of food. Yet, considering the preference of *Lithax* for the coarse substrates (and inseparably linked with this, the higher current speeds), its use of relatively large grains for case construction and its choise of pupation sites, the conclusion is justified that a loss of coarse substrates and a decrease in current velocity will cause the disappearance of *L.obscurus*. Especially the absence of suitable substrates in otherwise similar streams (natural, shaded, moderate to fast flow) is probably the cause of the restriction of *L.obscurus* (and Goeridae in general) to stony, gravelly streams.

4.2.2.2 Sericostoma personatum (Spence) (Trichoptera: Sericostomatidae).

Identification According to Botosaneanu (1967), *S.pedemontanum* is a synonym for *S.personatum*. In the Netherlands, Sericostomatidae are represented by two genera, *Sericostoma* and *Notidobia* (Geijskes & Fischer, 1971), of which only *S.personatum* was found in this investigation, and then only in the Snijdersveerbeek. Only recently, Wallace (1977) clarified the differences between *S.personatum* and *N.ciliaris*, making the identification of the two species quite simple. From Wallace's work it also became clear that Lepneva (1964) presented the pronotum of *S.personatum* as that of *N.ciliaris*. Adults were identified with Macan's key (1973) after rearing them from larvae in the rearing channel.

Life cycle The life cycle of *S.personatum* may vary geographically. Iversen (1973) concluded with Dittmar (1955) that in Northern Europe *S.personatum* has a three year life cycle. The univoltine cycle given by Nielsen (1942) and the 1.5-year cycle of Illies (1952) fit into this 3 year cycle. Elliot (1969) found a cycle of 1-1.5 years in Great Britain. Iversen (1973) explained the slower growth in Denmark and Sauerland as an effect of the lower temperature fluctuations and maxima and less-favourable food supply. In the Snijb both a 1.5 year and 3-year life cycle are possible when considering the data in Fig. 23, giving body length of the larvae in time. Measurements of head width indicated however that a three-year life cycle is most probable (Tolkamp & Verdonschot, to be published).

S.personatum has 7 larval instars, which are very difficult to separate on the basis of head capsule width or length (Iversen, 1973), Nielsen (1942) and Elliot (1969) found a discontinuous pattern, or at least distinct peaks for each instar. In the Snijdersveerbeek, last instar larvae measured at most 18-19 mm, which is slightly longer than the 15 mm Ulmer (1909) and the 16.2 mm Nielsen (1942) reported. Tolkamp & Verdonschot (to be published) have established that overwintering takes place in the egg stage and the first and second instar in the first year in the Snijdersveerbeek. In the second year, the third and fourth instars overwinter and the third year the sixth and seventh instar and the (pre-)pupae overwinter. Pupae are most abundant from April to June, while adults emerge from June to August (c.f. Svensson, 1972; Iversen, 1973).

Microdistribution in the Snijdersveerbeek *Sericostoma personatum* was predominantly found in association with coarse detritus, except for the Bare Gravel substrate (Table 22). This is in agreement with the food preferences, since *S.personatum* is a detritivore (shredder), feeding mainly on leaves (Décamps, 1968), although its gut does not contain cellulase (Bjarnov, 1972), which suggests that the bacteria and fungi attached to leaves and detritus are the main food items (Thorup & Iversen, 1974). Together with detritus, diatoms, algae and fungi are also ingested (Moon,

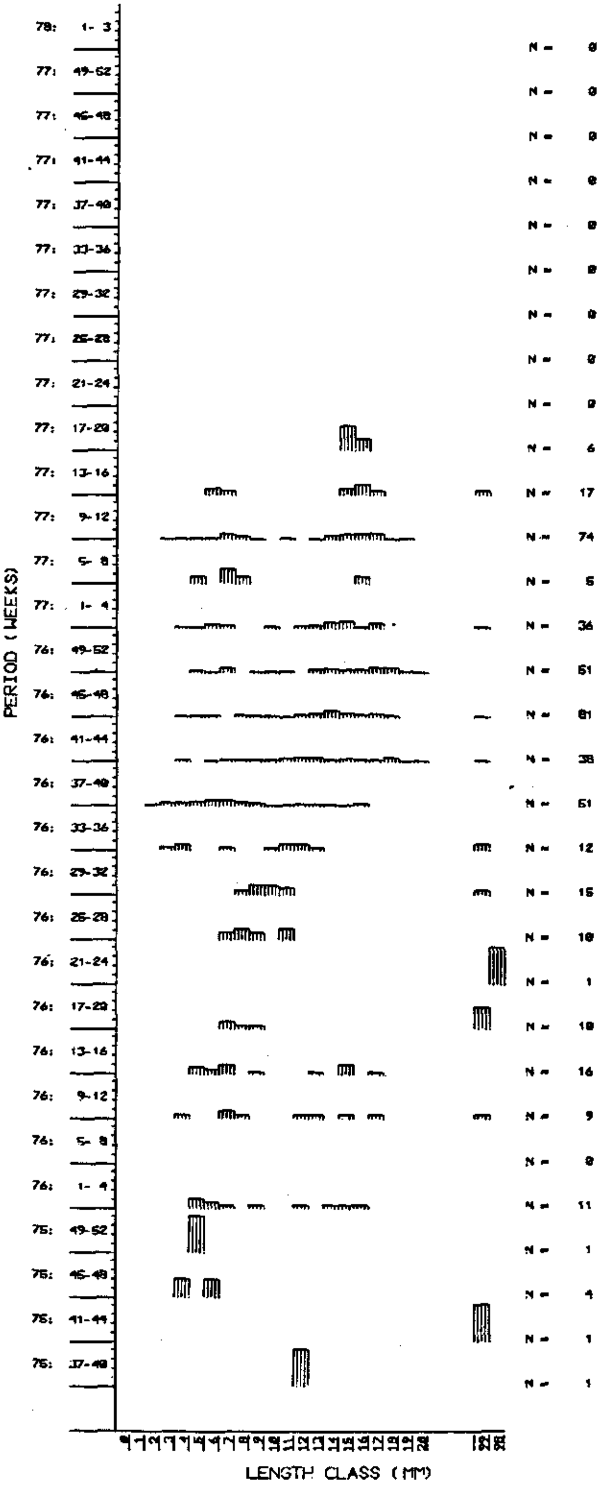


Fig. 23. Life cycle histograms of *Sericostoma personatum* showing the distribution (%) of larval body length, pupae (99) and adults (98) per four-week period.

Table 22. I.R. values for *Sericostoma personatum* (N = 346) in the field classification of the substrates in the Snijdersveerbeek.

Sort	Sand								Gravel			Detritus		
3	-0.3								*2.5*			-2.9		
4	-1.3			1.0					*2.8*	0.4		-2.9		
2	-0.8		-1.2	*3.0*			-1.0		*2.8*	0.4		-2.9		
1	-0.4	-0.7	-1.2	-0.8	*2.5*	*4.4*	0.3	-2.8	*2.8*	-1.1	1.1	*2.4*	-4.1	-2.8
	St	Sh	FD	L	CD	CD+L	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

1934; Slack, 1936), and sometimes insects are eaten as well (Dittmar, 1955; Lepneva, 1964). This is why Hickin (1967) classified *Sericostoma* as omnivorous, although the percentage of insects is only about 1% (Thorup & Iversen, 1974). Since diatoms and algae are more abundant on gravel in the Snijdersveerbeek, the over-representation in BG might be related to this type of food, although this can only be a tentative conclusion. In Table 22 the preference for S+CD+L (I.R. = 4.4) should be considered with care since this only concerns three samples.

In the grain-size classification (Table 23) we see that *Sericostoma* prefers the gravelly substrates, together with the detritus substrates. The over-representation in the finer substrates is probably mainly determined by the presence of coarse detritus, since only the I.R. values for $\bar{x}xx$ and 23x increase from the 1% to the 10% sorting.

The very high preference for coarse substrates is also clear from the field-

Table 23. I.R. values for *Sericostoma personatum* (N = 346) in the grain-size classification of the substrates in the Snijdersveerbeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,10%	-1.0	-2.2	*4.5*	*2.9*	-0.5	-0.8	1.8	-2.9	-0.5	-2.0	-	*2.8*	-4.2	-3.1
Sort 6,10%	-1.0	-1.0	-2.5	-0.5	*2.8*	*3.9*	1.8	0.9	-2.0	1.1	-	*2.8*	-4.2	-3.1
Sort 7,10%	-	-1.0	-2.1	-1.9	-1.0	-1.9	-2.3	-3.7	*6.9*	0.6	-1.8	*2.8*	-4.2	-3.1
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,10%	-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

Italic values indicate significant over-representation

Table 24. I.R. values for *Sericostoma personatum* per length class (A) and season (B) in the Snijdersveerbeek in Sort 8,10%.

Length class and Season	N	Substrate class and $Q_1M_dQ_3$ index													
		1 $\overline{xxx}$	2 $\overline{x5}x$ $\overline{x4}x$	3 $\overline{x3}x$	4 $\overline{x2}x$	5 $\overline{x1}x$	6 $\bar{x}1x$	7 $\bar{x}xx$	8 1xx	9 22x	10 23x	11 33x	12 CD	13 L	14 CD+L
A 1 - 5	46	-1.2	-0.9	0.1	-0.0	0.1	1.3	1.1	-0.8	-1.4	0.3	1.5	*3.3*	-2.1	-1.3
6 - 7	70	-1.4	0.1	-1.1	-0.3	0.9	1.4	*3.3*	-0.4	-1.1	1.0	-1.1	0.6	-1.7	-1.5
8 - 9	43	-1.1	-1.9	0.8	-0.5	-0.4	1.5	1.3	-0.7	0.3	*3.5*	-1.3	-0.5	-1.5	-1.2
10 - 12	40	-1.1	-0.7	*2.2*	*3.9*	0.4	0.4	0.5	-1.5	-0.7	0.1	-1.3	-0.4	-0.9	-1.2
13 - 20	131	-1.9	0.9	*4.8*	*4.6*	0.8	0.0	-0.1	-2.8	-0.8	-1.4	-1.5	*2.4*	-2.9	-1.6
99 - 98	16	-0.7	-0.3	-1.0	-0.1	*4.1*	-1.0	0.3	0.3	-1.1	0.1	-0.8	0.9	-0.4	-0.7
Total	346	-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
B Spring	78	-1.0	0.3	*3.4*	0.4	0.9	1.5	*2.4*	-0.4	-0.9	-1.4	-1.0	-0.0	-2.9	-2.0
Summer	82	-1.7	-3.1	*2.4*	0.4	0.6	-0.3	0.1	-1.2	-0.4	0.4	-2.2	*8.0*	-	-
Autumn	92	-1.7	-2.0	-1.7	*7.9*	-1.2	1.5	0.9	-2.3	-1.5	*2.8*	-0.5	1.2	-2.9	-0.7
Winter	94	-1.7	*3.1*	*2.3*	-0.9	*3.2*	1.2	0.6	-1.7	-0.7	-0.9	-0.1	-0.6	-1.5	-2.3

Italic values indicate significant over-representation

classification in Table 22 when considered on a less detailed level. Consideration of the preference of several length classes in Sort 8, 10% (Table 24A) shows that the smallest (0-5 mm) larvae prefer Coarse Detritus, while 5-7 mm larvae are mainly found in $\bar{x}xx$ (often combined with CD) and the 7-9 mm larvae especially in 23x (+ CD) substrates. Larvae larger than 9 mm distinctly prefer gravel ($\overline{x3}x$, $\overline{x2}x$). Pupae are predominantly found in $\overline{x1}x$.

However, all length classes show positive I.R. values in at least 5 substrate classes, which suggests that a wide range of mineral substrates can be inhabited by *S.personatum* and that the presence of detritus plays an important role. Comparison between seasons shows (Table 24B) that the animals are absent from the detritus substrates in winter and spring, when they are most abundant in gravel. The preference for detritus and sand substrates (Class 12 and 10, respectively) is most pronounced in summer and autumn, although in autumn gravel is preferred. The preference for substrates with a considerable proportion consisting of detritus is also reported by Higler (1975), who stated that they can be found burrowed in sand substrates or under or behind stones where the sand is often mixed with leaves. They prefer these places because they are night-active and hide during the day, a phenomenon often observed in laboratory experiments, where they burrow immediately during the day, but move over the surface at night, although they may be observed moving over the stream bed in shaded places during the day as well. Jones (1949) and Geijskes (1935) both reported that *S.personatum* is often found in the same habitat as *Ephemera danica*, namely in coarse gravel and stones near the banks, where the current is slower, but it is also found in sandy areas (Jones, 1951). The larvae are distinctly rheophilic and can be found in springs, streams and rivers (Higler, 1975), a distribution which agrees with the authors' observations in the Netherlands, and its presence in the

Snijdersveerbeek. The absence in the Ratumsebeek remains unexplained, however.

According to Nielsen (1942) *S.personatum* is never found in high densities, but this is certainly not true for the Snijdersveerbeek, where on several occasions (when collecting larvae for experiments) more than 40 specimens were found on 10-15 cm^2 of sand mixed with gravel to a depth of approx. 5 cm; a clay/loam bank prevented further penetration below.

Case building According to Wallace (1977), last instar larvae of *S.personatum* dwell in a case which is 13 mm long, but Hickin (1967) and Lepneva (1964) mention a case length of 15-16 mm. The case is made from long, narrow grains of, for example, 0.65 mm by 0.13 mm (Nielsen, 1942), which are arranged in a characteristic mosaic pattern in a single layer stuck together with thick, yellow-brown salivary secretion. The surface is completely smooth. The case is slightly curved, especially in smaller instars. It tapers towards the rear, except in the last instar, for which the case is practically parallel-sided because it is no longer necessary to enlarge the case,

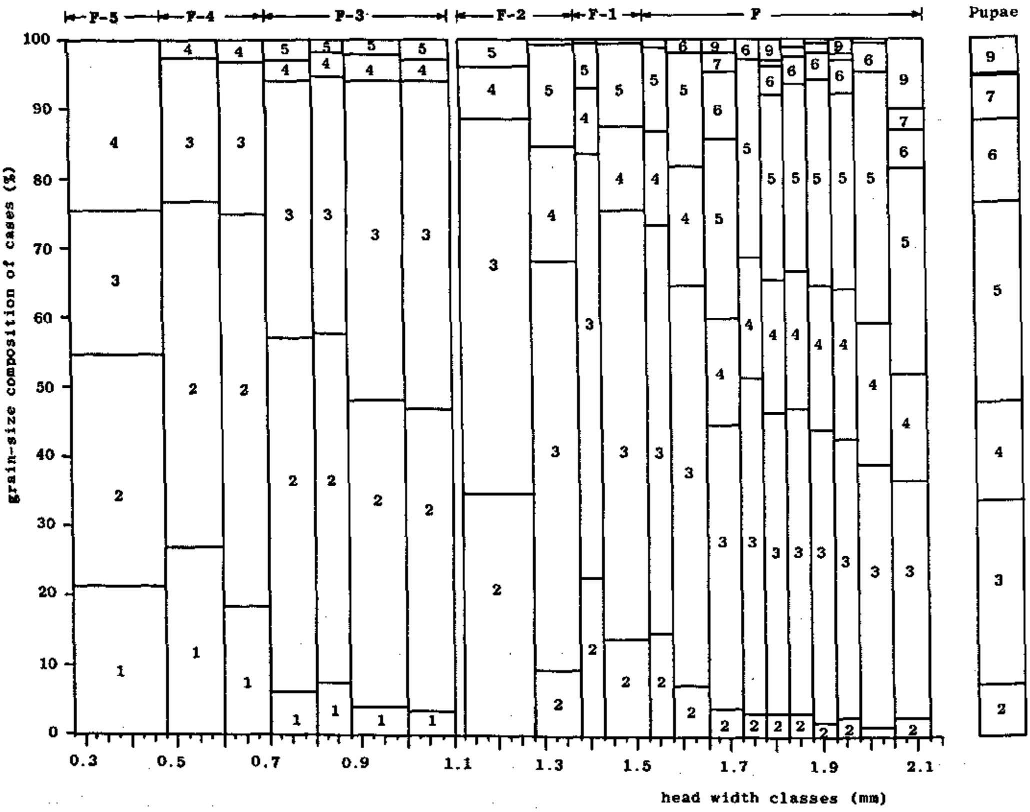


Fig. 24. Distribution (%) of grain-size fractions in natural cases of *Sericostoma personatum*. 1 = 0.050 - 0.105 mm; 2 = 0.105 - 0.150 mm; 3 = 0.150 - 0.210 mm; 4 = 0.210 - 0.250 mm; 5 = 0.250 - 0.350 mm; 6 = 0.350 - 0.500 mm; 7 = 0.500 - 0.850 mm; 8 = 0.850 - 1.0 mm; 9 = 1.0 - 2.0 mm.

restricting the building activity to maintenance. The rear end is closed with a round membrane that is perpendicular to the case and within which an opening formed like a spool is present.

Analyses of the grain sizes used in the cases showed an increase in grain size with increasing larval size (Fig. 24). First instar larvae, reared from eggs deposited and hatched in the rearing channel in the laboratory from adults that emerged there, build a case of grains smaller than 0.150 mm within a day. Going from the instar F-4 to F-2 a decrease from 21% to 0% was seen for the fraction smaller than 0.105 mm, while the 0.105-0.150 mm fraction remained at about 50% and the fraction of 0.150-0.210 mm increased from 24% to 42%. From the F-2 to the F instars the fraction 0.105-0.150 decreased to zero, while the fraction 0.210-0.350 mm increased significantly. The pupal case differs from the last-instar case in that it contains slightly more of the very coarse fractions (up to 2 mm), especially used for closing the case. Before pupation the case is extended with larger grains and attached to gravel or even stones in the stream bed (below the substrate surface), after which the front is closed with a sieve-like membrane with a central cleft of which the edges are bent outwards. The clefts in the front and rear membrane are situated perpendicular to each other.

When naked final instar larvae of *S.personatum* were offered all grain sizes mentioned in Table 6 for case building, the medium sand fraction (0.250 mm) was preferred (Experiment 1, Table 25). When this fraction was left out, the larvae used the finer and coarser sand fractions (Experiment 2, Table 25). When fine sand was also left out, they mainly used coarse sand (Experiment 3, Table 25), but if this was also absent (Experiment 4, Table 25) the larvae built an emergency case only and were unable to use coarser grains or leaf material for case building.

Comparing the grain-size composition of the cases with that of the substrates preferred by *S.personatum* in the Snijdersveerbeek, no direct relationship can be seen. All fractions needed for case building will be present in the substrate. However, it is striking that substrates with $Q_3 = 2$ (0.250 - 0.500 mm) (Table 23, Sort 7) are preferred, which means that coarse substrates (Sort 8) must include at least 25% of the fractions finer than 0.500 mm and coarser than 0.125 mm.

Table 25. Grain-size composition (percent) of cases built by final instar larvae of *Sericostoma personatum* in laboratory experiments.

	Proportion (%) of grain-size fraction (lower level, mm) in cases			
	0.050	0.125	0.250	0.500
Experiment 1	0	4.7	86.3	9.0
Experiment 2	0	57.5	Ab	42.5
Experiment 3	19.1	Ab	Ab	80.9
Experiment 4†	0	Ab	Ab	Ab

Ab = Grain-size fraction absent
†:In Experiment 4 no case was built

Substrate-selection experiments In a first series of experiments, the substrate selection at low and high current speeds was tested for F and F-1 instars (the instar was only roughly determined). At both current speeds these larvae (F, F-1) selected the coarsest particle size (16 mm); particle sizes of 1 to 8 mm followed. There was no significant preference for any of these four particle sizes at the low speed, but at high current speeds 1 mm and 2 mm particles attracted more larvae than 4 mm and 8 mm particles (Fig. 25 a and b), although the differences are not significant. The same experiment conducted with F-2 and F-3 instars showed again that current does not influence the substrate selection significantly (Fig. 24 c and d).

Calculation of the significance of the substrate selection with the chi-squared test showed that only in the experiment with the F-2 and F-3 larvae at slow current speeds (Fig. 25c) was the substrate selection not significant and only a tendency for coarser particle sizes was detected. A small experiment with F-1 and F-2 larvae on 1, 2, 4, and 8 mm particles showed that *S.personatum* significantly selected the coarsest grains (8 mm), while the differences between the remaining particle sizes were not significant (Fig. 25 e)

In conclusion, it can be stated that there were no significant differences in substrate selection between different instars of *S.personatum* in laboratory experiments. Unfortunately no experiments were carried out with organic substrates. The selection

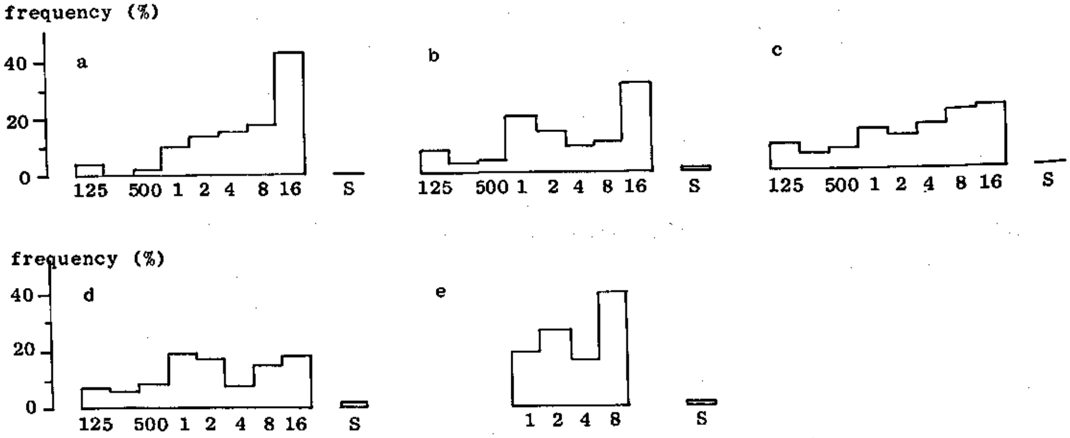


Fig. 25. Substrate selection in laboratory experiments by *Sericostoma personatum*. Grain-size fractions are indicated by the lower limit in µm (under 1 mm) and mm (over 1 mm). S = end retaining screen.

Figure no.	Instar	Body length /mm	Number of experiments	Number of larvae per experiment	Current velocity (cm/s)
a	F ; F-1	8-14	8	16	5
b	F ; F-1	8-14	8	32	10
c	F-2; F-3	6-10	4	16	5
d	F-2; F-3	6-10	8	16	10
e	F-1; F-2	7-11	3	32	10

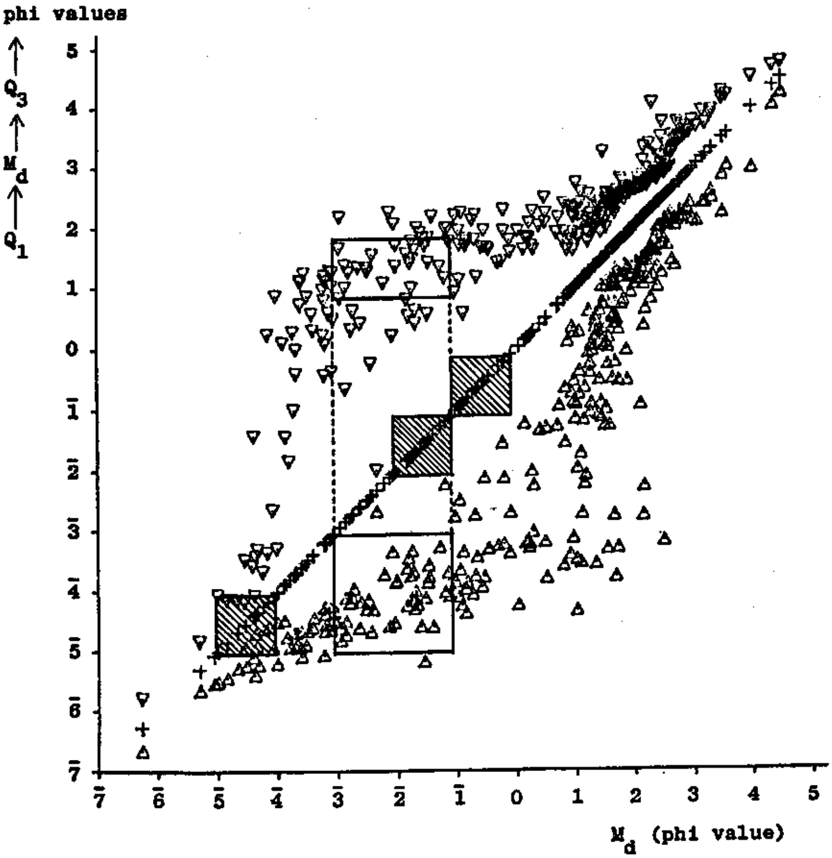


Fig. 26. Comparison of substrate preferences in the field (unshaded) with particle-size selection in laboratory experiments (shaded) for *Sericostoma personatum.*

of the coarse substrates is in full agreement with substrate preferences in the field, as observed in the Snijdersveerbeek, where $x\bar{3}x$ and $x\bar{2}x$ substrates are preferred, for which 50% or more of particles are coarser than 1 mm. For most of these substrates more than 25% is coarser than 16 mm. The similarity of the field and laboratory studies is further illustrated in Fig. 26, where both the substrates preferred in the field (based on Sort 5 to 8, 10%) and the particle-size selection in the laboratory experiments have been projected on the $Q_1M_dQ_3$ graph (Fig. 14).

4.2.2.3 Micropterna sequax (MacLachlan) (Trichoptera: Limnephilidae)

Life cycle *M. sequax* has a clearly univoltine life cycle in the Snijdersveerbeek and the Ratumsebeek (Fig. 27). Larvae were collected numerously in shovel samples, and also in additional collections. Pupae were found only incidentally (11 specimens in total) in the shovel samples and not at all collected by hand, since pupae are burrowed in the substrate, while larvae mostly occur on top of or in the upper layer.

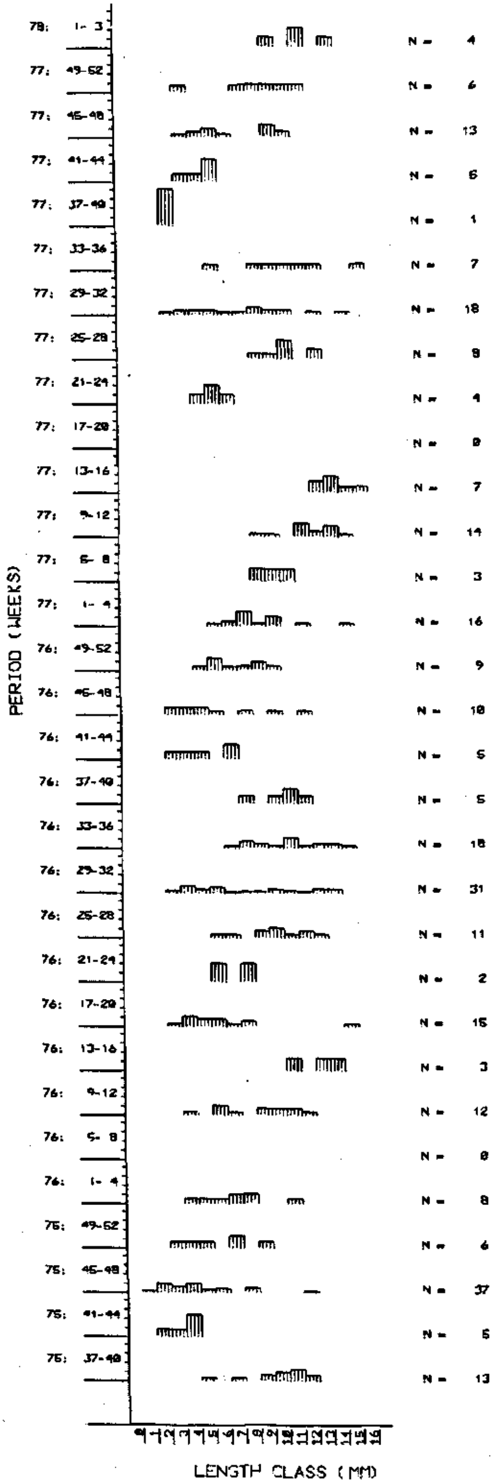


Fig. 27. Life cycle histograms of *Micropterna sequax* showing the distribution (%) of larval body length, pupae (99) and adults (98) per four-week period.

Pupae were found from March - September, which might indicate a long flight period. This was also concluded by Crichton (1971) for *Stenophylax* (= *Micropterna*) *sequax* (from Scotland) and he suggested that there is an imaginal diapause. However, according to Svensson (1972) mating takes place within a few hours to a few days after emergence. He found no imaginal diapause, which is typical for *Limnephilus* spp, and that the development of the genitalia takes place in the last larval and pupal instar.

In the Rab and Snijb, the first juvenile (second instar) larvae were found in July. They grow in autumn and overwinter in the fourth (F-1) and fifth (F) instar, which agrees with the conclusion of Dittmar (1955). According to the literature, the last instar larvae become 18-19 mm long. In the Snijb and Rab they reach on average 20-25 mm, with exceptionally some smaller specimens (fifth instar larvae on the basis of head width had a body length ranging between 12.5 and 25.2 mm, see Tolkamp & Verdonschot, to be published).

Microdistribution In the Rab, *M. sequax* occurred predominantly in detritus substrates and no over-representation was found on mineral substrates (Appendices 9 and 13). Of the 286 larvae, 252 occurred in detritus, 8 in gravel and 26 in sand with a negative Q_1. The larvae on mineral substrate were mostly last instars. Three pupae were found in coarse substrates only (Classes 3, 5, 6 in Sort 8, 10%, Table 26) in the shovel samples.

The preference for Coarse Detritus substrates and Leaf substrates in the Rab was clearly linked with the season. Preference for Coarse Detritus was only found in summer when leaf packs are scarce, while the preference for leaf packs is especially found in the autumn when leaves are abundant (cf. Scott, 1958 for *Stenophylax* spp.). In spring, only 6 animals were found; in winter 23. These low numbers are probably caused by the fact that the larvae and pupae burrow in places where no shovel samples were taken, a fact which will be illustrated further on in this subsection.

In the Snijb, *M. sequax* shows a different distributional pattern. Although the total number of specimens is lower than in the Rab, they are distinctly distributed

Table 26. I.R. values for *Micropterna sequax* (N = 194) in the field classification of the substrates in the Snijdersveerbeek.

Sort	Sand								Gravel			Detritus		
3	-2.0								1.2			*2.0*		
4	-3.3			0.7					*2.1*	-0.9		*2.0*		
2	-2.0		-3.1	*3.0*			-1.5		*2.1*	-0.9		*2.0*		
1	0.4	-3.7	-3.1	*3.4*	-0.4	*5.3*	-2.0	0.6	*2.1*	*2.1*	-2.2	1.9	*2.1*	-1.5
	St	Sh	FD	L	CD	CD+L	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

Table 27. I.R. values for *Micropterna sequax* (N = 194) in the grain-size classification of the substrates in the Snijdersveerbeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,10%	-0.7	1.9	1.0	-0.7	0.9	*2.2*	-0.9	-3.6	-0.4	-2.2	-	1.6	*2.0*	-0.2
Sort 6,10%	-0.7	-0.7	1.9	-0.6	-1.2	0.4	*3.3*	0.2	-2.6	-1.0	-	1.6	*2.0*	-0.2
Sort 7,10%	-	-0.7	1.5	*2.1*	-0.7	0.7	-1.8	-2.5	*2.2*	-1.9	-0.7	1.6	*2.0*	-0.2
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,10%	-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

Italic values indicate significant over-representation

over different substrate types. More larvae occurred in Sand (82) and Gravel (69) and not in Detritus (43). In Sort 3 this leads to a preference for Detritus and Gravel but this picture is totally different when considering a more detailed classification (Table 27). Here *M. sequax* prefers S+CD+L and S+L, followed by BG, G+L, CD and L substrates. In the grain-size classification (Table 27) this is reflected in the preference for $\bar{x}\bar{1}x$ (i.e. $\bar{2}\bar{1}2$, derived from Sorts 5 to 7), besides L and CD. In table 26 it can be seen that the classification on the $Q_1M_dQ_3$ index (Sort 8) seems to obscure the influence of the separate quartiles. In Sorts 5, 6 and 7 there is a clear tendency towards the substrates with coarse fractions ($Q_1 = \bar{6}, \bar{5}$; $M_d = \bar{5}$; $Q_3 = \bar{5}, \bar{4}$). This is less clear in Sort 8 ($\bar{x}\bar{5}x$, $\bar{x}\bar{4}x$). Still the presentation in Sort 8 will be the most reliable one because in the first six classes in Sort 7 the number of samples is very low. The low Q_1 and M_d values are combined with a high Q_3 value in the Classes 2 and 5 in Sort 8.

Considering the distribution between seasons (Table 28B), mineral substrates are favoured in winter, spring and summer and organic detritus substrates in autumn. The summer data only concern samples from the last week in summer (Week 37). *M. sequax* was not found in the previous 12 weeks. The autumn preference for Leaves is linked with larvae from 1-10 mm and that for Coarse Detritus with 16-20 mm larvae, while the 10-15 mm larvae are present in 22x and 23x (combined with detritus) (Table 28A). The largest larvae occur predominantly in $\bar{x}\bar{1}x$ and $\bar{x}1x$, while of the nine pupae, eight occurred exclusively in substrates coarser than $\bar{x}xx$ (with one specimen in CD+L), which means that at least 25% of the grain sizes are coarser than 1 mm. Preference of the pupae for a certain grain size combination could not be demonstrated significantly because of the low number of specimens. It is expected, however, that substrates preferred by last instar larvae will at least partly reflect the preference of the pupae. This will be tested in experiments.

Table 28. I.R. values for *Micropterna sequax* per length class (A) and season (B) in the Snijdersveerbeek in Sort 8,10%.

Length class and Season	N	Substrate class and $Q_1M_dQ_3$ index													
		1 xxx	2 x5x x4x	3 x3x	4 x2x	5 x1x	6 x1x	7 xxx	8 1xx	9 22x	10 23x	11 33x	12 CD	13 L	14 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
99	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 Spring	36	-0.7	-0.4	*2.2*	1.1	*6.3*	0.1	1.3	-1.4	-1.5	-1.5	-0.7	-2.1	-0.9	-1.4
Summer	21	-0.9	*2.9*	-0.6	-0.9	-1.0	-0.7	-1.4	-1.2	-1.0	*2.2*	-1.1	*2.2*	-	-
Autumn	84	-0.4	-0.3	-1.6	0.8	-0.6	-1.3	-1.3	-2.8	1.4	0.2	-1.6	*3.4*	*2.7*	-0.6
Winter	53	-0.5	0.8	-0.3	0.6	1.9	*3.6*	0.2	-1.6	-2.3	-0.6	-0.6	-1.2	-0.3	1.2

Italic values indicate significant over-representation

Mackay (1977) demonstrated for *Pycnopsyche scabripennis* that pupae burrow in particular substrates and may be easily missed. After investigation of the substrate preferences in the laboratory she was capable of finding pupae in Augusta Creek (Michigan, U.S.A.) where they were 'absent' previously. The same phenomenon occurs with *M. sequax*. Experiments in the rearing channel showed that larvae ready to pupate selected coarse substrates to burrow into and a subsequent careful check in the field showed that pupae were often concentrated in certain places with relatively coarse substrates, often outside the sampling sites chosen. This explains the low number of pupae in the regular samples in both streams.

Case building The case of the last instar larvae of *M. sequax* consists of a smooth inside cocoon surrounded by an outside case made of sand grains embedded in the salivary material of the cocoon. The case is slightly conical, weakly curved and almost circular in diameter, 18-19 mm long and 4.5 mm wide (Ulmer, 1909; Lepneva, 1964; Hickin, 1967), although in the Achterhoek larger specimens - up to 30 mm long - are found.

M. sequax changes its building material in the same sequence Nielsen (1942) described for *Stenophylax nigricornis*. Juvenile larvae all build mineral cases, but later instars use leaves and mineral matter in various combinations (Tolkamp & Verdonschot, to be published). In the laboratory, last instar larvae mainly used the 0.5-1.0 mm particles for case building, together with leaves and 1-2 mm sand. In the absence of the preferred particles, the preference shifted to 1-2 mm, leaves and 0.25-0.5 mm, or to leaves only (Fig. 28A). In the field the fourth (F-1) instar larvae build completely mineral and completely organic cases, while fifth (F) instars

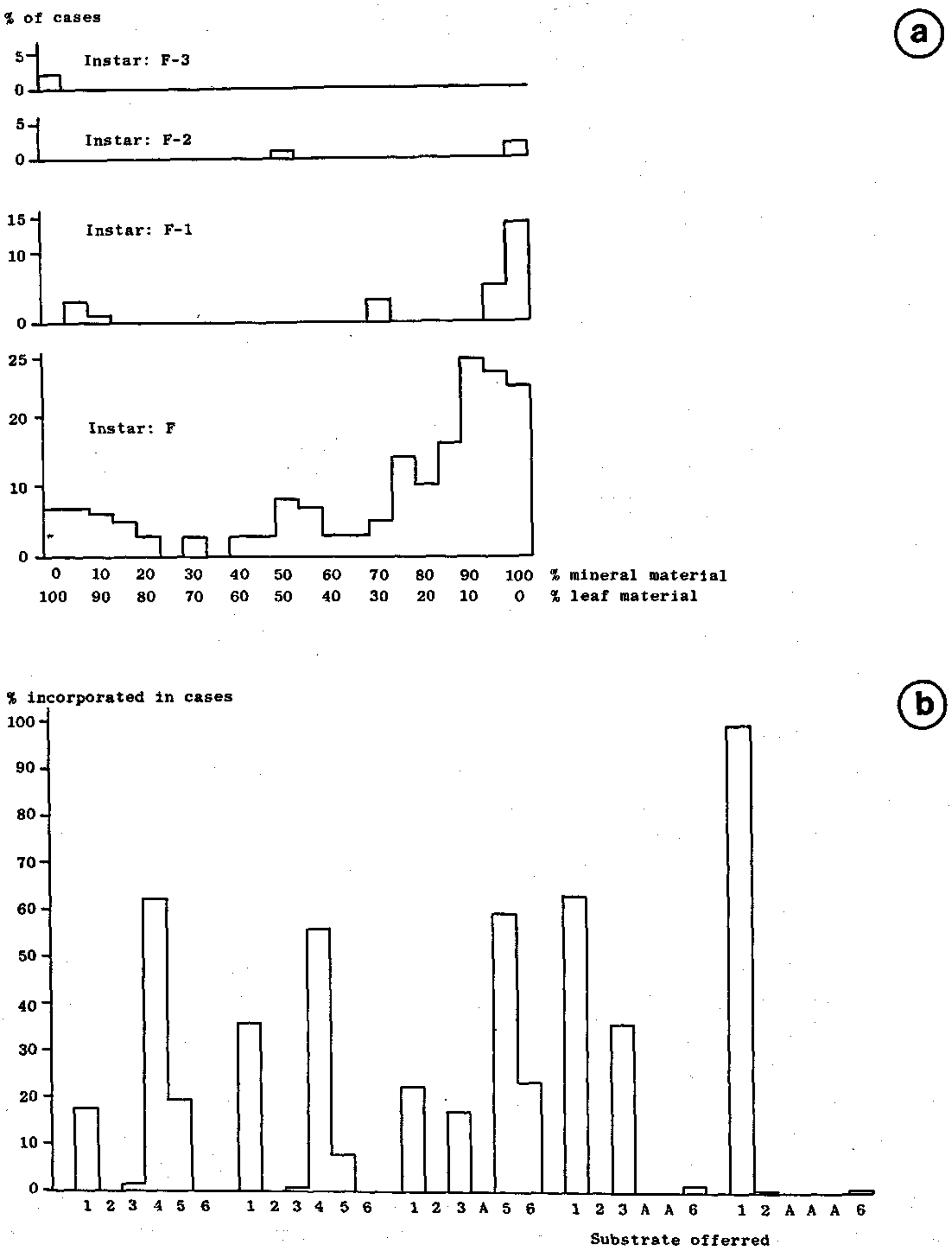


Fig. 28. a: Distribution (%) of organic and mineral matter in natural cases of *Micropterna sequax* for the second (F-3) to the last (F) instar.
b: Case building of *Micropterna sequax* under experimental conditions in the presence of various grain sizes. 1 = leaves; 2 = 0.125 - 0.250 mm; 3 = 0.250 - 0.500 mm; 4 = 0.500 - 1.0 mm; 5 = 1.0 - 2.0 mm; 6 = 2.0 - 4.0 mm; A = absent.

display these two and all possible combinations of leaves and sand (Fig. 28B). However, pupal cases are always completely mineral.

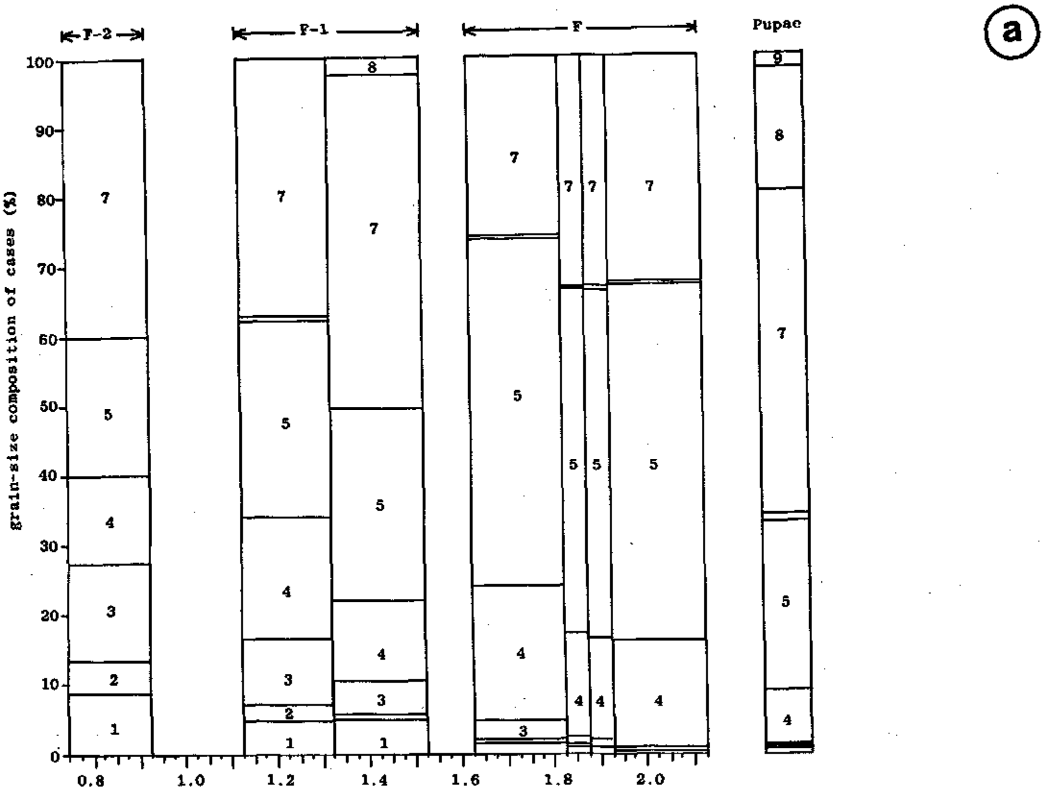
Analysis of the grain sizes used by the different instars showed that the third instar used for 40% the grain size fraction 1-2 mm, and for 20% the fraction 0.5 - 0.85 mm. The remaining 40% was divided over all finer fractions. The fourth and fifth instar used somewhat coarser grains (0.5 - 0.85 mm, 40 - 50%; 1-2 mm, 30%). These ratios of the particle sizes were present in the purely mineral cases (Fig. 29A), as well as the partly organic cases (Fig. 29B).

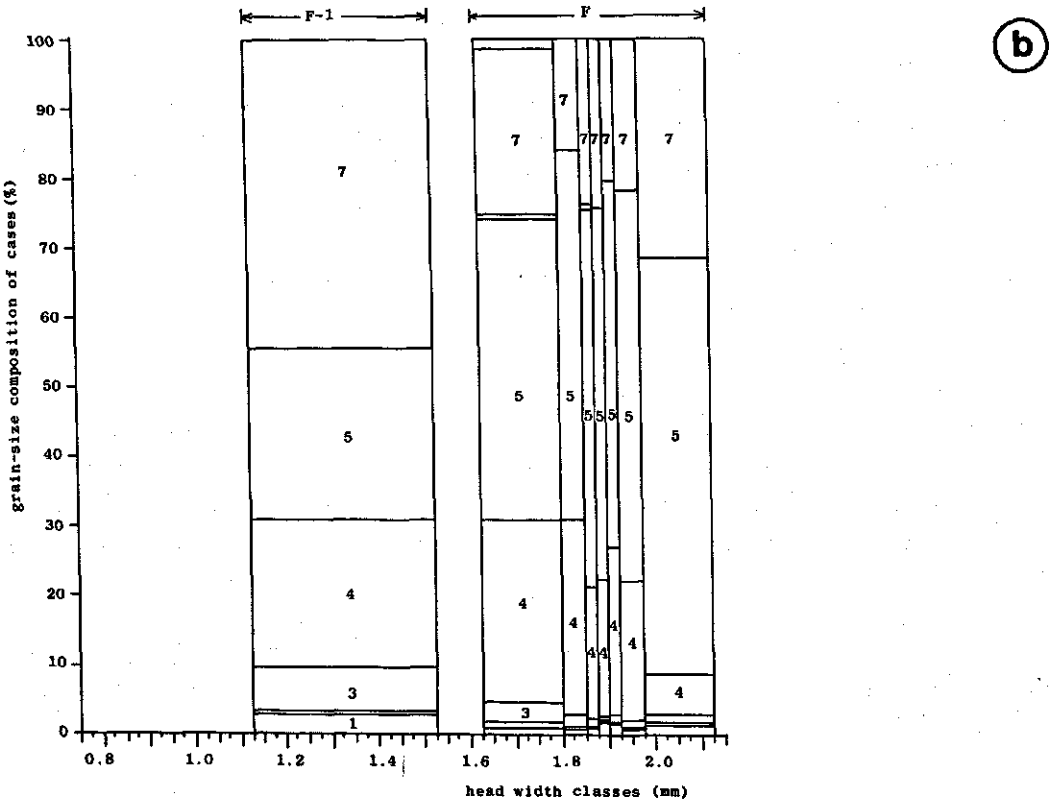
The pupal case is built of the same material as the case of the last instar, but it is much larger than this because the case is extended on both sides with coarse sand and gravel. Just before pupation the larvae attach 1-4 mm grains to the front of the case, completely closing it but for small openings between the grains. On the inside, a sieve membrane is made of salivary secretion. The larva turns in or outside the case, bites off the rear part and eventually extends this side with mineral material when a large portion had to be removed, e.g. because it consisted of detritus or was damaged in some way. Hereafter, the larva digs perpendicularly into the stream bed, often with the enlarged rear still protruding from the surface. In this position the new front is also closed with coarse sand and fine gravel, sometimes even attached to coarse gravel or pebbles. The inside of the front is also covered with a membrane. Observations of pupae in this position were made in the laboratory in the rearing channel, during experiments in the artificial stream, as well as in the field.

Nielsen (1942) already offered an explanation for this kind of alternating case-building behaviour. When larvae normally build mineral cases, the thick layers of leaves in autumn might prevent the larvae from reaching the sand bottom. When they normally build leaf cases, it is possible that younger and older larvae use coarse sand because leaf material may then be scarce. On the other hand a leaf case offers a much better camouflage when leaf substrates dominate in the stream, and likewise for a mineral case when organic substrates are scarce. The necessity to build a mineral case in the last instar, preparing for the pupal case, probably lies in the fact that predation on organic cases could be high, especially in periods with low amounts of organic material. Besides, organic cases are decomposed by bacteria and fungi (Mackay, 1972; Mackay & Kalff, 1973).

Burrowing in the substrate is clearly also a protective mechanism against predation and possibly drift. In the rearing channel it was observed that cases dug into the substrate completely or with only the rear protruding were left alone, but cases removed from the substrate and put on the surface were opened by larvae of the same species and the pupae consumed (Gallepp (1974) observed the same phenomenon for *Brachycentrus occidentalis*).

Substrate-selection experiments *Single grain-size fractions* Mackay (1977) performed experiments with *P.scabripennis* with a 16 mm pebble in the middle of the substrate trays and established that the larvae showed no special response to the pebble: no


a
F-2
F-1
F
Pupae
grain-size composition of cases (%)
0
10
20
30
40
50
60
70
80
90
100
0.8
1.0
1.2
1.4
1.6
1.8
2.0
1
2
3
4
5
7
8
9


b
F-1
F
grain-size composition of cases (%)
0
10
20
30
40
50
60
70
80
90
100
0.8
1.0
1.2
1.4
1.6
1.8
2.0
head width classes (mm)
1
3
4
5
7

animals burrowed directly below the pebble. In experiments where *M. sequax* could choose between 8 particle sizes, ranging from 0.050-8 mm, the influence of a 16 mm pebble placed in the middle of the trays was tested in a similar way. This pebble did not influence the particle-size selection or the preference for 2, 4 and 8 mm (compare Figs. 30a and 31b), although finer substrates with a pebble attracted relatively more animals than without a pebble. A similar experiment was carried out with a beech leaf placed under the pebble as well. Again no differences were observed (Fig. 30b compared with 30a and 311). In all following experiments the pebble was therefore omitted.

It is interesting to note that all observations done by day lead to the same result, but at night no substrate preference can be seen at all (Fig. 30c) because the caddis is night active. At night the larvae leave their burrowing sites and go in search of food, house building material, etc. Cummins (1964) concluded for *Pycnopsyche lepida* that they do not burrow in the dark, which suggests that the burrow responses are linked to photoperiod in a functional way. He also concluded that the larvae do not burrow when they build.

Given the choice between 0.125 - 16 mm particle sizes, *M. sequax* preferred coarse substrates (coarser than 2 mm) with peaks in 16 mm and 4 mm (Fig. 30d). Replacing particles of 0.125 mm by those of 32 mm, the preference for particles over 2 mm remained, but the differences between the coarser particles are not significant any more (Fig. 30e). When particles of 0.125 mm are replaced by leaves (a tray filled with beech leaves), *M. sequax* again preferred 16 and 4 mm above 8 and 2 mm or Leaves (Fig. 30f). When 16-mm particles are replaced by leaves, the preference shifted from 16 mm to leaves and 8-mm particles (Fig. 30g).

In a series of experiments where the preferred particle size(s) was (were) omitted, individually or in a combination, the preference always changed to the coarsest particle size present. However, 2, 4 and 16 mm are preferred more strongly than 8 mm. The combinations offered were: 0.050 mm or 0.125 mm, 0.250 mm, 0.500 mm and 1 mm combined with one coarser particle size (Fig. 31a-g), two coarser particle sizes (Fig. 31h-j), three coarser particle sizes (Fig. 31k-n) and 4 or 5 coarser particle sizes (Fig. 30d and e).

The conclusion from all these experiments is that *M. sequax* can burrow more readily in 2, 4 and 16 mm substrates than in 8 or 1 mm. In the presence of 1 mm substrates and the absence of coarser grains, the majority of the animals do not burrow any more but keep walking around, climbing the screens, or over the turned over trays, probably in search for more suitable sites. The aversion for 8 mm particles

Fig. 29. Distribution (%) of grain-size fractions in natural cases of *Micropterna sequax*. a: mineral cases b: cases partly consisting of organic matter. 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; 8 = 2.0 - 4.0 mm; 9 = 4.0 - 8.0 mm.

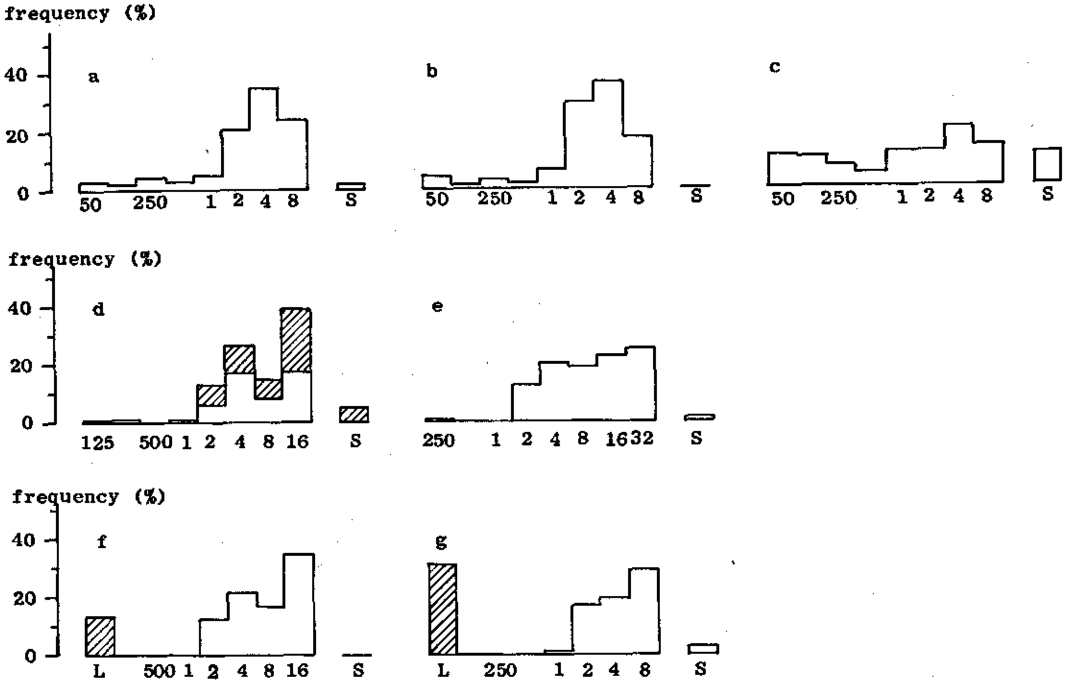


Fig. 30. Substrate selection in laboratory experiments by *Micropterna sequax*. Grain-size fractions are indicated by the lower limit of the fraction in µm (under 1 mm) and mm (over 1 mm). L = leaves ; S = end retaining screen.

Figure no.	Case type	Instar	Body length /mm	Number of experiments	Number of larvae per experiment	Note
a	mixed	F	> 15	20	16	+ 16 mm pebble
b	mixed	F	> 15	10	16	+ 16 mm pebble
c	mixed	F	> 15	10	16	idem b , at night
d	mixed	F	> 15	29	16	upstream(shaded),downstream (unshaded)
e	mixed	F	> 15	10	16	
f	mixed	F	> 15	10	16	+ leaf pack (shaded)
g	mixed	F	> 15	15	16	+ leaf pack (shaded)

was also apparent in experiments where other coarse particles were present (Fig. 31i, l and n).

All experiments indicate that *M. sequax* does not prefer grain sizes smaller than 1 mm, although they may be found here incidentally. In many instances they are then building or repairing their cases.

Mixtures of grain sizes The particle sizes 2, 4, 8 and 16 mm, which appeared to be preferred above 0.050 mm - 1 mm in all previous experiments, were offered together with mixtures (equal amounts of both particle sizes on volume basis) with 0.5 and 1 mm, respectively. In a first series, the larvae could choose from 4 substrates, only the four particles sizes or the four mixtures (Fig. 32a - c); in a second series the choice was from 8 substrates, namely the four particle sizes and the four mixtures with 0.5 mm and 1 mm, respectively (Fig. 32d, e).

For the first series, it is clear that the attraction of the preferred particle sizes as a substrate changes when these particle sizes are mixed with finer grains. The preference for 2 mm decreased drastically when mixed with 0.5 mm or 1 mm. The preference for 16 mm, 4 mm and 8 mm (decreasing in this sequence) (Fig. 32a) changed to the sequence 4 mm, 16 mm and 8 mm in the mixture with 0.5 mm (Fig. 32b), although the change is not significant. In the mixture whith 1 mm particles (Fig. 32c) the preference changed to 8 mm, 4 mm and 16 mm, which is a complete reversion of the sequence. A possible explanation is that the accessibility of the 8-mm substrate increases when the interstices are filled with grains. Normally the interstices of 8 mm are too small for *M.sequax* to enter and the 8-mm grains too heavy to push aside without much effort. For 16-mm particles it is not necessary and for 4-mm particles it is obviously no problem to push aside the grains. In the mixture with 16-mm particles, the removal of 1-mm grains is probably not enough to make the interstices accessible, while the 16-mm grains are too heavy to handle. Why the mixture of 8 mm with 1 mm is preferred might be connected with the instability of the mixture: the coarse grains may roll aside easier when the fine grains are removed. Particle sizes smaller than 1 mm are not preferred (Fig. 30), possibly because they offer too much resistance and demand too great an effort for penetration.

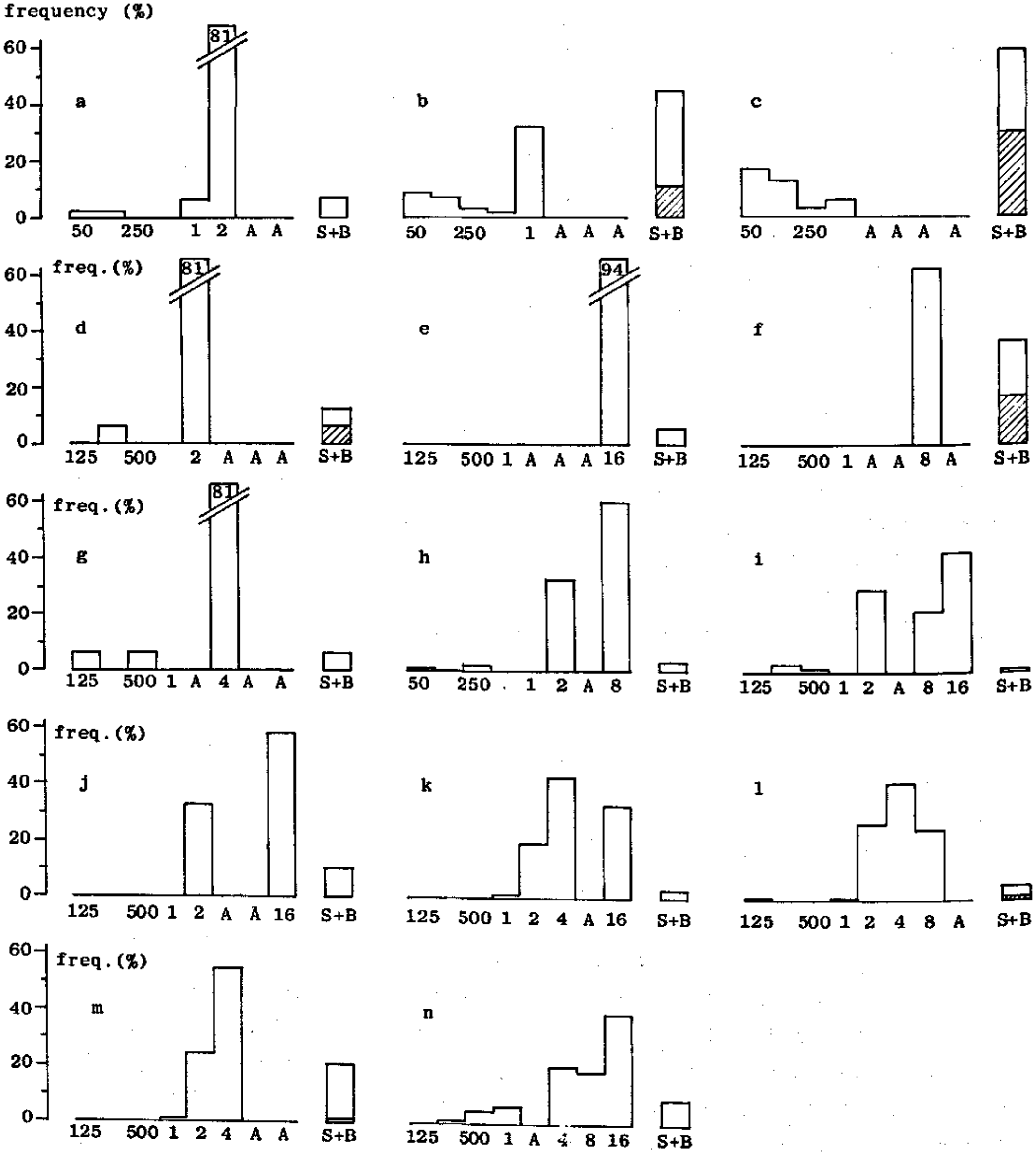
From the experiments discusses above, it is clear that 1 mm can still be used by part of the population, which means that the resistance of this particles size is not insurmountable (Fig. 31b), while in 0.5 mm and smaller particles, the animals hardly burrow at all, show no preference and keep moving around (Fig. 31c).

In the second series, in which the larvae had the choice between the four bare grain sizes and the four mixtures with 0.5-mm and 1-mm particles (Fig. 32d and e), *M.sequax* clearly preferred grain sizes not mixed with 0.5 mm or 1 mm particles, with a significant preference for 16 mm particles. No differences between the mixtures were observed.

Case type and substrate selection A series of experiments with *M.sequax* in different case types was conducted: animals with an 'almost' pupal case, already closed on one side with coarse grains (see subsection on case building),the so-called half pupae; animals with a mineral case; and animals with a partly mineral, partly organic case (mixed cases)(see table 5).

Half pupae preferred the three coarsest grain sizes (Fig. 32f) without any preference for a specific grain size. This agrees with the distribution in the field of the largest larvae and pupae, which preferred substrates with at least 25% coarser than 2 mm. All other case types showed the same preference as previous experiments (Fig. 32g, h), although larvae with a mineral case preferred 8 mm after the first choice of 16 mm. In the previous experiments larvae with mixed cases were always used, and it is logical that the same preferences for 16 and 4 mm were found. The difference between larvae with mineral and mixed cases can possibly be explained by the stronger penetrating ability of larvae with mineral cases. Partly organic cases are more easily damaged. On the other hand, the animals in mineral cases may be closer to pupation, because animals with partly organic cases still have to replace the organic material by mineral particles.

A series of experiments with larvae with mineral and mixed cases on substrates consisting of a monolayer of 2, 4, 8 or 16 mm grains on a base of 0.5 mm and 1 mm



(Fig. 32i and j), respectively, showed that the preference for 16 mm and 4 mm remains for both case types, but the relative preferences are reversed. Of course, the difference in grain size of the base may be of influence, but possibly also the larger penetrating ability of larvae in mineral cases may cause the preference for 4 mm. Larvae in 16 mm were mostly present on the base, not or only half burrowed beneath the 16 mm grains, while those in 4 mm had completely disappeared from view.

Differences between instars A series of experiments with larvae of different age on substrates of 0.125 - 16 mm showed that the preference for 16 mm is similar in all instars studied (Fig. 32k: F-2; Fig. 32l: F-1; Fig. 30d : F). F-1 and F-2 instar larvae were very active and less inclined to hide by burrowing into the substrate than the F instar larvae. This is illustrated by the large number of larvae on the end retaining screens.

An experiment on the influence of current speed on the substrate selection of the larvae showed that the preference of last instar larvae is not influenced by the current (Fig. 30d). Younger larvae (F2), however, positively selected the downstream substrates at high current speeds (10 cm/s) (Fig. 32m).

Leafpacks as substrate placed on a mineral base Offering *M.sequax* a leaf pack (beech) in a small 12 mm mesh basket, placed on top of the 0.125 mm substrate, together with the mineral substrates 0.125 - 16 mm, F-2 instar larvae preferred the leaf packs (Fig. 33a, b), while the animals are very active as seen by the large number of screen animals. Offering these larvae a mixture of 0.5 - 4 mm (all grain sizes in equal proportion of a quarter) and the single grain sizes 0.5, 1 and 2 mm, they showed preference for the mixture, although again a large number of animals was found

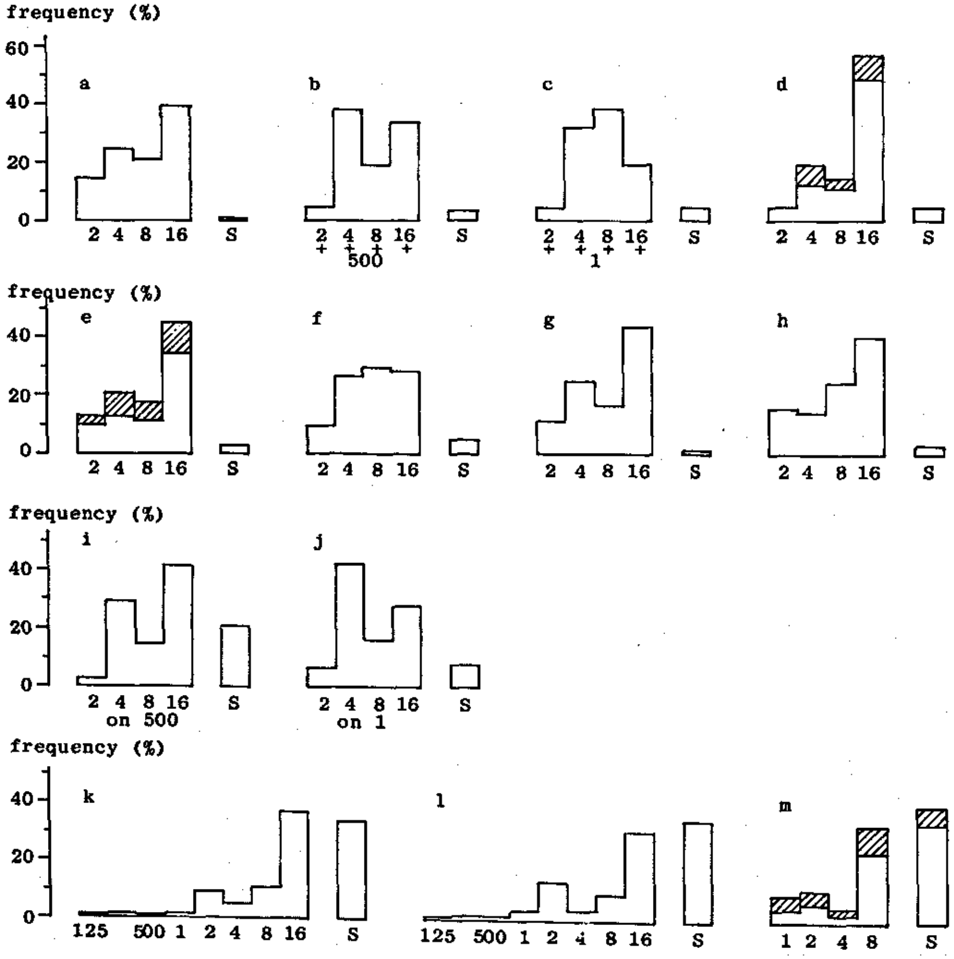
Fig. 31. Substrate selection in laboratory experiments by *Micropterna sequax*. Grain-size fractions are indicated by the lower limit of the fraction in µm (under 1 mm) and mm (over 1 mm). S = end retaining screen; B = bottom of reversed tray (shaded); A = absent.

Figure no.	Case type	Instar	Body length /mm	Number of experiments	Number of larvae per experiment	Note
a	mixed	F	> 15	5	16	4 and 8 mm absent
b	mixed	F	> 15	5	16	2,4 and 8 mm absent
c	mixed	F	> 15	5	16	1,2,4 and 8 mm absent
d	mixed	F	> 15	1	16	4,8 and 16 mm absent
e	mixed	F	> 15	1	16	2,4 and 8 mm absent
f	mixed	F	> 15	1	16	2,4 and 16 mm absent
g	mixed	F	> 15	1	16	2,8 and 16 mm absent
h	mixed	F	> 15	5	16	4 mm absent
i	mixed	F	> 15	4	16	4 mm absent
j	mixed	F	> 15	5	16	4 and 8 mm absent
k	mixed	F	> 15	14	16	8 mm absent
l	mixed	F	> 15	35	16	16 mm absent
m	mixed	F	> 15	5	16	8 and 16 mm absent
n	mixed	F	> 15	4	16	2 mm absent

on the screens (Fig. 33c). F-1 instar larvae with mixed cases (1/3 - 1/2 organic) on 0.250 - 2 mm, with a leaf pack on 0.250 mm, distinctly preferred the leaf pack and 2 mm, with a relatively low number of screen animals (Fig. 33d).

Giving a leaf pack on all mineral substrates (0.5 - 4 mm), the pack on 4 mm is preferred (Fig. 33e), while in sections without a leaf pack and the same mineral substrates (Fig. 33f), 2 and 4 mm are selected with a much higher number of screen animals. F-1 instar larvae on 1-8 mm, each provided with a leaf pack, preferred the leaf pack on 1 mm and there were no significant differences between the other leaf packs or the mineral substrate (Fig. 33g). Given the choice between 1-8 mm, the fractions of 2, 4, and 8 mm are equally chosen with large numbers of animals on the screens (Fig. 33h).

In an experiment where 0.125 - 16 mm particles were mixed with coarse detritus (small pieces of beech leaves) *M.sequax* showed no significant differences in grain-size selection (compare Figs. 33i and 30d), indicating that the selection of 16 and 4



mm substrate is a real preference for these particle sizes when food conditions are favourable, but Figs. 33a, d, and e indicate that when food conditions (leaf packs) are more favourable on other substrate types, food is the main selection criterion.

Concluding it can be stated that *M. sequax* prefers leaf packs above mineral substrates. However, when leaf packs are absent they clearly prefer coarse particle sizes (coarser than 2 mm), in particular 16 - 32 mm and 4-8 mm. The fraction 8-16 mm is less preferred; this might be related to the penetrability of the substrate. No significant differences were observed in substrate selection between the three last larval instars.

Comparison with the distribution in the field (Table 27) shows that substrates with a large proportion around 8-16 mm (Q_1 or $M_d = \bar{4}$) are avoided, but when most of the substrate is coarser than 8-16 mm ($Q_3 = \bar{4}$) the substrate may actually be preferred. The similarity in substrate preferences found in the field and the laboratory is further illustrated in Fig. 34, upon which both the particle sizes selected in experiments in the laboratory and the substrates preferred in the field (based on both Snijb and Rab data in Sorts 5 to 8, 10%) have been projected on the $Q_1M_dQ_3$ graph. Thus the results of the laboratory experiments confirm the substrate preferences observed in the field, especially concerning the shift of preferences from detritus substrates in autumn - when detritus is abundant - to coarse mineral substrates in winter and spring - when detritus substrates become less abundant and it forms a more integrated part of the mineral substrates. The preference of F-1 instar larvae (10-15

Fig. 32. Substrate selection in laboratory experiments by *Micropterna sequax*. Grain-size fractions are indicated by the lower limit of the fraction in µm (under 1 mm) and mm (over 1 mm). S = end retaining screen.

Figure no.	Case type	Instar	Body length /mm	Number of experiments	Number of larvae per experiment	Note
a	mixed	F	> 15	16	16	
b	mixed	F	> 15	10	8	mixtures with 0.5 mm
	mixed	F	> 15	2	16	mixtures with 0.5 mm
c	mixed	F	> 15	10	8	mixtures with 1.0 mm
	mixed	F	> 15	2	16	mixtures with 1.0 mm
d	mixed	F	> 15	5	32	bare (unshaded) and mixed with 0.5 mm (shaded)
e	mixed	F	> 15	5	32	bare (unshaded) and mixed with 1.0 mm (shaded)
f	½ pupal	F	> 15	2	12	
	½ pupal	F	> 15	12	8	
g	mixed	F	> 15	6	12	
	mixed	F	> 15	8	8	
h	mineral	F	> 15	8	8	
	mineral	F	> 15	6	12	
i	mixed	F	> 15	7	16	a monolayer on 0.5 mm
j	mineral	F	> 15	7	16	a monolayer on 1.0 mm
k	mixed	F-2	6-10	6	32	
l	mixed	F-1	10-15	6	32	
m	mixed	F-2	6-10	6	32	upstream(shaded),downstream (unshaded)

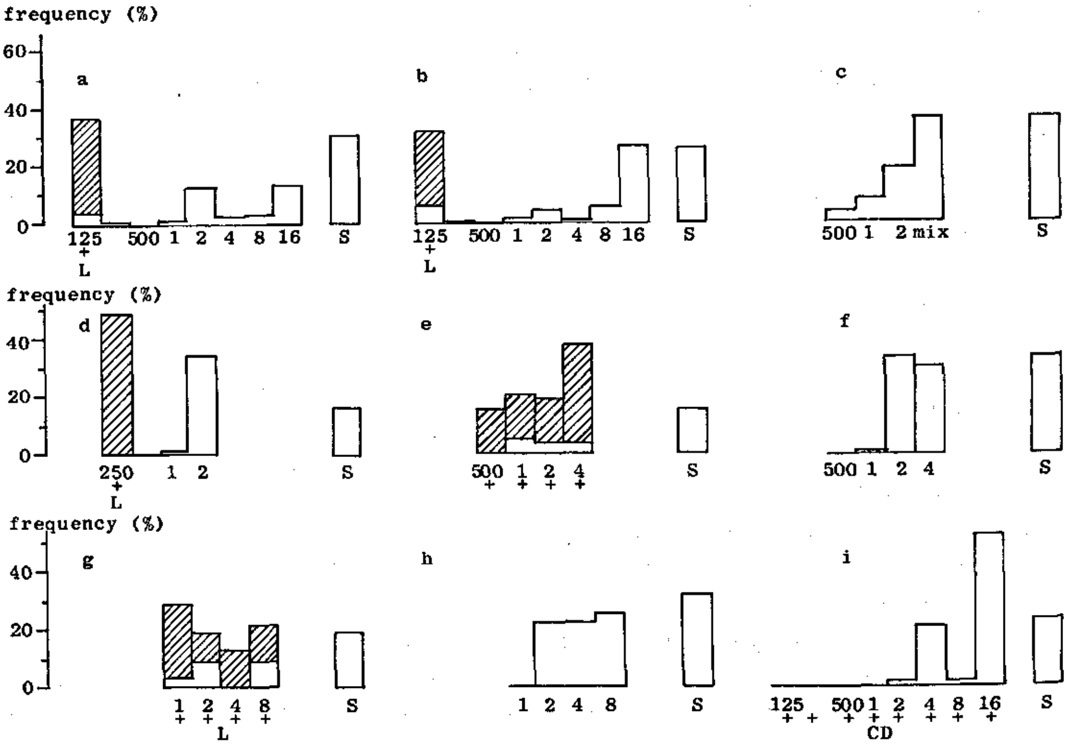


Fig. 33. Substrate selection in laboratory experiments by *Micropterna sequax*. Grain-size fractions are indicated by the lower limit of the fraction in µm (under 1 mm) and mm (over 1 mm). L = leaves; S = end retaining screen; CD = coarse detritus.

Figure no.	Case type	Instar	Body length /mm	Number of experiments	Number of larvae per experiment	Note
a	mixed	F-2	6-10	5	32	leaf pack (shaded) on 0.125 mm
b	mixed	F-2	6-10	5	32	leaf pack (shaded) on 0.125 mm
c	mixed	F-2	6-10	5	16	mixture of 0.5+1+2+4 mm
d	mixed	F-1	10-15	5	16	leaf pack (shaded) on 0.250 mm
e	mixed	F-1	10-15	5	16	leaf pack (shaded) on all
f	mixed	F-1	10-15	5	16	
g	mixed	F-1	10-15	4	8	leaf pack (shaded) on all
h	mixed	F-1	10-15	4	8	
i	mixed	F	> 15	3	16	all mixed with CD

mm) for sand substrates (Table 28) could not be confirmed in experiments (Fig. 33d-k), but it is problably explained by the presence of coarse detritus in the sand substrate, although it is less than 10%.

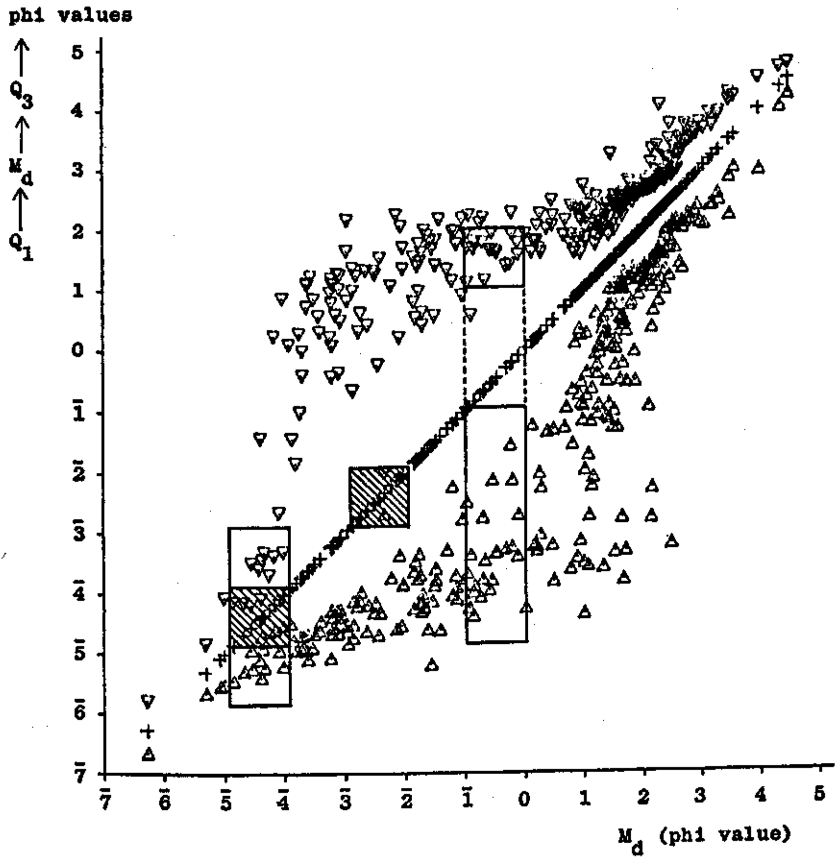


Fig. 34. Comparison of substrate preferences in the field (unshaded) with particle-size selection in laboratory experiments (shaded) for *Micropterna sequax.*

4.2.2.4 Chaetopteryx villosa (Fabricius) (Trichoptera: Limnephilidae)

Life cycle Chaetopteryx villosa has a univoltine life cycle (Fig. 35), with a relatively late flight period in autumn. In the rearing channel, emergence started mid-October and continued till early December, which agrees with the peak in November reported by Svensson (1972), although he stated a total flight period from mid-September until January. Décamps (1968) often found adults in the snow. Hickin (1967) gave a shorter period: only the second half of October, but Gledhill (1960) reported the first adults in the middle of August with a peak in emergence in the middle of October.

Adults always fly in upstream direction at night (Elliot, 1971) and deposit their eggs above the water. The eggs develop very fast, partly before winter while part of the eggs overwinters. In May, first instar larvae can be still found. Early hatched larvae overwinter in the first or second instar (Dittmar, 1955) and start

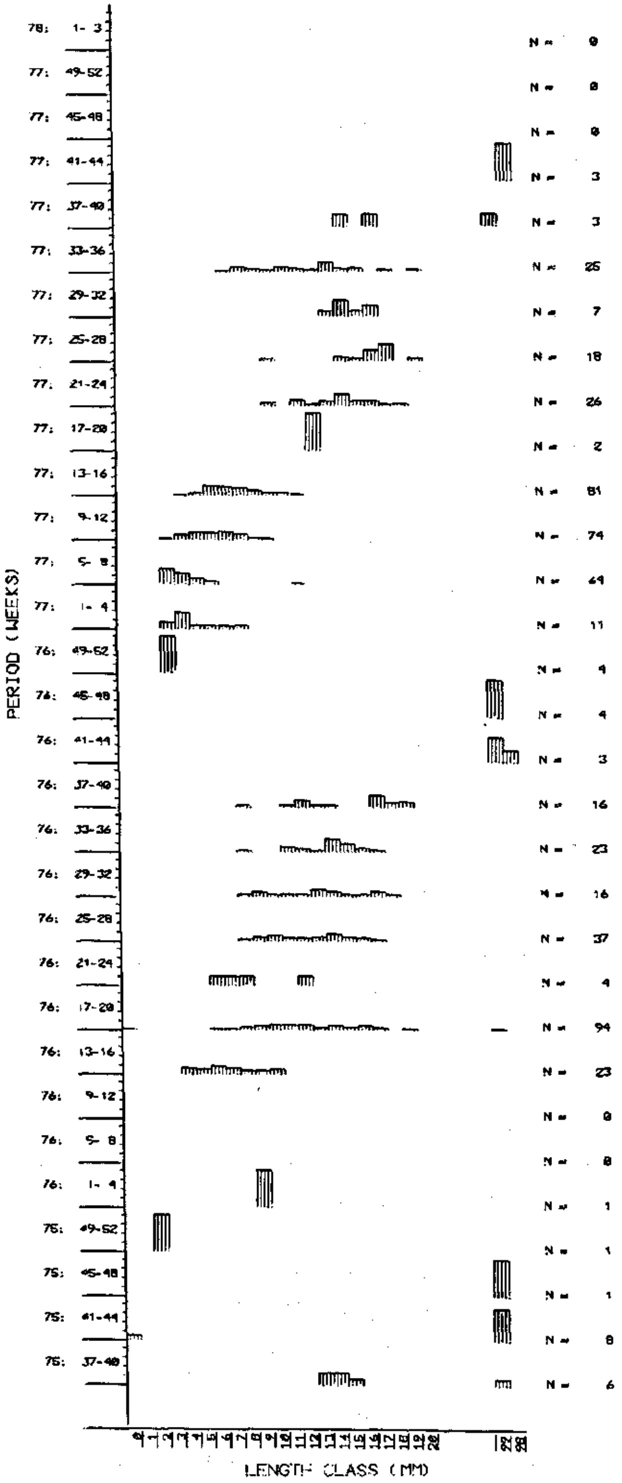


Fig. 35. Life cycle histograms of *Chaetopteryx villosa* showing the distribution (%) of larval body length, pupae (99) and adults (98) per four-week period.

growing again in April (Elliot, 1971), although in the Snijdersveerbeek this seems to be earlier (Fig. 35). Elliot (1971) distinguished 5 larval instars on the basis of the head capsule width. This is confirmed by measurements by Tolkamp & Verdonschot (to be published). Larvae become at most 16 mm long and 3 mm wide.

In summer the larvae undergo a resting period (Denis, 1978) in the last instar, in which they pass from spring to autumn. This observation does not fully agree with the larval sizes found in the present research, as growth was still observed in summer (Fig. 35).

Case building According to Elliot (1971) *Ch.villosa* larvae build a case of vegetable material in the first instar, often with various parts projecting in all directions (a so-called shoddy case). Starting from the fourth (F-1) instar, mineral matter is used also. In the fifth (F) instar mineral matter is often the only building material with perhaps some small pieces of leaf material at the rear end.

From the data of the Snijdersveerbeek this tendency is also apparent and will be described in detail by Tolkamp & Verdonschot (to be published). However, the choice of building material depends strongly on the inhabited environment, which indicates that mimesis may play an important role, as already reported for *M.sequax*. *Ch.villosa* uses leaf and mineral material in all instars, although the first three instars use relatively more organic material and the last two instars more mineral matter. Of the mineral material there was a significant preference for the 1-2 mm and 0.5 - 0.85 mm fractions in the last instars, with a decrease of the still finer fractions with increasing instar (Fig. 36).

Similar changes from vegetable to mineral matter have been observed for many members of the Limnephilidae family and have been described by Cummins (1964) and Mackay (1977) for *Pycnopsyche* spp. From research on *Potamophylax latipennis* by Zintl (1976) and on *Lepidostoma hirtum* by Hansell (1972; 1974) it is clear for at least these two species that a change in building material and style is not based on environmental factors but on a complex of endogenous factors. Elliot (1971) concluded the opposite for *Ch.villosa*. He correlated the change from organic to mineral building material after the third instar with a migration of the larva from vegetable to mineral substrates. The latter phenomenon is also observed in the present study, although it was not directly linked with the instars, because all instars used leaves as well as mineral particles.

Pupal cases resemble last instar cases, but they are closed with sieve-like membranes covered with coarse mineral particles. They resemble the pupal cases from *M.sequax*, but are smaller and often still contain some organic material. A similar closing system is used: the larva closes the front with 1-2 and 2-4 mm grains, opens the rear, sometimes removes the organic material and extends the case with mineral matter if necessary, burrows perpendicularly into the substrate and closes the new front with material at hand. The grain sizes used for closing both ends vary from 0.5 - 8 mm.

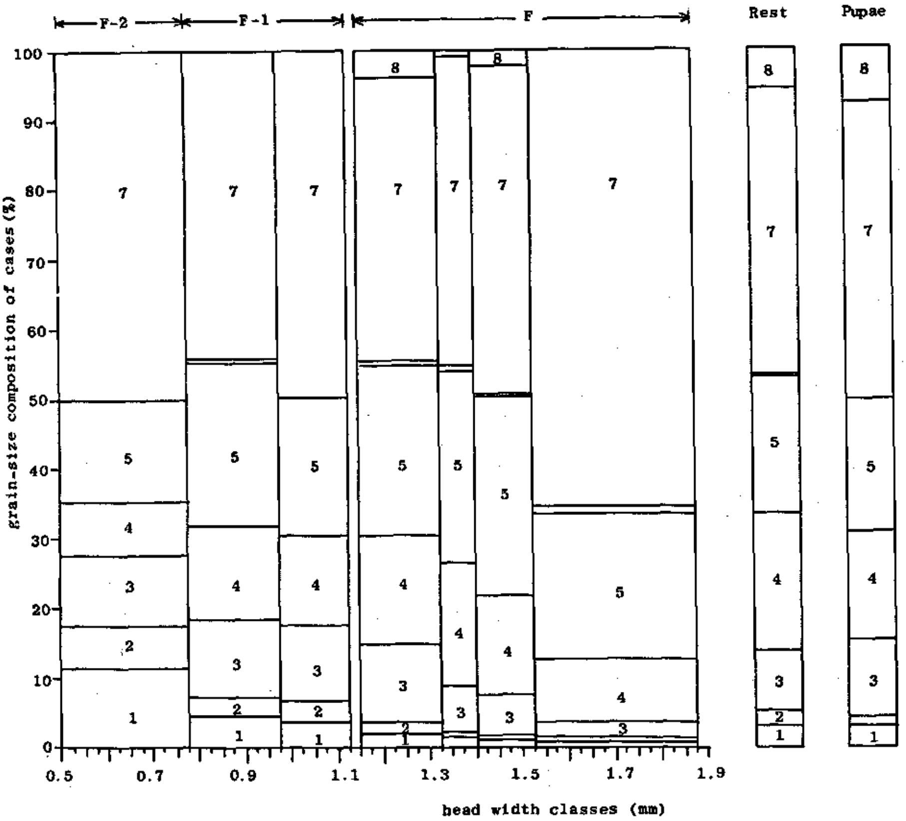


Fig. 36. Distribution (%) of grain-size fractions in natural cases of *Chaetopteryx villosa* . 1 = 0.105 - 0.210 mm; 2 = 0.210 - 0.250 mm; 3 = 0.250 - 0.350 mm; 4 = 0.350 - 0.500 mm; 5 = 0.500 - 0.850 mm; 6 = 0.850 - 1.0 mm; 7 = 1.0 - 2.0 mm; 8 = 2.0 - 4.0 mm; 9 = 4.0 - 8.0 mm.

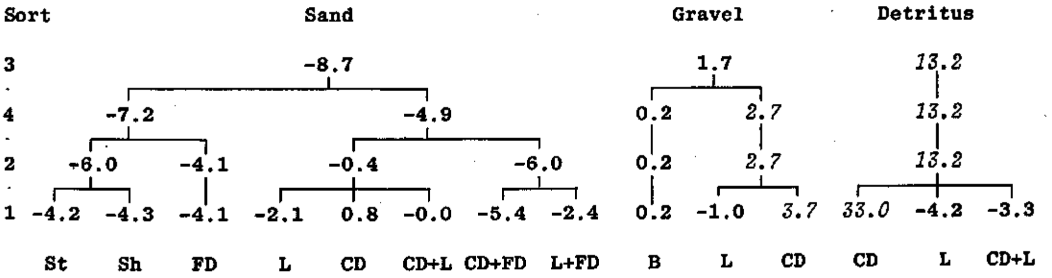
Elliot (1971) stated that the adults are quite capable of flying into the wind (at night, in upstream direction to compensate for drifting young larvae). However, during the day the adulst are bad flyers (personal observation). Observations by Tolkamp & Verdonschot that many more juvenile larvae are found in the upstream sections of the Snijb and more older larvae in the downstream sections confirm Elliot's observation on the presence of a colonization cycle (Müller, 1954).

Microdistribution In all substrate classifications, *Ch.villosa* obviously prefers the organic substrates (Table 29 and 30), although a slight preference for coarse mineral substrates (Gravel and Detritus) can be observed as well.

From Table 31A, giving the I.R. values for all length classes, it is clear that the preference for organic substrates is primarily caused by juvenile larvae (maximum length 7 mm). Larger larvae (12-20 mm) prefer mineral substrates with $Q_1 < \bar{1}$ and preferably $M_d \leq \bar{1}$ (coarser than 1 mm).

Animals of the length Class 8 - 11 mm were most abundant in Coarse Detritus, but

Table 29. I.R. values for *Chaetopteryx villosa* (N = 386) in the field classification of the substrates in the Snijdersveerbeek.



Italic values indicate significant over-representation

Table 30. I.R. values for *Chaetopteryx villosa* (N = 386) in the grain-size classification of the substrates in the Snijdersveerbeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,10%	*5.0*	-0.6	*2.6*	-0.1	-2.8	-2.2	-0.5	-5.8	-6.6	-3.8	-	*27.7*	-3.6	-3.6
Sort 6,10%	*5.0*	-1.0	-3.0	*3.1*	*2.7*	-0.9	-0.7	-1.6	-6.1	-6.6	-	*27.7*	-3.6	-3.6
Sort 7,10%	-	*5.0*	-1.8	-2.0	-1.0	-2.0	0.8	*5.7*	-3.8	-7.0	-2.7	*27.7*	-3.6	-3.6
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,10%	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

Italic values indicate significant over-representation

they have already partly moved to the coarse mineral substrates where the largest larvae are found. Pupae were exclusively found in mineral substrate with a preference for M_d between 2 and 8 mm (phi = $\bar{3}$ and $\bar{2}$) or $\bar{x}\bar{3}x$, $\bar{x}\bar{2}x$ substrate (Q_1 and $M_d \leq \bar{1}$). In leaf packs hardly any *Ch.villosa* larvae were found.

Similar preferences were probably present in the Ratumsebeek, but this could not be tested for the various instars by lack of sufficient material (only 60 specimens).

Considering the distribution between seasons, Table 31B shows that in winter and spring the highest preferences are found in Coarse Detritus, in addition to which in winter only negative I.R. values are found in mineral substrates. In spring there is also over-representation in $\bar{x}\bar{x}\bar{x}$ and $\bar{x}\bar{4}x$/$\bar{x}\bar{5}x$ (M_d resp. $\bar{7}$ and $\bar{4}$). In summer the preference is solely for mineral substrate, when organic substrates yield only negative I.R. values. In autumn there is a shared preference for mineral and organic substrates which concerns pupae, prepupae and burrowing larvae and feeding larvae. Comparison of

Table 31. I.R. values for *Chaetopteryx villosa* per length class (A) and season (B) in the Snijdersveerbeek in Sort 8,10%.

Length class and Season	N	Substrate class and $Q_1M_dQ_3$ index													
		1 $\bar{x}\bar{x}\bar{x}$	2 $\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	3 $\bar{x}\bar{3}x$	4 $\bar{x}\bar{2}x$	5 $\bar{x}\bar{1}x$	6 $\bar{x}1x$	7 $\bar{x}xx$	8 1xx	9 22x	10 23x	11 33x	12 CD	13 L	14 CD+L
A 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
99 - 98	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
B Spring	201	*2.1*	*3.5*	-2.4	-1.1	1.1	-3.2	-2.8	-4.6	-3.1	-2.0	-1.6	*16.0*	-2.8	-3.2
Summer	85	*2.9*	-1.3	*7.2*	-0.6	-0.5	*2.1*	0.4	-1.6	1.0	-3.8	-2.2	-0.7	-	-
Autumn	27	-0.9	-1.1	*4.5*	1.3	-1.3	-0.8	1.2	-1.2	-1.1	-1.8	-0.9	*3.8*	-0.6	-0.8
Winter	73	-1.5	-2.0	-1.8	-1.1	-2.2	-0.6	-1.5	-2.9	-2.7	-1.6	-1.5	*26.5*	-1.8	-2.0

Italic values indicate significant over-representation

these seasonal differences with the differences between the various instars shows a remarkable conformity in the distributional changes under the influence of larval size (age). *Ch.villosa* seems to be very well adapted to the seasonal changes in the abundance of substrate types and food resources (coarse detritus).

Chaeptopteryx is a detritivore and the larvae use the enzymes pectinase and xylanase to break down vegetable matter (Bjarnov, 1972). Dittmar (1955) found that the larvae occur in combination with macrophytes, where they feed on detritus, filamentous algae and diatoms, although they also predate on chironomids and caddis larvae. In the rearing channel, Ch.villosa was often observed feeding on cases, larvae or pupae (mostly those with still some organic material in their cases) of its own species.

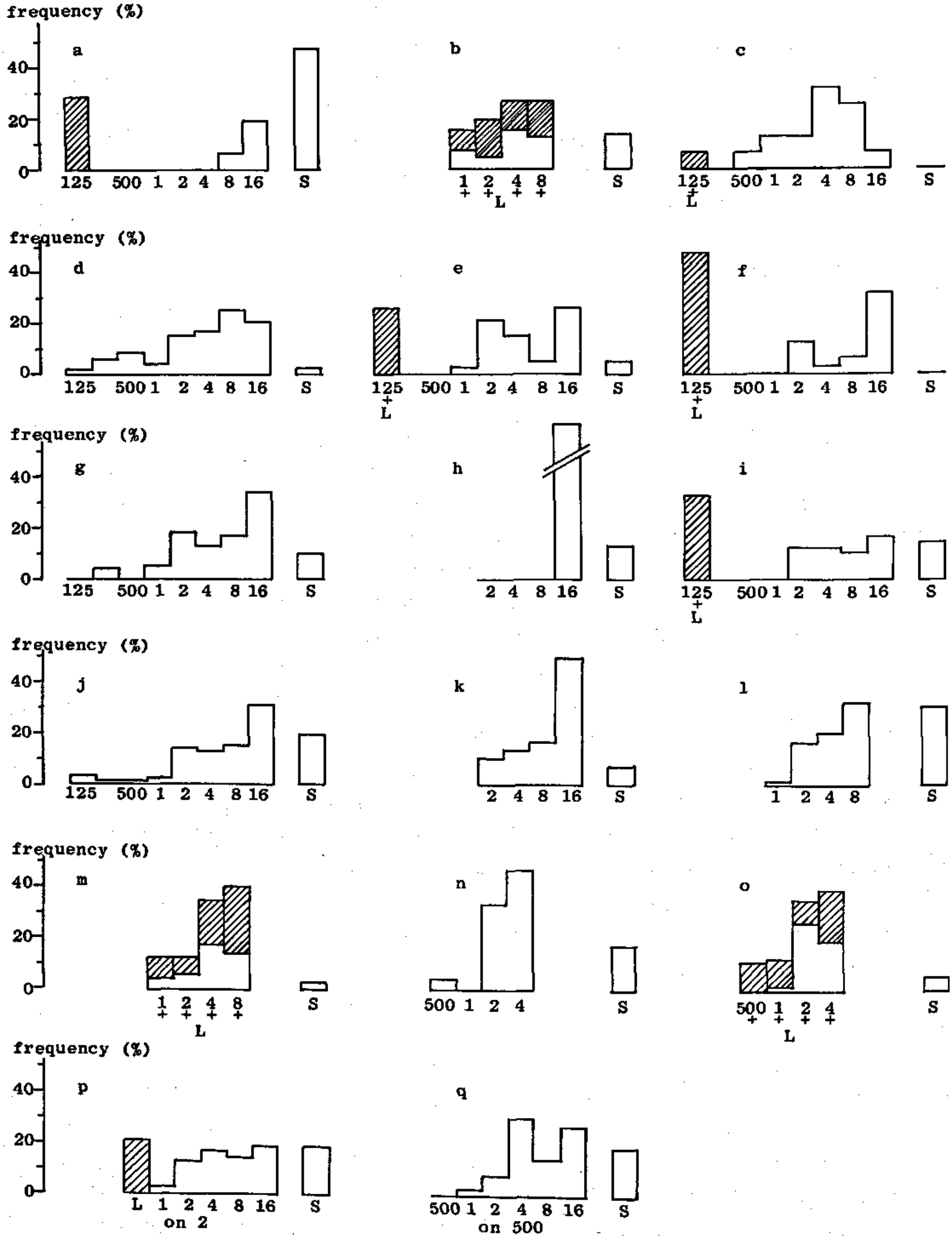
In winter, when detritus is abundant in the streams, the larvae are small and they build organic cases and inhabit detritus substrates on which they feed. During spring and into summer, when detritus substrates become more scarce the larvae grow and move to mineral substrates, although these will still contain enough organic material, or will be situated in the neighbourhood of detritus substrates, to provide food, which is consumed at night (personal observation). In summer and early autumn detritus substrates are very scarce and this might form part of the explanation for a possible resting period in this time of year. Apart from the observation by Petran (1977), Kamler & Riedel (1960) also found *Ch.villosa* to be the only thrichopteran occurring in desiccating sections of a stream. Illies (1952) stated for Ch.villosa that it is an inhabitant of lower courses and that it may penetrate into middle courses. The distribution of *Ch.villosa* in the Netherlands is not completely known, but it probably occurs mainly in the smaller (upper course type) streams. Since

Ch.villosa is an eurythermous and moderately rheophilous limnephilid it occurs in quiet places, in pools of small streams or stagnating larger streams where temperature fluctuations may be high (Dittmar, 1955; Kamler & Riedel, 1960; Hynes, 1970a). Beyer (1932) found that many Limnephilidae are eurythermous (e.g. *M.sequax, S.rotundipennis, H.interpunctatus*) and he thought that *Ch.villosa* might be cold stenothermous. The observations made by the other above mentioned authors and by the data from the present research do not confirm this.

In his study on the emergence patterns of various insects in the Breitenbach, Illies (1978) found a contradiction in the emergence of the mayflay *Baetis vernus* and *Ch.villosa*, which he attributed to quantitative and qualitative changes in substrate mosaic patterns in the investigated stream section (the green house). After analysing several factors (temperature, food, water level) he supposed that the temporal variability in substrate patterns (between years) was the only possible factor responsible for the reciprocal abundance of *Ch.villosa* and *B.vernus*, assuming that they have opposite habitat (substrate) preferences. The data of the present research support Illies' assumption. *Ch.villosa* clearly needs more than one substrate type to complete its life cycle in a stream, while *Baetis vernus* largely prefers the (sheltered places of) very coarse mineral substrates together with the sand + detritus substrates (Appendix 12). The latter is in accordance with the food preferences of *B.vernus* (algae and detritus). *Ch.villosa*, however, needs organic substrates in winter and spring, when the larvae are growing fast, and coarse mineral substrates in summer and autumn for resting and pupation. It is very likely that temporal substrate variation played a role in the greenhouse where the emergence of these species was recorded by Illies (1978). When sand and detritus substrates, perhaps together with some large stones, are present in spring, this habitat will be favourable for *B.vernus*, which emerges in May/June. *Ch.villosa* will avoid burrowing in these substrates to pass the summer. On the other hand, when coarse, gravelly substrates dominate, these will offer suitable burrowing sites for *Ch.villosa* to spend the summer and to pupate in August/September. These conditions are unfavourable for *Baetis vernus*.

Substrate-selection experiments All experiments with *Ch.villosa* were conducted with last instar larvae with various case types (Fig. 37). All experiments lasted 8 or 24 hours. This gave no differences in substrate selection. After 14 hours the distribution of the larvae in the dark was recorded as well. The latter results will not be presented. In general the main preferences seen by day remained at night, although the distribution was less pronounced and more grain sizes were inhabited at night. The most remarkable feature at night was that the larvae were most abundant on the end retaining screens or at the edges of the experimental area, where they were obviously in search for more suitable substrates or food. The results of the experiments with Ch.villosa are summarized in Fig. 37.

In all experiments where a leafpack was present on one or more of the mineral substrates, leaves were the preferred substrate type for all case types (Fig. 37a, b,


frequency (%)
40
20
0
a
125 500 1 2 4 8 16
S
b
1 2 4 8
+ + + +
L
S
c
125 500 1 2 4 8 16
+
L
S
frequency (%)
40
20
0
d
125 500 1 2 4 8 16
S
e
125 500 1 2 4 8 16
+
L
S
f
125 500 1 2 4 8 16
+
L
S
frequency (%)
40
20
0
g
125 500 1 2 4 8 16
S
h
2 4 8 16
S
i
125 500 1 2 4 8 16
+
L
S
frequency (%)
40
20
0
j
125 500 1 2 4 8 16
S
k
2 4 8 16
S
l
1 2 4 8
S
frequency (%)
40
20
0
m
1 2 4 8
+ + + +
L
S
n
500 1 2 4
S
o
500 1 2 4
+ + + +
L
S
frequency (%)
40
20
0
p
L 1 2 4 8 16
on 2
S
q
500 1 2 4 8 16
on 500
S

e, f, i, m, o). except for larvae with half-pupal cases, which preferred mineral substrates i.e. 4 and 8 mm (Fig. 37c). Together with a preference for leaves, the (partly) mineral case types selected particle sizes coarser than 2 mm, with a distinct preference for these mineral particles when leaf packs were absent (Fig. 37g and j). Larvae with half-pupal cases also selected the same particle sizes in the absence of a leaf-pack (Fig. 37d) although slight, but not significant, differences did occur. Larvae in organic cases, however, only showed a slight over-representation in 16 mm, but were abundant on the screens or walking around (Fig. 37a).

In the experiment where the larvae could choose between all grain sizes from 0.125 - 16 mm, the preference was clearly for the coarsest particle sizes, where 16 mm and 2 mm were selected mostly by the larvae in mineral cases (Fig. 37e, f, g). Larvae with half-organic, half-mineral, cases showed a distinct preference for 16 mm only, with an equal distribution over the other three coarse particle sizes (Fig. 37i, j).

In experiments with only a choice between these 4 coarse particle sizes, the same preferences of the half-mineral, half-organic cased larvae occurred (Fig. 37k), while larvae with mineral cases chose 16 mm exclusively (Fig. 37h). Larvae with cases consisting of one third organic and two thirds mineral material also selected the two coarsest particle sizes in the presence (Fig. 37m, o) as well as absence (Fig. 37l, n) of leaf packs, although in the presence of leaf packs the preference was higher for leaves, but especially for the leaf packs on the preferred mineral particle size (shaded area in Fig. 37m and o).

Larvae in organic cases show a similar selection of the leaf packs but not

Fig. 37. Substrate selection in laboratory experiments by last (F) instar larvae of *Chaetopteryx villosa*. Grain-size fractions are indicated by the lower limit of the fraction in µm (under 1 mm) and mm (over 1 mm). L = leaves; S = end retaining screen. (1/2 - 1/2 : 1/2 organic, 1/2 mineral)

Figure no.	Case-type	Number of experiments /mm	Number of larvae per experiment	Note (leaf packs : shaded) (mineral : unshaded)
a	organic	2	16	leaf pack on 0.125 mm
b	organic	5	16	leaf pack on all substrates
c	½ pupal	1	16	leaf pack on 0.125 mm
d	½ pupal	3	16	
e	mineral	4	16	leaf pack on 0.125 mm
f	mineral	1	32	leaf pack on 0.125 mm
g	mineral	3	32	
h	mineral	1	16	
i	1/2 - 1/2	2	24	leaf pack on 0.125 mm
j	1/2 - 1/2	6	24	
k	1/2 - 1/2	2	32	
l	1/3 - 2/3	5	16	
m	1/3 - 2/3	5	32	leaf pack on all substrates
n	1/3 - 2/3	5	16	
o	1/3 - 2/3	5	16	leaf pack on all substrates
p	1/3 - 2/3	5	24	monolayer on 2 mm
q	1/3 - 2/3	5	24	monolayer on 0.5 mm

linked to the mineral substrate, while the selection of the two coarsest grain sizes is less pronounced (Fig. 37b). When these larvae have the choice between a monolayer of several grain sizes on a base of 2 mm, together with a leaf pack on 2 mm, there is no distinct preference for any substrate (Fig. 37p). When placed on 0.5 mm, 4 mm and 16 mm are selected, which indicates that not only the surface of a substrate is important for selection of burrowing sites, but also the composition of the underlying material.

From all these experiments it is clear that for *Ch.villosa* leaf packs form the most preferred substrate, after which coarse particle sizes larger than 2 mm are favoured, especially 16 mm. The selection of leaf packs can be seen for all larval case types, but the preference for mineral substrate is higher for larvae with partly or completely mineral cases than for larvae with purely organic cases. Larvae very close to pupation significantly prefer coarse mineral substrates, which agrees with the field study (Table 31a: 16-20 mm larvae). An additional observation is that larvae found on the four finest substrates were often building or repairing their cases or starting to build their half-pupal case. Some of the half-pupae even closed their case during an experiment, which made it necessary to replace them.

Field experiments with artificial substrates In the Ratumsebeek various grain sizes were offered for colonization. These artificial substrates were collected after 14 and 28 days. In these (spring) experiments *Ch.villosa* occurred with 9 larvae in the replicates of 5 substrate types after 14 days; 6 of these larvae occurred in 32 mm (Table 32). After 28 days, with 9 substrate types, 42 larvae were found, 18 of which occurred in 32 mm (Table 32). This clearly indicates that *Ch.villosa* preferred the coarsest grain size above the finer substrates (see Table 16). Moreover, 8 mm was avoided after both periods and a similar explanation as that given for *M.sequax* might be applicable, namely the impenetrability of this grain size.

4.2.2.5 Plectrocnemia conspersa (Curtis) (Trichoptera: Polycentropodidae)

Microdistribution *Plectrocnemia conspersa* is the only net-spinning Trichoptera species found in reasonable numbers in the Snijb. In the Rab only a few individuals were

Table 32. Number of *Chaetopteryx villosa* larvae in artificial substrate in the Ratumsebeek in April/May 1978 after 14 and 28 days of colonization.

Days of colonization	Number of larvae by grain size (mm)									Total
	32	16	8	4	2	1	0.5	0.25	0.125	
14	6	2	.	.	1	-	-	-	-	9
28	18	6	.	5	2	2	.	5	4	42

- = fraction not offerred

found. Other net-spinning Trichoptera, such as *Hydropsyche angustipennis*, *Lype reducta* and *Tinodes waeneri* were only found incidentally. *T.waeneri* was only found in the Rab and never in shovel samples but always on larger stones.

In the Snijb the distribution of *Plectrocnemia conspersa* is restricted to the detritus substrates, especially CD or L. The combination of CD and L is not preferred although a slight over-representation occurred (Table 33). In the grain-size classification (Table 34) the same distribution is seen. The slight preference for S+CD in Table 33 returns in Table 34 as a minor over-representation in the finest mineral substrate (33x), which resembles mud or fine sand with fine detritus. Coarse substrates are only inhabited by few *P.conspersa* larvae, probably because the current is too fast and because sand and pebbles are not lying loosely packed, which would offer dwelling sites, but are embedded in sand. Relatively high numbers were found in x̄xx and 1xx substrates with 17 and 10 individuals, respectively, in 39 samples in each type.

Plectrocnemia conspersa mainly occurs in relatively cold upstream regions (Décamps, 1968; Edington, 1968; Edington & Hildrew, 1973), where they dwell in slowly running water with current speeds not exceeding 20 cm/s, and preferably lower than 10 cm/s (Nielsen, 1942; Edington, 1968). They do occur in sites with faster currents (rapids, riffles) but then always in sheltered places under stones. They are most abundant in pools with detritus and stones overgrown with moss or algae (Beyer, 1932; Nielsen, 1942; Wesenberg-Lund, 1943; Jones, 1951). Edington & Hildrew (1973) demonstrated the longitudinal zonation of Polycentropodidae, where *P.conspersa* is replaced by *Polycentropus flavomaculatus* (cf. Nielsen, 1942) in the downstream sections. This is attributed to the influence of temperature, but is in fact based on circumstantial evidence and is not yet proved. However, Philipson & Moorhouse (1976) showed that the temperature tolerance of several species of Polycentropodidae is very important in longitudinal zonation and that this is directly linked with their ventilation behaviour for the oxygen intake (Philipson, 1978).

Plectrocnemia conspersa prefers substrate types where prey density is high

Table 33. I.R. values for *Plectrocnemia conspersa* (N = 233) in the field classification of the substrates in the Snijdersveerbeek.

Sort	Sand								Gravel			Detritus		
3	-4.4								-6.4			*16.7*		
4	-6.0			0.2					-6.3	-2.2		*16.7*		
2	-6.2		-1.4	*3.1*			-2.2		-6.3	-2.2		*16.7*		
1	-4.6	-4.1	-1.4	-0.9	*3.7*	1.6	-1.9	-1.1	-6.3	-1.5	-1.7	*12.4*	*12.8*	1.7
	St	Sh	FD	L	CD	CD+L	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

Table 34. I.R. values for *Plectrocnemia conspersa* (N = 233) in the grain-size classification of the substrates in the Snijdersveerbeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,10%	-0.8	-2.2	-5.0	-4.2	-1.4	-2.2	0.2	-2.8	-4.9	1.4	-	*13.3*	*12.5*	1.1
Sort 6,10%	-0.8	-0.8	-2.2	-3.9	-2.7	-2.9	-2.1	-3.2	-4.2	-2.4	-	*13.3*	*12.5*	1.1
Sort 7,10%	-	-0.8	-1.2	-1.6	-0.8	-1.6	-1.9	-4.4	-4.6	-5.3	1.5	*13.3*	*12.5*	1.1
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,10%	-2.3	-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

Italic values indicate significant over-representation

(Hildrew & Townsend, 1977), regardless of the kind of prey, because they are not selective feeders. *P.conspersa* is a 'sit and wait' predator (Hildrew & Townsend, 1976) that catches its food by a characteristic, but irregular, net consisting of a small dwelling tube (e.g. under a stone) that expands at both ends to form a funnel-shaped catching area. Mostly the largest funnel is directed upstream (Nielsen, 1942; Edington, 1968; Tachet, 1971). This net is very large, which is characteristic for species inhabiting slow-running water (Wallace, Webster & Woodall, 1977). It is coloured brown by attached detritus particles, which was regularly observed in the rearing channel where *P.conspersa* started spinning nets as soon as it was introduced. In small streams the nets may cover large surfaces giving the impression that the stream is overgrown with fungi or some kind of thread forming bacteria (cf. Wesenberg-Lund. 1911). *P.conspersa* consumes all animals drifting or swimming against the net and trapped in it (Dittmar, 1955; Edington, 1968), but especially micro-crustacea and insect larvae are eaten (Nielsen, 1942). Townsend & Hildrew (1978) found that all instars eat stoneflies and chironomids, but the smaller larvae consume more micro-crustacea and the larger larvae more prey from terrestrial origin. Detritus formed an important part of the gut contents of larvae, but it is not known whether this reflects active feeding on detritus or is the remains of the gut contents of prey animals (Winterbourn, 1978), although it is known for some species of Polycentropodidae that they feed on detritus as well, especially species inhabiting slow-running water (Malas & Wallace, 1977).

Capture nets only function statisfactory in slow-running waters, since they are damaged by high currents (Edington, 1968). This makes it improbable that *Plectrocnemia* is dependant on drift for its food supply. More likely, animals swimming against the net form the main prey organisms (Hildrew & Townsend, 1976). When a positive correlation of *P.conpsersa* with a certain substrate type is seen, this will be a functional response of *P.conspersa* to prey density, which means that substrate preferences of the prey will determine the distribution of *P.conspersa* (Hildrew & Townsend, 1977). In the Snijb, detritus substrates were the most densely populated substrates (especially chironomids), which explains why *P.conspersa* prefers these substrates. Moreover, to be able to build a net, *P.conspersa* needs substrates that project from the stream bed, such as stones, leafpacks and sticks (CD). These will be the sites where one should find *P.conspersa* larvae, and the data presented above fully confirm this for the Snijdersveerbeek.

4.2.2.6 Ephemera danica (Müller) (Ephemeroptera: Ephemeridae)

Population density *E.danica* was found in 107 of the 382 samples in the Snijdersveerbeek with 436 specimens. The nymphs only occurred in the Sections 4, 5, 6 and 8 (325 samples): in 60% of the samples in Section 6; in 45% of the samples in Section 5; in 14% of the samples in Section 8; and in 10% of the samples in Section 4.

In the Ratumsebeek, 504 specimens were found in 80 samples (out of a total of 195). Comparison of the density per surface unit reveals that this is much higher in the Rab than in the Snijb: 6.22 and 4.07 specimens, respectively, per sample of 150 cm^2, giving 414 and 271 per square metre. Compared with the densities given by Percival & Whitehead (1926) of 1850-2075 per square meter this is rather low, but the figures are in the same order of magnitude as reported for the related Ephemeridae nymph *Hexagenia limbata*: 266 (Lyman, 1955) and 758 per square metre (Neave, 1932). They are however, much higher than the figure Needham (1917/18) presented for *E.simulans*, 32 per square metre or Hunt (1953) gave for *Hexagenia limbata*, 127-365 per square metre, with an average of 153 per square metre. Zimmerman et al. (1975) showed that the densities of *H.limbata* are greatly dependant on the age of the nymphs and are always highest for younger nymphs and lowest for final instars, gradually decreasing with the increasing of age (size). They quote Hudson & Swanson (1972), who state that migration is most intensive in populations of more than 100 specimens per square metre. These data on age-correlated density are confirmed for *E.danica* in this present research, which shows the same pattern (Table 9 and 10, Subsection 4.1.3.3.)

Life cycle In the two streams under investigation, the life cycle of *E.danica* appeared to be bivoltine (Fig. 38), which is in agreement with data known from other areas (Landa, 1968; Sowa, 1975b; Svensson, 1976, 1977), although some authors found that it may be univoltine (Thibault, 1971) or trivoltine (Svensson, 1977), dependant on such environmental factors as temperature and photo period. Pleskot (1958, 1960) stated that it is commonly accepted that *E.danica* is univoltine and illustrated this with the fact that she hardly found nymphs in July. Considering the stream (the Schwechat, in Austria) she investigated, it is more likely that these data are unreliable because of the crude sampling method used and the joining of samples from

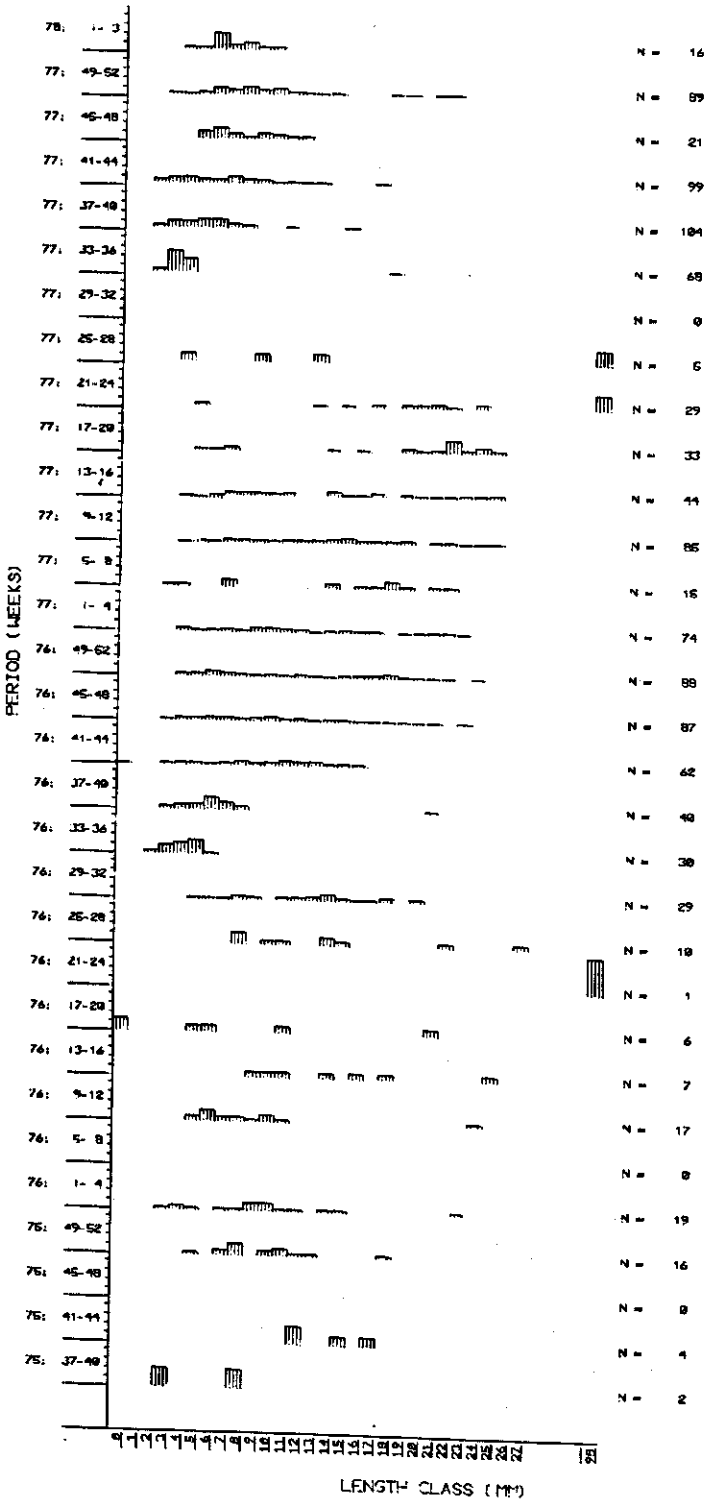


Fig. 38. Life cycle histograms of ***Ephemera danica*** **showing the distribution (%) of nymphal body length and adults (98) per four-week period.**

upstream and downstream areas of quite different temperature regimes.

In the Snijb and the Rab two cohorts are found on many occasions. The material was not investigated in enough detail (e.g. on wingpad development and distinction between males and females for older nymphs) to exclude with certainly the presence of univoltine specimens but their presence seems hardly likely. Some of the very large nymphs found in autumn might spend three years in the stream having missed the previous emergence period, although it is also possible that they have grown faster during the last summer than most others of the same age because of extremely favourable food conditions. In the Achterhoek, *E.danica* emerges from the end of May until the end of June (Weeks 21-26), after which the first young nymphs are found in August. They are by then already starting on their second or third moult. In the autumn there is a period of fast growth, while in the winter growth is retarded (cf. Thibault, 1971; Sowa, 1975; Svensson, 1977). The presence of very small nymphs from August into May indicates that at least some of the eggs or batches of eggs have retarded hatching.

The low number of small to average sized nymphs in the Rab in the spring of 1977 and the larger specimens in the autumn and winter 1977-1978 might be the result of the desiccation of parts of the stream in the summer of 1976. Early hatched nymphs may not have survived, leaving only the offspring of the 'resting' eggs, which is probably much smaller in number than that of early hatched eggs, considering the ratio between the number of small nymphs in Week 37-40 and those appearing after Week 45.

Microdistribution The field classification of the substrates shows clearly that in both streams the highest preference is for S+CD+FD in Sort 1 (Tables 35 and 36). Secondly, G+CD/FD and S+CD is preferred in the Snijb. In the Rab only a slight preference for G+L and S+FD was established. Detritus substrates were always avoided (only one specimen was caught in a leaf pack and this concerned a nymph ready to emerge from the stream and probably on its way to the water surface). Analysing Tables 35 and 36 at less detailed classification levels reveals that *Ephemera danica* prefers Sand far above Gravel in the Rab, but in the Snijb Gravel is chosen quite often, although always less than Sand, except in Sort 3.

In both streams, mineral substrates mixed and/or covered with Coarse and Fine Detritus are always preferred. This agrees with the preliminary conclusions drawn by Tolkamp & Both (1978), although some differences can be seen. However, the results of the laboratory analysis showed that some samples included in the S+FD substrate in the preliminary classification in fact belonged to the S+CD+FD substrate, because large amounts of CD were hidden below the surface and this knowledge had not been included in the field classification at that moment. Another reason for differences in the preferences found then and later may have resulted from the fact that the period January-April 1977 was not included in the preliminary data, which means that especially the smallest and largest specimens were under-represented in the arrangement of the preliminary results. This can have considerable influence on the total

Table 35. I.R. values for *Ephemera danica* (N = 436) in the field classification of the substrates in the Snijdersveerbeek.

Sort	Sand								Gravel			Detritus		
3	*2.1*								*2.7*			-7.5		
4	-4.9			*9.0*					-0.1	*5.0*		-7.5		
2	-5.4		-0.5	*2.7*			*9.3*		-0.1	*5.0*		-7.5		
1	-3.7	-4.0	-0.5	-3.0	*4.8*	0.9	*10.3*	0.4	-0.1	-1.3	*6.6*	-4.3	-5.3	-3.3
	St	Sh	FD	L	CD	CD+L	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

Table 36. I.R. values for *Ephemera danica* (N = 504) in the field classification of the substrates in the Ratumsebeek.

Sort	Sand								Gravel			Detritus		
3	*9.7*								-5.1			-9.8		
4	-2.9			*18.3*					-4.3	-2.7		-9.8		
2	-4.1		1.6	-1.5		*21.3*			-4.3	-2.7		-9.8		
1	-2.2	-3.9	1.6	-1.6	-1.0	-1.0	*24.2*	-0.4	-4.3	1.5	-3.4	-3.3	-9.1	-2.0
	St	Sh	FD	L	CD	CD+L +FD	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

results, because nymphs of different sizes show different substrate preferences (Tolkamp & Both, 1978).

Tables 37 and 38 give the I.R. values for the grain-size classifications. In both streams, the high preference for CD substrates (Class 14 or 12) at the 1% detritus level moves to the fine mineral substrates at the 10% level, which indicates that this concerns Sand substrates with 1-10% organic detritus. The distributional pattern seen in the field classification is repeated in Sorts 5-8: in the Snijb there is preference for Q_1 = 2, M_d = 3 and Q_3 = 3, seen in Sort 8 as 22x and 23x; but also for more gravelly substrate with Q_1 = $\bar{5}$, M_d = $\bar{3}$, $\bar{2}$, or $\bar{1}$ and Q_3 = 2 (Sorts 5-7), seen in Sort 8 as $\bar{x}\bar{3}x$, $\bar{x}\bar{2}x$ and $\bar{x}\bar{1}x$. In the Ratumsebeek, *Ephemera danica* prefers the well sorted materials with Q_1, M_d and Q_3 = 3, although Q_1 = $\bar{3}$ and $\bar{4}$, M_d = 2 and Q_3 = 3 or 4 is also favoured, which is confirmed in Sort 8 by 23x, 33x and $\bar{x}xx$. From this grain-size classification the difference between the two streams in the preference of *E.danica* for Gravel is again clear. In the Rab, *E.danica* occurs only in Sand substrates (M_d = 1 or more) with less than 50% gravel (Q_1 = $\bar{4}$, $\bar{3}$), while in the Snijb

Table 37. I.R. values for *Ephemera danica* (N = 436) in the grain-size classification of the substrates in the Snijdersveerbeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,1%	-1.1	-1.6	*5.3*	-0.5	0.6	-3.3	-4.4	-5.5	-1.9	-0.7	-	*10.2*	-5.3	-3.0
Sort 5,10%	-1.1	-2.1	*6.5*	0.5	0.8	-3.5	-2.9	-5.5	*8.0*	0.9	-	-3.2	-5.3	-3.3
Sort 6,1%	-1.1	-	-1.6	-1.8	*3.5*	1.1	*2.0*	-3.1	-5.0	0.1	-	*10.2*	-5.3	-3.0
Sort 6,10%	-1.1	-1.1	-2.1	-1.9	*5.8*	*2.3*	*2.1*	-2.2	-1.3	*7.2*	-	-3.2	-5.3	-3.3
Sort 7,1%	-	-1.1	-1.5	-2.1	-1.1	-1.7	-1.5	-4.6	*2.8*	-2.4	-0.7	*10.2*	-5.3	-3.0
Sort 7,10%	-	-1.1	-3.4	-2.1	-1.1	-1.7	-1.5	-4.6	*4.2*	*5.1*	0.9	-3.2	-5.3	-3.3
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,1%	-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
Sort 8,10%	-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

Italic values indicate significant over-representation

Table 38. I.R. values for *Ephemera danica* (N = 504) in the grain-size classification of the substrates in the Ratumsebeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,1%	-1.0	-1.0	-3.5	*2.4*	*7.1*	-3.0	0.4	-2.8	-4.4	-1.6	-	*12.4*	-8.8	-1.7
Sort 5,10%	-1.0	-1.0	-3.5	*2.1*	*9.0*	-2.5	0.4	-2.7	*2.7*	*10.9*	-	-3.3	-9.1	-2.0
Sort 6,1%	-	-	-1.6	-1.4	-3.2	-3.0	-2.0	*2.0*	*2.0*	-0.4	-	*12.4*	-8.8	-1.7
Sort 6,10%	-	-	-1.6	-1.4	-3.2	-3.2	-2.0	1.3	*5.7*	*10.4*	-	-3.3	-9.1	-2.0
Sort 7,1%	-	-	-	-	-	-	-1.6	-0.8	-8.3	*9.8*	-0.4	*12.4*	-8.8	-1.7
Sort 7,10%	-	-	-	-	-	-	-1.6	-0.8	-8.9	*16.2*	*8.6*	-3.3	-9.1	-2.0
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,1%	-1.6	-1.4	-3.2	-3.0	-2.0	*2.0*	*10.1*	-2.8	-4.8	0.5	-1.6	*12.4*	-8.8	-1.7
Sort 8,10%	-1.6	-1.4	-3.2	-3.3	-2.0	1.3	*12.2*	-2.7	-1.0	*6.6*	*10.9*	-3.3	-9.1	-2.0

Italic values indicate significant over-representation

Gravel substrates ($M_d = \bar{1}$ or less) with less than 50% Sand ($Q_3 = 2$) are also preferred.

Calculation of the I.R. values for several length classes of *E.danica* nymphs in Sort 5 for the Ratumsebeek leads to the conclusion that the over-representation in substrates with $Q_1 = \bar{4}$ (Table 38) is caused by nymphs of 5-20 mm and in $Q_1 = \bar{3}$ by nymphs of 0-10 mm. The latter (length class 1-10) are also responsible for the preference in Q_3 = 3, while the largest specimens (20-27 mm) prefer especially Q_1 = 2. Considering the median grain size (Sort 6) hardly any difference between length classes can be seen in the Ratumsebeek, although 10-20 mm nymphs have a stronger preference for M_d = $\bar{1}$ or 1 than 2 or 3.

In the Q_3 classification (Sort 7) only the small nymphs (0-10 mm), especially the smallest ones (0-5 mm), prefer both Q_3 = 3 and Q_3 = 4; the large specimens favour only Q_3 = 3. These differences between younger and older nymphs return in a condensed

Table 39. I.R. values for *Ephemera danica* per length class (A) and season (B) in the Snijdersveerbeek in Sort 8,10%.

Length class and Season	N	Substrate class and $Q_1M_dQ_3$ index													
		1 $\bar{x}\bar{x}\bar{x}$	2 $\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	3 $\bar{x}\bar{3}x$	4 $\bar{x}\bar{2}x$	5 $\bar{x}\bar{1}x$	6 $\bar{x}1x$	7 $\bar{x}xx$	8 1xx	9 22x	10 23x	11 33x	12 CD	13 L	14 CD+L
A 0	3	-0.3	1.5	-0.4	1.8	-0.4	-0.4	-0.6	-0.6	-0.5	-0.6	*2.5*	-0.5	-0.5	-0.3
1 - 5	87	-1.0	-2.0	*3.7*	-1.6	*6.9*	-2.3	0.0	-1.6	1.5	1.2	0.2	-1.2	-2.1	-1.7
6 - 10	179	-1.4	-2.6	*2.6*	1.0	-0.5	-2.1	0.9	-3.8	*3.8*	*4.8*	*2.0*	-1.2	-3.1	-2.1
11 - 15	116	-1.3	-0.6	*4.0*	*4.9*	-0.8	-1.9	0.1	-3.2	*3.1*	*3.1*	-0.8	-2.5	-3.3	-2.0
16 - 20	35	-1.0	-0.5	1.9	-0.2	-1.5	*2.7*	-0.3	-1.4	*3.7*	1.4	-1.2	-1.5	-1.8	-1.1
21 - 27	16	-0.7	0.6	*3.0*	-1.0	1.0	-1.0	0.3	-1.3	1.5	-0.6	0.4	-1.0	-1.2	0.6
Total	436	-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
B Spring	78	-1.0	-1.8	*2.8*	-0.5	-1.8	-1.0	-2.4	-1.4	*8.0*	*5.8*	-0.0	0.6	-2.9	-2.0
Summer	88	-1.2	-2.9	*4.0*	-2.6	*8.3*	-2.5	1.0	-1.3	-1.5	0.8	0.8	-1.4	-	-
Autumn	110	-1.9	-2.1	-0.8	*11.8*	-1.9	-1.5	-0.1	-3.6	*3.7*	*3.8*	-1.9	-2.7	-3.3	-1.5
Winter	160	-1.0	1.4	*5.0*	-2.2	0.8	-0.8	*4.8*	-4.0	1.9	*2.5*	1.7	-3.0	-3.4	-2.3

Italic values indicate significant over-representation

Table 40. I.R. values for *Ephemera danica* per length class (A) and season (B) in the Ratumsebeek in Sort 8,10%.

Length class and Season	N	Substrate class and $Q_1M_dQ_3$ index													
		1 $\bar{x}\bar{x}\bar{x}$	2 $\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	3 $\bar{x}\bar{3}x$	4 $\bar{x}\bar{2}x$	5 $\bar{x}\bar{1}x$	6 $\bar{x}1x$	7 $\bar{x}xx$	8 1xx	9 22x	10 23x	11 33x	12 CD	13 L	14 CD+L
A 1 - 5	198	-1.0	-2.0	-2.0	-4.0	-3.5	-3.0	*11.0*	-1.5	*2.7*	*4.1*	*7.1*	-1.8	-5.9	-1.5
6 - 10	170	-0.9	-0.3	-1.9	-0.4	-1.8	*2.3*	*8.4*	-2.0	-2.6	-2.2	*12.8*	-2.1	-5.2	-0.3
11 - 15	44	-0.5	1.2	-1.0	-0.5	1.6	*6.1*	1.8	-0.4	-2.0	-0.5	-1.1	-1.1	-2.9	-1.0
16 - 20	41	-0.5	0.2	-1.0	0.1	*3.0*	*2.0*	-0.1	0.3	-1.1	*2.6*	-1.0	-1.0	-2.5	-1.0
21 - 27	50	-0.5	-1.0	-1.0	-1.2	-0.3	-1.8	-0.2	-1.8	-0.9	*15.2*	-1.1	-1.1	-2.8	-1.0
99	1	-0.1	-0.1	-0.1	-0.3	-0.3	-0.3	-0.4	-0.3	-0.4	-0.3	-0.2	-0.2	1.8	-0.1
Total	504	-1.6	-1.4	-3.2	-3.3	-2.0	1.3	*12.2*	-2.7	-1.0	*6.6*	*10.9*	-3.3	-9.1	-2.0
B Spring	65	-	-	-1.4	-0.9	-0.7	-3.1	-1.0	-2.4	0.9	*9.3*	-	-	-2.8	-
Summer	99	-1.1	-	-2.0	-0.7	-1.4	1.4	*5.5*	-1.4	-3.7	*11.2*	*2.7*	-2.2	-3.3	-1.6
Autumn	263	-	-	-	0.2	-2.0	1.2	*13.5*	-0.2	*2.8*	-	*8.7*	-	-10.5	-1.0
Winter	77	-	-0.5	-	-1.7	1.3	1.2	1.2	1.2	-1.5	-1.6	*6.4*	-	-2.4	-1.4

Italic values indicate significant over-representation

form in Sort 8 (Table 40A). The preference for $\bar{x}xx$ and 33x is caused by 0-10 mm nymphs; for 23x by 0-5 mm and 15-27 mm animals and the slight over-representation in $\bar{x}1x$ by animals of 5-20 mm length. It should be noted that 10-15 mm nymphs prefer $\bar{x}1x$ substrates ($Q_1 = \bar{5}, \bar{4}, \bar{1}$; $M_d = 1$; $Q_3 = 3$).

Analysis of the Snijdersveerbeek data for the nymphal size classes of *Ephemera* in Sort 8 (Table 39A) confirms the preliminary conclusions previously drawn for part of the data (Tolkamp & Both, 1978). Larger nymphs prefer gravelly substrates: 20-27 mm nymphs are mostly found in $\bar{x}\bar{3}x$ and 15-20 mm nymphs in $\bar{x}1x$, although also in sand (22x) with detritus. Smaller nymphs occur in gravel as well as in sand : 0-5 mm nymphs especially in $\bar{x}\bar{1}x$ and $\bar{x}\bar{3}x$ substrates and 5-15 mm nymphs in both 22x, 23x, 33x substrates with detritus and in $\bar{x}\bar{3}x$ and $\bar{x}\bar{2}x$ substrates. From all other classifications (Sort 5-7) the same picture emerged.

Comparison of the I.R. values for the several nymphal size classes in Sort 2 (not presented) with the directly comparable preliminary results does show some differences, for reasons mentioned earlier.

Between seasons the distributional pattern follows the preferences of the more abundant length classes present (Tables 39B and 40B). In the Snijb, *E.danica* prefers sand with detritus substrates (22x, 23x) in spring, when all nymphal size classes are quite numerous. This preference shifts to more gravelly substrates in summer ($\bar{x}\bar{1}x$, $\bar{x}\bar{3}x$) when especially the small nymphs are abundant. In autumn this distributional pattern remains, although as the nymphs grow a shift back to sand can be observed. In winter the preferences are more or less equally distributed over gravel and sand.

In the Rab, a similar change of preference from sand to more coarse substrates after spring is present; although substrates as coarse as the ones preferred in the Snijb showed no over-representation, they were very scarce in the Rab anyway.

These shifts in preference coincide with the decrease and increase of the water flow in the streams, which is high in winter and spring and low in summer and autumn. In the Ratumsebeek this is much more pronounced because of the much larger drainage area. Some of the differences in substrate preference might be linked to differences in the current-speed pattern of the two streams and their effects on the substrate composition and spatial distribution. In the Snijb, Gravel is originally present in the stream bottom because of the fluviatile gravel deposits and it occurs over the total width of the bed, bare or covered with a layer of sand or detritus. In the Rab, Gravel is present in far smaller quantities and it often consists of iron-condensates, formed in the stream, and accumulations of the heavier material remaining after erosion of banks and bed. The Rab stream bed is much wider and the maximum current speeds are much higher. In the Rab, the gravel is more or less restricted to the riffles or the middle of the bed, places where the current is highest. Sand and Detritus substrates are more abundant in the pools and along the banks.

Since *E.danica* nymphs prefer mineral substrates combined with detritus (especially fine detritus), which occur only in places with a low current velocity, the absence of *E.danica* from coarse, gravelly substrates in the Rab could be a reaction to the absence of detritus, which is swept away by the current. Moreover, also the fine sand ingested for its bacterial growth (Zimmerman & Wissing, 1978) is absent here.

Summarizing the data presented above it can be stated that *Ephemera danica* prefers substrates with at least 25%, and preferably 75% finer than 0.5 mm, or 25% coarser than 4 mm but finer than 32 mm, although for the latter is not certain because of the limited number of samples in this substrate type. The importance of the presence of fine detritus in combination with mineral substrates is best illustrated in the most detailed field classification, and the knowledge that the fine sand substrates in Sort 8 contain large amounts of fine detritus confirms this very well. This relationship with fine detritus will certainly be linked with *E.danica's* feeding habits, since it is a detritivore or collector (Cummins, 1973), living from the microbial flora and the organic material in fine detritus. They may also ingest large amounts of inorganic sediment for the microbial growth on it (Zimmerman & Wissing, 1978). Ephemeridae are called 'mud-eaters' (Bengtsson, 1924; Hunt, 1953), although it has to be oxygen rich mud (Wautier & Pattee, 1955; Eriksen, 1963a, b; 1964; 1966; 1968), which emphasizes the fact that detritus feeders is probably a better description.

Although *Ephemera* is a eurythermous genus (Percival & Whitehead, 1926; Kamler, 1966), *E.danica* occurs in streams with less high temperature fluctuations than *E.vulgata* (Beyer, 1932; Fox et al., 1934; Pleskot, 1953). This is probably why *E.danica* is found in streams, while *E.vulgata* occurs predominantly in the mud substrates of ponds and larger streams (Fox et al, 1934; Moller Pillot, 1971). Percival & Whitehead (1926) found only few *E.danica* in mud and they occurred predominantly in sandy streams in the substrates with the coarsest fraction between 0.05 and 1.0 mm (65% coarse sand, 2% fine sand and 1% silt). The abundance of *E.danica* decreased with an increasing amount of silt and clay (finer than 0.05 mm), while nymphs never migrated to neighbouring substrates with a higher silt content. *E.danica* lives in the bottom in small tunnels, which are burrowed with their strong front legs and mandibles and kept open with the aid of an axial water current over the back of the nymphs that is the result of their dorsally placed gills (Eastham, 1932; Uhlmann, 1975, p. 66). Apparently a small amount of clay is necessary to stick coarser grains together in order to obtain a stable tunnel structure. Eastham (1939) suggested that the preference of *E.danica* for certain substrates might be determined by the need for tunnels of some permanency, easy to make and easy to leave and permitting an axial water current without the tunnel walls collapsing. A high silt/clay content might be detrimental because the particles can obstruct gill movement and clog them, preventing proper respiration.

Most authors reporting on substrate preferences of *Ephemera danica* give as the characteristic habitat the sand substrate in the current (Geijskes, 1935; Pleskot, 1953; Collins, 1971), the quieter places near the banks with mud or clay fractions (Percival & Whitehead, 1926; Beyer, 1932; Dittmar, 1955), the sheltered places in stony-gravelly bottoms, where fine gravel (Percival & Whitehead, 1930), sand, mud and detritus (Sowa, 1975a) accumulate, or coarse substrates near the banks, where the current is slack (Jones, 1949). These data agree with those found in the Ratumsebeek and the Snijdersveerbeek, although the results of these investigations emphasize the importance of the presence of organic detritus and fine sand.

Substrate-selection experiments A series of experiments was conducted to establish the effect of current velocity on the substrate selection of *Ephemera danica*. Substrates ranging from 0.050 mm to 8 mm were offered at high (10 cm/s) and low (5 cm/s) current velocities, and substrate selection was determined after 24 hours. The nymphs were introduced into the stagnant stream on each grain size in densities of 1, 2 or 4 per tray. After introduction they were exposed to the current. Comparison of replicates showed no significant differences between replicates or the densities used.

There is a distinct effect of the current on the substrate selection (compare Fig. 39a and 39c). With a strong current significantly more nymphs were found on the downstream screens and burrowed in the downstream substrates, more or less independantly of grain size (Fig. 39b). With a slow current this effect is not noticed (Fig. 39d). This leads to the conclusion that for a low current velocity the substrate selection of *Ephemera* is voluntary, but for a high current velocity enforced. Fig. 39c shows that *E.danica* prefers 2-4 mm grains, and this preference decreases to both coarser and finer particle sizes, with the exception of 0.050 - 0.125 mm. In the latter a slight overrepresentation can be seen.

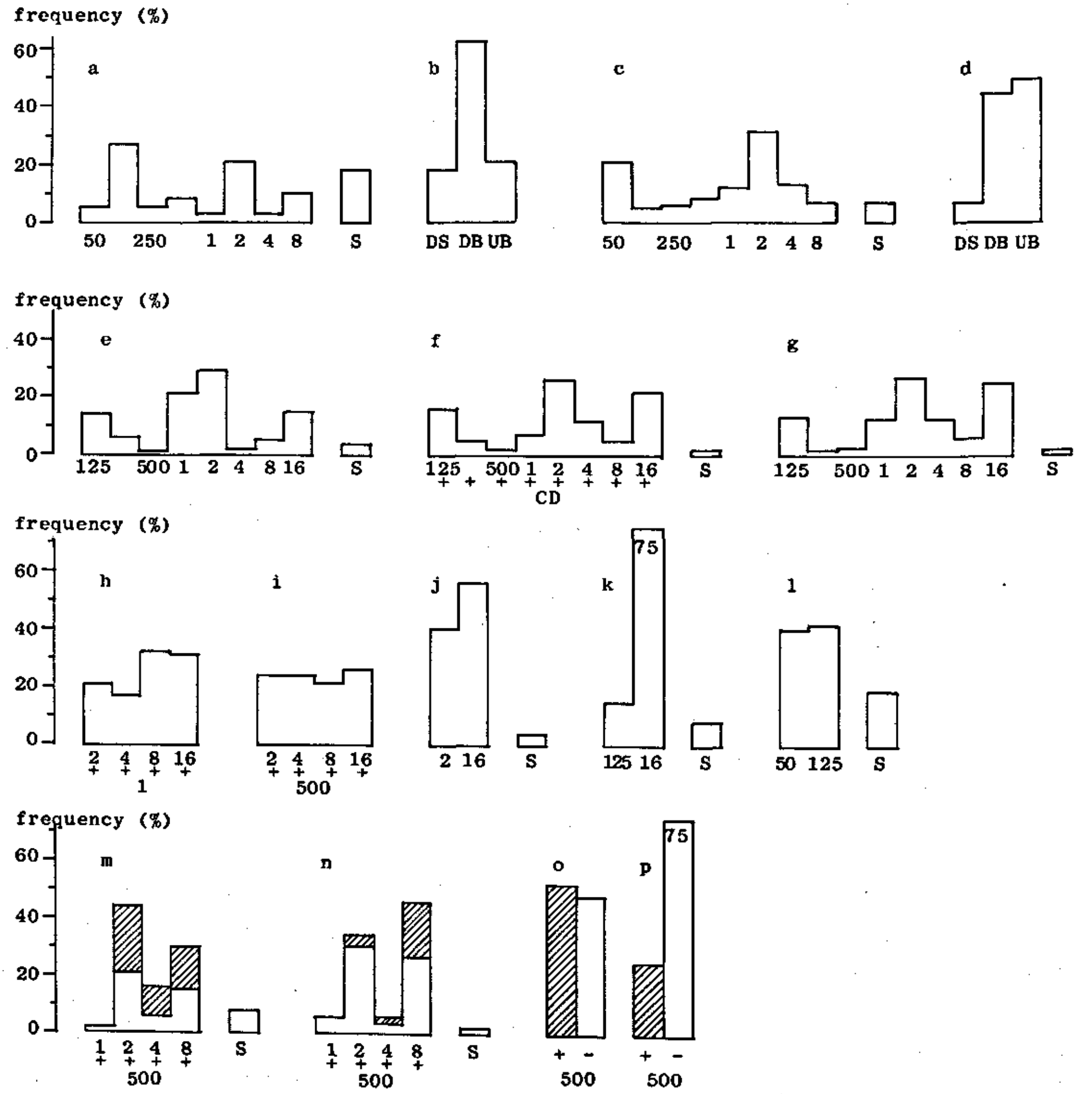
In experiments where the 0.050 mm particle size was substituted by one of 16 mm the same preference for 2-4 mm was seen (Fig. 39e and 39g). However, also 1, 0.125 and 16 mm showed over-representation. No significant differences were present between the two experiments. When mixed with fine and coarse detritus, practically the same substrate selection was found (Fig. 39f), indicating that the presence of food substances did not influence the substrate selection in these experiments.

Experiments with 2, 4, 8 and 16 mm grains mixed with 0.5 or 1 mm (Fig. 39h and 39i) showed that *E.danica* has no significant preference for any of these mixtures. Particle sizes 8 mm and 16 mm mixed with 1 mm are chosen more often but the differences are only small. Comparison of Fig. 39k with Fig. 39c, 39e and 39g, demonstrates that mixing the four coarse particle sizes with 0.5 mm or 1 mm sand levels down the differences in substrate selection, although 8 mm seems to become more accessible.

In a series of experiments where only two of the preferred substrates were offered, *E.danica* favoured 16 mm above 2 mm or 0.125 mm (Fig. 39j and 39k), but no difference was observed between 0.050 and 0.125 mm (Fig. 39l). Also, an experiment was started where grains of 0.125 - 16 mm were mixed with approximately one-third 0.050 mm substrate. The experiment showed that mixing with this very fine sand strongly levelled down the differences between the different grain sizes, although over 40% of the nymphs did not burrow but sat on the screens, while 10% died during the experiment, probably because of lack of food and because they had been subjected to experiments for more than 48 hours. This had been avoided in previous experiments and care was taken that in following experiments well fed, fresh nymphs were used.

Experiments with two size classes of *E.danica* (15-20 mm and 20-25 mm) were conducted, giving them choice between 1, 2, 4 and 8 mm particles covered with a thin layer of 0.5 mm sand and bare 1, 2, 4 and 8 mm substrate. Large nymphs preferred 2 mm and 8 mm and no influence of the 0.5 mm covering was noticed (Fig. 39m). Smaller nymphs displayed the same grain-size selection (Fig. 39n) but they differed from the larger nymphs in their strong preference for bare particle sizes compared with the covered ones (Fig. 39o and 39p).

Compared with the results of the field investigation the preference of large *Ephemera* nymphs for gravelly substrates is thus confirmed by the selection of 2-4 mm particles in the laboratory experiments. The (less distinct) selection of smaller particles sizes also agrees with the occurrence in finer substrates (22x, 23x) in the



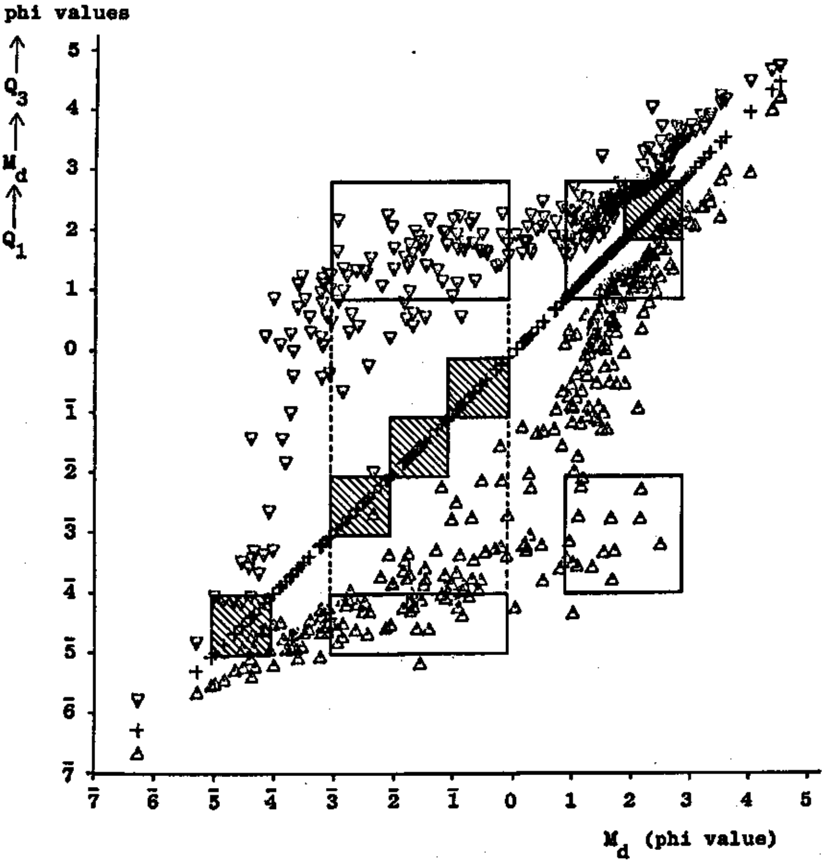


Fig. 40. Comparison of substrate preferences in the field (unshaded) with particle-size selection in laboratory experiments (shaded) for *Ephemera danica*.

Fig. 39. Substrate selection in laboratory experiments by *Ephemera danica*. Grain-size fractions are indicated by the lower limit of the fraction in µm (under 1 mm) and mm (over 1 mm). S = end retaining screen; DS = downstream screen ; DB = downstream burrowed; UB = upstream burrowed (fig. d); CD = coarse detritus.

Figure no.	Body length /mm	Number of experiments	Number of nymphs per experiment	Current velocity (cm/s)	Note
a+b	20-25	3	16	10	
	20-25	2	32	10	
c+d	20-25	6	8	5	
	20-25	4	16	5	
e	20-25	2	40	5	
f	20-25	2	40	5	mixed with coarse detritus
g	20-25	5	24	5	
h	20-25	3	24	5	mixed with 1.0 mm
i	20-25	3	24	5	mixed with 0.5 mm
j	20-25	3	16	5	
k	20-25	3	16	5	
l	20-25	3	16	5	
m+o	20-25	2	24	5	bare(unshaded),covered with 0.5 mm (shaded)
n+p	15-20	2	24	5	

field. The differences seen between large and small nymphs in the experiments with mixtures of particles sizes agree with the differences in preference seen between these nymphs in the Ratumsebeek, where the large nymphs occur predominantly in finer substrate (23x), while smaller nymphs preferred coarser substrates.

Conclusions drawn from the field research are thus confirmed by the laboratory experiments, as illustrated in Fig. 40, in which particle-size selection in the experiments is projected on the $Q_1M_dQ_3$ graph together with the substrate preferences seen in Sorts 5-8, 10%. The nymphs select 2-4 mm, 16-32 mm and 0.125-0.250 mm particles in the laboratory. These particle sizes correspond with the Q_3 and M_d particle sizes of the substrates selected in the field.

4.2.2.7 Nemoura cinerea (Retzius) (Plecoptera: Nemouridae)

Microdistribution In the Snijdersveerbeek the population of *Nemoura cinerea* was rather small and only 155 specimens were present in 26 samples. In the Ratumsebeek, 2896 specimens were caught in 87 samples. In both streams, the highest numbers were present in leaf packs. This is clear in both the field classification (Table 41) and the grain-size classification, although only Sort 8, 10% is presented (Table 42).

Over-representation also occurs on very coarse substrates in the Ratumsebeek. This preference is only seen in the winter season (Table 42B), which is by the way the only period when this substrate class is present, and it concerns all length classes (i.e. 1-3 and 3-6) (Table 42A), although relatively more small (0-3 mm) specimens were found on mineral substrate (Classes 2 and 4-7 in Sort 8) than larger (3-6 mm) ones. This is in comparison with the total number of each length class. The only statistical clue for this statement lies in the small difference between the I.R. values for the 1-3 mm length class in $\bar{x}5x$, $\bar{x}4x$ and Leaf substrates, the additional occurences of positive I.R. values in $\bar{x}2x$ and $\bar{x}1x$ substrates and the less negative values in the other mineral classes compared to length class 3-6 mm.

Table 41. I.R. values for *Nemoura cinerea* (N = 2896) in the field classification of the substrates in the Ratumsebeek.

Sort	Sand								Gravel			Detritus		
3	-28.1								-1.9			*44.2*		
4	-20.2			-19.6					*4.5*	-11.8		*44.2*		
2	-15.6		-13.8	-5.7		-19.1			*4.5*	-11.8		*44.2*		
1	-6.2	-16.9	-13.8	-3.9	-4.7	-4.6	-19.2	-1.7	*4.5*	-3.9	-11.1	-8.5	*53.7*	-4.7
	St	Sh	FD	L	CD	CD+L +FD	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

Table 42. I.R. values for *Nemoura cinerea* per length class (A) and season (B) in the Ratumsebeek in Sort 8,10%.

Length class and Season	N	Substrate class and $Q_1M_dQ_3$ index													
		1 xxx	2 x5x x4x	3 x3x	4 x2x	5 x1x	6 x1x	7 xxx	8 1xx	9 22x	10 23x	11 33x	12 CD	13 L	14 CD+L
A 1 - 3	680	-1.9	*13.4*	-3.7	0.9	*2.6*	-0.8	-3.6	-5.1	-10.5	-2.3	-3.2	-3.9	*15.4*	-1.3
4 - 6	1768	-3.0	*15.4*	-6.0	-3.5	-2.1	-5.0	-7.3	-8.0	-17.2	-9.0	-5.7	-6.7	*42.4*	-4.7
7 - 9	438	-1.5	-3.0	-3.0	-5.4	-4.9	-5.2	-6.7	-2.7	-8.6	-4.5	-3.4	-3.4	*32.9*	-1.0
10 - 12	8	-0.2	-0.4	-0.4	-0.9	-0.8	-0.9	-1.0	-0.7	-1.2	-0.7	-0.5	-0.5	*5.2*	-0.4
99	2	-0.1	-0.2	-0.2	-0.4	-0.4	-0.4	-0.5	-0.4	-0.6	-0.4	-0.2	-0.2	*2.6*	-0.2
Total	2896	-3.9	*17.3*	-7.7	-4.5	-2.4	-6.3	-10.1	-9.8	-22.0	-9.9	-7.3	-8.5	*53.7*	-4.7
B Spring	1125	-	-	-5.8	-5.7	-5.8	-6.9	-11.5	-8.6	-11.3	-13.4	-	-	*59.8*	-
Summer	30	-0.6	-	-1.1	-1.6	-1.5	-0.7	-2.0	-1.4	-2.8	-1.1	-0.9	-0.7	*6.3*	*12.9*
Autumn	169	-	-	-	*2.8*	-2.2	-3.7	-3.1	-2.1	-5.0	-	-2.1	-	*7.5*	0.4
Winter	1572	-	*3.5*	-	-7.8	-1.1	-3.5	-3.6	-7.0	-10.4	-8.6	-7.4	-	*41.2*	-5.1

Italic values indicate significant over-representation

For all length classes, preference is always highest for leaves. In spring and autumn the distribution is mainly restricted to these leaf packs, while in summer the preference is higher for L+CD, although the I.R. values should be considered sceptically since only two samples were taken in this substrate class in summer, only one of which contained *N.cinerea* (12 specimens), against four of the ten samples in winter in Leaves (16 specimens). The data for the Snijdersveerbeek have not been presented because of the very strong resemblance to the Ratumsebeek data, with the exception that over-representation in leaf packs occurred in both seasons (winter and spring) in the Snijdersveerbeek only. Similarity in results was also seen for the length classes in the Snijdersveerbeek, although slight over-representation was found in CD and CD+L in spring for large (6-10 mm) specimens which is probably the result of the disappearance of leaf packs in spring.

Nemoura cinerea nymphs are herbivorous and feed mainly on vegetable matter as detritus and dead leaves, although they also ingest moss tissue and algae, dependant on the abundance of the various food types present (Hynes, 1941). Thus it is not surprising to find a strong relationship of these stonefly nymphs to detritus substrates, a fact reported by several authors (Geijskes, 1935; Dittmar, 1955).

N.cinerea is widely distributed in Europe (ubiquist) and occurs in various, strongly-differing biotopes, such as trickles from springs, lowland streams and rivers. It is also frequently found in littoral zones of ponds and lakes (Brinck, 1949; Hynes, 1941). However, in the Netherlands it is only found in (slowly) running water and is most abundant in small woodland streams, which often desiccate in summer.

The life cycle of *N.cinerea* is well adapted to life in leaf packs and summer-dry streams (Bontenbal et al., 1979). In the study area, the life cycle of *N.cinerea* is clearly univoltine, with growth in autumn, winter and spring, when leaf packs are abundant. Adults fly from early April and continue to do so well into June, and first instar nymphs are present from August to February, although most nymphs hatch late in autumn (October/November). This means that when food conditions are unfavourable in the stream, *N.cinerea* is in the adult or egg stage. Unfavourable nutrititional conditions that extend the life cycle from univoltine to almost bivoltine, as reported by Lillehammer (1975), were not observed in the streams under study.

4.2.2.8 Limnius volckmari (Panzer), Elmis aenea (Müller), and Oulimnius tuberculatus (Müller) (Coleoptera: Elminthidae)

Microdistribution *Limnius volckmari* occurred in the Snijdersveerbeek with 27 specimens (larvae and adults) in 11 samples; 423 specimens (larvae and adults) were found in 92 samples in the Ratumsebeek. The distributional pattern was exactly the same in both streams, with a significant preference for Gravel substrates and Stable Sand (Table 43). This preference is clear in all substrate classifications and the highest preferences are found on substrates with $M_d = \bar{1}$ (1-2 mm), although all substrates with $Q_1 < \bar{2}$ (2-4 mm) show over-representation (Table 44).

Elmis aenea was found in 40 samples in the Snijdersveerbeek (133 specimens) and in 29 samples in the Ratumsebeek (53 specimens). *E.aenea* showed a similar preference as *L.volckmari*, but was restricted to Gravel substrates only (Table 45). Again, the distribution was similar in both streams. The higher preference for coarser substrates than *L.volckmari* showed is especially clear in Sort 5-8, 10%, where only the coarsest substrates show significant over-representation. *Elmis aenea* avoids classes 4, 6 and 7 in Sort 8, 10% and the preference for Class 5 ($\bar{x}\bar{1}x$) is shown by larvae only. Adults occur in highest numbers in $\overline{xxx}$ and $\bar{x}\bar{3}x$, while larvae show the highest preference for $\overline{xxx}$ and a lower preference for Classes 2 and 5 (Table 46).

In the Ratumsebeek *Oulimnius tuberculatus* shows the same preferences as *L.volckmari* with the highest preference for Class 5 in Sort 8, 10%. Only 25 larvae and 23 adults were found in 28 samples in the Ratumsebeek. Larvae showed no significant

Table 43. I.R. values for *Limnius volckmari* (N = 423) in the field classification of the substrates in the Ratumsebeek.

Sort	Sand								Gravel			Detritus		
3	-4.2								*15.7*			-8.3		
4	0.1			-6.6					*11.8*	*11.0*		-8.3		
2	*2.2*		-4.0	-1.5		-6.7			*11.8*	*11.0*		-8.3		
1	*5.2*	-2.8	-4.0	-1.5	-1.1	-2.2	-5.7	-3.0	*11.8*	-0.8	*11.9*	-2.1	-7.7	-2.6
	St	Sh	FD	L	CD	CD+L +FD	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

Table 44. **I.R. values for *Limnius volckmari* (N = 423) in the grain-size classification of the substrates in the Ratumsebeek, including the distinction between larvae and adults in Sort 8,10%.**

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,10%	0.6	*3.7*	*7.9*	*5.8*	*11.6*	1.4	-1.6	-3.9	-7.7	-2.7	-	-2.1	-7.7	-2.6
Sort 6,10%	-	-	*4.6*	*4.2*	*5.9*	*5.0*	*14.6*	*2.0*	-2.9	-6.2	-	-2.1	-7.7	-2.6
Sort 7,10%	-	-	-	-	-	-	*7.4*	*6.7*	*7.3*	-3.5	-0.3	-2.1	-7.7	-2.6
$Q_1M_dQ_3$ index	$\overline{xxx}$	$\overline{x5}x$ $\overline{x4}x$	$\overline{x3}x$	$\overline{x2}x$	$\overline{x1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,10%	*7.4*	*2.8*	*5.9*	*5.0*	*14.6*	*2.0*	*3.9*	-3.9	-6.0	-4.9	-2.7	-2.1	-7.7	-2.6
Larvae(N=410)	*7.5*	*2.6*	*6.1*	*4.4*	*14.5*	*2.1*	*4.1*	-3.8	-5.8	-4.9	-2.6	-2.3	-7.6	-2.6
Adults(N= 13)	0.3	1.4	-0.5	*3.5*	*2.1*	-0.2	-0.5	-0.9	-1.5	-0.9	-0.6	1.2	-1.0	-0.5

Italic values indicate significant over-representation

Table 45. **I.R. values for *Elmis aenea* (N = 133) in the field classification of the substrates in the Snijdersveerbeek.**

Sort	Sand								Gravel			Detritus		
3	-7.3								*11.6*			-2.8		
4	-4.9			-5.5					*13.3*	1.2		-2.8		
2	-4.1		-2.9	-3.4			-4.3		*13.3*	1.2		-2.8		
1	-2.4	-3.4	-2.9	-1.7	-2.8	-1.0	-3.8	-2.0	*13.3*	1.6	0.4	-0.5	-2.3	-2.0
	St	Sh	FD	L	CD	CD+L	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

preference although coarser substrates yielded more positive I.R. values than the finer substrates. Adults were significantly over-represented in Classes 2 and 5 of Sort 8, 10%. In the Snijdersveerbeek only 2 adults of *O.tuberculatus* and 23 larvae were caught in 11 samples. These larvae only occurred in substrates coarser than class 7 in Sort 8, 10% which is similar to the results for *L.volckmari* in the Ratumsebeek (see Appendix 9).

These results confirm that the common name for this group of beetles, 'riffle beetles' is well chosen. This name indeed indicates their preferred habitat. These very small beetles can withstand very strong currents (Dittmar, 1955; Dorier & Vaillant, 1955). They attach themselves to the substrate with their sprawling, large-clawed legs. The larvae are very well streamlined and some species (e.g. *Elmis aenea*)

Table 46. I.R. values for *Elmis aenea* (N = 133) in the grain-size classification of the substrates in the Snijdersveerbeek, including the distinction between larvae and adults in Sort 8,10%.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,10%	*41.8*	*2.1*	*4.4*	*5.9*	-1.7	-2.2	-2.9	-3.4	-5.1	-2.4	-	-1.4	-1.2	-2.1
Sort 6,10%	*41.8*	-0.6	-2.0	*8.4*	*2.3*	-0.9	*7.1*	-0.7	-5.8	-4.6	-	-1.4	-1.2	-2.1
Sort 7,10%	-	*41.8*	-1.3	-1.2	-0.6	-1.2	*2.0*	*6.6*	-1.1	-3.0	-1.8	-1.4	-1.2	-2.1
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,10%	*13.4*	*6.0*	*2.6*	-0.9	*7.1*	-0.8	-3.4	-3.4	-3.3	-4.0	-2.4	-1.4	-1.2	-2.1
Larvae(N=107)	*12.5*	*6.7*	0.1	-1.5	*8.1*	-1.0	-3.0	-3.0	-3.0	-3.6	-2.1	-1.2	-1.2	-2.0
Adults(N= 26)	*4.9*	-0.1	*5.8*	1.0	-0.5	1.2	-1.6	-1.6	-1.5	-1.8	-1.0	-0.6	-0.3	-0.9

Italic values indicate significant over-representation

can seal off the ventral side of their body with numerous hairy spines, producing a tight grip on the surface (Hynes, 1970a).

Elminthidae are most common on small stones and gravel in moderately swift waters (Percival & Whitehead, 1929; Jones, 1949), sometimes covered with dense algal growth (Berg et al, 1948; Jones, 1951). Comparing the distribution of *E.aenea* and *L.volckmari* as shown in Tables 43 and 45, it is clear that the presence of detritus is more important for *L.volckmari* than it is for *E.aenea*. *L.volckmari* has equal preferences for Bare Gravel and Gravel + Coarse Detritus, while *E.aenea* strongly prefers Bare Gravel (and Pebbles). This preference of *L.volckmari* for coarse substrates with detritus does not show in any of the grain-size classifications (Table 44), which means that the amount of trapped detritus was smaller than 1% of the sample weight. This emphasizes the importance of using a field classification together with a grain-size classification. The importance of detritus for *L.volckmari* would have been obscured in the grain-size classification, and the difference between *E.aenea* and *L.volckmari*, with preferences for very coarse gravel and medium gravel, respectively, would have been unnoticed in the field classification.

Of course one should bear in mind that in the grain-size classification so called mineral samples (Classes 1-11) still may contain up to 1% or 10% detritus, although this mainly concerns samples with $Q_1 \geq 2$ (cf. Subsection 4.1.3.2). Rabeni & Minshall (1977) showed that 1-3.5 mm substrates collected more detritus than coarser or finer substrates and that the presence of detritus may be the primary reason responsible for insect colonization. The relationship with mineral substrates remains, however, since the nature of the mineral substrate determines the amount of detritus trapped in the interstices.

Egglishaw (1964, 1969) concluded that the distribution of *Esolus parallelopipedus*, another member of the Elminthidae is strongly correlated with the presence of detritus, although this was more important for the adults than for the larvae. Edwards (1975) showed that *Esolus parallelopipedus* has a similar distribution as *Limnius volckmari*. Larvae of *E.parallelopipedus* showed no correlation with current velocity and only a weak correlation to substrate composition, suggesting that substrate is more important than current velocity. Adults of *E.parallelopipedus* were positively correlated with current velocities of 30-50 cm/s and a median particle size of 20-40 mm.

The data of the present study are not sufficient, however, to justify the statistical treatment of larvae and adults separately. The I.R. values for larvae and adults in Table 44 and 46 should only be considered as indicative, since the differences are not significant.

It is not possible to give any detailed results of the seasonal distribution of *Elmis aenea* since most animals (82 of the total of 107) were caught in spring and showed a substrate preference similar to the distribution presented in Table 50. It is noteworthy that in summer a slight over-representation is seen in CD as well (5 specimens of the 21). A similar observation was made for *Lithax obscurus* in summer (see Subsection 4.2.2.1) and this might be related to the availability of food (algae and detritus) (Jones, 1951; Hynes, 1961).

Limnius volckmari occurred in highest numbers in summer, autumn and winter, but in all seasons Class 5 (Table 44) was preferred ($\bar{x}\bar{1}x$). Only in spring was a high I.R. value (7.7) found in $\bar{x}\bar{3}x$, but this concerned only one sample, with 13 specimens out of the total of 44. Adults and all larval instars except the first may be present throughout the year (Holland, 1972). The population found will mostly be a mixture of younger and older larvae and adults.

4.2.2.9 Gammarus pulex (L.) (Malacostraca: Amphipoda, Gammaridae)

Life cycle In the Snijdersveerbeek and the Ratumsebeek all sizes of *G.pulex* are present in all seasons (Fig. 41). Reproduction takes place mainly in spring (Weeks 17-20: May) and summer (Weeks 21-28: June, July), but also in autumn until October/November (Weeks 33-36). In winter and early spring (Weeks 41-16) there is a resting period, after which juveniles appear again in abundance. Adults die probably in June-July, which would explain the decrease in large specimens (above 9-10 mm) in this period (Fig. 41).

The annual temperature fluctuations of the stream are comparable with those found by Hynes (1955) (varying from 5-15°C mostly), and it seems probable that the life cycle of G.pulex is also in accordance with that described by Hynes (1955). Roux (1970) described a continuous reproduction of *G.pulex* in four streams with very small annual fluctuations in temperature (between 10 and 15°C) and also that a resting period in reproduction occurs in autumn in streams with a strong seasonal fluctuation of the water temperature (less than 5°C in winter, more than 15°C in summer). The

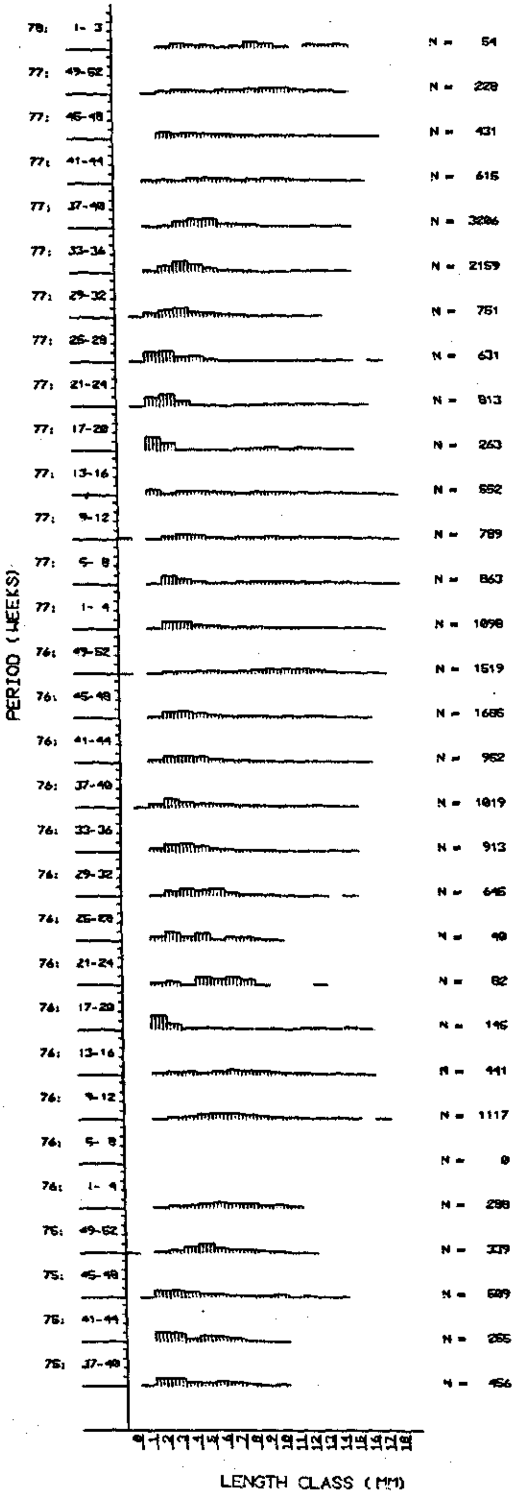


Fig. 41. Life cycle histograms of *Gammarus pulex* showing the distribution (%) of animal body length per four-week period.

latter cycle is comparable with the observations of Hynes (1955), who found that breeding slowed down in September and started again in December. He found that species born in spring reach maturity in July and August, breed through September, rest until December/January and breed again throughout spring. They then die, which causes a decrease in numbers in June/July. Specimens born later in summer overwinter as juveniles and reach maturity in March, after which they breed until June and then probably die. Hynes stated for overwintering specimens a period of about 7 months to mature ($T = 5\text{-}10^{o}C$) and for summer growers a period of 3-4 months ($T = 10\text{-}15^{o}C$).

Roux (1970) suggested that the reproductive rhythm found by several authors is due to a synergetic influence of water temperature and day lengths. Nilsson (1974) showed that temperature is the determining factor for growth of *G.pulex* and Roux (1975) demonstrated that temperature affects the time between the moults. Iversen & Jessen (1977) found in Rold Kilde that breeding is insignificant or absent in winter and that the new generation appears in March-April, but is most abundant in summer. Growth of juveniles is slightly reduced in winter. They observed that part of a generation survives until the third summer, which gives a maximum age of two years. They contribute the differences with the results of Hynes (1955) to the lower summer temperatures in Rold Kilde. In the two Dutch lowland streams no indication of a reduced breeding or growth was observed, which confirms the conclusions of Roux (1970) and Hynes (1955).

Microdistribution *Gammarus pulex* is the most dominant species in both streams regarding the number of samples in which it occurred: in 282 of the 382 samples in the Snijb and in 154 of the 195 samples in the Rab. In the Rab it was also the most dominant species in numbers (9958 specimens) whereas this was *M.* gr. *praecox* in the Snijb (20138 specimens), followed by *G.pulex* (11125 specimens). *G.pulex* occurred in practically all samples in the upstream sections in the Snijb and it became less frequent in the more downstream sections. This is probably connected with its tendency to move upstream (Meijering, 1972) and with the increasing substrate heterogeneity.

Based on the field classification of the substrates (Sort 1-4), *G.pulex* shows a significant preference for detritus substrates (Table 47 and 48), especially for Coarse Detritus. This is confirmed by the grain-size classifications (Table 49). There is also a clear over-representation in Sand samples mixed with Coarse Detritus and/or Leaves in the Snijb, while Gravel with Leaves is also preferred in the Rab. Comparing this with the grain-size classifications it can be seen that there is only a slight preference for $Q_1 = \bar{1}$ with 1% organic matter and $Q_1 = \bar{1}$ and $\bar{2}$ and $M_d = \bar{6}$ with 10% organic matter. In the Rab only a little over-representation for $Q_3 = \bar{1}$ is seen (I.R. = 3.2), but this concerns 1 sample so it is not reliable. The preference in the Snijb for rather fine substrates with a coarse top fraction is also clear from Sort 8, 10% where $\bar{x}xx$ contains most animals after detritus substrates. From the slight shifting of the preferences from detritus substrates to mineral substrates with 1-10% organic matter in Sorts 5-8, 1% to 10% (Table 49), it is apparent that

Table 47. I.R. values for *Gammarus pulex* (N = 11125) in the field classification of the substrates in the Snijdersveerbeek.

Sort	Sand								Gravel			Detritus		
3	0.1								-41.9			*56.9*		
4	-25.9			*30.2*					-39.5	-16.5		*56.9*		
2	-27.2		-4.6	*52.6*			-3.0		-39.5	-16.5		*56.9*		
1	-15.1	-24.7	-4.6	*9.2*	*53.5*	*14.5*	-6.1	*5.2*	-39.5	-5.9	-15.6	*35.2*	*32.4*	*34.2*
	St	Sh	FD	L	CD	CD+L	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

Table 48. I.R. values for *Gammarus pulex* (N = 9918) in the field classification of the substrates in the Ratumsebeek.

Sort	Sand								Gravel			Detritus		
3	-50.7								-28.5			*103.2*		
4	-43.2			-27.5					-28.0	-8.4		*103.2*		
2	-39.4		-17.8	-15.6		-23.0			-28.0	-8.4		*103.2*		
1	-25.5	-30.9	-17.8	-7.1	-14.1	-10.4	-18.3	-10.6	-28.0	*8.7*	-11.8	*160.5*	*49.5*	*22.6*
	St	Sh	FD	L	CD	CD+L +FD	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

Table 49. I.R. values for *Gammarus pulex* (N = 11125) in the grain-size classification of the substrates in the Snijdersveerbeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,1%	-5.4	-5.9	-34.7	-30.3	-7.8	-3.0	*6.6*	-8.6	-19.9	-4.3	-	*39.4*	*28.6*	*37.3*
Sort 5,10%	-5.4	-3.4	-34.2	-23.6	-8.7	*6.5*	*18.1*	-10.5	-14.9	-7.5	-	*55.3*	*32.0*	*35.5*
Sort 6.1%	-5.4	-	-10.6	-22.6	-25.0	-20.2	-13.9	-5.7	-13.1	-19.7	-	*39.4*	*28.6*	*37.3*
Sort 6,10%	-5.4	*3.7*	-10.2	-22.4	-23.9	-20.8	-14.4	-4.3	0.3	-16.2	-	*55.3*	*32.0*	*35.5*
Sort 7,1%	-	-5.4	-6.6	-3.8	-4.8	-7.1	-11.2	-28.5	-26.4	-21.6	-2.3	*39.4*	*28.6*	*37.3*
Sort 7,10%	-	-5.4	-3.5	-3.8	-4.8	-7.1	-11.2	-28.5	-27.4	-9.7	-1.6	*55.3*	*32.0*	*35.5*
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,1%	-13.4	-22.8	-23.8	-20.2	-13.9	-2.6	-8.9	-8.6	-9.9	-18.8	-4.3	*39.4*	*28.6*	*37.3*
Sort 8,10%	-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*

Italic values indicate significant over-representation

mineral substrates combined with detritus are also selected as a habitat. A preference for Gravel with Leaves in the Rab (Table 48) is seen in Sort 8, 10% in the preference for $\bar{x}\bar{x}\bar{x}$ substrate.

Division of the distribution over substrates into length classes in Sort 5 shows that the slight preference for $Q_1 = \bar{1}$ (1% detritus level) and $\bar{1}$ and $\bar{2}$ (10% detritus level) in the Snijb is caused by small specimens (1-6 mm) that prefer substrates with at least 25% of the grains coarser than 1 mm (see Table 50A, Sort 8, Classes 6 and 7). The preference for $M_d = \bar{1}$ is caused by animals from 6 to 18 mm, and especially the ones from 15-18 mm. Table 50A illustrates further for the Snijb that the smallest specimens (1-3 mm) are most abundant in CD or CD+L, while larger specimens (16-18 mm) are more abundant in CD+L or L. This shift in preference between the three types of detritus occurs gradually from CD through L to CD+L from small to large animals. In the Rab exactly the same shift from CD to CD+L was observed. The preference for $Q_3 = \bar{1}$ appeared to be caused by small (1-3 mm) animals, and for G+L in the field classification by 3-6 mm animals.

In summer the preference for detritus substrates seen in all other seasons shifts to 'mineral' substrates in Sort 8, 10% (Table 50B). This shift is not present in Sort 8, 1% when CD shows the highest I.R. values, indicating that purely detritus substrates are more scarce in summer, forcing the animals to be content with the combination of mineral substrate with small amounts of detritus.

Species of the genus *Gammarus* can be called aspect determining in many lowland streams, mountain streams and also slow flowing rivers (of good water quality and with enough input of organic material). Often one can speak of *Gammarus* streams (Meijering, 1971). Also the choice of the *Gammarus* group for the second best water-

Table 50. I.R. values for *Gammarus pulex* per length class (A) and season (B) in the Snijdersveerbeek in Sort 8,10%.

Length class and Season	N	Substrate class and $Q_1M_dQ_3$ index 1 $\bar{x}\bar{x}\bar{x}$	2 $\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	3 $\bar{x}\bar{3}x$	4 $\bar{x}\bar{2}x$	5 $\bar{x}\bar{1}x$	6 $\bar{x}1x$	7 $\bar{x}xx$	8 1xx	9 22x	10 23x	11 33x	12 CD	13 L	14 CD+L
A 0	2	-0.2	-0.4	-0.4	-0.4	-0.4	*2.5*	-0.5	-0.5	-0.4	1.6	-0.3	-0.4	-0.4	-0.3
1 - 3	2763	-5.2	-9.7	-11.5	-8.3	-5.0	*2.3*	*10.8*	-3.1	-3.4	1.3	0.0	*32.6*	-3.1	-0.8
4 - 6	4136	-7.3	-13.5	-13.2	-11.4	-9.4	*3.0*	*13.3*	-4.7	-5.1	-8.7	-4.3	*41.2*	*10.9*	*7.9*
7 - 9	2241	-6.7	-9.6	-9.8	-11.3	-7.2	-3.1	*2.8*	-7.3	-3.3	-8.1	-4.6	*17.2*	*28.0*	*26.5*
10 - 12	1334	-3.1	-9.3	-8.6	-9.0	-5.0	-3.9	-2.5	-5.1	-4.2	-8.2	-4.4	*13.1*	*24.4*	*34.5*
13 - 15	576	-2.4	-6.7	-6.0	-5.8	-4.7	-5.4	-3.5	-3.5	-3.2	-4.1	-4.9	*7.5*	*22.2*	*25.4*
16 - 18	73	-0.1	-2.5	-2.1	-2.2	-2.1	-2.1	-2.4	-2.7	-2.0	-2.3	-1.8	0.0	*9.8*	*17.5*
Total	11125	-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*
B Spring	1656	-4.6	-10.9	-7.7	-9.5	0.2	-5.3	-0.3	-5.4	-10.0	-7.5	-2.7	*21.7*	*15.0*	*15.1*
Summer	1750	-6.3	-5.0	-9.3	-4.0	-8.7	*2.6*	*12.7*	1.9	*10.0*	*5.9*	-3.2	-3.1	-	-
Autumn	3917	-7.5	-7.8	-9.5	-13.9	-12.7	*5.9*	*7.5*	-8.4	*2.3*	-14.5	-4.8	*44.8*	-2.5	*21.2*
Winter	3802	-5.7	-16.1	-15.9	-12.0	-6.9	-0.4	*4.0*	-7.9	-18.6	-7.0	-4.0	*28.2*	*35.4*	*24.3*

Italic values indicate significant over-representation

quality class in the system of Moller Pillot for the assessment of the water quality of lowland streams (Moller Pillot, 1971) is connected with this. Meijering (1971) suggested to call *G.pulex* the 'common freshwater shrimp' and *G.fossarum* the 'stream freshwater shrimp', based on their differing preferences for slower or faster current velocities and on the more limited distribution of *G.fossarum.* Gammarids are probably the most commonly known inhabitants of detritus substrates, where they may occur very abundantly.

G.pulex is a detritivore which feeds mainly on the microflora on leaves (Haeckel, Meijering & Rusetzki, 1973; Barlöcher & Kendrick, 1975; Moore, 1975; Kostalox & Seymour, 1976; Monk, 1976; Willoughby & Sutcliffle, 1976; Nilsson, 1977; Nilsson & Otto, 1977; Lautenschlager, Kaushik & Robinson, 1978). It also feeds on a varied assortment of detritus, including living and dead plants and animals. In fact they are thus omnivorous (Percival & Whitehead, 1929; Badcock, 1949; Hynes 1970a, p. 427; Roux, 1975). In the Snijdersveerbeek, *G.pulex* was found abundantly in detritus but also on for example a drowned rabbit. In the laboratory *G.pulex* fed readily on any dead animal that happened to be in the rearing channel (e.g. *Ephemera danica* nymphs and pupae of *M.sequax*), often feeding together with *M.sequax* larvae on the latter's prey.

The abundance of *G.pulex* in detritus substrates as demonstrated above, is determined by its preference for leaves (and associated microflora) as food, as well as by its preference for sheltered sites with relatively slow flow (e.g. Badcock, 1949; Albrecht, 1953; Hynes, 1954, 1970a, p. 146; Meijering, 1972; Franke, 1977). Food as well as protection can both be found in detritus/leaf packs but also by the (secondary) selection of coarse mineral substrates where current is reduced in the crevices and interstices, especially when also some detritus is trapped. Rees (1972) found for *G.pseudolimnaeus* a preference for 16-32 mm substrate and he also demonstrated a significant relationship between the body length of *G.pseudolimnaeus* and the particle size of the substrate. In less preferred substrates, the oxygen consumption increased, which he explained as being the result of the absence of the 'proper particle size stimulus' (cf. Eriksen, 1963a). Meijering (1972) stated that *G.pulex* is restricted to the zones that are almost current free, behind and under stones when the current velocity of the main water body is high.

Differences in substrate preference between differently-sized specimens were observed by many authors, who mainly looked for differences in grain sizes of mineral substrates, and not for differences between organic substrates. Petran (1977) found the smallest specimens of *G.fossarum* more abundant in fine substrates (M_d = 0.6 mm) and larger specimens more abundant in coarse material (M_d = 24.5 and 26 mm) in the field samples, with similar differences in artificial substrates placed in the stream. Probably the availability of space is the main reason for these differences. When interstices between stones are too small to offer shelter for larger animals, only small ones will be present (Whitehead, 1935).

The different preferences of larger and smaller *G.pulex* in the Snijb and Rab can only be explained with space as the selection mechanism. It could very well be the explanation for the over-representation of only smaller specimens in mineral substrates (Table 50A) but it does not cover the differences between the three organic substrates types. Here the ability to feed on the substrate might be important as well as the carrying capacity of the substrate types involved (Nilsson & Sjöstrom, 1977). Juvenile gammarids often feed on the faeces of the older ones (Hynes, 1954), and they may feed on fine detritus as well. From field observations it is clear that coarse detritus substrates contain much more fine detritus than leaf packs, which might explain the preference of small *G.pulex* for CD. Larger animals dwell more on Leaves or the combination of CD and L, but the observed difference between the medium and larger sized animals remains puzzling.

Differences in food preferences between animals of different size could be an explanation. Especially when food preferences of medium and larger sized animals overlap, competition for food and space will determine the balance as soon as the carrying capacity of the substrate is approached for a population of a certain size class composition (Nilsson & Sjöstrom, 1977).

More likely, however, the difference in preference between medium-sized and larger-sized animals is inherent to the organic substrate. Leaf packs disappear in the course of winter, spring and summer and are gradually incorporated in the coarse detritus substrates as smaller fragments. Medium-sized specimens are especially abundant in winter, when leaf packs are still dominant. As time goes on, the animals grow and move with the (remains of the) leaves to the CD substrate.

Field experiments In the Ratumsebeek the colonization rate for *G.pulex* of the 8 mm and 4 mm grain size appeared to be the same as Nilsson & Sjöstrom (1977) found in Höje Å (Fig. 42), although there the colonization started sooner, probably because of a stronger drift rate compared to the Ratumsebeek. For all other grain sizes the number of observations is too small to justify any conclusions.

Tables 51 and 52 give the number of *G.pulex* for 6 size classes after 14 and 28 days colonization, respectively. It is apparent that smaller specimens colonize much faster than larger ones, a phenomenon which agrees with another observation by Nilsson & Sjöstrom (1977), who explained this as being related to the presence of each size class in the drift, which is highest for the smallest sizes. Summarized over all size classes, the preference of *G.pulex* after 28 days colonization decreases in the sequence 8, 4, 16 and 32 mm (See Subsection 4.1.7, Table 16). Looking at size classes (Table 53) animals smaller than 6 mm determine the preference for 8 and 4 mm, and the larger individuals, which are present in smaller numbers, the preference for 16 and 32 mm. This illustrates that availability of interstitial space may influence the size group of *Gammarus* that will inhabit the substrate (cf. Whitehead, 1935).

Comparison of these experimental data with those of the field investigation without including the detritus substrates leads to some interesting conclusions. Table 54 gives the I.R. values for Sort 6, 10% in the Rab, and comparing these with

Table 51. Number of *Gammarus pulex* in two artificial substrate trays in the Ratumsebeek after 14 days of colonization.

Length class /mm	Particle size (lower limit)/mm					Total
	32	16	8	4	2	
1 - 3	338	330	137	222	135	1162
3 - 6	25	47	54	176	25	327
6 - 9	26	55	84	11	-	176
9 - 12	53	125	86	-	-	264
12 - 15	31	43	21	-	-	95
15 - 18	6	3	1	-	-	10

Table 52. Number of *Gammarus pulex* in two artificial substrate trays in the Ratumsebeek after 28 days of colonization.

Length class /mm	Particle size (lower limit)/mm									Total
	32	16	8	4	2	1	0.5	0.25	0.125	
1 - 3	234	329	529	595	97	1	2	2	4	1793
3 - 6	267	535	1157	790	91	-	2	8	4	2844
6 - 9	44	51	32	9	-	-	-	-	-	136
9 - 12	106	153	39	-	1	-	-	-	-	299
12 - 15	66	75	2	-	-	1	-	-	-	144
15 - 18	8	5	-	-	-	-	-	-	-	13

Table 53. I.R. values for *Gammarus pulex* in two artificial substrate trays in the Ratumsebeek after 28 days of colonization.

Length class /mm	Particle size (lower limit)/mm								
	32	16	8	4	2	1	0.5	0.25	0.125
1 - 3	*2.5*	*9.2*	*23.4*	*28.0*	-7.3	-14.0	-14.0	-14.0	-13.8
3 - 6	-2.8	*12.3*	*47.3*	*26.1*	-12.7	-17.8	-17.7	-17.3	-17.6
6 - 9	*7.4*	*9.2*	*4.4*	-1.6	-3.9	-3.9	-3.9	-3.9	-3.9
9 - 12	*12.6*	*20.8*	1.0	-5.8	-5.8	-5.8	-5.8	-5.8	-5.8
12 - 15	*12.5*	*14.8*	-3.5	-4.0	-4.0	-3.8	-4.0	-4.0	-4.0
15 - 18	*5.5*	*3.0*	-1.2	-1.2	-1.2	-1.2	-1.2	-1.2	-1.2

Italic values indicate significant over-representation

the I.R. values for the same size classes in the experiments in Table 53 reveals that the results only partly agree. Small individuals mainly colonize the coarse artificial substrate and are also present in the shovel samples taken in coarse substrate. However, larger specimens only colonize the coarsest artificial substrates, but are nearly absent in the coarse shovel samples and abundant in the fine sand substrates, which are often mixed with 1-10% organic detritus.

Compared with Sort 6, 1%, which means that then only mineral samples with less than 1% organic detritus are included, the preference of the smaller individuals hardly changes, indicating that this is a true selection of the mineral particles.

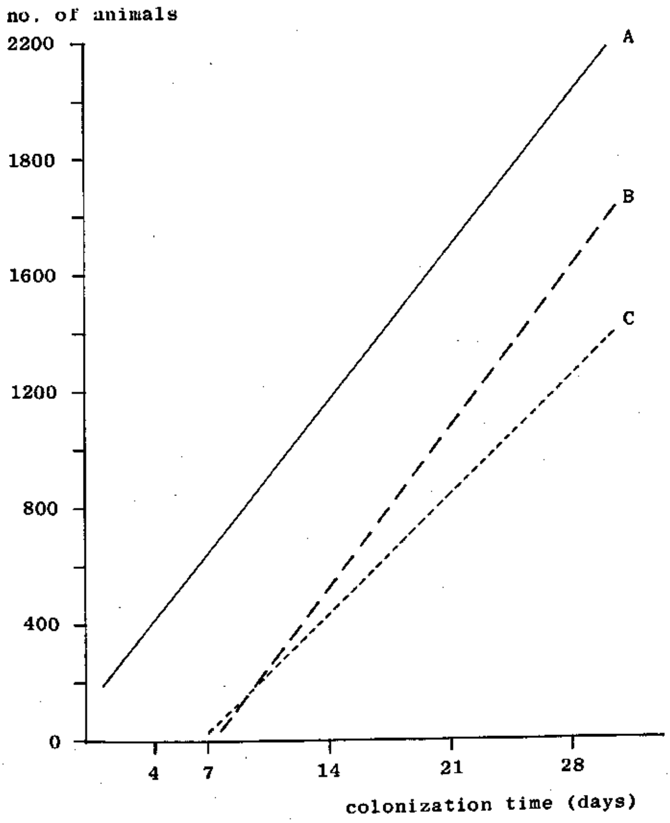


Fig. 42. Colonization rate of *Gammarus pulex* in artificial substrates in the field.
A) according to Nilsson & Sjöström (1977)
$y = 75.4\ x + 113.1$; $r = 0.997$; $N = 5$; $P < 0.005$
B) in 8 mm substrate in the Ratumsebeek
$y = 77.6\ x - 654.6$; $r = 0.956$; $N = 5$; $P < 0.01$
C) in 4 mm substrate in the Ratumsebeek
$y = 59.8\ x - 402.9$; $r = 0.954$; $N = 6$; $P < 0.005$

Table 54. I.R. values for *Gammarus pulex* in the mineral classes of Sort 6,10% in the Ratumsebeek.

	Total	Median particle size (M_d)/mm							
		16	8	4	2	1	0.5	0.25	0.125
Number of samples	148	1	4	4	18	14	19	67	21
Length class/mm	N								
1 - 3	1176	-2.8	*3.9*	*11.2*	-0.7	0.5	*7.7*	-5.2	-3.9
3 - 6	919	-2.5	-0.2	*3.8*	0.7	*2.9*	*3.4*	-2.1	-3.6
6 - 9	212	-1.2	-2.4	-2.4	1.8	-0.2	*2.6*	-2.0	*2.0*
9 - 12	131	-0.9	-1.4	-1.9	1.3	-3.5	0.8	-2.3	*6.6*
12 - 15†	39				3	1	3	8	24
15 - 18†	6				2				4

Italic values indicate significant over-representation
†: actual number of specimens because no significant over-representation

However, for the larger specimens the preference shifted from 0.125 mm to 2 mm and 0.5 mm, because all samples with 1-10% organic detritus were now included in the detritus samples (compare with Appendix 6, on shifting of samples in classes). However, the relative difference with small-sized individuals remains. Obviously, larger-sized *G.pulex* do not select the substrate for its grain size but for the amount of available food (detritus, leaves).

4.2.2.10 Dicranota Zetterstedt sp. (Diptera: Limoniidae)

Identification *Dicranota* larvae are easily recognisable Limoniidae larvae with 5 pairs of ventral pseudopods. They were only identified to genus because no key was available for the identification of the larvae and no adults were found or reared. Although Hennig (1968, vol.II) mentioned only one possible species for Europe (*D.bimaculata*), Mendl (1978) gives another species for the lowland area (*D.guerini*). Which species is found in the Achterhoek streams is uncertain; perhaps they both occur there.

Life cycle Hennig (1968, p. 420) states that Limoniidae probably have 4 larval instars like the Tipulidae, to which they are closely related. According to Levy (1919) *Dicranota bimaculata* pupates in February, although he was unable to rear the pupae to adults. Pomeisl (1953) also stated that *Dicranota* larvae are very hard to keep alive in the laboratory. Mendl (1973) found two flight periods in the Breitenbach (April/ May and September/October) and he concluded that there are 2 generations a year. From the data in Fig. 43 it is clear that in the Ratumse- and Snijdersveerbeek, *Dicranota* has indeed two generations in a year. Although no adults were caught the first flight period will be around week 13-16 (April) and the second in week 33-36 (August/ September), which corresponds with the observations of Mendl (1973).

Microdistribution *Dicranota* occurred with 209 specimens in 108 samples in the Snijdersveerbeek, and with 74 specimens in 43 samples in the Ratumsebeek. In the field classification (Sort 1) in the Snijdersveerbeek the I.R. values indicate significant over-representation in S+CD and Sh.S (Table 55), while no significant positive I.R. values occurred in any other sand substrate except those with fine detritus. Positive I.R. values also occurred in BG and G+CD. In the Ratumsebeek significant positive I.R. values were only found in BG and G+CD (Appendix 9).

Dicranota presents a nice example of the differences that can be found when using different levels of field classifications (Table 55). In Sort 3 with only 3 substrate classes no significant over-representation is present (all I.R. values below 2.0). In Sort 4, with 5 classes, over-representation is present in Sand without Coarse Detritus, which shifts to S+L/CD in Sort 2 (with 7 classes), while the Sand classes without CD only give moderate, not-significant I.R. values. In Sort 1, the most detailed classification, with 14 classes, the above mentioned preferences were

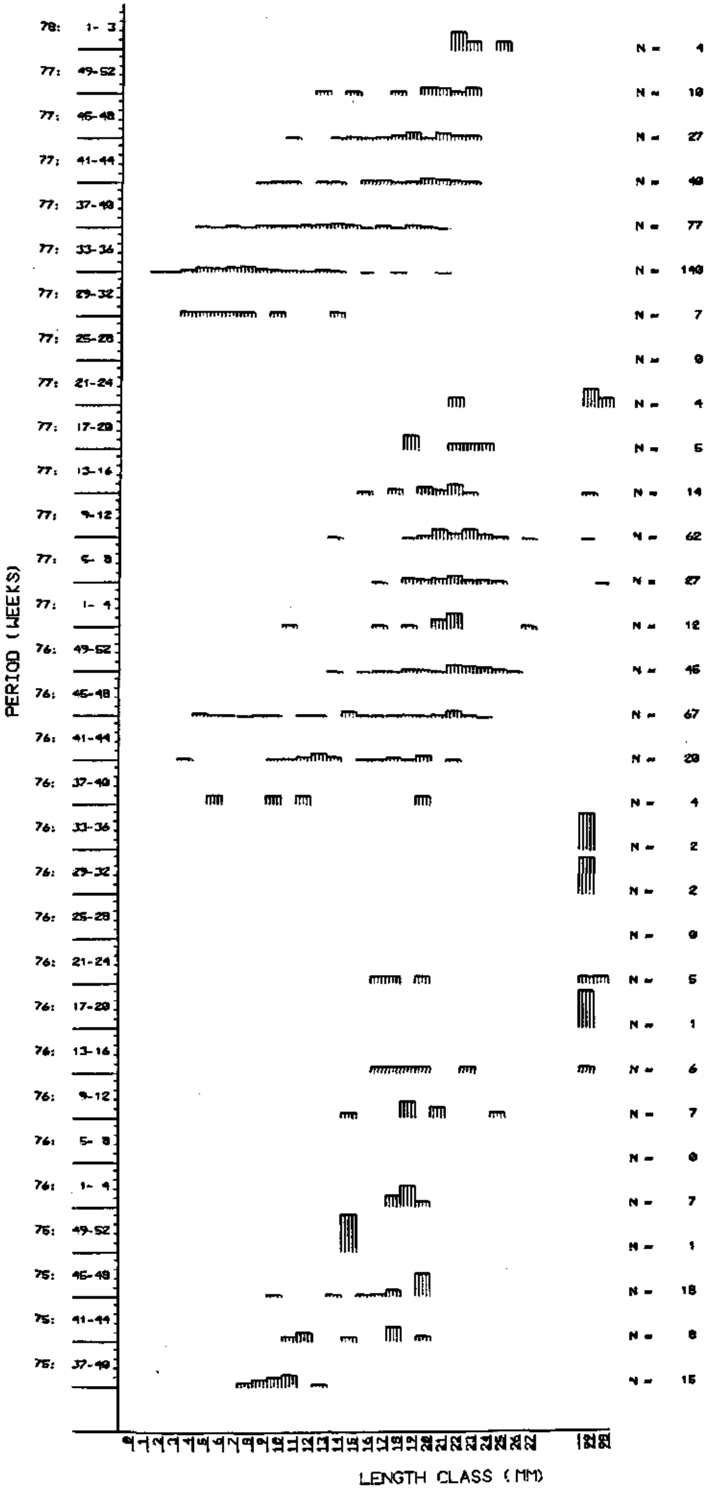


Fig. 43. Life cycle histograms of *Dicranota* sp. showing the distribution (%) of larval body length per four-week period.

Table 55. I.R. values for *Dicranota* spp. (N = 209) in the field classification of the substrates in the Snijdersveerbeek.

<table>
<tr><th>Sort</th><th colspan="8">Sand</th><th colspan="3">Gravel</th><th colspan="3">Detritus</th></tr>
<tr><td>3</td><td colspan="8">1.1</td><td colspan="3">0.5</td><td colspan="3">-2.6</td></tr>
<tr><td>4</td><td colspan="3"><i>2.3</i></td><td colspan="5">-1.0</td><td>0.6</td><td colspan="2">-0.1</td><td colspan="3">-2.6</td></tr>
<tr><td>2</td><td colspan="2">1.7</td><td>1.8</td><td colspan="3"><i>2.8</i></td><td colspan="2">-3.5</td><td>0.6</td><td colspan="2">-0.1</td><td colspan="3">-2.6</td></tr>
<tr><td>1</td><td>0.4</td><td><i>2.2</i></td><td>1.8</td><td>0.3</td><td><i>2.9</i></td><td>1.1</td><td>-2.7</td><td>-2.5</td><td>0.6</td><td>-1.3</td><td>0.7</td><td>-0.9</td><td>-2.7</td><td>-0.4</td></tr>
<tr><td></td><td>St</td><td>Sh</td><td>FD</td><td>L</td><td>CD</td><td>CD+L</td><td>CD+FD</td><td>L+FD</td><td>B</td><td>L</td><td>CD</td><td>CD</td><td>L</td><td>CD+L</td></tr>
</table>

Italic values indicate significant over-representation

found, which agree with the result of Sort 2, but indeed give more detailed information. Stable Sand is not preferred, while of the S+D samples, CD is the most important and the combination with Coarse and Fine Detritus is less preferred.

Considering the grain-size classification for *Dicranota* in the Snijdersveerbeek (Table 56) it is obvious from the differences between the 1% and 10% classification that substrates with less than 1% coarse organic matter are preferred above substrates with 1-10% CD, although this only concerns the finer sand substrates ($Q_1 > 2$) and not the coarse substrates which mostly have less than 1% detritus anyway. Only the substrates with $Q_1 = \bar{1}$ show an increase in I.R. values going from 1% to 10% CD, but this only affects the picture from Sort 8 in Class 7 ($\bar{x}xx$), while Class 5 ($\bar{x}\bar{1}x$) is unaltered. At the same time however, the I.R. values in the fine substrates ($Q_1 > 2$)

Table 56. I.R. values for *Dicranota* spp. (N = 209) in the grain-size classification of the substrates in the Snijdersveerbeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,1%	-0.7	-0.4	-0.4	1.0	*2.1*	-0.4	0.9	-2.1	*2.7*	*3.2*	-	-0.7	-2.7	0.1
Sort 5,10%	-0.7	-0.8	-0.7	0.7	*2.2*	-0.6	*3.8*	-2.5	1.2	1.4	-	-0.6	-2.8	-0.4
Sort 6,1%	-0.7	-	0.9	-2.0	0.4	-0.0	*3.5*	0.9	-1.6	*5.0*	-	-0.7	-2.7	0.1
Sort 6,10%	-0.7	-0.7	0.4	-2.1	0.2	0.1	*3.5*	0.7	-0.7	*2.2*	-	-0.6	-2.8	-0.4
Sort 7,1%	-	-0.7	-1.1	1.9	0.6	-0.1	-0.2	-3.7	1.8	*2.7*	-0.1	-0.7	-2.7	0.1
Sort 7,10%	-	-0.7	-1.7	1.9	0.6	-0.1	-0.2	-3.7	1.7	*2.1*	0.0	-0.6	-2.8	-0.4
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,1%	-0.2	-1.7	0.7	-0.0	*3.5*	0.9	-0.2	-2.1	0.2	*3.8*	*3.2*	-0.7	-2.7	0.1
Sort 8,10%	-0.4	-2.0	0.5	0.1	*3.5*	0.7	1.7	-2.5	-0.5	1.9	1.4	-0.6	-2.8	-0.4

Italic values indicate significant over-representation

decrease, resulting in values smaller than 2.0 in Sort 8, 10%, indicating that *Dicranota* prefers substrates with less than 1% CD. From the drastic shift of over-representation in Sort 5 between 1 and 10% and the relatively unaltered I.R. values in Sort 6 and 7, the conclusion must be dawn that the Q_1 is especially important in connection with the amount of Coarse Detritus present. Furthermore it can be concluded that *Dicranota* dwells preferably in Fine Sand substrates ($Q_1 > 2$) with only small amounts of CD and in Fine Gravel substrates ($Q_1 = \bar{1}$; $M_d = \bar{1}$). In the 10% classification the preference for Fine Sand is less pronounced and higher for Fine Gravel/Coarse Sand. In the Ratumsebeek, *Dicranota* always preferred the coarser substrates (Classes 1, 3, 4, 5 in Sort 8, 10%: $\bar{x}\bar{x}\bar{x}$, $\bar{x}\bar{3}x$, $\bar{x}\bar{2}x$, $\bar{x}\bar{1}x$) with the highest over-representation in $\bar{x}\bar{1}x$, corresponding to the distribution in the Snijdersveerbeek.

From the results of the field experiments presented in Section 4.1.7 (Table 16) it is clear that *Dicranota* occurred mainly in the 0.5 - 1 mm grain size fraction (phi index = 1), but also in the fractions 1-2 and 0.25 - 0.50 mm, which corresponds with the median grain size of the $\bar{x}\bar{1}x$ substrates.

Analysis of the distribution of differently-sized animals in three length classes showed no significant differences, although small larvae occurred preferably in $\bar{x}\bar{1}x$, 33x and $\bar{x}xx$ substrates, while larger ones preferred 23x and CD substrates (Table 57), which might be connected with their journey to damp sites (near the banks) above the water surface for pupation (Miall, 1893). Medium-sized animals showed no significant preference at all, although they mostly occurred in the same substrates as the other sizes.

Since *Dicranota* is carnivorous, predating mainly on Chironomidae and Oligochaeta (Levy, 1919; Wesenberg-Lund, 1943; Hynes, 1961) one might expect a relation between the distribution of prey organisms and *Dicranota*. When these results are compared with the distribution of Oligochaeta (i.e. Tubificidae) the preference in Sort 8, 10% for 23x and 33x corresponds with that of the Oligochaeta for these substrates. Also many Chironomidae larvae show preferences for the same substrates as *Dicranota* (see Appendix 12). A more detailed study of this relationship including gut content analysis will be necessary for establishing relationships between the distribution of *Dicranota* and its

Table 57. I.R. values for *Dicranota* spp. per length class (A) and season (B) in the Snijdersveerbeek in Sort 8,10%.

Length class and Season	N	Substrate class and $Q_1M_dQ_3$ index													
		1 $\bar{x}\bar{x}\bar{x}$	2 $\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	3 $\bar{x}\bar{3}x$	4 $\bar{x}\bar{2}x$	5 $\bar{x}\bar{1}x$	6 $\bar{x}1x$	7 $\bar{x}xx$	8 1xx	9 22x	10 23x	11 33x	12 CD	13 L	14 CD+L
A 1 - 5	65	0.8	-1.9	1.4	-1.1	*4.6*	-2.0	*2.5*	-1.4	-1.9	0.5	*3.8*	-1.6	-2.0	-0.1
6 - 10	84	-0.3	-0.8	0.8	1.1	*3.1*	1.3	0.1	-1.6	-0.7	0.0	0.3	-1.6	-1.0	0.1
11 - 20	60	-1.3	-0.9	-1.4	0.0	-1.9	1.8	0.4	-1.3	1.9	*3.0*	-1.6	*2.4*	-1.9	-0.7
Total	209	-0.4	-2.0	0.5	0.1	*3.5*	0.7	1.7	-2.5	-0.5	1.9	1.4	-0.6	-2.8	-0.4

Italic values indicate significant over-representation

food animals since possible prey was abundant in all substrate types.

The above presented data on the microdistribution partly agree with earlier data, although these cover a wide range of substrates. Geijskes (1935) stated that Limoniidae and Tipulidae belong to the mud fauna as well as to the detritus fauna, but that *Dicranota* occurs in sandy bottoms. This agrees with the observation of Petran (1977) who found that *Dicranota* prefers fine substrates. Edwards (1975) caught *Dicranota* specimens in sites with an abundance of fine substrates enriched with organic matter and found less specimens with increasing current speed and coarser median particle size, which agrees with Egglishaw's (1969) conclusion. However, Jones (1951) reported that *Dicranota* and *Limnophila* occur among stones and coarse gravel in slack water near the banks. Although these distributional data are not contradictory, it illustrates that *Dicranota* occurs in a wide range of substrates, varying from fine sand and mud to coarse gravel and stones, preferably combined with fine detritus. This picture also emerges for the Snijdersveerbeek, where sand substrates combined with fine or coarse detritus are preferred, although *Dicranota* is absent in samples with large amounts of coarse detritus.

Miall (1893) found that pupae never live under water, but that they migrate to damp places above the water surface, e.g. banks or sand ridges in the stream bed. This agrees with the presence of *Dicranota* in especially the samples that were taken from inner bends and sand banks in the Snijdersveerbeek. Mendl (1978) noted that *D.guerini* dwells in streams and small rivers, but that *D.bimaculata* is found within the direct reach of the water surface in the damp banks of these water types. This emphasizes the necessity to identify the genus to species level and the above-cited differences in preferred habitat might be related to different species.

4.2.2.11 Limnophila Marquart spp. (Diptera: Limoniidae)

Microdistribution Although four different *Limnophila* species were distinguished (Appendix 1: taxa no's 197, 198, 199 and 208) the identification remained uncertain and it may have concerned more species. From the distribution of *Limnophila* in the Snijdersveerbeek (Tables 62 and 63) it can be seen that *Limnophila* prefers both Gravel and Sand substrates. Table 58 shows that especially bare substrates (without CD or L) are inhabited, which is also apparent from the decrease of the positive I.R. values comparing the 1% and 10% classification in Tabel 59, except for Class 7 in Sort 8. Since it concerns several species, it is possible that the preference for Coarse Gravel and Fine Sand refers to different species. This cannot be tested since 342 of the 385 specimens were classified as one taxon, the genus *Limnophila*, which may concern several species, while the remaining 43 larvae belonged to the other three taxa (9 to *Limnophila* sp. a, 1 to Limnophila sp. b and 33 to *Limnophila* gr. *fuscipennis*).

In the Ratumsebeek only 62 specimens were found and these occurred mainly in Bare Sand substrates (Appendix 9). In the grain-size classification a preference for

Table 58. I.R. values for *Limnophila* spp. (N = 385) in the field classification of the substrates in the Snijdersveerbeek.

Sort	Sand								Gravel			Detritus		
3	*2.6*								1.1			-6.2		
4	*3.8*			-0.4					*2.2*	-1.2		-6.2		
2	*3.1*		*2.2*	*2.7*			-2.7		*2.2*	-1.2		-6.2		
1	1.5	*3.2*	*2.2*	*4.2*	0.2	1.7	-3.4	0.9	*2.2*	-1.0	-0.8	-2.6	-4.7	-3.3
	St	Sh	FD	L	CD	CD+L	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

Table 59. I.R. values for *Limnophila* spp. per length class (A) and season (B) in the Snijdersveerbeek in Sort 8,10% and for the total in Sort 8,1% (C).

Length class and Season	N	1 x̄x̄x̄	2 x̄5x x̄4x	3 x̄3̄x	4 x̄2x	5 x̄1̄x	6 x̄1x	7 x̄xx	8 1xx	9 22x	10 23x	11 33x	12 CD	13 L	14 CD+L
		Substrate class and $Q_1M_dQ_3$ index													
A 0	1										+				
1 - 4	116	-0.7	*2.0*	-0.5	-0.6	*3.4*	-1.9	-1.1	-1.7	*3.1*	0.1	*6.0*	-2.5	-2.6	-2.0
5 - 8	155	-2.1	1.7	-0.6	-0.4	*2.5*	0.6	1.6	-0.7	-1.3	1.1	*2.6*	-1.1	-2.7	-1.9
9 - 12	77	-1.5	1.0	-0.8	-0.0	0.6	*2.0*	*2.6*	-0.7	1.1	-1.0	0.4	-0.5	-2.3	-1.6
13 - 20	36	-1.0	-0.0	-1.5	0.4	-0.1	1.9	1.2	-0.4	*3.6*	-0.6	0.4	-1.6	-1.8	-1.1
Total	385	-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
B Spring	67	-0.9	*4.9*	-1.0	*2.7*	-0.7	0.3	-0.5	1.2	0.3	*2.3*	-0.9	-1.7	-2.6	-1.9
Summer	52	-1.4	-1.3	-0.1	-0.9	0.4	1.9	*2.3*	-1.9	-1.6	0.3	1.1	0.7	-	-
Autumn	97	-0.6	-2.0	1.7	0.4	-0.8	-0.7	1.2	-1.5	0.6	*3.1*	*2.3*	-1.1	-2.1	-1.4
Winter	169	-2.3	*2.8*	-2.3	-1.5	*6.1*	0.2	*2.8*	-1.6	*2.9*	-1.3	*5.0*	-2.4	-4.0	-2.8
C Total	385	-2.5	*3.3*	-1.7	-0.9	*3.8*	1.0	0.9	-1.6	*4.3*	*2.1*	*6.5*	-3.7	-2.7	-2.2

Italic values indicate significant over-representation
+ : only one specimen not measured.No I.R. values calculated

x̄1x, x̄xx and 1xx was present, while no over-representation was seen in coarse substrates. Table 59 presents the I.R. values for 4 length classes (and 1 unmeasured specimen) (Table 59A) of *Limnophila* and those for the seasons (Table 59B) in the Snijdersveerbeek. These data show that the distribution of the larvae is different in summer and autumn than in winter and spring. The latter seasons are the only periods with many larvae in coarse substrates: most larvae occur in Classes 7 and 10 in summer and autumn. Looking at this distribution for each length class shows that smaller larvae (0-8 mm), which are more numerous than larger ones (7:3), determine the overall (total) distribution seen in Table 59C. Like the smaller larvae, larger ones (8-20 mm) occurred in practically every substrate type, but preferably in the finer substrates.

According to Lévy (1919) *Limnophila* is carnivorous, like *Dicranota* and *Pedicia*, and they dwell preferably in mud and detritus substrates. In experiments with artificial substrates Petran (1977) found that Limoniidae and Tipulidae prefer fine-grained substrates as Chironomidae and Tubificidae do, expecially in the slower running sections of the stream. This may be a predator-prey relationship.

Jones (1949) found *Limnophila* between stones and coarse gravel and according to Geijskes (1935) the Limoniidae belong to the mud and detritus fauna, as do the Tipulidae. Although *Limnophila* did occur in Sand + Leaves, the data from the Snijdersveerbeek and the Ratumsebeek hardly support the possibility that *Limnophila* dwells in detritus substrates. They prefer Fine Sand, which is mostly combined with Fine Detritus (mud), but they also occur in several coarser substrate types. This emphasizes the danger of generalizing from data concerning families or groups of species and the need to identify to the most detailed level.

4.2.2.12 Ptychoptera Meigen spp. (Diptera: Ptychopteridae)

Microdistribution In the Snijdersveerbeek *Ptychoptera* occurred mainly in sandy substrates with a strong preference for S+FD, which can also be described as mud, although it is oxygen-rich, at least at the surface. Other substrates in the field classification were all a combination between CD and/or FD and Sand, although especially the FD played an important role (Sort 2, Table 60).

In the grain-size classification the finest substrates are preferred (Table 61). Only a small shift in preference from Class 12 (CD) to 11 (33x) is observed when comparing the 1% and 10% classifications, indicating that the amount of coarse detritus is not very important. The fine organic material, which is primarily a part of finer substrates, plays a more important role as was seen in the field classification. According to Wagner (1978) the larvae and pupae of *Ptychoptera* occur in loosely packed, soft substrates that are enriched with organic mud. There, they feed on organic matter. They burrow perpendicular in the substrate, breathing through their long, retractible siphon, which extends to the water surface. The maximum length of the siphon determines the maximum water depth that can be tolerated (for longer periods). This is probably why *Ptychoptera* was not found in the Ratumsebeek, since this stream is often too deep in the pools and the current is too strong in the shallower places.

Geijskes (1935) classified *Ptychoptera* as a typical mud-species, like the Tubificidae, *Sialis* and Chironomidae. *Ptychoptera* occur mainly in waters with a lenitic character, where they can tolerate pollution quite well (Berg, 1948; Zitek-Zwyrtek, 1971; personal observation). Most species live in seeping springs and spring-swamps, but they also occur in slowly running streams (Thomas, 1977a, b). The literature cited confirms the observations made in the Snijdersveerbeek, where *Ptychoptera* are especially related to the substrates with much detritus, present in quiet parts of the stream.

Table 60. I.R. values for *Ptychoptera* sp. (N = 251) in the field classification of the substrates in the Snijdersveerbeek.

Sort	Sand								Gravel			Detritus		
3					*7.7*					-7.1			-4.1	
4		*3.8*				*7.4*			-6.8	-2.5			-4.1	
2	-0.2		*7.8*		*3.7*		*6.5*		-6.8	-2.5			-4.1	
1	-2.5	*2.9*	*7.8*	1.6	*3.0*	1.5	*4.8*	*4.8*	-6.8	0.0	-2.9	-2.3	-3.3	-1.2
	St	Sh	FD	L	CD	CD+L	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

Table 61. I.R. values for *Ptychoptera* sp. (N = 251) in the grain-size classification of the substrates in the Snijdersveerbeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,1%	-0.8	-2.0	-5.7	-5.2	-2.1	-0.9	*5.2*	-1.0	*8.4*	*9.6*	-	*3.3*	-3.2	-0.7
Sort 5,10%	-0.8	-2.3	-5.4	-5.2	-0.2	-1.1	*4.1*	-1.3	*6.4*	*11.6*	-	0.7	-3.3	-1.2
Sort 6,1%	-0.8	-	-2.0	-3.7	-4.1	-3.5	-3.5	-1.8	*6.0*	*6.1*	-	*3.3*	-3.2	-0.7
Sort 6,10%	-0.8	-0.8	-2.3	-3.4	-3.9	-3.6	-2.1	-2.0	*5.4*	*6.3*	-	0.7	-3.3	-1.2
Sort 7,1%	-	-0.8	-1.2	-1.6	-0.8	-1.6	-2.0	-3.9	-5.1	*5.3*	*9.5*	*3.3*	-3.2	-0.7
Sort 7,10%	-	-0.8	-1.8	-1.6	-0.8	-1.6	-2.0	-3.9	-4.0	*4.7*	*11.1*	0.7	-3.3	-1.2
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,1%	-2.6	-3.7	-3.9	-3.5	-3.5	-1.4	*2.4*	-1.0	*9.5*	*2.0*	*9.6*	*3.3*	-3.2	-0.7
Sort 8,10%	-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

Italic values indicate significant over-representation

4.2.2.13 Orthocladius van der Wulp spp. (Diptera: Chironomidae, Orthocladiinae)

Microdistribution *Orthocladius* occurred in 31 samples with 631 specimens in the two most downstream sections (6 and 8) in the Snijdersveerbeek; the other 11 specimens were found in 1 sample in Section 4. According to Moller Pillot (personal communication) it concerns at least two different species, although no specific species names are known yet.

In the Ratumsebeek, only three specimens were found, each in a different sample. In the Snijb, *Orthocladius* showed a distinct preference for Gravel substrates combined with Detritus (Table 62, Sort 2), especially Leaves (Table 62, Sort 1), in the

Table 62. I.R. values for *Orthocladius* spp. (N = 642) in the field classification of the substrates in the Snijdersveerbeek.

Sort	Sand								Gravel			Detritus		
3	-16.4								*24.0*			-3.3		
4	-13.1			-9.9					-0.6	*43.5*		-3.3		
2	-11.1		-7.0	-4.1			-9.4		-0.6	*43.5*		-3.3		
1	-9.3	-6.1	-7.0	*3.2*	-6.1	-2.3	-8.4	-4.3	-0.6	*79.9*	*4.7*	*2.5*	-3.9	-4.3
	St	Sh	FD	L	CD	CD+L	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

Table 63. I.R. values for *Orthocladius* spp. (N = 642) in the grain-size classification of the substrates in the Snijdersveerbeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,10%	-1.3	-2.7	*28.7*	*4.3*	-4.7	0.1	-6.4	-6.7	-11.3	-5.0	-	0.1	-3.8	-4.7
Sort 6,10%	-1.3	-1.3	-4.3	1.2	*49.4*	*2.2*	1.8	-2.8	-12.2	-10.4	-	0.1	-3.8	-4.7
Sort 7,10%	-	-1.3	-2.9	-2.6	-1.3	-2.6	0.9	*4.5*	0.8	*2.7*	-3.9	0.1	-3.8	-4.7
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,10%	-1.3	-1.6	*51.9*	*2.2*	1.8	-2.2	-8.1	-6.7	-7.2	-8.7	-5.0	0.1	-3.8	-4.7

Italic values indicate significant over-representation

field classification, and this corresponds to the preference for $\bar{x}\bar{3}x$ (i.e. $\bar{5}\bar{3}x$) in the grain-size classification (Table 63, Sort 5-8). Comparing the preference in Sort 5-7, 10% with the preference in Sort 8, 10% (Table 63), the preference for $Q_1 = \bar{5}$ (Sort 5) and $M_d = \bar{3}$ (Sort 6) is also seen in the preference for $\bar{x}\bar{3}x$ in Sort 8, emphasizing the importance of the coarse grains. However, the Q_3 seems to be less important since the over-representation seen in Sorts 5 and 6 is divided over $Q_3 = \bar{1}$-3 in Sort 7.

Orthocladiinae larvae and especially genera related to *Orthocladius* (e.g. *Euorthocladius*, *Rheorthocladius*, *Synorthocladius* and *Trichocladius*) are regarded as typical for the stony habitat in running water (e.g. Nietzke, 1937; Thienemann, 1954). *Orthocladius* larvae build loose tubes on stones (Geijskes, 1935). Orthocladiinae larvae are more rheophilous and more abundant on stones and vegetation than Chironominae (Thienemann, 1954, Lindegaard, 1972). Cummins (1972) stated that Orthocladiinae are more abundant in erosional zones, which agrees with its distribution in the Snijb as far as the gravelly substrates are concerned. In sandy substrates (e.g. Bare Sand) Chironominae are more abundant (Subsection 4.1.6, Table 14).

4.2.2.14 Micropsectra gr. praecox (sensu Tshernowskij) (Diptera: Chironomidae, Tanytarsini)

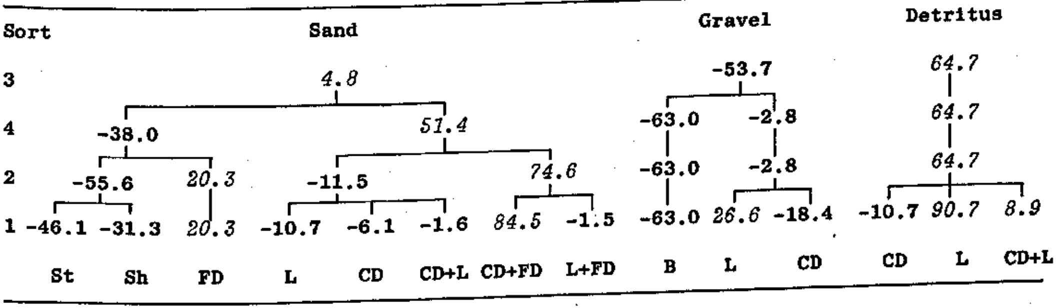
Microdistribution *Micropsectra* larvae were distinguished in two larval groups: *M.* gr. *praecox* and *M.* gr. *trivialis*, the latter having a much longer spine on the inner corner of the antennal base. Undoubtedly the *praecox* group consists of several species, but for further identification no keys were available.

The *Micropsectra* larvae build very long tubes of sand and detritus. They normally are present in and on the upper layer of the bottom in places with a weak current, where the tubes of former generations may have formed tick layers. They also occur in vegetation and sheltered places, where they also build long sand tubes (Lindegaard, 1972).

In the Snijb, *M.* gr. *praecox* is the most numerous species of all macro-invertebrates found, while it is the second most numerous one in the Rab. In both streams it occurs predominantly in detritus substrates (Appendix 9). In the Snijb, the preference is about equal for Leaves and S+CD+FD, with S+FD and G+L as secondly preferred substrates (Table 64). This G+L substrate in fact concerned rather fine sand combined with some coarse material ($Q_1 = \bar{3}$) with less than 10% organic material, because the preference is only seen in Sort 5, 10% (Table 65). The importance of detritus is illustrated by the increase of I.R. values in 23x and 33x substrates in Sort 8, 10% and the decrease in CD comparing with the 1% classification. This corresponds very well with similar changes in I.R. values in Sort 5, 6 and 7 (Table 65).

In the Rab, *M.* gr. *praecox* was most abundant in the CD substrate in both the field classification and the grain-size classification, with only minor preferences for Sand + CD or L and FD substrates, which corresponds with the 23x and 33x substrates in Sort 8, 10%.

Table 64. I.R. values for *Micropsectra* gr. *praecox* (N = 20138) in the field classification of the substrates in the Snijdersveerbeek.



Italic values indicate significant over-representation

Table 65. I.R. values for *Micropsectra* gr. *praecox* (N = 20138) in the grain-size classification of the substrates in the Snijdersveerbeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,1%	-7.3	-16.2	-47.6	-45.7	-23.3	-12.0	-7.6	-33.6	-22.8	*20.1*	-	*57.8*	*93.9*	*5.1*
Sort 5,10%	-7.3	-19.0	-44.8	-46.6	*11.1*	-8.3	-4.7	-33.4	*25.7*	*30.1*	-	*25.8*	*88.6*	*4.5*
Sort 6,1%	-7.3	~	-21.7	-29.7	-35.5	-28.5	-29.4	-31.0	-31.5	-12.1	-	*57.8*	*93.9*	*5.1*
Sort 6,10%	-7.3	-7.0	-24.0	-26.3	-33.8	-29.4	-3.6	-29.8	-25.2	*37.3*	-	*25.8*	*88.6*	*4.5*
Sort 7,1%	-	-7.3	-10.3	-14.5	-7.3	-14.4	-17.6	-37.5	-49.8	-43.4	*23.4*	*57.8*	*93.9*	*5.1*
Sort 7,10%	-	-7.3	-16.1	-14.5	-7.3	-14.4	-17.6	-37.5	-33.0	-9.3	*34.2*	*25.8*	*88.6*	*4.5*
$Q_1M_dQ_3$ index	$\overline{xxx}$	$\overline{x5}x$ $\overline{x4}x$	$\overline{x3}x$	$\overline{x2}x$	$\overline{x1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,1%	-22.7	-31.4	-43.0	-28.5	-29.4	-28.4	-13.9	-33.6	-9.4	-23.7	*20.1*	*57.8*	*93.9*	*5.1*
Sort 8,10%	-22.8	-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*

Italic values indicate significant over-representation

Lindegaard (1972) remarked that it is still uncertain whether the larvae found in the bottom belong to the same species as the ones in the vegetation. The same reasoning applies to the differences found in the Snijb, with two quite different substrate types (leaf packs and S+CD+FD) preferred, while this is also different from the preferences observed in the Ratumsebeek. Further investigation of the larval material from both streams might reveal that it does concern different species.

The combined material from both streams shows that *Micropsectra* gr. *praecox* has two main flight periods: one in March-April (Weeks 9-16) and one in August-September (Weeks 33-40) (Fig. 44).

Differently sized larvae of *M.* gr. *praecox* showed no differences in substrate preference, but between the four seasons differences in distribution were seen (Table 66A). In the Snijdersveerbeek, *M.* gr. *praecox* only prefers Coarse Detritus in spring; it is not so densely populated in any other season. In summer, when pure detritus substrates are rare in the stream, mineral substrate combined with detritus is preferred, while in autumn and winter the main preferences are for Leaves and secondly for Sand/Mud + Detritus (Table 66B). In the Ratumsebeek, small larvae (0-5 mm) prefer CD or CD+L (in summer), while larger larvae (5-10 mm) occur mainly in CD+L or 23x (+ detritus). The preference for 23x and 33x substrates by larger larvae is mainly seen in winter, while in autumn most larvae are found in CD+L, although no samples were taken in the CD substrate in autumn and winter, making interpretation of the data difficult.

Comparison of these data with the grain-size selection in the field experiments (Tables 15 and 16) shows that after a period of 14 days of colonization, the larvae

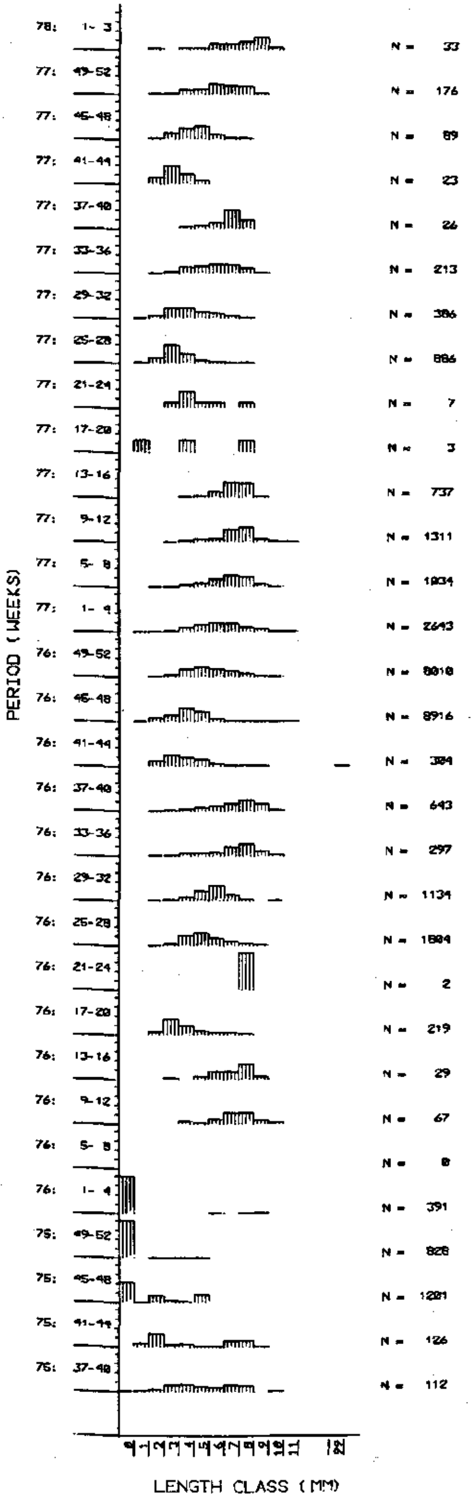


Fig. 44. Life cycle histograms of *Micropsectra* gr. *praecox* showing the distribution (%) of larval body length and pupae (99) per four-week period.

Table 66. I.R. values for *Micropsectra* gr. *praecox* per length class (A) and season (B) in the Snijdersveerbeek in Sort 8,10%.

Length class and Season	N	Substrate class and $Q_1M_dQ_3$ index													
		1 $\bar{x}\bar{x}\bar{x}$	2 $\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	3 $\bar{x}\bar{3}x$	4 $\bar{x}\bar{2}x$	5 $\bar{x}\bar{1}x$	6 $\bar{x}1x$	7 $\bar{x}xx$	8 1xx	9 22x	10 23x	11 33x	12 CD	13 L	14 CD+L
A 0	1846	-7.3	-12.4	-2.6	-11.0	-8.9	-10.2	*24.4*	-13.7	*38.0*	-5.7	*33.3*	-9.4	-13.0	1.5
1 - 5	9499	-16.3	-18.3	-23.9	-20.2	*7.4*	-18.9	-11.0	-21.7	-6.8	*11.7*	*17.8*	-9.9	*94.7*	*3.7*
6 - 10	8789	-15.7	-20.4	-22.8	-18.4	-9.0	-16.7	-17.5	-21.7	-12.6	*35.2*	*11.8*	*53.6*	*41.4*	*2.3*
11 - 20	3													+	
99	1								+						
Total	20138	-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*
B Spring	2249	-5.4	-10.1	-9.4	-11.9	-7.5	-10.8	-13.2	-6.5	-7.7	-1.3	-4.7	*87.8*	-14.1	-10.4
Summer	3663	-11.3	-13.3	-16.2	-9.0	-7.4	-18.3	*2.3*	-12.9	-10.0	*48.3*	*23.1*	-8.9	-	-
Autumn	7013	-14.5	-6.7	-14.8	-19.0	*24.6*	-0.6	-5.1	-21.4	-11.8	-18.2	*7.2*	-7.1	*66.6*	*18.0*
Winter	7213	-15.1	-22.0	-21.5	-17.0	-21.4	-17.5	-11.4	-23.0	*13.9*	*26.4*	*21.2*	-9.1	*65.9*	1.4

Italic values indicate significant over-representation
+ : No I.R. values calculated

are present in equally high numbers in all grain sizes, while they are over-represented in the 4 mm and 8 mm fractions after 28 days. It is highly likely that this is not a preference for the mineral particle size but for the detritus trapped between the mineral grains. More data (e.g. measurements of the amounts of trapped detritus) must be gathered to be able to explain the over-representation of *M.* gr. *praecox* in these coarse-mineral particle sizes.

4.2.2.15 Paracladopelma Harnisch spp. (Diptera: Chironomidae, Chironominae)

Microdistribution Two species of *Paracladopelma* were found in both streams: *P.laminata* and *P.camptolabis*. However, only the larvae longer than 2 mm were identified to species level, because differences between the species were not constant in the smaller specimen.

In the Snijdersveerbeek, 185 specimens were found, 64 of which could not be identified to species level. Of the 47 larvae found in the Ratumsebeek, only 17 could be completely identified. The distributional pattern was the same in both streams for both species considering the field classification (Table 67), although the number of animals is rather low for statistical analysis. Both species show the highest preference for S+FD, followed by Bare Sand substrates (Sh.S and St.S). The small larvae prefer S+CD together with S+FD.

In Sort 8, 10% some differences between the two species appear (Table 68). *P.camptolabis* dwells preferably in 1xx sand, and although *P.laminata* occurred in this substrate, it preferred 23x. Small *Paracladopelma* larvae were found predominantly in $\bar{x}xx$, where also some of the larger larvae of the two species were found.

The two species only sporadically occurred together in the same sample: of the

Table 67. I.R. values for *Paracladopelma* in Sort 1 in the Snijdersveerbeek.

Taxa no.	Taxa name	N	Sand								Gravel			Detritus		
			St	Sh	FD	L	CD	CD+L	CD+FD	L+FD	B	L	CD	CD	L	CD+L
301	*P. camptolabis*	69	*3.4*	*4.8*	*7.3*	-1.2	0.5	-0.7	-2.8	-1.4	-3.8	-1.3	-1.8	-0.1	-2.5	-1.4
307	*P. laminata*	52	-1.6	*5.3*	*6.1*	-1.0	-1.7	-0.6	0.5	0.4	-2.1	0.7	-0.9	-1.6	-2.2	-1.2
299	*Paracladopelma* spp.	64	-2.0	-1.1	*11.0*	0.6	*7.5*	-0.7	-1.1	-1.4	-2.3	-1.2	-2.2	-1.7	-2.4	-1.4
	Total	185	0.1	*5.1*	*14.2*	-1.0	*3.8*	-1.2	-2.1	-1.4	-4.8	-1.1	-2.9	-1.9	-4.1	-2.3

Italic values indicate significant over-representation

Table 68. I.R. values for *Paracladopelma* in Sort 8,10% in the Snijdersveerbeek.

Taxa no.	Taxa name	Number of samples	$Q_1M_dQ_3$ index											Detritus		
			$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
301	*P. camptolabis*	28	-1.4	-2.4	-2.1	-2.1	-1.6	0.4	0.7	*9.0*	0.6	1.0	-0.5	-0.8	-2.5	-2.5
307	*P. laminata*	19	-1.2	-0.7	-1.3	-0.8	-0.6	-1.2	0.3	*2.0*	1.4	*4.4*	0.6	-1.9	-2.2	-1.3
299	*Paracladopelma* spp.	16	-1.4	-2.3	-2.0	-2.1	0.6	-0.9	*13.9*	-1.8	-0.5	0.2	-1.0	-2.1	-2.4	-1.5
	Total	60	-2.3	-3.2	-3.1	-2.9	-0.9	-0.9	*8.8*	*5.6*	0.8	*3.0*	-0.6	-2.7	-4.1	-2.5

Italic values indicate significant over-representation

19 samples with *P.laminata* present, only three samples also contained *P.camptolabis*. This could be ecological segregation, one species excluding the other by some mechanism, e.g. food competition. More likely, the differences in substrate preference play a role in separating the two species: *P.laminata* preferring finer substrates than *P.camptolabis*, although more detailed information is needed to confirm this.

4.2.2.16 Prodiamesa olivacea (Meigen) (Diptera: Chironomidae, Orthocladiinae)

Microdistribution *Prodiamesa olivacea* is with its white body and long black paralabial hair-tufts one of the most easily recognisable Orthocladiinae larvae. It was quite numerous in the Snijdersveerbeek (950 specimens in 105 samples) and the Ratumsebeek 240 specimen in 28 samples), giving an average of 8-9 specimen per sample in both streams.

A direct relationship with detritus in combination with Sand substrates is apparent in both streams, which is illustrated for the Snijdersveerbeek in Table 69 for the field classification. Here the main preference is for S+CD+FD, with a minor over-representation in S+CD+L. The preference is present through all four classification levels, except for the slight over-representation in leaf packs (118 specimens in 34 samples). The preference for S+CD+FD is a preference that is repeated in the grains-size classification, which is not always so, as demonstrated for some of the detritus-preferring Chironomidae (see Subsection 4.2.2.18). In Sort 5-8, 1% the main preference is for CD substrate (Table 70), followed by the finest mineral substrate in all classifications except Sort 6, indicating that substrates preferred by *Prodiamesa* contain more than 1% CD. In the 10% classifications the preference has shifted from CD to the finest mineral substrates, which means that *P.olivacea* occurs predominantly in very Fine Sand substrates combined with 1-10% coarse organic detritus. As demonstrated in Appendix 6, these are also the substrates with the largest amounts of fine organic detritus.

The slight over-representation in Leaves is constant in both the 1% and 10% classifications, indicating that it concerns leaf packs without much mineral matter. In the field classification for the Rab the preference was highest for S+L+FD and S+FD followed by S+CD+FD. In the grain-size classification the preferences were practically identical with those seen for the Snijb, except for the fact that in the Rab Class 9 (22x) was mainly preferred in both the 1% and 10% classifications, while detritus substrates showed no over-representation in any classification. However, an increase in the I.R. values for the finest mineral substrates occurred in the 10% classification, together with a decrease of the I.R. values in CD, indicating that samples with 1-10% CD and containing *P.olivacea* were masked in the 1% classifications.

The distribution of differently sized larvae in three length classes (0-6, 6-10 and 10-17 mm) showed no differences in substrate preference. Nor were there any seasonal variations in the distributional pattern over the substrates. In the field experiments (Table 16), a selection of the 4 mm particle size was seen. Probably the

Table 69. I.R. values for *Prodiamesa olivacea* (N = 950) in the field classification of the substrates in the Snijdersveerbeek.

Sort	Sand								Gravel			Detritus		
3	*13.3*								-15.4			-2.8		
4	-11.6			*33.8*					-14.0	-6.8		-2.8		
2	-12.0		-2.5	1.9			*41.6*		-14.0	-6.8		-2.8		
1	-10.7	-5.8	-2.5	-1.1	*3.7*	-2.0	*46.9*	-0.5	-14.0	-3.3	-6.0	-6.2	*3.6*	-5.0
	St	Sh	FD	L	CD	CD+L	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

Table 70. I.R. values for *Prodiamesa olivacea* (N = 950) in the grain-size classification of the substrates in the Snijdersveerbeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,1%	-1.6	-4.3	-11.0	-9.9	-5.5	-4.1	-6.6	-7.6	-5.6	*4.4*	-	*32.9*	*3.3*	-5.4
Sort 5,10%	-1.6	-4.9	-10.6	-10.4	-5.7	-4.4	-5.7	-7.3	*22.7*	*13.7*	-	*6.5*	*3.3*	-5.3
Sort 6,1%	-1.6	-	-4.7	-7.2	-7.6	-7.0	-7.1	-6.9	-10.9	-1.4	-	*32.9*	*3.3*	-5.4
Sort 6,10%	-1.6	-1.6	-5.2	-7.0	-6.9	-7.1	-7.3	-7.1	-3.2	*24.4*	-	*6.5*	*3.3*	-5.3
Sort 7,1%	-	-1.6	-2.2	-3.2	-1.6	-3.2	-3.9	-8.1	-12.3	-12.2	*5.1*	*32.9*	*3.3*	-5.4
Sort 7,10%	-	-1.6	-3.5	-3.2	-1.6	-3.2	-3.9	-8.1	-11.9	*8.2*	*14.5*	*6.5*	*3.3*	-5.3
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,1%	-5.0	-7.6	-7.3	-7.0	-7.1	-6.3	-7.5	-7.6	-4.3	-3.6	*4.4*	*32.9*	*3.3*	-5.4
Sort 8,10%	-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

Italic values indicate significant over-representation

same explanation as given for the over-representation of *M.* gr. *praecox* in this grain-size fraction applies, namely the high amount of detritus trapped in the 4 mm fraction.

Geijskes (1935) and Nietzke (1937) assigned *Prodiameda olivacea* to the 'mud-inhabitants', a group of species consisting of *Micropsectra praecox, Polypedilum laetum, Polypedilum pedestre, Polypedilum convictum, Ablabesmyia geijskesi, Chironomus, Macropelopia, Psectrotanypus* and others, a community also described by Lindegaard (1972), who gives an even longer list of species in this habitat. Jones (1951) found *P.olivacea* mainly in sand-mud-detritus substrates. Marlier (1951) described the *Micropsectra preacox* community, where *Prodiamesa olivacea* is one of the predominant species.

In the Snijb, *M.* gr. *praecox* occurred most dominant in Leaf substrates and less in the finest sand (mud), although the largest numbers of *M.* gr. *praecox* and *P.olivacea* always occurred in the same range of substrates (Class 9-13 in Sort 8, 10%), with the only difference in the mainly preferred type (Leaves and 23x Sand, both in combination with Fine Detritus). In the Ratumsebeek, *Micropsectra* gr. *praecox* occurred mainly in the CD substrates, while *P.olivacea* was predominantly found in 22x Sand (Class 9). However, all references and the results from both streams reported here indicate that *P.olivacea* prefers soft substrates, consisting of Fine Sand and Fine Detritus (mud) with abundant Coarse Detritus, which is present in places with a weak current. *P.olivacea* is a free-living detritivore that is very well adapted to live in the sand habitat, where it eats the sand for micro-organisms (Bryce, 1960). It is an educated guess that it will also consume large amounts of fine detritus.

4.2.2.17 Epoicocladius flavens (Malloch) (Diptera: Chironomidae, Orthocladiinae)

Microdistribution The life cycle of *E.flavens* and its association with *Ephemera danica* (Ephemeroptera) has been excellently described by Svensson (1976). He found less than 2% of the total number of *E.flavens* larvae free in the substrate; the rest was associated with *Ephemera danica* nymphs.

In the Snijb and the Rab, the second to fourth instar larvae (longer than 1 mm) were always found in samples containing *E.danica* nymphs, but since the number of larvae on the live nymphs was not determined, it is not possible to say whether some occurred free or whether all were attached to *E.danica*. In the Snijb, only four *E.flavens* larvae were found (with 436 *E.danica* nymphs in the samples). In the Rab, however, 130 larvae occurred together with 504 *E.danica* nymphs, although in all samples containing *E.flavens* larvae only 190 *E.danica* nymphs were present. This gives a rather low infestation ratio (0.26) on the total average and is still low (0.68) when only considering the samples containing both larvae and nymphs.

Comparison of the distribution of *Epoicocladius flavens* in the Rab with that of *Ephemera danica* should give a similar distribution if the larvae choose their hosts at random. If they prefer larger nymphs, a difference in the total distribution should be found, but agreement with that of the larger nymphs.

In the field classification (Table 71) *E.flavens* shows a clear preference for S+CD+FD, with a much lower positive I.R. value in S+L+FD. This agrees very well with the preference of *E.danica* (Table 36), especially since the over-representation in S+FD and G+L is caused by the 6-15 mm size class and larger specimens are more or less retricted to S+CD+FD. In the grain-size classification (Table 72) the preference of *E.flavens* in Sort 8, 10% agrees best with that of the largest *E.danica* nymphs (Table 40). The same shifts of preference exist between the 1% and 10% classification.

Analysis of these data for each nymphal size class shows again that *E.flavens* follows the largest *E.danica* nymphs. Differences between Table 72 and Table 38 can be related to the presence of many small nymphs (see Table 40). Although 23x is preferred,

Table 71. I.R. values for *Epoicocladius flavens* (N = 130) in the field classification of the substrates in the Ratumsebeek.

Sort	Sand								Gravel			Detritus		
3	*4.0*								-0.6			-5.4		
4	-3.8			*10.6*					0.3	-1.8		-5.4		
2	-3.6		-1.3	-0.8		*12.3*			0.3	-1.8		-5.4		
1	-2.1	-3.1	-1.3	-0.8	-0.6	-1.4	*13.3*	2.0	0.3	0.4	-2.0	-1.8	-4.8	-1.6
	St	Sh	FD	L	CD	CD+L +FD	CD+FD	L+FD	B	L	CD	CD	L	CD+L

Italic values indicate significant over-representation

Table 72. I.R. values for *Epoicocladius flavens* (N = 130) in the grain-size classification of the substrates in the Ratumsebeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,1%	*2.9*	-1.2	-1.8	*2.5*	-2.6	-0.8	-1.2	-2.2	-2.6	-0.8	-	*10.8*	-4.0	-2.0
Sort 5,10%	*2.9*	-1.2	-1.8	*2.3*	-2.9	-0.7	-1.2	-1.8	*8.9*	-1.8	-	-1.8	-4.8	-1.6
Sort 6,1%	-	-	-0.8	0.2	-1.6	-1.3	1.5	0.5	-4.3	1.4	-	*10.8*	-4.0	-2.0
Sort 6,10%	-	-	-0.8	0.2	-1.6	-1.4	1.5	0.1	-3.1	*14.4*	-	-1.8	-4.8	-1.6
Sort 7,1%	-	-	-	-	-	-	-0.8	-0.2	-3.8	-0.1	*2.9*	*10.8*	-4.0	-2.0
Sort 7,10%	-	-	-	-	-	-	-0.8	-0.2	-4.3	*9.6*	-0.2	-1.8	-4.8	-1.6
$Q_1M_dQ_3$ index	$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,1%	-0.8	0.2	-1.6	-1.3	1.5	0.5	-1.9	-2.2	-3.4	*2.1*	-0.8	*10.8*	-4.0	-2.0
Sort 8,10%	-0.8	0.2	-1.6	-1.4	1.5	0.1	-1.9	-1.8	-1.5	*19.1*	-1.8	-1.8	-4.8	-1.6

Italic values indicate significant over-representation

E.flavens occurred (on *E.danica* nymphs) in all grain sizes from Class 4-10 in Sort 8, 10% with an additional three larvae in Class 2 ($\bar{x}\bar{5}x$, $\bar{x}\bar{4}x$). Since only 5 pupae were found in the shovel samples, no reliable statement can be made on their distribution. All larval size classes showed the same distributional pattern, with the main preference for Class 10 (23x).

Although only 5 *E.flavens* pupae were collected in the substrate samples, many *E.danica* nymphs were found with the remains of pupal tubes attached to the sternum between the middle legs, often on both sides, indicating that two pupae had been attached. Since the pupal stage only lasts a few days, they are easily missed with a sampling frequency of once in two weeks. Hence, nothing can be concluded on the distribution of *E.flavens* pupae.

4.2.2.18 Chironomidae of detritus substrates

Of the 20 Chironomidae species found with more than 100 specimens during this investigation, the following 7 showed a major preference for Coarse Detritus and/or Leaf substrates in both the field and the grain-size classifications (Appendices 9, 12 and 13):

253/254	*Conchapelopia (melanops)*
269	*Corynoneura* spp.
272	*Brillia modesta*
275	*Diplocladius cultriger*
277	*Rheocricotopus* spp.
279	*Eukiefferiella* gr. *discoloripes*
310	*Polypedilum laetum* agg.

Comparison of Appendix 9 with Appendices 12 and 13 shows that preferences for sand or gravel substrates in the field classification are not seen in the mineral classes in the grain-size classifications. This indicates that detritus is more important for these species than mineral matter. All species listed above were mentioned by Lindegaard (1972) as species with vegetation as their specific habitat. Nietzke (1937) classified these species, except *Conchapelopia*, in the group of species occurring mainly in aquatic vegetation or (less abundant) on stones. Geijskes (1935) mentioned, among others, *Brillia, Corynoneura, Rheocricotopus* and *Limnophyes* for the detritus habitat. For detailed notes on the ecology of these species, the paper by Lindegaard (1972) can be consulted. Since the classifications Sort 2-4 and Sort 5-7 do not add any vital information on the substrate preferences of these species, only Sort 1 and Sort 8 will be presented. (Table 73 and Appendices 12 and 13).

Conchapelopia melanops (Wiedemann) (Diptera: Chironomidae, Tanypodinae)

Microdistribution *Conchapelopia* larvae cannot be identified to species level when the pupal thoracal horns are still absent. Since all larvae and pupae that could be identified to species level were *C.melanops*, all *Conchapelopia* larvae were considered to belong to this species.

Conchapelopia is the only Tanypodinae preferring Detritus substrates above mineral substrates (cf. Appendices 9, 12 and 13). Although relatively more larvae were found in S+D and G+D than in pure Detritus substrates, the densities per sample were much higher in the latter. Comparison of Sort 8, 1% with Sort 8, 10% (Table 74) shows an increase of the I.R. values in most of the mineral substrates, together with an increase in the organic substrates. This indicates that at least part of the population lives in mineral substrates with 1-10% organic matter. However, this does not concern different instars since analysis of the distribution of different length classes revealed no significant differences in distribution.

Table 73. I.R. values in Sort 1 for the Chironomidae dwelling preferably in Detritus substrates in the Snijdersveerbeek.

Taxa no.	Taxa name	Sand								Gravel				Detritus	
		St	Sh	FD	L	CD	CD+L	CD+FD	L+FD	B	L	CD	CD	L	CD+L
253	*C.melanops*	-5.6	-4.8	-4.4	-1.5	0.1	*9.8*	1.3	0.6	-4.3	-0.0	0.0	*18.1*	1.9	*6.1*
269	*Corynoneura* spp.	-6.8	-5.7	-4.3	*2.1*	-3.3	0.6	-3.5	0.9	-5.4	*3.6*	-3.7	*16.8*	*20.3*	0.3
272	*B.modesta*	-7.8	-6.2	-5.7	-2.4	-2.8	-1.3	-5.9	-2.7	-9.2	-0.7	-4.4	*14.5*	*30.4*	*18.6*
275	*D.cultriger* †	-6.3	-6.1	-4.7	-1.4	-3.4	-2.4	-7.1	-1.7	-4.5	-1.4	-2.4	-2.1	*27.9*	0.5
275	*D.cultriger*	-2.2	-4.0	-4.3	0.4	-3.0	-1.4	-4.2	-1.9	-2.4	*2.6*	-2.8	0.7	*15.9*	*13.2*
277	*Rheocricotopus* spp.	-12.4	-10.3	-8.9	1.9	-6.5	*4.7*	-10.1	-2.3	-10.6	*20.1*	-7.4	*12.1*	*54.5*	-2.2
279	*E.* gr. *discoloripes*	-14.2	-11.3	-10.4	-5.2	-1.8	-1.4	-11.8	-6.6	-12.2	*49.3*	-8.3	*34.1*	*36.9*	-2.4
310	*P. laetum* agg.	-12.1	-7.2	-4.2	-4.9	*14.2*	*8.1*	-10.0	-5.7	0.2	-2.6	-6.9	*12.2*	*29.9*	-4.3

Italic values indicate significant over-representation
† : Ratumsebeek data

Table 74. I.R. values in Sort 8,1% and Sort 8,10% and seasonal distribution in Sort 8,10% for *Conchapelopia melanops* in the Snijdersveerbeek.

	$Q_1M_dQ_3$ index											Detritus		
	$\bar{x}\bar{x}x$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,1%	-2.2	-4.0	-0.1	-0.3	-1.8	-3.6	-3.9	-4.0	-3.2	-3.1	-2.0	*9.6*	1.7	*9.6*
Sort 8,10%	-2.4	-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*
Spring	-1.0	-2.8	-1.7	-1.3	-0.9	-2.0	-2.7	-1.7	-2.2	-2.2	-1.0	*13.6*	-0.6	*3.1*
Summer	-1.5	-1.6	*4.0*	1.4	0.7	-2.0	0.9	-2.1	-1.7	-2.2	-1.9	*11.3*	-	-
Autumn	-0.8	-1.7	-0.8	0.3	-2.1	-0.3	-3.3	-2.4	1.9	*3.3*	-1.5	*2.7*	1.2	*3.9*
Winter	-1.3	-1.6	-2.2	-1.5	-1.3	-2.0	1.0	-2.5	-2.3	0.8	*2.3*	*3.4*	*3.8*	*4.0*

Italic values indicate significant over-representation

Lindegaard (1972) mentioned that *Conchapelopia* lives primarily on *Elodea* vegetation in places where the current is weak. He assumed that *Eukiefferiella* and *Cricotopus* species, which also occur in this habitat, will be the main food organisms for the predatory *Conchapelopia* larvae. In the two investigated Dutch streams any of the species dwelling in the detritus habitat might serve as food for *Conchapelopia*. However, only an analysis of the gut contents can clarify this in detail.

In the two streams studied, *Conchapelopia* was found with all larval sizes present during the whole year. No significant differences in substrate preference were seen between larvae of different size (1-5 and 5-10 mm). Preference for CD was present in all seasons but highest in spring and summer (Table 74). In winter preference for all Detritus substrates was equally high and shared with Fine Sand with Detritus (33x). In autumn Sand substrates were favoured after CD+L.

In the colonization experiments of several grain-size fractions in the Rab (Tables 15 and 16, Subsection 4.1.7), *Conchapelopia* preferred the 2 and 4 mm fractions after both colonization periods (like *Macropelopia nebulosa*, another Tanypodinae larva). More data on the conditions occurring in the artificial substrates in the field are necessary to explain this preference.

Corynoneura Winnertz spp. (Diptera: Chironomidae, Orthocladiinae)

Microdistribution The genus *Corynoneura* was represented by at least two species: *C.minuta* and *C.scutellata*. *C.minuta* corresponds to the *Corynoneura* sp. II of Lindegaard (1972) and *C.scutellata* resembles his sp. I.

Treated at the generic level, this mixture of species showed a clear preference for organic substrates, especially Coarse Detritus or Leaves. In the Snijb only a slight over-representation occurred in S+L and G+L (Table 73). In the Rab *Corynoneura* occurred predominantly in leaf packs. Berg et al. (1948) and Lindegaard (1972) found *Corynomeura* mainly in vegetation where detritus is often abundant.

Brillia modesta (Meigen) (Diptera: Chironomidae, Orthocladiinae)

Microdistribution *B.modesta* is the most common *Brillia* species found, and the only one in the Rab. In the Snijb, another species was present in low numbers: *B.longifurca* (19 specimens).

Both species occurred in the same substrate types. In all substrate classifications *B.modesta* showed preference for Detritus substrates in general, and for Leaves in particular (Table 73 and Appendices 9, 12 and 13). In both streams, CD+L was the second preference, followed in the Snijb by CD as the third choice. Considering the actual numbers of *Brillia modesta* larvae in the Snijdersveerbeek, 92% of all larvae was present in one of the three organic substrates in Sort 8, 10%. Only 35 larvae were found in the mineral substrates. In the field classification this was 90% for the detritus substrates and the 42 remaining larvae occurred in the mineral substrates combined with CD or L.

In the Rab, only three larvae (2%) did not occur in the detritus substrates in any classification. These data emphasize that organic substrates form the specific habitat of *Brillia*. Geijskes (1935) found them mainly between leaves, but also in moss, detritus and algae. Berg et al. (1948) found *Brillia* between beech leaves in a slow running spring. Hynes (1970a) mentioned that *Brillia* is a wood-eating species, which agrees with the observations by N.H. Anderson (personal communication) that *Brillia* dwells mainly in coarse detritus substrates with a lot of decaying wood present. It is possible that this concerns a difference in the *Brillia* species, since *B.modesta* showed a distinct preference for Leaf substrates without much detritus in the form of sticks, bark, fruits or decaying wood. More likely is the assumption that it concerns an adaptation to the most-readily-available food source.

Diplocladius cultriger Kieffer (Diptera: Chironomidae, Orthocladiinae)

Microdistribution This free-living Orthocladiinae was found in both streams, where it occurred in the Rab mainly in Leaf packs and with equal preference for Leaf packs and CD+L in the Snijb (Table 73). Lindegaard (1972) found *Diplocladius cultriger* predominantly in vegetation together with *Eukiefferiella* species. This combination is also apparent for the Leaf substrate in the Snijb, although some differences remain concerning the secondly preferred substrate.

D.cultriger was most abundant in autumn, winter and spring. In summer only very small numbers were found in both streams, which agrees with the data and references Lindegaard (1972) presented. He concluded that *D.cultriger* is a spring species.
All larval length classes distinguished (1-4 mm, 4-6 mm and larger specimens) showed similar substrate preferences in all seasons.

Rheocricotopus Thienemann spp. (Diptera: Chironomidae, Orthocladiinae)

Microdistribution Only on a few occasions were *Rheocricotopus* larvae identified to species level, and then two species were recognized: *R.dorieri* and *R.fuscipes*, the latter probably being the most abundant one (Moller Pillot, personal communication). However, all *Rheocricotopus* spp. were treated at the generic level.

Rheocricotopus was extremely abundant in leaf packs, with smaller numbers in Coarse Detritus substrates and a few specimens on stones combined with a few leaves (Table 73). This is a distribution quite similar to that of *Eukiefferiella* gr. *discoloripes*. The same increase in I.R. values of the preferred detritus substrate (Leaves) and decrease of I.R. values in the 'mineral' substrates is observed in comparing Sort 8,1% and Sort 8,10%. In Sort 5-7 also over-representation was seen in the coarsest mineral substrate, but this concerned only one sample (see Appendix 4).

Thienemann (1954, p. 629) gave as the characteristic biotope for *Rheocricotopus* the slower- or faster-running rivers and streams, and even springs, in lowlands and middle or high mountain areas, mostly between plants but also on stones, even in polluted streams.

Lindegaard (1972) mentions that *Rheocricotopus fuscipes* is a spring form as all specimens occurred from March to May with a maximum in April. In the Snijb and the Rab the larvae were always present with maximum densities in spring, autumn and winter, indicating that it concerns more generations a year or a mixture of species. *Rh.effusus* is known to have three generations during spring and summer (Lindegaard, 1972).

Eukiefferiella gr. discoloripes (sensu Moller Pillot, 1980) (Diptera: Chironomidae, Orthocladiinae)

Microdistribution This green Orthocladiinae larva was quite abundant in the Snijdersveerbeek, but was found only incidentally in the Ratumsebeek. It proved to be a true representative of Nietzke's (1937) plants-stones group as it preferred detritus and gravel substrates (Table 73): G+L, CD and L in Sort 1. In Sort 8, only CD and L were preferred and no 'mineral' substrates, indicating that of the combination gravel-leaves, the leaves were more important. The I.R. values in the CD and L classes in Sort 8 increased from the 1% to the 10% classification without any increase in the I.R. values in the 'mineral' classes, which indicates that detritus samples with only 1-10% organic material are not the preferred substrate for *Eukiefferiella* gr. *discoloripes*.

This result corresponds well with the observations of Thienemann (1936, p. 50) as reported by Berg et al. (1948), who found that *Eukiefferiella* larvae demand good oxygen conditions in fast-running water, where they dwell between algae and moss on stones. Berg et al. (1948) also found them on stones. The reason for the small population of *E.* gr. *discoloripes* in the Ratumsebeek is not known.

Eukiefferiella verralli larvae (included in the *discoloripes* group) feed on detritus and although they are rheobiontic, they are most abundant in places not exposed to the strongest current (vegetation) where detritus accumulates (Lindegaard, 1972). This type of distribution corresponds closely with that of *Eukiefferiella* gr. *discoloripes* in the Snijdersveerbeek.

E. gr. *discoloripes* is present throughout the year, with a minimum in numbers in summer in the Snijdersveerbeek. Pupae were found in March, and probably the flight period will be the same as Lindegaard (1972) reported: March - June and incidentally during the whole summer, since small larvae were most abundant from October to December and large larvae from February to April.

Polypedilum laetum agg. (sensu Moller Pillot, 1979) (Diptera: Chironomidae, Chironominae)

Identification *P.laetum* is a *Polypedilum* species that can be easily confused with *P.pedestre*. All material was checked with the most recent key (Moller Pillot, 1979) and many identifications were checked by Moller Pillot.

Microdistribution *P.laetum* was only found once in the Rab, downstream of the investigated stream section. In the Snijb, large numbers of larvae were found. They occurred predominantly in detritus substrates, showing a similar distribution as *Conchapelopia melanops*. Leaves, CD and S+CD+L were mostly preferred (Table 73), which agrees with Hynes' (1970a) statement that *Polypedilum* belongs to the wood-eaters, although he did not specify the species.

In the field classification, a minor over-representation was seen in Bare Gravel, but this appeared to be a distinct preference for $\overline{31}$x substrates, which is concluded from Table 75. Moreover, this concerned only one sample with 150 specimens. The increase of the I.R. values in CD and L substrates indicates that substrates mainly consisting of organic material are preferred and not the combination with Sand. This agrees with the substrate where Berg et al. (1948) found *P.laetum*: on stones and vegetation.

Breakdown of the preferences to two larval length classes (Table 76A) shows that the preference for $\overline{31}$x results from the smaller larvae (0-5 mm), although these show an even higher preference for Leaves. Larger larvae (5-8 mm) mainly occur in Detritus substrates and a number of not measured larvae preferred Coarse Sand ($\bar{x}$xx).

Table 75. I.R. values for *Polypedilum laetum* agg. (N = 1125) in the grain-size classification of the substrates in the Snijdersveerbeek.

	Substrate class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	phi index											detritus		
	$\bar{7}$	$\bar{6}$	$\bar{5}$	$\bar{4}$	$\bar{3}$	$\bar{2}$	$\bar{1}$	1	2	3	4	CD	L	CD+L
Sort 5,1%	-1.7	-3.2	-5.5	-10.3	*19.0*	-6.2	-2.1	-8.2	-9.4	-2.5	-	*5.7*	*22.4*	-0.5
Sort 5,10%	-1.7	-3.2	-5.7	-10.8	*17.7*	-6.4	*6.8*	-8.9	-10.5	-5.6	-	*14.7*	*24.2*	-4.4
Sort 6,1%	-1.7	-	-4.8	-1.9	-5.0	-6.3	*10.6*	-7.4	-11.4	-6.4	-	*5.7*	*22.4*	-0.5
Sort 6,10%	-1.7	-1.7	-4.1	-2.0	-5.2	-6.5	*10.0*	-7.6	-8.4	-8.6	-	*14.7*	*24.2*	-4.4
Sort 7,1%	-	-1.7	-2.4	-3.4	-1.7	-2.9	-4.2	-2.9	-2.4	-12.6	-1.4	*5.7*	*22.4*	-0.5
Sort 7,10%	-	-1.7	-2.0	-3.4	-1.7	-2.9	-4.2	-2.9	-3.0	-11.3	-3.4	*14.7*	*24.2*	-4.4
$Q_1M_dQ_3$ index	$\overline{xxx}$	$\overline{x5}$x $\overline{x4}$x	$\overline{x3}$x	$\overline{x2}$x	$\overline{x1}$x	$\bar{x}$1x	$\bar{x}$xx	1xx	22x	23x	33x	CD	L	CD+L
Sort 8,1%	-5.4	-2.2	-4.5	-6.3	*10.6*	-7.9	-3.9	-8.2	-7.9	-5.4	-2.5	*5.7*	*22.4*	-0.5
Sort 8,10%	-5.7	-2.2	-4.7	-6.5	*10.1*	-8.1	*2.4*	-8.9	-9.5	-5.8	-5.6	*14.7*	*24.2*	-4.4

Italic values indicate significant over-representation

Table 76. I.R. values for *Polypedilum laetum* agg. per length class (A) and season (B) in the Snijdersveerbeek in Sort 8,10%.

Length class and Season		N	Substrate class and $Q_1M_dQ_3$ index													
			1 $\bar{x}\bar{x}\bar{x}$	2 $\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	3 $\bar{x}\bar{3}x$	4 $\bar{x}\bar{2}x$	5 $\bar{x}\bar{1}x$	6 $\bar{x}1x$	7 $\bar{x}xx$	8 1xx	9 22x	10 23x	11 33x	12 CD	13 L	14 CD+L
A	0	53							35†					18†		
	1 - 5	919	-5.1	-0.8	-3.7	-6.1	*12.7*	-7.3	-0.2	-8.0	-8.5	-4.7	-4.8	*8.9*	*28.0*	-4.9
	6 - 10	153	-2.1	-2.7	-2.8	-1.6	-3.0	-3.0	-0.4	-2.9	-3.5	-2.6	-2.5	*13.5*	*11.8*	0.8
	Total	1125	-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
B	Spring	459	-2.4	-2.9	0.5	-4.9	-5.5	-4.9	-6.6	-6.5	-5.5	-5.5	-2.4	*13.5*	*34.8*	-3.7
	Summer	122	-2.1	-1.4	-0.7	0.2	-2.0	-3.4	*10.5*	-0.2	-2.4	-0.2	-2.7	*3.6*	-	-
	Autumn	452	-3.8	-4.1	-3.0	-4.9	*22.5*	-3.1	0.7	-7.2	-6.7	-2.3	-1.9	*7.2*	*5.0*	-2.4
	Winter	92	-1.7	*10.1*	-2.9	-1.9	-2.0	-2.2	-1.1	-0.4	-3.0	-2.0	-1.4	*4.3*	*3.2*	-1.0

Italic values indicate significant over-representation
† : Actual numbers are given. No I.R. values calculated

Seasonally there are also differences (Table 76B). In spring, Detritus substrates were preferred, while in autumn most larvae occurred in $\bar{x}1x$ Gravel and Detritus. In summer, only mineral substrates show over representation, while in winter Coarse Gravel ($\bar{x}\bar{5}x$, $\bar{x}\bar{4}x$) is preferred together with Detritus. This clearly indicates that the autumn-winter-spring generation has other preferences than the summer generation. A fact that might be connected with the availability of the preferred substrates.

In summer, when detritus substrates are scarce, the generation spends a much shorter time in the stream. In autumn and winter, when detritus substrates are abundant but larval growth is minimal, the young larvae prefer mineral substrates, while in spring, a period of fast growth, they obviously move to detritus.

5 General discussion

As demonstrated in Subsection 4.1.5. and elucidated for several species in Subsection 4.2.2, most macroinvertebrate species are strongly related to certain substrate types composed of mineral or organic material or a combination of both. These results support the hypothesis that many lowland-stream species have distinct substrate preferences, often with narrow ranges concerning the preferred particle size (combinations). The results concerning the species dealt with in detail have already been compared with literature data in Subsection 4.2.2 and in general agree with or give additional or more detailed information on the substrate preferences.

One should, however, keep in mind that relationships with certain substrate types or particle sizes, concluded from over-representation in these substrates, are not necessarily the result of preferences for the substrate. Preference implies the active choice of 'optimal' conditions by the animals, and conclusions about substrate preference should therefore be based on laboratory experiments in combination with field data. It is not practicable, however, to perform laboratory experiments testing the substrate or particle-size selection for all species present in a stream.

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.

The presence of a species in a habitat is the result of its bahavioural response to the environmental conditions prevailing on the spot (Meadows & Campbell, 1972). Cummins (1975) stated that the relationship of the microdistribution and abundance of macroinvertebrates with various specific physical-chemical parameters may be of only an indirect nature. The animal distributions may actually be controlled by some other factor, which itself is more directly related to a physical-chemical parameter. Substrate composition, or the range of particle sizes present in a habitat, is determined by the current (velocity, flow regime and turbulence), while these are also responsible for the amount of accumulated organic detritus, the growth of macrophytes and the oxygen supply. Thus it is possible that a relationship between the microdistribution of a species and the substrate is in fact controlled by the current velocity or the amount of food (detritus) present. However, on the basis of the knowledge of the correlation between various specific parameters and the substrate it is possible to indicate for each species which parameter will be responsible for the selection of a certain substrate type.

The most important mechanisms seen in Subsection 4.2.2. are either directly linked to the substrate, because it restricts or enhances the possibilities for burrowing, attaching (clinging, sucking), hiding or the provision of the material necessary for case or tube building, or indirectly, because of factors associated with substrate conditions, e.g. microbial, algal or detrital food, or prey density, current-velocity, -regime and -turbulence and oxygen supply. In summary it can be stated that the three factors mainly responsible for substrate selection are: particle size, current velocity and food conditions, as also illustrated in the diagram presented by Cummins & Lauff (1969) (Fig. 1). Of course these factors are often of a combined influence and not easily separated, but it will be possible to illustrate their individual roles.

5.1 PARTICLE SIZE

Species reacting directly to substrate particle size can be found especially among the species dwelling on coarse substrates, where the surface is large enough to allow attachment and clinging (*Simulium*) or smooth enough to allow sucking (*Ancylus*) or the sealing off of the ventral side of the body (*Elmis* larvae). Although these relationships with coarse substrates are inseparably connected with higher current velocities, these species are not found on fine substrates with similar (high) currents. Coarse mineral substrates are comparable to macrophytes, branches or objects as plastic bags, kettles, bottles, etc., which all have in common that the surface area is large and smooth.

Other species distinctly related to the particle size of the substrate are those that ingest the mineral substrate in order to collect the attached microbial and algal growth. This was demonstrated for several Oligochaeta by Juget (1979), who showed a positive correlation between the ingested particle size, the presence of these particle sizes in the substrate and the width of the intestines. This may be one of the reasons why the small Oligochaeta (mainly Tubificidae) are mostly restricted to the fine substrates, while the larger *Eiseniella* dwells in coarser substrates (Appendices 9 and 12), since the former feeds on detritus and mud (smaller than 0.13 mm (Juget, 1979)) while the latter feeds on bacteria and diatoms scraped from larger sand grains (0.3-1.3 mm) or filamentous algae (Ward, 1976). *Ephemera danica* could be an example of such a relationship as well, since Ephemeridae are known to ingest large amounts of inorganic sediment, together with their main food source, fine detritus and the associated microbial growth and seston. It was demonstrated that the distribution of *Ephemera danica* is linked with the presence of fine detritus in the substrate, and the conclusion might follow that the factor food will be an important selection mechanism for *Ephemera danica*. However, Eriksen (1963) demonstrated for *E.similans* that the tolerable amount of fine mineral material that may be present is limited because of its detrimental effect on the oxygen content of the interstitial water. For *E.simulans* the oxygen content of the interstitial water reaches the critical value of 1.20 mg/l when 8-10% of the substrate consists of fine sand (0.125-0.250 mm). Under these conditions it is necessary that the burrow remains in open contact with the stream water. In this event a certain (small) amount of very fine particles (silt, lutum) is necessary to glue larger particles together to obtain a stable tunnel structure (Eastham, 1939). However, the amount of very fine particles must not be too high, because the gill movement of Ephemera may be obstructed. Thus it can be concluded that *Ephemera danica* needs substrates with enough fine organic detritus to feed on, but coarse enough in mineral particle-size composition to allow a good interchange of oxygen between the interstitial water and the stream, or with a large enough proportion of fine particles (smaller than 0.05 mm) to make the substrate sticky, but not too much to clog the gills of the nymphs.

It is very likely that other burrowing species are related to the particle-size composition of the substrate in a similar manner. The selection of particular substrates for pupation by last instar larvae of *M.sequax* could be caused by the fact that substrate composition is related to current velocity and oxygen supply. Pupae are unable to migrate to more suitable places when conditions change. To survive it is therefore obligatory to select sites where such changes are least likely. The aggregation of the pupae of *Lithax obscurus*, *Agapetus fuscipes* and *Potamophylax luctuosus* on stones and branches projecting from the stream bed, often near the banks, is probably the result of the same phenomenon.

Other species showing a direct relationship with the particle size are those that use the mineral and organic material for case building or tube formation. It was demonstrated in case building experiments that *Sericostoma personatum* uses mainly 0.25-0.50 mm grains for its case and that the range of materials that can be used lies between 0.125 mm and 1.0 mm. This means that *Sericostoma personatum* will need a substrate of which a considerable proportion falls within this grain size range, although it is not known yet what the minimum amount should be. Furthermore, *Sericostoma personatum* dwells preferably in coarse substrates, which means that the case-building material has to be found among the smaller fractions and that the substrate selection is related to some other factor, which is probably the presence of Coarse Detritus, as demonstrated before, and a moderate to fast current velocity.

The caddis larvae *Lithax obscurus* and *Agapetus fuscipes* both prefer gravelly substrates, where they live on top of stones or, when the current is very strong, behind stones. They both use mineral matter to construct their cases. *Agapetus fuscipes* uses grain-size fractions ranging from 0.25-0.85 mm in the F-3 instar, but this gradually shifts to 0.5-0.85 mm and 1-2 mm fractions in the F-1 instar, and mainly the 1-2 mm fraction in the final instar and the pupal case. Comparing the distribution of *Agapetus fuscipes* in the Ratumsebeek with the particle-size selection for case building, it is clear that selection of 1-2 mm grains in the final and pupal stage is related to the presence of this fraction in the underlying material. Substrates with a median particle size ranging from 0.5 mm to 2 mm are clearly preferred ($M_d = \bar{1}$ and 1, respectively ; Appendix 13), together with very coarse substrates ($\bar{x}\bar{5}x$, $\bar{x}\bar{4}x$), for which Q_3 varies around 0.5 mm. This means that enough suitable grains will be present for the (largely) final instar larvae and pupae on this substrate. Smaller larvae use relatively more small grains and they occur predominantly on finer substrates than larger larvae. A similar conclusion applies to *Lithax obscurus* (cf. Table 21).

5.2. CURRENT VELOCITY

Since substrate and current are two inseparably connected factors (Schmitz, 1961; Scherer, 1965) it is very difficult to distinguish whether the individual factors or their combination determine macroinvertebrate preferences, although the latter is most probable. The current is responsible for the variation of the grain-size composition over very short distances (mosaic patterns and longitudinal substrate bands). The current influences, for example, the oxygen content of the interstitial water, the amount of trapped detritus, the number of crevices and the growth of periphyton. Together with the interactions between volume of flow and channel dimensions, the current is responsible for the zonation in the substrate composition from head water to delta or from spring to confluence, whereby the median particle size and the coarseness of the detritus decrease (Behning, 1928; Beyer, 1932; Pennak, 1971; Cummins, 1975). According to Ulfstrand (1968) the direct effect of the current on the faunal distribution has often been over-estimated, especially for animals living in running water but dwelling out of the current, dependant as they may be on oxygen and food supply.

The substrate composition of the stream bottom is determined by the interaction of erosion and sedimentation. This principle is used by many authors (e.g. Cummins, 1975) to distinguish three main zones in streams and rivers, which are also present in lowland streams: erosional (riffles with coarse substrate and high current velocities), depositional (pools with fine substrate and low current velocities) and intermediate zones (with gravel-sand substrate and moderate current velocities). Although significant differences in substrate composition and current velocity form the major differences between these zones, Cummins (1966) stresses that the food-chain bases are also different: in erosional habitats, 'Aufwuchs' or periphyton predominates as the major food source, while in depositional habitats the input of detritus acts as such. All these factors are of influence on the faunal composition of these zones. According to Cummins (1975) each zone is characterized by a specific benthic fauna, which in general is more or less restricted to its environment by morphological, physiological and ethological adaptations (Hora, 1936; Ambühl, 1959;

Pleskot, 1961; Jaag & Ambühl, 1963; Bournaud, 1963; Scherer, 1965; Cummins, 1972; Uhlmann, 1975).

Three faunal groups can be distinguished:

- Fauna of the erosional zone, which can attach itself to the substrate by sucking (*Ancyclus*), clinging (*Simulium*) or avoid the current by flattening (*Heptagenia*) or dwelling in crevices (*Gammarus*) or which have specially adapted cases enabling them to withstand the current (*Goera*).
- Sprawling, climbing (*Habrophlebia*, Limnephilidae) or burrowing (*Ephemera, Ptychoptera*) fauna of the depositional zone, often with a mechanism to avoid fouling of the respiratory surfaces (*Caenis*, *Ephemera*). Mud-chiroromids are also found in this zone.
- Fauna often more or less restricted to the intermediate zone, dwelling in moderate flow and burrowing in sand-gravel substrates (*Ephemera*, *Micropterna*, *Sericostoma*).

The more complex substrates, composed of various combinations of the organic and mineral components, form the major part of the stream bottom, especially in lowland streams, where most substrate types are composed of sand combined with detritus; coarse substrates are never abundant.

In the Snijdersveerbeek and the Ratumsebeek most substrates sampled with the shovel were situated in a relatively moderate current in the intermediate or depositional zone, except for Bare Gravel, Bare Sand and leaf packs against obstacles in the current.

Only a few species were significantly over-represented in the two mineral substrates directly exposed to the current. The species found in Bare Gravel were all well adapted to live in stronger currents on the surface of the substrate (*Baetis vernus*, *Lithax obscurus*, *Agapetus fuscipes*, *Elmis aenea* larvae, *Rheotanytarsus* spp.), burrowing in it (*Micropterna sequax*, *Limnophila* spp.,*Sericostoma personatum*, *Eiseniella tetraedra*) or living in existing crevices and interstitial spaces (*Amphinemura standfussi*, *Limnius volckmari*, *Elmis aenea* adults). Most of these species feed on periphyton and detritus, with its associated microbial growth (scrapers or grazers). Only *Limnophila* is predacious.

Because the current brings the oxygen and the food to the animals, the current velocity in the stream may be extremely important for species' microdistribution, but most animals will avoid direct exposure to the current unless they possess special adaptations (Hynes, 1970a).

Habrophlebia fusca needs a well-oxygenated habitat, but it is a very poor swimmer. Its preference for leaf packs and coarse detritus and leaf accumulations is therefore not surprising, since these substrates often accumulate against or behind obstacles in the main current, but protect the animals inside. The same principle applies to *Gammarus pulex*, which is also a poor swimmer without special attachment mechanisms to withstand the current. Only when *G.pulex* is small, can it dwell in the interstices of coarse mineral substrates.

Current, in combination with substrate particle size, is also responsible for substrate stability and may thus influence species' microdistribution. It was demonstrated by several authors that instable substrates are poor habitats (Petran, 1977), only inhabited by Oligochaeta and some Chironomidae species. In the Ratumsebeek and the Snijdersveerbeek the same conclusion was reached. In shifting sand, only Oligochaeta (mainly Tubificidae), Chironomidae (*Polypedilum breviantennatum*, *Stictochironomus*, *Prodiamesa olivacea*), some other Diptera (*Ptychoptera*, *Palpomyia*, *Limnophila*), Hydracarina and *Pisidium* showed over-representation, while only Oligochaeta, *Stictochironomus*, *Polypedilum breviantennatum* and *Pisidium* showed preference for this substrate.

Transport of fine mineral material (silt and sand) by the current resulting in scouring of more stable substrates may also be responsible for the absence of species from substrates normally preferred. On many occasions, especially after periods of high discharge, *Agapetus fuscipes* could not be found in its usual habitat of Coarse Gravel or on stones, but was it hidden under the stones or in finer substrates. The preference of *Simulium* for Coarse Detritus and Leaves may also be linked to the scouring effects of transported sand on the gravel substrate, forcing the larvae to move to places where the current is strong enough to provide sufficient food to their filtering cephalic fans, but slow enough to be free of mineral particles. These conditions can be found on top of detritus accumulations or stones and branches (or plants), which project into the water column, but are high enough above the stream bed itself.

5.3 FOOD CONDITIONS

Provided a wide range of other factors is suitable, the presence of detritus has probably a stronger influence on the microdistribution of most macroinvertebrates than any other factor. Although food as a factor was not studied, most taxa could be related to the substrates they preferred by their food preferences and feeding habits. Cummins (1972, 1975) developed a theory about the relationship between locomotion, feeding, growth, respiration and selection of physical-chemical parameters in determining macroinvertebrate distribution and abundance. In his flow scheme Cummins (1975) distinguished macro- and micro-movements. Macro-movements include rapid migration and drift induced by a sub-optimal physical-chemical environment. Animals leave places where the factors like current, substrate, temperature, oxygen and light do not meet their needs. They also leave when food conditions are bad or competition is too strong. Having found the optimal combination of physical-chemical conditions, micro-movements lead to habitat selection. These movements start with orientation towards current direction and turbulence, while the ultimate habitat selection is largely determined by the nature, particle size and amount of available food. This theory puts more weight on the importance of food for the ultimate selection of the habitat within a given section of a stream that is chosen on the basis of other factors. However, when sufficient food of a suitable composition to support a population is available in a stream section, other factors will determine the detailed microdistributional pattern of macroinvertebrates. Then substrate particle size is possibly the main factor.

Comparison of the microdistributional patterns of several species in the Ratumsebeek with those in the Snijdersveerbeek provides a nice illustration of this theory. The Snijdersveerbeek has small dimensions and a large input of allochthonous organic material that is distributed over the whole width and length of the stream. This creates a situation where for fine or coarse particle detritivores and their predators, sufficient food of suitable particle sizes will be available throughout the stream. The Ratumsebeek, however, is larger, also with a large input of allochthonous organic matter that is mainly distributed along the margins of the stream bed because of the much stronger current velocities, especially after periods of heavy rainfall. This restricts the bulk of the available detritus to the finer substrates along the banks, accumulated against obstacles in the middle of the streambed, trapped in the interstices of coarse substrates, or covered with transported mineral material. Only after extended periods with a low discharge were accumulations of leaves and coarse detritus found in the middle of the stream bed, in deeper pools. In Cummins' (1972) terminology the pools and the margins of the stream are the macro-depositional zones, while the accumulations in the current form the micro-depositional pockets.

In the Snijdersveerbeek, the practically overall favourable food conditions make it possible for the macroinvertebrates to select their habitat on the basis of factors like substrate particle size, current velocity, oxygen conditions and proximity of substrates needed for case building. In the Ratumsebeek food conditions are less favourable, at least in the middle of the streambed, forcing the animals to be content with less preferred physical-chemical conditions in favour of availability of food. Several examples of this negative influence of the absence of suitable food on the microdistribution of macroinvertebrates were already indicated in Subsection 4.2.2. Perhaps the best examples are formed by the differences in distributional patterns of *Ephemera danica*, *Micropterna sequax* and *Sericostoma personatum*. The latter caddis-fly species was not found in the Ratumsebeek at all, although the grain-size composition selected by this species was abundantly present. Apart from macrodistributional factors, one of the reasons for its absence in the Ratumsebeek could very well be the absence of the proper combination of substrate and food in the same habitat.

Ephemera danica and *Micropterna sequax* show small but distinct differences in micro-distribution in the two streams. In the Ratumsebeek, *M.sequax* occurs mainly in Detritus substrates, while it was more or less evenly distributed over Sand + Detritus, Bare Gravel and Detritus (Sort 2, Appendix 3) in the Snijdersveerbeek. Even this preference for Bare Gravel in the Snijdersveerbeek fits the theory since the animals in Bare Gravel are still within easy reach of Detritus substrates or have no further need of food (pupae). In the Ratumsebeek, Bare Gravel substrates were restricted to the erosional zone and only here could pupae be found, while in the Snijb the Bare Gravel also occurs in the intermediate zone where the current is moderate. *E.danica* occurred in both streams, mainly in the Sand + Coarse and Fine Detritus substrates, but it showed a much narrower distribution over the streambed in the Rab in the field classification. (Sort 2, Appendix 9). In the grain-size classifications (Tables 37 and 38) the differences in preferred substrate composition were even more pronounced. In the Snijb, the nymphs occurred in equal densities in Gravel and Fine Sand substrates, while they were restricted to Coarse Sand and Fine Sand in the Rab.

From these data it may be concluded that especially the species showing differences in microdistributional patterns between the two streams inhabit the intermediate zone with gravel-sand substrates and moderate to low current velocities in the Snijdersveerbeek and the depositional zone with sand-detritus substrates and low current velocities in the Ratumsebeek. In the Rab, the erosional zone contains the right substrate composition of sand and gravel, but other factors like current, turbulence and food are unfavourable for many species, while the intermediate zone is rare because coarse substrates are more less restricted to the channel part where the main current is present.

The data on the microdistribution of the individual species in Subsection 4.2.2 clearly demonstrate that species' substrate preferences are strongly linked with their feeding habits and food preferences. Tables 77 and 78 illustrate for both streams the relationship between feeding mechanism and major food type for the four functional trophic groups (Cummins, 1973) and the distribution over the substrate types distinguished in Sort 2 (Appendix 9).

Scrapers and grazers, feeding largely on periphyton and fine organic matter with its associated microflora, prefer Gravel and Bare Sand substrates. This concerns, for example, *Lithax obscurus* and *Agapetus fuscipes*, dwelling on Gravel and Bare Sand, Hydrophilidae, Elminthidae and *Dryops* spp. dwelling on Gravel, and *Pisidium*, occurring mainly on Bare Sand and + Fine Detritus.

Species feeding on coarse organic detritus and leaves (shredders or coarse particulate detritivores) are predominantly found in Detritus substrates or mineral substrates combined with detritus. However, differences in microdistribution between the species remain and these are probably not caused by differences in food preference or feeding habit but by factors like substrate particle size and current velocity. Most Limnephilidae larvae (e.g. *Micropterna sequax*, *Chaetopteryx villosa*, *Potamophylax luctuosus*, *Halesus radiatus* and *Glyphotaelius pellucidus* and also *Sericostoma personatum* prefer substrates where coarse detritus is present in sufficient amounts. *S.personatum* prefers Sand + Detritus substrates but occurs in Coarse Detritus substrates when it is small (Table 24). When young, both *M.sequax* and *Ch.villosa* prefer Leaves, but move to mineral substrates combined with detritus when they are older (Tables 28 and 31). *H.radiatus* and *P.luctuosus* and *G.pellucidus* were only found in small numbers, but they are distinctly associated with Detritus substrates, in the larval stage at least. Pupae of *Potamophylax luctuosus* where mostly found on the underside of large stones, branches or logs. These pupae have a case of coarse sand and fine gravel, while the larvae have a leaf case up to the final instar, when they

Table 77. I.R. values for the trophic groups in the Snijdersveerbeek in Sort 2.

Trophic group	Substrate class and substrate type						
	1	2	3	4	5	6	7
	BS	S+FD	S+D	S+D+FD	BG	G+D/FD	D/FD
Predators	-11.8	*4.5*	*3.5*	*12.9*	-10.3	*4.3*	*4.8*
Scrapers/Grazers	*3.3*	-3.0	-6.9	-7.8	*11.1*	*5.9*	-6.7
Shredders excluding *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 excluding *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*

Italic values indicate significant over-representation

Table 78. I.R. values for the trophic groups in the Ratumsebeek in Sort 2.

Trophic group	Substrate class and substrate type						
	1	2	3	4	5	6	7
	BS	S+FD	S+D	S+D+FD	BG	G+D/FD	D/FD
Predators	-4.0	0.5	1.8	*10.1*	-4.2	-2.2	-1.4
Scrapers/Grazers	*8.8*	-5.2	-2.9	-11.0	*11.8*	*14.4*	-11.5
Shredders excluding *G.pulex*	-20.5	-15.8	-1.1	-21.0	-1.0	-16.3	*55.0*
Shredders excluding *G.pulex* and *N.cinerea*	-13.8	-7.8	*7.3*	-9.0	-9.1	-6.4	*32.2*
Gammarus pulex	-39.4	-17.8	-15.6	-23.0	-28.0	-8.4	*103.2*
Nemoura cinerea	-15.6	-13.8	-5.7	-19.1	*4.5*	-11.8	*44.2*
Collectors excluding *M.* gr. *praecox*	-16.0	-7.3	-6.9	*2.3*	-16.1	-8.7	*38.2*
Micropsectra gr. *praecox*	-18.1	0.2	0.5	*9.2*	-11.4	0.4	*19.2*
Total	-15.4	-10.3	-3.6	-2.5	-12.7	-4.1	*37.1*

Italic values indicate significant over-representation

start building a mineral case, probably for protection in the pupal stage against predators and shredders. The leaf case of *P.luctuosus* is quite similar to that of *G.pellucidus*. These cases, with their round pieces of beech leaves form an extremely good camouflage in leaf packs and are one of the finest examples of the ability of Trichoptera to adapt their cases to their environment.

Other species feeding on Coarse Detritus and Leaves are predominantly found in the pure Detritus substrates. e.g. Tipulidae and *Helodes* larvae. *Gammarus pulex* is the most abundant shredder in both streams and prefers both pure Detritus substrates (larger specimens) and Sand + Coarse Detritus (smaller ones) (Table 54). Plecoptera nymphs (*Nemoura cinerea* and *Amphinemura standfussi*) prefer Detritus substrates, although *A.standfussi* is also over-represented on Bare Gravel, where it probably feeds on the attached fine detritus and diatoms (Dittmar, 1955; Madsen, 1974). Coarse Detritus feeders seem to avoid substrates where large amounts of Fine Detritus are present, even when Coarse Detritus is abundant, which is illustrated by the strongly negative IR values in the Classes 1, 2 and 4 in Table 77.

Collectors, feeding on fine particulate organic detritus (fine particle detritivores) by filtering (*Simulium* spp., *Rheotanytarsus* spp., many Orthocladiinae species) or deposit feeding (*Ephemera danica*, most Chironomini and Tanytarsini species) dwell preferably in mineral substrates combined with detritus. Substrates devoid of detritus are not avoided by most of these species, but they are certainly not preferred except for the species dwelling in Shifting Sand as mentioned in Section 5.2. *Simulium* spp. and *Rheotanytarsus* spp. are known to occur abundantly on gravel substrates up to very high current velocities (Hynes, 1970a) and, indeed, small numbers were found in bare mineral substrates, but *Simulium* occurred predominantly in Coarse Detritus or leaf packs that were often situated in a good current but higher above the streambed, where there is much less scouring by transported sand. *Rheotanytarsus* spp. preferred Sand + Coarse Detritus substrates but were also found on Bare Gravel and in Coarse Detritus.

Most Orthocladiinae species (e.g. *Eukiefferiella* spp., *Brillia* spp., *Corynoneura* spp., *Diplocladius cultriger*, *Rheocricotopus* spp. prefer Coarse Detritus or Leaves, and the species composition found here, corresponds quite well with that given for vegetation by Lindegaard (1972). These species feed here on the trapped Fine Detritus and attached algal growth. *Orthocladius* feeds strictly on diatoms and it is therefore not surprising to find it mainly on gravelly substrates where they dwell in tubes attached to the mineral substrate (Lindegaard, 1972). Perhaps this and similar species should be called scrapers or grazers.

Prodiamesa olivacea is a free living Orthocladiinae species dwelling preferably in Sand with Coarse and Fine Detritus, the same habitat preferred by *Micropsectra* gr. *praecox*, which agrees with the observations by Marlier (1951) and Lindegaard (1972). However, *M.* gr. *praecox* shows a wider distribution than *Prodiamesa olivacea* since it is also abundantly present in pure Detritus substrates and S+FD. Other Tanytarsini species show quite different substrate preferences, e.g. *Cladotanytarsus* for Bare Sand and Gravel + Detritus, while *Tanytarsus curticornis* prefers Gravel + Detritus but is over-represented in most other substrate types except Bare Sand.

Most Chironomini larvae prefer the substrates consisting of a mixture of Sand and Detritus, although some species are also abundant in pure Detritus substrates (*Polypedilum laetum*, *Phaenopsectra*). Some species were even found in shifting sand substrates (*Stictochironomus*, *Polypedilum breviantennatum*, *Paracladopelma* spp.), which might indicate that these species can also feed on the microbial growth on fine mineral substrates, or diatoms possibly present in this habitat.

Epoicocladius flavens, a chironomid living phoretically on *Ephemera danica*, feeds on the detritus passing over the mayfly nymphs with the axial current generated by the gill movements. It occurs in the same substrate as preferred by *Ephemera danica*, which feeds on the same material, namely Sand + Coarse and Fine Detritus. Another mayfly feeding on Fine Detritus is *Habrophlebia fusca*, which was only found in the Ratumsebeek. Here it occurred predominantly in Leaves or Coarse Detritus +

Leaves, where Fine Detritus and attached microbial and algal growth is abundant, but where the leaves offer a good protection against the current. *Baetis* is a better swimmer, feeding on the same material but dwelling on Bare Gravel or Sand + Detritus in the Snijb and in leaf packs in the Rab.

Predators are more evenly distributed over the different substrate types than any other trophic group. They predominate in Sand with Coarse and Fine Detritus, but are also over-represented in all other substrate types except for Bare Sand and Bare Gravel. Within this group, the differences between the individual species are considerable. *Plectrocnemia conspersa* prefers Detritus substrates, while *Hydropsyche angustipennis*, the other net spinning caddis, occurs mainly in Gravel. They both feed on animals (largely Chironomidae) drifting in or swimming against their capturing nets. Of the Tanypodinae, *Macropelopia nebulosa* prefers Sand with Fine Detritus, Sand with Coarse and Fine Detritus and Gravel with Coarse Detritus, a distribution similar to that of *Apsectrotanypus trifascipennis*. *Conchapelopia melanops* prefers Detritus substrates and *Procladius* and *Zavrelimyia* Sand with Detritus and Detritus. These preferences closely agree with the habitat description and species combinations given by Lindegaard (1972).

Other predacious Diptera larvae (e.g. *Limnophila*, *Dicranota*, *Palpomyia*) are more evenly distributed over Sand and Gravel substrates, although differences between the two streams can be observed. Detailed analysis of predator gut contents would be necessary to link predator density and distribution to prey distribution, although for some predators a positive relationship between prey density and predator abundance was demonstrated (e.g. for *Plectrocnemia conspersa*; Hildrew & Townsend, 1976).

Although Tables 77 and 78 illustrate the main preferences of the trophic groups, they do not give any insight in the community structure within a substrate type. To this end, the relative proportion of each trophic group within each substrate type must be considered (Tables 79 and 80). Then it can be seen that scrapers and grazers

Table 79. Percentage occurrence of the trophic groups within the substrate types in Sort 2 in the Snijdersveerbeek.

Trophic group	Substrate class and substrate type							Total
	1 BS	2 S+FD	3 S+D	4 S+D+FD	5 BG	6 G+D	7 D/FD	
Predators	8	6	5	6	9	7	3	5
Scrapers/Grazers	8	1	1	1	13	4	1	2
Shredders excluding *G.pulex*	5	1	3	1	13	5	9	5
Gammarus pulex	29	17	47	13	13	11	24	22
Collectors excluding *M.* **gr.** *praecox*	29	18	22	18	48	35	24	25
Micropsectra **gr.** *praecox*	21	56	23	62	4	38	40	40
Unknown	1	+	-	-	1	+	+	+
N = 100 %	3956	4129	5563	10877	3256	4825	17765	50371

+ : less than 0.5 %
- : zero

Table 80. Percentage occurrence of the trophic groups within the substrate types in Sort 2 in the Ratumsebeek.

Trophic group	Substrate class and substrate type							Total
	1 BS	2 S+FD	3 S+D	4 S+D+FD	5 BG	6 G+D	7 D/FD	
Predators	7	10	9	10	5	4	2	4
Scrapers/Grazers	21	6	7	3	19	24	1	6
Shredders excluding *G.pulex* and *N.cinerea*	2	1	16	2	3	1	6	5
Gammarus pulex	22	30	20	28	23	40	53	42
Nemoura cinerea	13	+	11	3	27	1	13	12
Collectors excluding *M.* gr. *praecox*	30	31	21	34	17	15	18	22
Micropsectra gr.*praecox*	5	21	17	19	6	14	7	9
Unknown	+	+	-	1	+	+	1	+
N = 100 %	2384	671	617	2993	2040	790	13989	23484

+ : less than 0.5 %
- : zero

are only present in considerable numbers in Bare Sand and Gravel substrates, while predators form a more or less constant proportion of the population (5-10%) in all substrate types except Detritus substrates, where the extremely high numbers of *G.pulex* and *M.* gr. *praecox* result in a low percentage occurrence of the predators. Shredders are dominated by *Gammarus* in the Snijdersveerbeek and *G.pulex* and *M.* gr. *praecox* in the Ratumsebeek. With the exception of these species, shredders are most abundant in Bare Gravel (*Amphinemura standfussi, Micropterna sequax* and *Chaetopteryx villosa*, and Detritus substrates (*Amphinemura standfussi, Chaetopteryx villosa* and *Helodes*). Collectors predominate in numbers in all substrate types, which is mainly caused by the high numbers of Chironomidae. Expressed in biomass, these figures would probably be more in favour of the shredders, which are in general, much larger than the collectors. From Tables 79 and 80, which show the percentage occurrence of the four trophic groups, it is clear that gravel obviously presents the most favourable conditions for a heterogeneous trophic structure, offering suitable food conditions to all different trophic levels of the stream community. In these tables the dominant species have been treated separately, to illustrate the proportion of the other species in the groups of the shredders and collectors.

6 Conclusions

The data presented in the previous chapters provide a sufficient basis for accepting the two working hypotheses concerning substrate composition and substrate patterns (Chapter 1, Section 1.3).

6.1 SUBSTRATE COMPOSITION

It has been demonstrated that most benthic macroinvertebrate species occurring in the Snijdersveerbeek are distributed unevenly over the various substrate types, which are composed of mineral matter, organic detritus or a combination of both. A species was considered to prefer a substrate type when it was present in significantly higher numbers than on or in other substrate types. Of the 84 species present with a total number of 20 specimens or more in one of the two streams, or present in more than 10 samples, 42 were over-represented in only one of the seven substrate types distinguished (Sort 2, Appendix 9). Nineteen preferred detritus substrates, 13 gravel (3 Bare Gravel, 10 Gravel mixed with Detritus) and 10 were most abundant in sand (2 in Bare Sand, 1 in Sand with Coarse Detritus and 7 in Sand with Coarse and Fine Detritus). In general, preferences of species for a certain substrate type observed in the Snijdersveerbeek were confirmed in the Ratumsebeek. Some species showed small differences in substrate preferences between the streams, but these could be explained on the basis of dimensional differences between the streams (Section 5.3).

Substrates were classified in several substrate types on the basis of field observations (Subsection 4.1.1), laboratory analysis of the grain sizes and the nature (and particle size) of the organic detritus (Subsection 4.1.2.2). Considering the distribution of the macroinvertebrates over the substrate types, three main groups of species could be distinguished, with preference for coarse mineral substrates (Gravel), fine mineral substrates (Sand) and organic substrates (Leaves or Coarse Detritus), respectively. These groups were similar in both the field and laboratory grain-size classifications. On a more detailed level, the field classification demonstrated the importance of the presence or absence of fine and coarse detritus and leaves in combination with mineral substrates, within these main substrate types, for the microdistribution of the macroinvertebrates. The classification on the basis of grain sizes determined in the laboratory emphasized the role of mineral particle-size composition on the microdistribution of the macroinvertebrates.

Substrate composition is strongly related to food conditions, current velocity and oxygen conditions. These parameters are closely related and changes in the physical environment will influence them concurrently. Coarse substrates generally occur in places with higher current velocities, where oxygen saturation is high and the amounts of fine organic detritus are low. Fine substrates occur together with low current velocities, accumulations of fine and coarse organic detritus and often less favourable oxygen conditions. Current velocity, oxygen content and the amount of detritus are intermediate where substrates consisting of a mixture of fine and coarse sediments are found.

Leaf packs form a special habitat where oxygen content, current velocity and amount of fine detritus may vary considerably, depending on their position in the stream bed. If accumulated against obstacles projecting from the stream bed (e.g. branches and stones), conditions will be similar to those in coarse mineral substrates; if accumulated near the banks or on the bottom of pools, conditions will be similar to those in fine mineral substrates.

Because animal microdistributions are strongly related to the mineral and organic composition of the substrate, the substrate composition is an excellent parameter to classify species habitats or community biotopes. This principle has successfully been used by many of the early workers on stream ecology (e.g. Thienemann, 1912; Beyer, 1932; Geijskes, 1935; Nietzke, 1937; Berg et al., 1948; Marlier, 1951; Dittmar, 1955) and has not lost its importance since.

6.2 SUBSTRATE PATTERNS

For many macroinvertebrate species dwelling in lowland streams, not only the substrate, current or food conditions prevailing in their habitats are necessary for their existence, the proximity of other habitats is also essential. The heterogeneous environment of natural lowland streams forms the basis for the heterogeneous macroinvertebrate community. They can occur in the same biotope because of the spatial variation of environmental conditions.

The characteristic lowland-stream community is formed by a large variety of species with quite different habitat preferences. Many authors have demonstrated that the mosaic substrate patterns, the alternation of riffles and pools and the occurrence of erosional and depositional sites in natural streams are the main reasons for the existence of the heterogeneous stream community (e.g. Illies, 1952; Schmitz, 1961; Cummins, 1966), because most species occurring in a stream dwell in distinctly defined habitats, as demonstrated in the preceding chapters.

Reice (1974) stated that sediment particle size is probably an organizing factor in stream-community dynamics and that different community level processes can be expected to increase their rates in proportion to the spatial heterogeneity and stability of their environment.

Malmqvist et al. (1978) concluded in their study of the influence of detritus on the distribution of the bottom-animal communities that environmental heterogeneity and substrate stability are the two most important variables influencing the community. Detritus as a food source may not only influence the species composition but also the structural modification of the bottom.

Rabeni and Minshall (1977) performed experiments with artificial substrates in pools and riffles, concluding that the maximum animal densities they found were positively correlated with the amount of trapped coarse organic detritus. Their conclusions that detritus is the most important factor influencing the microdistribution of insects, and that substrate structure and grain size determine the distribution of the detritus, is in agreement with Egglishaw's (1964, 1968, 1969).

The importance of organic detritus for running-water communities has been demonstrated by numerous authors (e.g. Sprules, 1947; Schwoerbel, 1961; Cummins, 1962, 1964, 1966; Thorup, 1966; Mackay & Kalff, 1969; Lindegaard, 1972; Fischer & Likens, 1973; Williams & Hynes, 1974; Lindegaard & Thorup, 1975; Hildrew & Townsend, 1976). At the same time, the influence on the microdistribution also received as much attention (e.g. preceding references plus Minshall, 1967, 1968; Kaushik & Hynes, 1968, 1971; Cummins, 1973; Hynes et al., 1974; Boling et al., 1975). Detritus forms an integral part of the stream bottom. It may cover the mineral substrate or vice versa, or may be mixed with it. In its various stages of degradation from leaves to fine-detritus particles it functions as a food source as well as an attachment site. It also forms an important component of substrates largely consisting of mineral particles. It loosens mineral substrate packing, increases porosity and thus the penetrability.

Mineral substrates always form the base for organic matter. Mosses grow on solid objects and detritus and leaves are deposited on the bottom and get trapped in the mineral substrate, although the nature and particle size of the trapped detritus depend on the particle size of the mineral substrate (Minshall & Minshall, 1977; Williams & Mundie, 1978). Rooted aquatic plants can often be regarded as a separate habitat, like floating ones, but there is often a combination with trapped detritus (Higler, 1977; Mackey, 1976, 1977).

The concurrent presence of several not-preferred substrate types together with the preferred type may be essential for the survival of certain species when conditions are unfavourable in their preferred habitat. Places with a relatively low current velocity and more stable substrates, e.g. behind obstacles where detritus can accumulate, form refuges for many species living in places that become unstable or offer too little food at times of high discharge. *Ephemera danica* nymphs move from gravelly substrates in the middle of the stream to sand with fine detritus near the banks and behind obstacles when the current velocity increases in winter, which increases the instability of the gravel substrates and reduces the amount of food (Subsection 4.2.2.6). Similarly, gravelly substrates with many interstices will form a refuge for many species, protecting them against the current and thus forming a reservoir from where other substrates can be stocked again when conditions improve (Mackay, 1969).

Species may need different substrate types because they need other grain sizes or materials to build their cases than are present in their preferred habitat (e.g.

many Trichoptera, such as *M.sequax*, *Ch.villosa*, *P.luctuosus*). Pupae need places where they will be assured of suitable protection against predators and of continuing good oxygen conditions. They cannot defend themselves nor change their position should conditions deteriorate (e.g. *M.sequax*, *Ch.villosa*, *L.obscurus*, *A.fuscipes*). Mackay (1977) demonstrated for *Pycnopsyche scabripennis* that pupae seem to be burrowed only in substrates where a considerable proportion of gravel of 4-8 mm and 8-16 mm is present, while the larvae prefer organic substrates. She suggested that the extent of these particle sizes available for aestivation and pupation may even limit the abundance of this species. Many Trichoptera species normally dwelling in organic substrates pupate in sites where they can attach their cases to some solid object, such as logs, branches, sticks, cobbles, bricks, kettles, e.g. *Halesus radiatus*, *Glyphotaelius pellucidus*. Other species, normally occurring in gravelly substrates, but often in places sheltered from the direct force of the current, move to stones or branchés situated in much stronger currents to pupate (e.g. *Lithax obscurus*, *Agapetus fuscipes*). Here they can be assured of a good oxygen supply while the chance of being smothered by transported sediment is minimal. Because pupal cases are firmly attached to the substrate they are not swept away by strong currents. Larvae may avoid these sites because they would have to expend too much energy just to withstand the current (Bournaud, 1974).

Some species even change their case-building material prior to pupation, when their larval cases consist of organic material, probably to obtain better protection against predators and shredders. This is expecially so when pupation takes place at the end of spring, when detritus substrates become scarcer. Cummins (1964) demonstrated this for *Pycnopsyche lepida*, and in the Ratumsebeek *Potamophylax luctuosus* is a good example of this material and habitat change. Both *Micropterna sequax* and *Chaetopteryx villosa* demonstrate a similar change in substrates preferred during their development. Comparing life cycle, substrate preferences, food habits and case building of these two limnephilid caddis-fly species, only one conclusion can follow: they show similar substrate, food and habitat preferences, and they build similar cases. But, their comparable development stages are not concurrent, which means they prefer the same habitats at different times of the year, so competition will be minimal. These species form a remarkable example of spatial and temporal ecological segregation. In summer and autumn, when *Ch.villosa* has reached its final instar and is in a resting stage or is a pupa, juvenile *M.sequax* larvae appear. At this time *Ch.villosa* is present in gravel substrates, while *M.sequax* dwells predominantly in detritus. In autumn some *Ch.villosa* larvae can also be found in Coarse Detritus. Until the first week of October this concerns larvae just before pupation, which were probably consuming their last meals before closing their cases. *M.sequax* larvae occurring in Coarse Detritus in autumn, were only found after the second week of October, which means the two species are seldom found together in the same substrate. In winter and spring, when *M.sequax* larvae are fully grown, they move to mineral substrates to build a mineral case and burrow, while feeding on the coarse detritus present in these sites or in the proximity. At the same time juvenile *Ch.villosa* larvae dwell predominantly in their organic cases in Coarse Detritus substrates. Only in spring and summer do they move to mineral substrates and build (partly) mineral cases, but by then *M.sequax* has already pupated or emerged. These two species form a pair that could be called the European equivalent of the species studied by Cummins (1964): *Pycnopsyche lepida* and *P.guttiger*. These two *Pycnopsyche* species are also spatially separated at times when they occur together in a stream. *P.lepida* shows the same changes in case-building material and substrate preference as *M.sequax*.

6.3 EFFECT OF REGULATION

The main goal behind the present research was to demonstrate that the limitation of many benthic macroinvertebrate species to natural or semi-natural lowland streams (and the absence of these species from regulated streams) is strongly connected to the differences in substrate composition and heterogeneity between natural and regulated streams. In a study on the microdistribution of benthic macroinvertebrates, the amount of material that has to be analysed may soon become too much to deal with in the time available. Therefore it was not possible to include some regulated streams in the research.

However, given the distinct substrate preferences demonstrated by most species and knowing that many of the substrates found in natural streams do not occur or are much less abundant in regulated ones, the conclusion is obvious that the substrate composition may be an important parameter responsible for the differences in benthic faunal composition. The stream bottom of natural lowland streams consists of a large variety of substrates, alternating in space and time in mineral particle-size composition and the amount and nature of organic detritus under the influence of current velocity and the form of the stream bed. The presence of these mosaic patterns is essential for the existence of the characteristic macroinvertebrate community in lowland streams.

Most macroinvertebrates living in these streams occur in characteristic habitats within the stream bed, where conditions concerning the availability of suitable food substances, particle size of the mineral substrate, current velocity and oxygen supply are optimal. By far the largest number is detritivore or herbivore, feeding on the allochthonous detritus originating from the vegetation on the banks. Some species can use the leaves almost immediately after they have entered the stream system, others depend on microbial activity to convert the leaves into more digestible components (most macroinvertebrates do not possess cellulase) or on the activity of other macroinvertebrates to break down the leaves to smaller particles (faeces, fine detritus, coarse detritus), often very rich in micro-organisms.

The abundance of the various degradation stages of the allochthonous organic matter in the stream habitats is strongly correlated with the current velocity and the mineral particle sizes. Current is responsible for the constant redistribution of the detritus over the stream bed and over the various substrate types. Coarse mineral substrates, often situated in higher currents, will trap both fine and coarse detritus in the interstices. Fine mineral substrates are more abundant when current velocities are lower, along the banks and in front of and behind obstacles and in inner bends. These are the places where most of the coarse and fine detritus accumulations can be found. When current velocities are low throughout the stream, in time of low discharge, the area with detritus accumulations can extend over the whole stream bed, although this concerns mainly the fine detritus, because whole leaves or parts of them are less abundant in the stream system in these periods (late spring, summer and early autumn).

It is essential that detritus can accumulate in sheltered places, because it forms the basis of the heterotrophic food web of a lowland stream. In these places the detritus can be broken down, partly to smaller particles, which are transported to other places, and partly digested. Without these accumulation sites the stream would soon be swept clean of detritus and become devoid of its main food source. Moreover, the accumulation of very thick layers of fine detritus (mud) in which anaerobic conditions would occur within a short distance below the surface, as often seen in regulated streams, is prevented by the constant sequence of allochthonous input, accumulation in sheltered places, degradation by fungi, micro-organisms, macroinvertebrates and mechanical reduction of the particle size by shredders and the interaction of current and mineral particles, and the constant redistribution of the organic particles by the current. It is therefore essential that pools and riffles are maintained in addition to stream meanders. Both mechanisms are used by the stream to expend its energy and to redistribute its bottom material and transport its waste downstream, where it can be broken down further in depositional habitats with their characteristic fauna (large, slow rivers and lakes and ponds).

Many of the differences in species composition between natural and regulated streams can be explained on the basis of changed environmental conditions as a consequence of the enlarged dimensions and the discharge regime of the stream. These changes concern the form of the stream bed, the water depth, the degree of meandering, the alternation of riffles and pools, the frequency of spates and droughts, the light intensity reaching the water surface, the current velocity, the minimum and maximum water temperature and their fluctuations, the particle-size composition of the substrate and the input of allochthonous material. Mineral substrate composition of the stream bottom, current velocity and the nature and origin of the organic detritus are the major habitat parameters that change. Erosional and intermediate zones disappear, together with the associated fauna. Leaf packs and coarse (leaf) detritus substrates are not present and of course neither is the fauna associated with these allochthonous organic substrates. Fine mineral substrates combined with fine organic detritus form the most abundant substrate in regulated streams, together with large fields of macrophytes. The fine detritus does not originate from the break-down of leaf material from allochthonous sources, but from decaying microphytes and macrophytes produced in the stream itself. Fluctuations in temperature and oxygen regime are much greater in regulated streams because of the direct exposure to the sunlight and the resulting increase in primary production. The amounts of fine detritus accumulating per unit area are also much larger because current velocities are kept low by weirs at regular distances along the streams and by the extremely high storage capacities of (enlarged) stream channels.

The regulated sand collector (Section 7) in between the two natural sections in the Snijdersveerbeek forms an example of such changes. This section runs parallel to a road and has functioned as a sand collector for 20 years, after a series of three small pools between Sections 4 and 7 were filled in. However, until 1976 it consisted of a small stream channel within the wider stream bed, where current and substrate resembled that of Section 6, except for a pool at the downstream end of Section 7 that was approximately 20 m long and 3 m wide. The water left this section through a culvert. Under the water works scheme of the land reclamation for Aalten, plans were made to regulate the Snijdersveerbeek downstream of Section 6. On the basis of the occurrence of several rare macroinvertebrate species in this stream and especially in the downstream sections it was agreed that this part of the plans would not be carried out. Section 8 is inhabited by the largest number of species of all different sections, some of the species occurring only in this section, e.g. *Goera pilosa*, *Athripsodes cinereus*, *Hydropsyche augustipennis* (Tolkamp, 1975b). Much to the surprise of everyone, including local farmers, the sand collector was regulated anyway in the summer of 1976. Within two days, the trees were cut, the trunks removed, and the section widened from 3 to 7 m with a slope of 1: 1 and the bottom-level lowered 80-100 cm. The width of the water in the bed increased from 50 to 165 cm and the water level had to increased from 25 cm (in the pool before the culvert) to 105 cm before one drop of water could flow through the culvert, a situation that occurred for the first time in late December, which means that Section 8 was dry in this period. The summer of 1976 was extremely dry, but in the following years the same situation occurred for shorter periods.

The substrate of the regulated section consisted of a uniform layer of fine sands (233, 334) mixed with a large amount of fine detritus. No macrophytes have grown there since 1976 and the detritus probably came from the upstream sections. Occasionally some gravel was present in Section 8, but always covered with a thick layer of sand and fine detritus.

The fauna predominating in the regulated section is very different from the other, natural sections of the stream. Appendix 14 compares the species and their numbers found in 5 shovel samples in sand and gravel substrates and 4 hand samples of leaf packs in Section 6, with 2 handnet samples in Section 7. In the regulated section, with its sand/mud substrate, only a few species are present that also occur in the upstream sections, while their abundances are quite different. Heteroptera and Odonata were only found in small numbers or not at all in the upstream or downstream sections, nor were the majority of the Chironomidae species found in the sand collector (cf. Appendix 9). It can be concluded that changing a stream into a long narrow pond by regulation results in the destruction of the stream fauna and the settlement of a pond or ditch fauna.

Summary

A lowland stream can be distinguished from other types of streams by its strongly varying discharge, water level, current velocity, bottom composition and vegetation pattern. A large number of benthic macroinvertebrate species are restricted to this type of environment and form the characteristic animal community of the natural lowland stream.

A large number of physical factors directly influence the distribution of macroinvertebrates over the various habitat types that can be found in a stream. Current velocity, substrate composition and the nature and amount of food are the most important ones.

Chapter 1, the introduction, deals with the relationship between these factors and their influence on the stream ecosystem. As a starting point for investigations into the role the substrate plays in the development and preservation of the macroinvertebrate communities in natural, undisturbed lowland streams, two closely related working hypotheses were formulated:

- Many benthic lowland stream macroinvertebrate species show distinct preferences for a specific substrate composition.
- For many of these species the small-scale spatial variation in substrate composition of the stream bed is essential for their existence.

The research was carried out in two unperturbed lowland streams, the Snijdersveerbeek and the Ratumsebeek. These two streams are described in Chapter 2.

In Chapter 3, Section 3.1 the method used to classify substrates in the field on visual characteristics, the selection of the sampling sites and the method of sampling substrate and macroinvertebrates at the same time with the micro-macrofauna shovel are described. In Section 3.2 a detailed description is given of the procedures carried out in the laboratory: collection and identification of the macroinvertebrates; particle-size analysis of the substrate; and determination of the nature and amount of organic detritus. Section 3.3 treats the methods used in the laboratory to test the results of the field study: performing substrate selection experiments for several macroinvertebrate species in a laboratory stream channel. Section 3.4 deals with the methods used to study the colonization of artificial substrates in the field. In Section 3.5, the methods used for statistical analysis of the collected data are described.

In Chapter 4, Section 1 the results of the field study are given. On the basis of the field classification of the substrates, each sample is classified to a substrate type characterized by the ratio between the dominant mineral (e.g. gravel,

sand and organic (e.g. leaves, coarse detritus, fine detritus) components. Four classification levels are used. Comparison of these levels illustrates that it is important to make a distinction between mineral and organic substrates, between coarse and fine mineral substrates, between coarse and fine organic substrates and between the various combinations of these types (Fig. 12).

From the particle-size analysis in the laboratory of the mineral components of the samples, the substrate characteristic ($Q_1M_dQ_3$ graph) is determined for both streams (Figs. 14 and 15). Several substrate types are distinguished using the first, second (median) and third quartile, or their combination, in the $Q_1M_dQ_3$ index (Appendices 4 and 5). Substrates consisting of more than 10% (1% in a parallel classification) organic detritus are distinguished as separate types: coarse detritus, leaves and the combination of these two.

The preference of a species for one or more substrate types was indicated by the Index of Representation. This method gave satisfactory results and was more convenient than other statistical methods (Subsection 4.1.3.1).

The importance of the joint use of the two classification levels for the organic material is illustrated in Subsection 4.1.3.2.

It was demonstrated that a high abundance of a species (*Ephemera danica*, a mayfly) may influence the total microdistributional pattern over the various substrate types, because juvenile animals are more numerous than older ones, although this does not influence the specific substrate preference as measured by the Index of Representation (Subsection 4.1.3.3).

Although only small differences in the total number of species between the substrate types are found, the differences are larger when the specimens are considered per taxonomic unit (Tables 13 and 14; Subsection 4.1.6). In all substrate types, chironomid midge larvae are dominant in terms of number of species and number of specimens. However, there are distinct differences between the various sub-families. Substrate types consisting of purely mineral material (bare sand, bare gravel) are poorest in specimens, but not in species. Bare gravel, for example, is richest in species, followed by detritus substrates. Bare gravel shows the most evenly balanced distribution of the number of specimens over the various taxonomic units.

In Subsection 4.1.4 clustering of the 14 substrate types (characterized by the $Q_1M_dQ_3$ index) on the basis of the species composition and the relative abundance of each species per substrate type demonstrates that the faunal composition differs strongly among the gravel substrates. It is also shown that there are differences between coarse sand, fine sand, leaves and coarse detritus, and that within these types the differences are less pronounced. For the main substrate types, only small differences are found between the two streams (Figs. 17 and 18).

In Subsection 4.1.5 the grouping of the species on the basis of their substrate preference(s) is described. The grouping is done using the field classification (Appendix 9) and the grain-size classification of the substrates (Appendices 12 and 13). Several species appear to have similar substrate preferences, making it possible to distinguish faunal groups, each with a certain substrate preference. It is clear that a detailed substrate analysis is not reflected in the preferences of the faunal groups, which mainly show distinct preferences for gravel, sand or a combination of these two types.

In Section 4.2 detailed data on substrate preference are presented for 26 taxa from the various taxonomic units representing the species composing the faunal groups. Mechanisms leading to substrate selection and eventual differences in substrate preference between different development stages of an organism are discussed. The results of the analysis of the field data are compared with data from the literature and, for a restricted number of species, with the results of substrate-selection experiments in the laboratory and colonization experiments in the field. It is shown that it is necessary to use a detailed substrate analysis for the assessment of the substrate preferences of individual species.

The results for the individual species are discussed in Chapter 5, emphasizing the role of the main factors that determine the substrate preferences (particle size, current velocity, and food conditions).

In Chapter 6, the conclusions concerning the working hypotheses formulated in Chapter 1 are discussed:

- Most benthic macroinvertebrates are related to certain substrate types. Three main groups can be distinguished, composed of species with preferences for coarse mineral substrate (gravel), fine mineral substrate (sand) and organic material (leaves or detritus), respectively. The particle size of the mineral component of the substrate as well as the nature and amount of the organic detritus influence the microdistribution of most of the investigated species. Factors related to the substrate, such as food availability, oxygen- and current conditions, are also important.
- Various macroinvertebrate species need several substrate types at the same time or consecutively to be able to maintain themselves in a lowland stream. Changes in food supply or food selection, as well as alterations in case-building material (for caddis flies) or in the proportion of factors related to the substrate, such as current velocity (for the mayfly *Ephemera danica*) make this necessary.

If a species prefers various substrate types, these preferences do not occur at the same moment (seasonal differences) or at the same development stage.

The alteration in substrate composition, changes in flow regime and the changed nature and origin of the food web basis, are the most important reasons for the differences in faunal composition between the communities of natural and regulated lowland streams. Because current velocity directly affects the substrate composition, and stream hedgerows are directly related to the structure of the food web in the stream (leaves are the basic food), it is essential that not only the hydrological consequences of hydrological operations in the stream are considered, but also the effects on the stream ecosystem. This implies that the natural current regime must be maintained and that hedgerows and forests along the banks must not be cleared to make way for inspection paths.

Samenvatting

Laaglandbeken vormen een voor Nederland karakteristiek beektype, gekenmerkt door een grote dynamiek in afvoerfrequentie, waterstand, stroomsnelheid, bodemsamenstelling en vegetatiepatroon. Vele benthische diersoorten, voornamelijk behorend tot de macrofauna, komen alleen of bij voorkeur in dit milieutype voor en vormen daarmee de kenmerkende dierlijke levensgemeenschap van een ongestoorde laaglandbeek.

Voor de verspreiding van macrofauna-organismen over de verschillende habitattypen welke men in een beek kan aantreffen (microdistributie) zijn een aantal fysische milieufactoren van belang, waarvan de stroomsnelheid van het water, de samenstelling van het substraat en de aard en de hoeveelheid van het voedsel de belangrijkste vormen.

In de inleiding in hoofdstuk 1 wordt ingegaan op de samenhang tussen de factoren en de invloed van deze factoren op het beekecosysteem.

Het doel van het onderhavige onderzoek is het verkrijgen van inzicht in de rol die de samenstelling en de variatie van het substraat spelen bij het ontstaan en in-stand-blijven van de voor ongestoorde laaglandbeken karakteristieke macrofauna-levensgemeenschap. Dit is vervat in twee samenhangende hypotheses:

- Veel bodembewonende laaglandbeek-macrofaunasoorten vertonen duidelijke voorkeuren voor een specifieke substraatsamenstelling.
- Voor veel van deze soorten is de kleinschalige ruimtelijke variatie in substraatsamenstelling van de beekbodem essentieel voor hun (voort)bestaan.

Het onderzoek werd verricht in twee ongestoorde laaglandbeken, de Snijdersveerbeek en de Ratumsebeek, welke beschreven worden in hoofdstuk 2.

Paragraaf 3.1 beschrijft de wijze waarop substraten in het veld werden gekarakteriseerd, de selectie van de bemonsteringsplaatsen en de methode van gelijktijdige bemonstering van substraat en macrofauna met de micro-macrofauna-schoffel.

Paragraaf 3.2 gaat in op de verwerking van de monsters in het laboratorium, het uitzoeken, conserveren en determineren van de macrofauna, de korrelgrootteanalyse van het substraat en de bepaling van de hoeveelheid organische stof in ieder monster.

In paragraaf 3.3 zijn de methodieken beschreven waarmee de resultaten van de veldinventarisatie in het laboratorium werden getoetst door het verrichten van substraatselectieexperimenten in een laboratoriumstroomgoot voor diverse macrofaunasoorten.

Paragraaf 3.4 geeft de methode toegepast voor de bestudering van de kolonisatie van in het veld aangeboden substraten, zogenaamde kunstmatige substraten, terwijl paragraaf 3.5 de wiskundige verwerking van de verzamelde gegevens weergeeft.

In paragraaf 4.1 worden de methodische resultaten van het veldonderzoek besproken. Op grond van de veldclassificatie wordt ieder monster ingedeeld bij een substraattype, gekarakteriseerd door de verhouding tussen de in het veld herkenbare dominante minerale (bijvoorbeeld grind en zand) en organische (bijvoorbeeld blad, grove detritus en fijne detritus) componenten. Hierbij worden vier classificatieniveaus gebruikt, welke door onderlinge vergelijking het belang illustreren van het maken van onderscheid tussen mineraal en organisch substraat, tussen grof en fijn mineraal substraat, tussen grof en fijn organisch substraat en tussen de diverse combinaties van deze substraten (fig. 12).

Op basis van de korrelgrootteanalyse van de minerale delen van de monsters is de substraatkarakteristiek voor de beide beken opgesteld (fig. 14 en 15) en worden er diverse substraattypen onderscheiden met behulp van het eerste, tweede (mediaan) en derde kwartiel of hun combinatie in de $Q_1M_dQ_3$-index (appendix 4 en 5), waarbij substraten bestaande uit meer dan 10% (1% in een parallelle indeling) organische detritus als aparte types worden onderscheiden in grove detritus, blad en de combinatie van beide.

Er wordt aangetoond dat de gekozen methode om de voorkeur van een organisme voor een of meer substraattypen te herkennen door middel van de 'Index of Representation', goed voldoet in vergelijking met andere statistische methoden (paragraaf 4.1.3.1). Het belang van het gebruik van de beide classificatie-grenzen voor het organisch materiaal werd geïllustreerd in paragraaf 4.1.3.2. Tevens wordt aangetoond dat hoge dichtheden van een soort (*Ephemera danica*, een haft) wel het algehele verspreidingsbeeld over de diverse substraattypen kan beïnvloeden omdat juveniele dieren veelal talrijker zijn dan oudere, maar dat de met behulp van de 'Index of Representation' aangetoonde specifieke voorkeur hierdoor niet wordt gemaskeerd (paragraaf 4.1.3.3).

Hoewel er ten aanzien van het totaal aantal soorten slechts geringe verschillen tussen de substraattypen werden gevonden, blijken er grotere verschillen wanneer de aantallen soorten en individuen niet als totaal maar per taxonomische eenheid worden beschouwd (tabel 13 en 14, paragraaf 4.1.6). Hierbij blijkt dat chironomiden (muggelarven) zowel wat betreft het aantal soorten als het aantal individuen in alle substraattypen domineren, waarbij er echter duidelijke verschillen bestaan tussen de diverse subfamilies. Substraattypen bestaande uit puur mineraal materiaal (kaal zand, kaal grind) zijn het armst aan individuen, maar niet aan soorten. Kaal grind is zelfs het rijkst aan soorten, gevolgd door detritussubstraten. Kaal grind is tevens het substraattype dat de meest evenwichtige verdeling van het aantal individuen over de diverse taxonomische eenheden te zien geeft.

In paragraaf 4.1.4 wordt door middel van een clustering van de 14 door de $Q_1M_dQ_3$ index gekarakteriseerde substraattypen op basis van de soortensamenstelling en de talrijkheid van iedere soort per substraattype aangetoond dat de faunistische samenstelling van de diverse grindsubstraten onderling sterk verschilt. Tevens komt naar voren dat er verschillen zijn in faunistische samenstelling tussen grof zand, blad en grove-detritussubstraten maar dat binnen deze substraattypen de verschillen minder groot zijn. Tussen de beide beken werden slechts geringe verschillen in de hoofdtypen grind, zand en detritus gevonden (fig. 17 en 18).

In paragraaf 4.1.5 wordt de groepering van de soorten op basis van hun substraatvoorkeur beschreven. Deze werd zowel uitgevoerd op basis van de veldclassificatie (appendix 9) als op basis van de korrelgrootteclassificatie van de substraten (appendix 12 en 13).

Diverse soorten blijken dezelfde substraatvoorkeur(en) te hebben, zodat het mogelijk is om faunistische groepen te onderscheiden, elk met een bepaalde substraatvoorkeur. Er komt naar voren dat een gedetailleerde substraatanalyse niet terug te vinden is in de voorkeuren van de groepen soorten, die veelal reageren op het onderscheid grind, zand, detritus of een combinatie van deze hoofdtypen.

Paragraaf 4.2 behandeld voor 26 soorten, vertegenwoordigers van genoemde faunistische groepen, verdeeld over de diverse taxonomische eenheden, de gedetailleerde substraatvoorkeuren, waarbij ingegaan wordt op de mechanismen die leiden tot substraatselectie en eventuele verschillen in voorkeur onder invloed van het ontwikkelingsstadium van het organisme. De resultaten van de analyse van de veldgegevens worden vergeleken met de literatuurgegevens en, voor een beperkt aantal soorten, met de resultaten van laboratoriumexperimenten en kolonisatieexperimenten met kunstmatig substraat in het veld. Er blijkt dat het voor de vaststelling van de substraatvoorkeur van individuele soorten wel belangrijk is om een zo gedetailleerd mogelijke substraatanalyse te hanteren.

Paragraaf 4.4 geeft een overzicht van de belangrijkste resultaten van de veldexperimenten.

In hoofdstuk 5 volgt de geïntegreerde discussie van de hiervoor gepresenteerde resultaten voor de individuele soorten, waarbij de nadruk wordt gelegd op de hoofdfactoren die de substraatpreferentie bepalen, namelijk korrelgrootte, stroomsnelheid en voedsel.

In hoofdstuk 6 worden de conclusies gegeven aan de hand van de eerder gestelde hypotheses:

1. De meeste bodembewonende macrofaunaorganismen zijn gerelateerd aan bepaalde substraattypen. Drie hoofdgroepen kunnen worden onderscheiden, bestaande uit soorten met een voorkeur voor respectievelijk grof mineraal substraat (grind), fijn materiaal substraat (zand) en organisch substraat (blad of detritus). Zowel de korrelgrootte van de minerale component van het substraat als de aard en de hoeveelheid van het organisch materiaal beïnvloeden de microdistributie van de meeste onderzochte organismen. Hierbij spelen tevens met het substraat gerelateerde omstandigheden zoals voedselaanbod, zuurstofgehalte en stroomsnelheid een rol.
2. Diverse soorten macrofauna hebben meer substraten tegelijkertijd of in successie nodig om zich te kunnen handhaven in een laaglandbeek. Hierbij spelen zowel wijzigingen in het voedselaanbod of de voedselkeuze een rol, als wisselingen in het

materiaal gebruikt voor huisjesbouw (bij kokerjuffers) of gewijzigde, aan het substraat gerelateerde factoren als de stroomsnelheid (bijvoorbeeld voor de haft *Ephemera danica*).

Wanneer een soort meer substraten prefereert, blijkt na gedetailleerde analyse van de gegevens dat deze in de regel niet op hetzelfde tijdstip voorkomen (seizoensverschillen) of dat verschillende ontwikkelingsstadia verschillende substraattypen prefereren.

Beschouwing van deze conclusies in het licht van de verschillen in faunistische samenstelling van de levensgemeenschappen van natuurlijke en gereguleerde laaglandbeken leidt tot de conclusie dat de wijzigingen in substraatsamenstelling tesamen met het gewijzigde stromingsregiem en de aard en herkomst van de basis van het voedselnetwerk als de belangrijkste oorzaken voor deze verschillen zijn aan te wijzen. Omdat de stroomsnelheid direct van invloed is op de substraatsamenstelling, terwijl beekbegeleidende houtopstanden direct gerelateerd zijn met de opbouw van het voedselnetwerk in de beek (blad is basisvoedsel), is het van wezenlijk belang dat er bij de planning van hydrologische ingrepen in het beekecosysteem niet alleen met de hydrologische consequenties wordt gerekend, maar ook met de hydrobiologische, hetgeen impliceert dat het natuurlijk stromingsregiem moet worden gehandhaafd, terwijl de beekbegeleidende bossen en houtwallen niet moeten wijken voor schouwpaden.

Appendices

Appendix 1. Macroinvertebrate species and taxa found in the Snijdersveerbeek and the Ratumsebeek.

0 : taxon not considered for calculation of number of species

00 : taxon not considered as such; identification uncertain; perhaps not aquatic.

4 3 : taxon 3 is part of the overlapping taxon 4, although it may be a well defined species. Taxon 3 is always considered as being included in the overlapping taxon 4.

Nomenclature follows the keys used for identification (see Identification References). When only a genus name is stated, it may concern more than one species (spp.), unless all specimens are expected to belong to one species, but the species name is unknown (sp.).

Numeral taxa codes are unique for this research and were used for computer analysis of the data.

Tricladida:		
4	3	*Polycelis tenuis* (Ijima)
	4	*Polycelis* Ehrbg. spp.
	9	*Dendrocoelum lacteum* (Müller)
Oligochaeta:		
	11	Oligochaeta spp.
11	12	Tubificidae spp.
11	13	Naididae spp.
11	14	Lumbriculidae spp.
	18	*Eiseniella tetraedra* (Savigny)
	19	*Stylaria lacustris* (L.)
Hirudinea:		
	21	*Erpobdella octoculata* (L.)
	22	*Erpobdella testacea* (Savigny)
	23	*Glossiphonia complanata* (L.)
	25	*Helobdella stagnalis* (L.)
	28	*Theromyzon tessulatum* (Müller)
Malacostraca:Crustacea:		
	32	*Gammarus pulex* (L.)
	33	*Gammarus roeselii* (Gervais)
	35	*Asellus aquaticus* (L.)
	36	*Asellus meridianus* Racovitza
Hydracarina:		
	38	Hydracarina spp.
Araneae:		
	39	*Argyroneta aquatica* (Clerck)
Plecoptera:		
	40	*Amphinemura standfussi* Ris
	42	*Nemoura cinerea* (Retzius)
Ephemeroptera:		
	47	*Ephemera danica* Müller)
	48	*Habrophlebia fusca* (Curtis)
	49	*Centroptilum luteolum* (Müller)
52	50	*Baetis vernus* Curtis
52	51	*Baetis muticus* (L.)
	52	*Baetis* Leach. spp.
	53	*Paraleptophlebia submarginata* (Stephens)

56 *Caenis horaria* (L.)
57 *Caenis robusta* Eaton
Odonata:
59 Zygoptera spp.
61 *Aeshna mixta* Latreille
63 *Somatochlora arctica* Zetterstedt
74 *Ceriagrion tenellum* (Villers)
Hemiptera:
0 75 Corixinae larvae spp.
76 *Velia caprai* Tamanini
77 *Notonecta glauca* L.
81 *Notonecta viridis* Delcourt
83 *Gerris gibbifer* Schummel
84 *Sigara striata* (L.)
85 *Sigara falleni* (Fieber)
86 *Sigara distincta* (Fieber)
87 *Sigara lateralis* (Leach)
88 *Sigara semistriata* (Fieber)
93 *Hesperocorixa sahlbergi* (Fieber)
96 *Nepa rubra* (L.)
97 *Hydrometra stagnorum* (L.)
98 *Gerris najas* (De Geer)
Trichoptera:
99 *Hydropsyche angustipennis* (Curtis)
100 *Plectrocnemia conspersa* (Curtis)
101 *Lype reducta* (Hagen)
103 *Agapetus fuscipes* Curtis
105 *Lithax obscurus* (Hagen)
107 *Goera pilosa* (Fabricius)
109 *Sericostoma personatum* (Spence)
0 112 *Halesus* Stephens spp.
113 *Halesus digitatus* (Schrank)
114 *Halesus tesselatus* (Rambur)
116 *Limnephilus auricula* Curtis
117 *Halesus radiatus interpunctatus* (Zetterstedt)
118 *Potamophylax rotundipennis* (Brauer)
122 *Potamophylax luctuosus* (Piller & Mitterpacher)
0 125 Potamophylacini spp.
126 *Enoicyla pusilla* (Burmeister)
127 *Chaetopteryx villosa* (Fabricius)
128 *Micropterna sequax* MacLachlan
130 *Hydatophylax infumatus* (MacLachlan)
131 *Limnephilus sparsus* Curtis
132 *Limnephilus extricatus* MacLachlan
133 *Anabolia nervosa* Curtis
134 *Glyphotaelius pellucidus* (Retzius)
135 *Limnephilus lunatus* Curtis
136 *Limnephilus rhombicus* (L.)
0 142 Limnephilidae spp.
143 *Bereodes minutus* (L.)
0 144 Leptoceridae spp.
145 *Mystacides longicornis* (L.)
146 *Athripsodes cinereus* (Curtis)
147 *Athripsodes aterrimus* (Stephens)
148 *Athripsodes bilineatus* (L.)
149 *Molanna angustata* Curtis
Megaloptera:
0 152 *Sialis* Latreille spp.
153 *Sialis lutaria* (L.)
154 *Sialis fuliginosa* Pictet
Coleoptera:
150 *Coelostoma* Brul spp.

	151	*Agabus paludosus* (Fabricius)
	155	*Agabus* Leach larvae spp.
	157	*Agabus bipustulatus* (L.)
	158	*Platambus maculatus* (L.)
	160	*Ilybius* Er. larvae spp.
	163	*Noterus* Clairville spp.
	165	*Laccophilus* Leach spp.
	168	*Hydroporus* Clairville spp.
	169	*Colymbetus fuscus* (L.)
	170	*Stictotarsus duodecimpustulatus* Fabricius
	172	*Haliplus* Latreille spp.
	173	Hydrophilidae spp
	174	*Helophorus aquaticus* L.
	175	*Helophorus* Leach spp.
	176	*Limnebius* Leach spp.
	178	Hydrophilidae spp. larvae
	179	*Anacaena limbata* (Fabricius)
	180	*Anacaena globulus* (Paykull)
	181	*Laccobius* Erchs. spp.
181	182	*Laccobius sinuatus* Motsch / *striatulus* (Fabricius)
	183	*Gyrinus substriatus* Stephens
	184	*Dryops* Ol. spp.
	185	*Elmis aenea* (Müller)
	186	*Limnius volckmari* (Panzer)
	187	*Oulimnius tuberculatus* (Müller)
	189	*Ochthebius* Leach. spp.
	190	*Helodes minuta* L. larvae
	191	*Chaetharthria seminulum* Herbst
	192	*Megasternum boletophagum* Mrsh.
Diptera:		
	193	*Tipula* L. spp.
193	194	*Tipula* gr. *lunata* sensu Theowalt,1957
193	195	*Tipula* gr. *pruinosa* sensu Theowalt,1957
193	196	*Yamatotipula* Matsumura spp.
198	197	*Limnophila* Marquart sp. a
	198	*Limnophila* Marquart spp
198	199	*Limnophila* gr. *fuscipennis* sensu Tolkamp, 1976
	200	*Pedicia* Latreille
	202	*Gnophomyia* subg. *Leiponeura* sensu Hennig, 1968
	203	*Gnophomyia* Osten-Sacken spp.
	204	*Elephantomyia* Osten-Sacken spp.
	205	*Dicranota* Zetterstedt
198	208	*Limnophila* Marquart sp. b
	210	*Anopheles* Meigen spp.
215	214	*Dixa* Meigen spp.
	215	*Dixa* gr. *maculata* sensu Disney,1975
	216	*Bezzia* Kieffer spp.
	217	*Palpomyia* Megerle spp.
	218	*Palpomyia tibialis* Meigen
	219	*Simulium erythrocephalum* De Geer
	220	*Simulium latipes* Meigen
	221	*Simulium aureum* Fries
	222	*Simulium* gr. *ornatum* Meigen
0	223	*Simulium* Latreille spp.
	224	*Simulium brevicaule* Dorier & Grenier
	225	*Psychoda* Latreille spp.
225	226	*Pericoma* Walker spp.
0	227	*Simulium naturale* Davies
	231	*Beris* Latreille spp.
	232	*Dixella* Dyer & Shannon spp.
	233	*Tabanus* L. spp.
	234	*Haematopoda* Meigen spp.

	236	*Aphrosylus* Walker spp.
	238	Bibionidae spp.
	239	*Hemerodromia* Meigen spp.
	240	Ephydridae spp.
	241	*Ptychoptera* Meigen
	242	Tetanoceridae spp.
	243	*Osmylus fulvicephalus* (Scopoli) (Neuroptera)
	244	*Macropelopia* Thienemann spp.
244	245	*Macropelopia nebulosa* (Meigen)
	248	*Apsectrotanypus trifascipennis* (Zetterstedt)
	249	*Procladius* Skuse spp.
	250	*Teichomyza* Marquet spp. (Ephydridae)
	251	*Hydraena excisa* (Coleoptera)
00	252	Coleoptera larvae spp.
	253	cf.*Conchapelopia* sensu Moller Pillot, 1978
253	254	*Conchapelopia melanops* (Wiedemann)
	256	*Zavrelimyia* Fittkau spp.
	258	*Metriocnemus* van der Wulp spp.
	260	*Clinotanypus nervosus* (Meigen)
0	263	Orthocladiinae spp. (juv.)
0	264	Chironomini spp. (juv.)
	265	*Cricotopus (Cricotopus)* van der Wulp
	266	*Cricotopus bicinctus* (Meigen)
	268	*Orthocladius* van der Wulp spp.
	269	*Corynoneura* Winnertz spp.
	270	*Thienemanniella* Kieffer spp.
	271	*Prodiamesa olivacea* (Meigen)
	272	*Brillia modesta* (Meigen)
	273	*Odontomesa fulva* (Kieffer)
	274	*Brillia longifurca* Kieffer
	275	*Diplocladius cultriger* Kieffer
	276	*Nanocladius* Kieffer
	277	*Rheocricotopus* Thienemann
	278	*Psectrocladius* Kieffer spp.
	279	*Eukiefferiella* gr. *discoloripes* sensu Moller Pillot 1980
	280	*Chaetocladius* Kieffer spp.
	281	*Eukiefferiella brevicalcar* (Kieffer)
	282	*Eukiefferiella claripennis* (Lundbeck)
	283	*Epoicocladius flavens* (Malloch)
	285	*Limnophyes* Eaton spp.
0	286	Tanytarsini spp
	287	*Micropsectra* gr. *praecox* sensu Tshernowskij
	288	*Tanytarsus curticornis* (cf. Mothers)
	289	*Micropsectra* gr. *trivialis* sensu Tshernowskij
	290	*Tanytarsus* van der Wulp spp.
	291	*Stempellina* Bause spp.
	292	*Cladotanytarsus* Kieffer spp.
	293	*Rheotanytarsus* Bause spp.
	294	*Paratanytarsus* Bause spp.
	296	*Chironomus* Meigen spp.
	297	*Glyptotendipes* Kieffer spp.
	298	*Dicrotendipes* gr. *notatus* sensu Moller Pillot, 1979
0	299	*Paracladopelma* Harnisch spp.
	300	*Cryptochironomus* Kieffer spp.
	301	*Paracladopelma camptolabis* agg. sensu Moller Pillot, 1979
	302	*Paratendipes* Kieffer spp.
	303	*Microtendipes* gr. *chloris* sensu Moller Pillot,1979
	306	*Phaenopsectra* Kieffer spp.
	307	*Paracladopelma laminata* agg. sensu Moller Pillot,1979
	308	*Stictochironomus* Kieffer
	310	*Polypedilum laetum* agg. sensu Moller Pillot, 1979
	311	*Polypedilum breviantennatum* Tshernowskij

	312	*Polypedilum* gr. *nubeculosum* sensu Tshernowskij
312	313	*Polypedilum* gr. *convictum* sensu Tshernowskij
	314	*Hydrobaenus pilipes* (Malloch)
277	315	*Rheocricotopus* cf.*dorieri* sensu Pankratova, 1970
0	317	Diptera pupae spp.
0	318	Chironomini pupae spp.
0	319	Orthocladiinae pupae spp.
Mollusca:		
	321	*Planorbarius corneus* (L.)
	323	*Gyraulus albus* (Müller)
	325	*Anisus leucostoma* (Millet)
	327	*Lymnaea peregra* f.*ovata* (Müller)
	328	*Lymnaea truncatula* Müller
	330	*Lymnaea palustris* (Müller)
	331	*Lymnaea auricularia* (L.)
	332	*Lymnaea glabra* (Müller)
	338	*Physa fontinalis* (L.)
	340	*Ancylus fluviatilis* Müller
	341	*Pisidium* C.Pfeiffer spp.
	342	*Sphaerium* Scopoli spp.
Various:		
	343	*Sisyra* Burmeister spp. (Neuroptera)
	344	Lepidoptera spp.
	345	*Hydrobius fuscipes* L. (Coleoptera)
	346	Unknown Orthocladiinae larva (Diptera)
198	351	Limnobiidae spp. (Diptera)
00	352	Coleoptera spp.
	354	*Helocharus lividus* Forst. (Coleoptera)
277	355	*Rheocricotopus* gr. *fuscipes* sensu Thienemann, 1944 (Diptera)
0	356	Diptera spp.
0	357	Pupae of unknown order
0	358	Tanytarsini pupae spp. (Diptera)
184	359	*Dryops luridus* Er. (Coleoptera)
0	360	*Ironoquia dubia* (Stephens) exuvium (Trichoptera)
Pisces:		
	361	*Gasterosteus aculeatus* (L.)
	362	*Pungitius pungitius* (L.)
	363	*Noemacheilus barbatulus* (L.)
Cyclostomata:		
	364	*Lampetra planeri* (Bloch)

Appendix 7. Number of specimens of *Ephemera danica* in high density samples in the Ratumsebeek for 5 length classes in Sort 2.

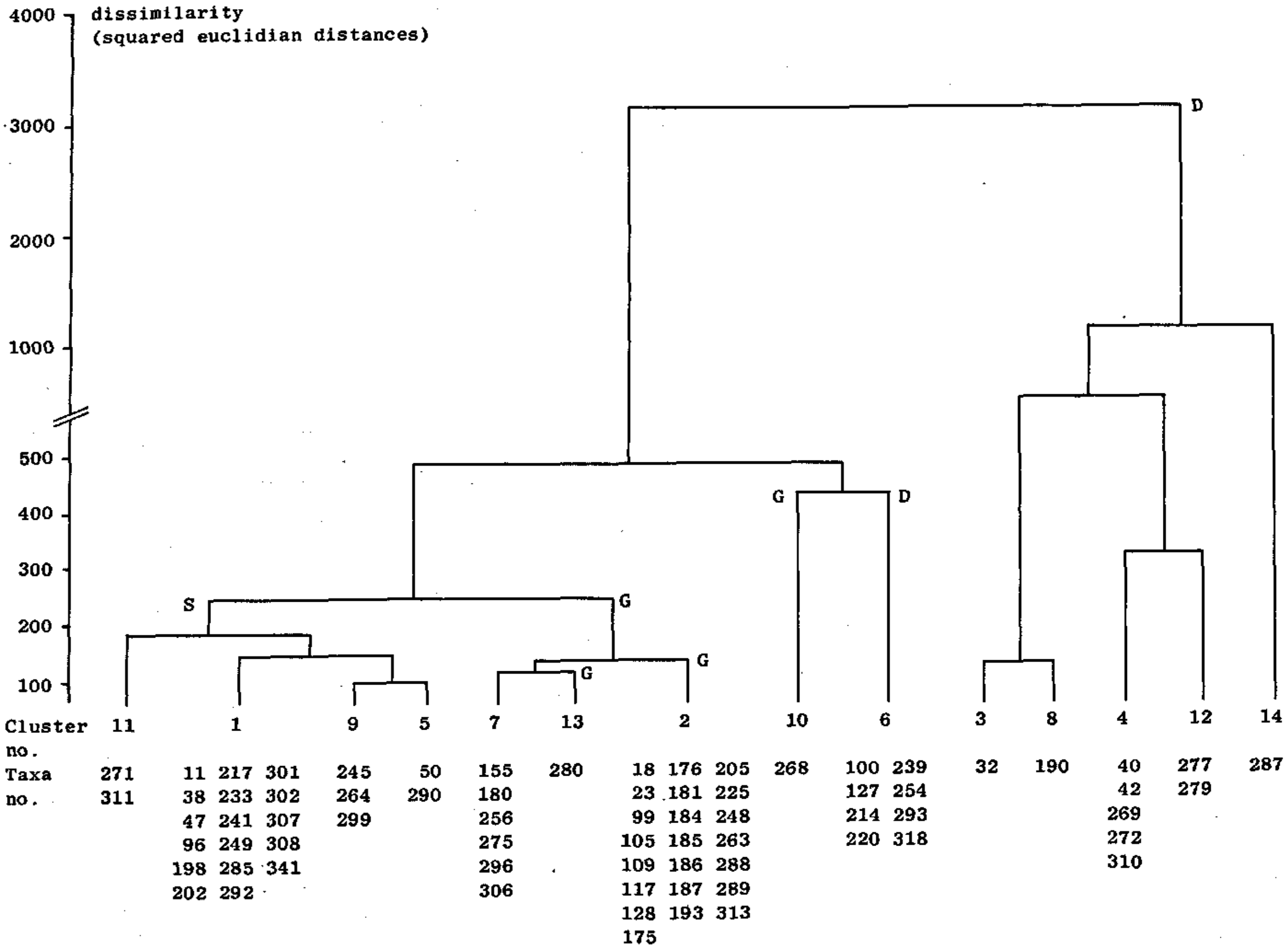
Sample no.	Year	Week	Number of specimens	Sort 2 class	Body length/mm				
					0-5	5-10	10-15	15-20	> 20
55	1977	19	15	4	1			2	12
60	1977	21	10	4	1		1	2	6
106	1977	35	26	4	26				
109	1977	35	32	1	32				
129	1977	40	38	4	32	6			
130	1977	40	29	4	11	18			
133	1977	40	26	4	14	12			
142	1977	43	14	1	13	1			
146	1977	43	78	4	31	42	5		
164	1977	49	31	2	4	17	8	1	1
176	1978	03	11	4	2	9			
Total			310		167	105	14	5	19

Appendix 8. Number of specimens of *Ephemera danica* in high density samples in the Snijdersveerbeek for 5 length classes in Sort 2.

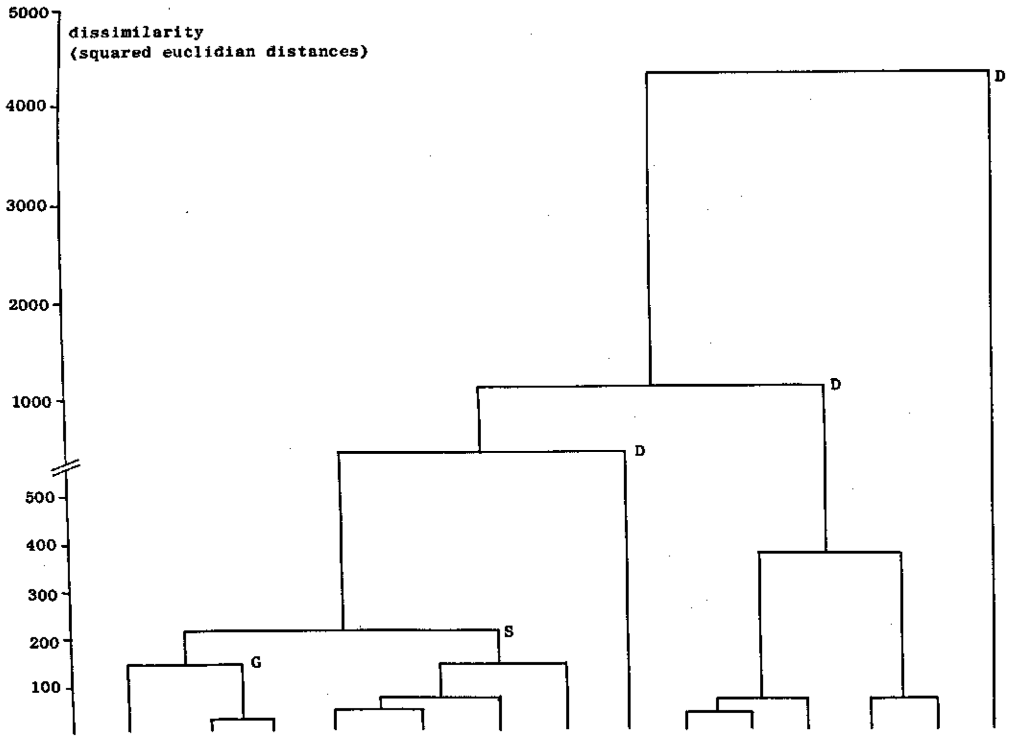
Sample no.	Year	Week	Number of specimens	Sort 2 class	Body length/mm				
					0-5	5-10	10-15	15-20	> 20
35	1976	04	14	6	2	8	4		
83	1976	34	20	6	20				
86	1976	37	10	3	2	8			
90	1976	37	10	4	5	5			
95	1976	43	14	4	2	3	8	1	
97	1976	43	15	6	1	5	9		
98	1976	43	12	2	1	5	5	1	
103	1976	45	12	4	2	7	3		
121	1977	03	20	3	4	8	7		1
122	1977	03	11	1	1	5	3	1	1
126	1977	03	10	5		3	4	3	
147	1977	12	19	4		2	7	8	2
155	1977	15	16	3	1	7	4	4	
Total			183		41	66	54	18	4

Appendix 9. I.R. values for the main taxa in Sort 2 for the Snijdersveerbeek and the Ratumsebeek. Italic values indicate significant over-representation. Sam = number of samples in which the taxon occurred. *n* = number of specimens. B = Bare, S = Sand, G = Gravel, D = Coarse Detritus / Leaves, FD = Fine Detritus. Boxes indicate the main substrate preferences of faunal groups: I : Gravel, II: Gravel / Sand, III: Sand, IV: Gravel / Sand / Detritus, V: Sand / Detritus, VI: Gravel / Detritus, VII: Detritus.

Taxa no.	Taxa name	Snijdersveerbeek									Ratumsebeek								
				Substrate class									Substrate class						
				1	2	3	4	5	6	7			1	2	3	4	5	6	7
		Sam	*n*	BS	S+FD	S+D	S+D+FD	BG	G+D	D	Sam	*n*	BS	S+FD	S+D	S+D+FD	BG	G+D	D
I. 18	*Eiseniella*	80	311	-5.7	-4.9	-4.2	-5.7	*18.6*	*3.4*	-5.4	-	-	-	-	-	-	-	-	-
99	*Hydropsyche*	11	27	-2.5	-1.4	-1.5	-1.9	*5.2*	*2.7*	-1.2	-	-	-	-	-	-	-	-	-
103	*Agapetus*	8	13 →	4	-	-	-	6	1	2	47	211	*4.9*	-3.2	-1.8	-5.9	*5.3*	*10.7*	-6.6
105	*Lithax*	150	451	*5.6*	-5.0	-4.8	-6.8	*8.4*	1.6	-4.7	55	218	-0.5	-3.8	-3.2	-6.0	*8.4*	*3.6*	0.8
107	*Goera*	11	14	-0.1	-1.0	-1.1	-1.4	*2.4*	*2.3*	-1.5	-	-	-	-	-	-	-	-	-
146	*Athripsodes*	2	2 →	1	-	-	-	-	1	-	10	22	0.2	1.3	-1.0	-2.0	-1.3	*10.2*	-2.3
175	*Helophorus*	10	39	0.0	-0.6	-1.8	-2.3	-1.8	*7.8*	-0.2	-	-	-	-	-	-	-	-	-
181	*Laccobius*	11	28	0.3	-0.8	-1.6	-2.0	1.7	*3.8*	-1.7	-	-	-	-	-	-	-	-	-
184	*Dryops*	19	30	-2.2	-1.5	-1.0	-1.1	1.9	*5.3*	-0.9	1	1 →	-	-	-	-	-	-	1
185	*Elmis*	40	133	-4.1	-2.9	-3.4	-4.3	*13.3*	1.2	-2.8	29	63	-1.7	-1.9	-0.3	-2.2	*7.4*	-1.0	-0.6
186	*Limnius*	11	27	-0.1	-1.4	-1.5	-1.9	*5.2*	0.2	-2.1	92	423	*2.2*	-4.0	-1.5	-6.7	*11.8*	*11.0*	-8.3
187	*Oulimnius*	11	25	-0.7	-1.4	-1.5	-1.9	*6.5*	-0.9	-2.0	28	48	*2.9*	-1.6	-1.5	-3.0	*4.8*	-0.3	-2.5
233	*Tabanus*	28	40 →	7	6	5	10	3	5	4	24	31	-0.3	-0.7	0.5	1.4	-1.8	*4.3*	-1.3
268	*Orthocladius*	32	642	-11.1	-7.0	-4.1	-9.4	-0.6	*43.5*	-3.3	3	3 →	-	-	1	1	1	-	-
303	*Microtendipes*	1	2 →	-	-	-	2	-	-	-	14	50	-2.7	-0.7	-1.5	-2.1	-1.8	*21.6*	-2.9
II. 47	*Ephemera*	107	436	-5.4	-0.5	*2.7*	*9.3*	-0.1	*5.0*	-7.5	81	504	-4.1	1.6	-1.5	*21.3*	-4.3	-2.7	-9.6
50	*Baetis*	45	250	-1.6	-1.1	*7.2*	-4.9	*8.7*	-2.1	-6.3	27	103	-3.1	-2.6	-2.2	-3.0	1.6	-1.9	*7.7*
109	*Sericostoma*	125	346	-0.8	-1.2	*3.0*	-1.0	*2.8*	0.4	-2.9	-	-	-	-	-	-	-	-	-
198	*Limnophila*	155	385	*3.1*	*2.2*	*2.7*	-2.7	*2.2*	-1.2	-6.2	39	62	*3.9*	0.9	0.7	-1.0	-0.8	-0.1	-3.4
245	*Macropelopia*	59	401	-8.8	*14.6*	-0.5	*7.0*	-7.3	*11.9*	-6.5	27	87	-3.0	*6.7*	-1.0	*6.5*	-3.2	-1.6	-2.4
248	*Apsectrotanypus*	39	102	-4.8	-1.0	-2.0	*8.2*	-4.6	*6.4*	0.5	1	1 →	-	-	-	1	-	-	-
288	*Tanyt.curticornis*	22	48	-3.3	1.8	-0.1	1.7	-1.6	*3.4*	0.4	-	-	-	-	-	-	-	-	-
290	*Tanytarsus*	27	374	-8.4	*6.5*	-5.0	*17.4*	-8.4	*13.1*	-7.5	6	96	-4.9	0.6	-2.1	*16.2*	-3.9	-2.2	-4.4
292	*Cladotanytarsus*	16	90	*7.4*	-1.1	-2.8	-3.3	-3.0	*5.5*	-3.9	1	6	*3.7*	-0.6	-0.6	-1.1	-1.0	-0.6	-1.2
296	*Chironomus*	14	92	-4.6	-2.6	-2.8	*5.7*	-3.9	*9.4*	1.2	8	23	-2.4	-1.2	-1.0	*4.7*	-1.4	-1.1	1.0
III. 11	Oligochaeta	132	383	-2.7	*3.9*	*6.9*	*4.9*	-3.4	0.8	-5.8	116	491	*2.5*	*5.1*	-0.6	*4.6*	0.1	0.2	-9.0
38	Hydracarina	54	125	0.5	-0.5	1.3	*3.3*	-2.8	0.5	-1.5	25	102	1.1	*2.0*	-1.3	*4.9*	-3.0	-1.9	-2.5
96	*Nepa rubra*	12	32	*5.8*	-0.9	-1.7	-2.1	-1.4	1.1	-2.3	-	-	-	-	-	-	-	-	-
202	*Gnophomyia*	12	21 →	4	-	2	6	1	3	5	2	22	0.2	-1.2	*14.9*	-2.0	-1.9	-1.1	-2.3
205	*Dicranota*	108	209	1.7	1.8	*2.8*	-3.5	0.6	-0.1	-2.6	43	74	-0.8	-1.3	-1.3	-3.2	*6.2*	*2.7*	-1.4
217	*Palpomyia*	126	317	-2.9	0.6	-0.8	*8.9*	-0.4	-1.2	-3.2	68	159	*2.5*	-0.2	0.6	0.3	*2.3*	*2.4*	-6.0
239	*Hemerodromia*	34	91	-2.8	1.9	-1.4	*4.6*	-0.2	-0.3	-0.8	-	-	-	-	-	-	-	-	-
241	*Ptychoptera*	85	251	-0.2	*7.8*	*3.7*	*6.5*	-6.8	-2.5	-4.1	-	-	-	-	-	-	-	-	-
249	*Procladius*	34	142	-5.2	1.3	-2.7	*17.6*	-4.5	-2.1	-2.4	26	152	-6.0	-1.3	1.1	*16.6*	-4.9	-2.1	-3.2
264	juv.Chironimini	12	119	*15.2*	-3.0	-2.9	-2.8	-5.0	-3.4	-2.9	-	-	-	-	-	-	-	-	-
271	*Prodiamesa*	105	950	-12.0	-2.5	1.9	*41.6*	-14.0	-6.8	-2.8	28	240	-1.5	*10.3*	-2.1	*12.3*	-6.2	-3.5	-7.1
283	*Epoicocladius*	3	4	-1.0	-0.6	-0.6	*3.3*	-0.9	1.0	-0.6	29	130	-3.6	-1.3	-0.8	*12.3*	0.3	-1.8	-5.4
299	*Paracladopelma*	16	64	-2.3	*11.0*	*6.2*	-1.6	-2.3	-2.5	-3.3	6	30	*4.5*	-1.4	-1.2	-1.5	-2.2	-1.2	0.3
301	*P.camptolabis*	28	69	*5.6*	*7.3*	-0.4	-3.1	-3.8	-2.2	-2.5	1	1 →	-	-	-	1	-	-	-
307	*P.laminata*	19	52	*2.1*	*6.1*	-2.1	0.7	-2.1	-0.5	-2.9	9	16	*3.0*	0.9	-0.9	-1.7	0.9	-0.9	-2.0
300	*Cryptochironomus*	6	18	-2.0	-1.2	*5.2*	*4.8*	-1.9	-1.3	-1.7	20	34	1.5	2.5	-0.5	1.1	-0.2	-1.3	-2.9
302	*Paratendipes*	15	84	-4.2	-0.2	-2.7	*16.8*	-4.2	-0.8	-3.2	21	110	1.4	-2.7	0.9	*9.7*	-4.2	-2.4	-4.4
308	*Stictochironomus*	84	268	1.8	*6.8*	*2.7*	*5.4*	-4.7	-2.4	-6.5	51	210	*8.3*	-0.5	-1.5	0.4	-3.7	-1.2	-4.3
311	*P.breviantennatum*	179	1247	0.1	*13.7*	*2.3*	*16.8*	-13.7	-4.4	-7.7	48	203	*8.3*	-1.8	-2.1	-3.5	*3.6*	-0.1	-6.4
341	*Pisidium*	78	225	*6.1*	*5.3*	-1.9	0.5	-3.1	-3.0	-4.1	83	328	*11.4*	1.5	1.0	-3.4	-3.6	*2.2*	-6.0
IV. 128	*Micropterna*	92	194	-2.0	-3.1	*3.0*	-1.5	*2.1*	-0.9	*2.0*	54	286	-6.7	-3.9	-3.6	-6.0	-5.6	-3.8	*22.1*
280	*Chaetocladius*	27	346	-8.1	-4.5	*7.0*	-6.6	1.2	*12.0*	*3.0*	15	32	-2.5	-1.8	*2.9*	0.0	-1.4	-1.3	*3.3*
293	*Rheotanytarsus*	70	612	-2.4	-4.5	*12.0*	-6.1	*3.3*	-4.8	*2.7*	1	1 →	1	-	-	-	-	-	-
V. 4	*Polycelis*	12	20	*2.6*	-0.4	-0.6	-1.7	-2.1	-1.4	*2.6*	18	31	-2.4	-1.4	-0.4	-0.7	-1.8	-1.3	*6.1*
23	*Glossiphonia*	21	32	1.0	1.0	0.1	-0.7	-1.8	-1.8	*2.1*	11	14 →	3	3	-	3	1	-	6
32	*Gammarus pulex*	282	11125	-27.2	-4.6	*52.6*	-3.0	-39.5	-16.5	*56.9*	154	9918	-39.4	-17.8	-15.6	-23.0	-28.0	-8.4	*103.2*
36	*Asellus meridian.*	-	-	-	-	-	-	-	-	-	32	58	-3.6	-2.0	-1.0	*3.6*	-1.7	-1.1	*4.0*
135	*Limn. lunatus*	7	15	-1.3	-1.1	-1.1	0.6	-1.2	*6.3*	-0.9	17	61	-3.2	-2.0	*7.3*	*2.0*	-2.8	-1.8	*2.4*
155	larvae *Agabus*	55	134	-5.3	-1.3	0.7	*2.2*	-4.7	1.7	*8.7*	1	1 →	-	-	-	-	-	-	1
160	larvae *Ilybius*	15	20	-2.1	-1.2	*3.3*	0.1	-2.1	0.1	*3.1*	3	3 →	1	-	-	2	-	-	-
256	*Zavrelimyia*	42	105	-4.5	0.0	*4.0*	*5.9*	-4.3	-1.0	*2.6*	10	16	-2.0	-1.0	-0.9	*3.6*	-1.0	-1.0	1.1
285	*Limnophyes*		4	0.5	-1.3	1.0	-1.7	-0.2	-0.7	*2.0*	20	41	-2.3	-1.7	0.1	*2.0*	-1.0	-1.5	*2.9*
287	*Microps.praecox*	223	20138	-55.6	*20.3*	-11.5	*74.6*	-63.0	-2.8	*64.7*	82	2111	-18.1	0.2	0.5	*9.2*	-11.4	0.4	*19.2*
289	*M.trivialis*	15	47	-3.3	-1.9	0.5	*2.5*	-1.2	0.7	*3.3*	-	-	-	-	-	-	-	-	-
306	*Phaenopsectra*	19	67	-3.9	-2.3	-1.6	*6.5*	-3.5	-2.6	*7.2*	17	30	-2.4	-1.4	-1.2	0.6	-1.7	-0.4	*4.8*
313	*Pol.*gr.*convictum*	16	22 →	-	3	3	4	4	5	3	6	9 →	-	-	1	2	2	-	3
VI. 40	*Amphinemura*	42	408	-7.9	-5.6	-5.3	-7.3	*4.6*	-4.1	*21.4*	26	313	-7.5	-4.6	*3.3*	-7.6	-3.4	-4.0	*17.1*
127	*Chaetopteryx*	95	386	-6.0	-4.1	-0.4	-6.0	0.2	*2.7*	*13.2*	27	60	-2.6	-1.0	-1.7	-1.5	-0.2	-1.2	*5.9*
180	*Anacaena*	13	53	-2.6	-1.5	-2.1	-1.6	-2.1	*10.1*	1.8	1	1 →	-	-	-	-	-	-	1
VII. 21	*Erpobdella octo.*	-	-	-	-	-	-	-	-	-	41	74	-3.2	-1.8	0.9	-1.5	-2.3	-2.0	*7.9*
42	*Nemoura cinerea*	26	155	-5.4	-3.1	-3.1	-4.6	-5.0	-3.6	*23.4*	87	2896	-15.6	-13.6	-5.7	-19.1	*4.5*	-11.8	*44.2*
48	*Habrophlebia*	-	-	-	-	-	-	-	-	-	74	727	-7.3	-6.1	*2.7*	-6.0	-6.0	-4.5	*21.7*
100	*Plectrocnemia*	88	233	-6.2	-1.4	*3.1*	-2.2	-6.3	-2.2	*16.7*	8	9 →	-	-	2	3	1	-	3
117	*Halesus radiatus*	14	27	-2.1	-1.4	-0.9	-0.4	-2.0	-1.6	*7.8*	4	4 →	-	-	1	-	-	-	3
122	*Potamophylax luct.*	-	-	-	-	-	-	-	-	-	15	30	-2.8	-0.7	-1.2	-1.1	-2.2	-1.2	*7.0*
190	larvae *Helodes*	79	1054	-15.0	-8.7	-4.8	-11.0	-13.0	0.4	*51.4*	33	207	-7.1	-3.5	*7.3*	-5.4	-5.6	-3.0	*16.4*
193	*Tipula*	37	46	-2.6	-0.8	0.0	-1.3	1.4	-0.7	*3.8*	7	14	1.3	-1.0	-0.8	*2.8*	-0.9	-0.9	-1.8
220	*Simulium*	25	302	-6.4	-4.8	-5.1	-6.5	-3.9	-4.7	*28.4*	8	12	-1.7	-0.9	1.9	-1.5	0.1	-0.8	*3.0*
225	*Psychodidae*	15	21	-2.2	-1.3	-0.6	-1.1	0.8	0.7	*3.5*	4	4 →	2	-	-	1	-	-	1
254	*Conchapelopia*	86	257	-7.4	-4.4	*2.3*	1.4	-4.3	0.0	*13.6*	18	47	-3.4	-1.8	-1.5	-1.3	-2.4	-0.3	*8.2*
263	juv.Orthocladiinae	15	30 →	7	2	4	1	12	1	3	2	7	-1.3	-0.7	-0.6	-0.3	-1.1	-0.6	*3.3*
269	*Corynoneura*	84	388	-8.9	-4.3	-1.5	-2.7	-5.4	-1.4	*24.0*	35	225	-7.4	-3.9	-3.2	-6.6	-5.5	-3.1	*22.5*
272	*Brillia modesta*	50	433	-9.9	-5.7	-3.8	-6.5	-9.2	-4.2	*37.8*	28	151	-6.2	-3.2	-2.3	-5.1	-4.9	-2.4	*18.5*
274	*B.longifurca*	12	19	-2.1	0.5	-1.3	-1.0	-1.5	-1.4	*6.7*	1	1 →	-	-	-	-	-	-	1
275	*Diplocladius*	53	244	-4.2	-4.3	-2.6	-4.6	-2.4	-1.2	*17.6*	44	366	-8.8	-4.7	-3.8	-7.6	-4.5	-2.7	*24.6*
277	*Rheocricotopus*	119	1288	-16.1	-8.9	-3.0	-10.0	-10.6	*3.5*	*45.6*	43	1177	-16.8	-8.9	-6.8	-14.5	-12.7	-7.4	*51.2*
279	*Eukiefferiella*	97	1489	-18.2	-10.4	-4.5	-13.5	-12.2	*17.1*	*44.6*	3	6	-1.2	-0.6	-0.5	-1.1	-1.0	-0.6	*3.8*
310	*Polyped.laetum*	76	1125	-14.0	-4.2	*11.7*	-11.5	0.2	-7.3	*26.7*	1	1 →	-	-	-	-	-	-	1
318	pupae Chironomini	68	174	-6.5	-2.3	*2.8*	0.4	-4.1	*3.5*	*7.5*	17	74	-4.1	-2.2	-1.9	-0.5	-2.9	-0.9	*8.3*



Appendix 10. Dendrogram representing the grouping of the 72 most abundant taxa in the Snijdersveerbeek in Sort 8,10%, based on the similarity of I.R. values. Taxa numbers refer to the numbers in Appendix 1. The letters S (Sand) , G (Gravel) and D (Detritus) indicate the main preferences of the taxa in the clusters below. They were added after analysis of the basic data.



Cluster no.	1	7	8	2	10	6	11	14	4	12	9	5	13	3
Taxa no.	4 254 21 280 36 285 50 296 122 306 127 318 135	103 186	105 185 187 205 303	11 38 245 271 302	146 300 198 308 217 311 233 341 299	47 202	249 283 286 290	287	40 48 272	269 275	128 190	42	277	32

Appendix 11. Dendrogram representing the grouping of the 51 most abundant taxa in the Ratumsebeek in Sort 8,10%, based on the similarity of I.R. values. Taxa numbers refer to the numbers in Appendix 1. The letters S (Sand), G (Gravel) and D (Detritus) indicate the main preferences of the taxa in the clusters below. They were added after analysis of the basic data.

Appendix 12. I.R. values for the 43 most-abundant taxa (more than 100 specimens) in the Snijdersveerbeek in Sort 8,10%.

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		
		$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
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
246	*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*	-2.6	-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	*72.9*	-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*	*6.8*
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

Italic values indicate significant over-representation
Boxes indicate groups of taxa with similar over-representation

Appendix 13. I.R. values for the 26 most-abundant taxa (more than 100 specimens) in the Ratumsebeek in Sort 8,10%.

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		
		$\bar{x}\bar{x}\bar{x}$	$\bar{x}\bar{5}x$ $\bar{x}\bar{4}x$	$\bar{x}\bar{3}x$	$\bar{x}\bar{2}x$	$\bar{x}\bar{1}x$	$\bar{x}1x$	$\bar{x}xx$	1xx	22x	23x	33x	CD	L	CD+L
103	*Agapetus fuscipes*	-1.0	*9.9*	1.3	0.4	*10.8*	*10.2*	-1.4	-1.4	-5.6	-3.8	-2.3	-2.3	-6.8	-2.1
105	*Lithax obscurus*	*4.6*	0.3	*2.1*	*6.2*	*5.9*	*2.6*	-2.1	-3.4	-5.9	-3.8	-1.9	*5.7*	-1.0	-0.7
186	*Limnius volckmari*	*7.4*	*2.8*	*5.9*	*4.9*	*14.6*	*2.0*	*3.9*	-3.9	-6.0	-4.9	-2.7	-2.1	-7.6	-2.6
217	*Palpomyia*	-0.9	*3.2*	1.5	*3.2*	-0.4	-0.1	1.5	1.7	*2.0*	0.4	-2.0	-2.0	-5.4	-1.8
308	*Stictochironomus*	-1.0	-2.1	-1.6	-2.4	-1.6	-2.5	*7.3*	1.1	*5.9*	-1.3	-2.3	-2.3	-3.6	-1.1
311	*Polypedilum breviantennat.*	-1.0	-2.0	-2.0	*3.3*	*4.0*	-1.1	*3.3*	-2.1	*5.6*	-2.3	-1.8	-2.3	-5.8	-1.5
341	*Pisidium*	0.3	-2.2	-0.3	-0.8	-1.3	-2.3	*3.2*	0.9	*10.8*	-0.4	-0.8	-2.2	-7.2	-2.6
47	*Ephemera danica*	-1.6	-1.3	-3.2	-3.3	-2.0	1.3	*12.2*	-2.7	-1.0	*6.6*	*10.9*	-3.3	-9.1	-2.0
11	**Oligochaeta**	-1.6	*2.8*	-2.2	-1.7	*2.3*	-3.3	-0.3	-1.0	*8.9*	*8.1*	-0.2	-3.6	-9.0	0.6
38	**Hydracarina**	-0.7	-0.8	-1.5	-2.4	-2.0	-3.2	*2.5*	-1.3	*4.3*	*7.0*	-1.6	-1.6	-4.2	*6.2*
249	*Procladius*	-0.9	-1.8	-1.8	-3.5	-3.0	-2.8	-3.7	-2.1	*4.8*	*16.3*	*3.6*	-2.0	-5.4	*7.9*
283	*Epoicocladius flavens*	-0.8	0.2	-1.6	-1.4	1.5	0.1	-1.9	-1.8	-1.5	*19.1*	-1.8	-1.8	-4.8	-1.6
302	*Paratendipes*	-0.8	-1.5	-1.5	-3.2	-2.8	-1.8	*5.3*	0.1	1.3	*9.9*	-0.5	0.1	-4.4	-1.5
271	*Prodiamesa olivacea*	-1.1	-2.2	-2.2	-4.7	-4.1	-2.6	-3.4	-2.8	*17.3*	*5.3*	*6.0*	-2.5	-6.7	-0.9
50	*Baetis vernus*	0.6	-1.5	*4.1*	-0.8	0.2	-0.6	-2.3	-2.5	-3.5	-2.6	-1.6	-1.6	*9.6*	-1.5
42	*Nemoura cinerea*	-3.8	*17.3*	-7.7	-4.5	-2.3	-6.3	-10.1	-9.8	-22.0	-9.9	-7.3	-8.5	*53.7*	-4.7
40	*Amphinemura standfussi*	-1.3	0.6	-2.5	-3.0	-3.7	-4.1	-5.6	*6.6*	-7.0	-4.6	-2.8	-2.8	*17.8*	*8.9*
48	*Habrophlebia fusca*	-1.4	-3.6	-1.0	-4.0	-5.3	1.8	-5.9	0.0	-10.5	-4.9	-0.6	*6.6*	*16.1*	*17.4*
272	*Brillia modesta*	-0.9	-1.8	-1.8	-3.7	-3.0	-3.8	-4.4	-2.7	-5.1	-2.9	-2.0	-3.0	*18.2*	*9.6*
128	*Micropterna sequax*	-1.2	-2.0	-3.0	-4.9	-3.4	-3.4	-4.1	-3.7	-6.7	-4.4	-2.7	*20.6*	*16.2*	*2.5*
190	*Helodes* larvae	-1.0	-2.1	-1.6	-4.1	-3.9	-4.3	-4.8	*5.4*	-5.2	-3.7	-3.3	*14.6*	*13.0*	-0.1
387	*Micropsectra* gr. *praecox*	1.6	-6.3	-4.9	-7.7	-2.4	-6.0	-4.4	-5.3	-2.0	0.9	*2.3*	*64.9*	-10.9	*26.8*
32	*Gammarus pulex*	*3.2*	-13.9	-4.5	-19.8	-17.3	-16.1	-23.0	-12.7	-33.9	-19.3	-13.8	*160.5*	*49.2*	*22.6*
269	*Corynoneura*	-0.1	-2.2	-1.7	-4.6	-3.5	-4.5	-5.4	-3.7	-6.2	-3.9	-2.4	*3.4*	*24.3*	-1.7
275	*Diplocladius cultriger*	-1.4	-2.0	-2.4	-3.6	-2.2	-4.5	-6.6	-4.8	-7.7	-4.1	-3.1	-2.1	*27.9*	0.5
277	*Rheocricotopus*	-1.2	-4.9	-4.1	-10.0	-8.5	-10.1	-12.2	-8.0	-14.0	-8.9	-5.5	-1.7	*53.2*	*13.4*

Italic values indicate significant over-representation
Boxes indicate groups of taxa with similar over-representation

Appendix 14. Comparison of the faunal composition of the Sand (S), Gravel (G) and Leaf (L) substrates in the natural section of the Snijdersveerbeek (Section 6) with that of the Sand and Fine Detritus (S+FD) substrate in the regulated section (7) downstream of Section 6.

	Section 6			Section 7
Taxon	S	G	L	S+FD
Lumbriculidae	1			
Eiseniella tetraedra	3	20		
Gammarus pulex	7	4	27	1
Hydracarina	2	3	1	6
Ephemera danica	46	32		2
Plectrocnemia conspersa	2		10	
Agapetus fuscipes		1		
Lithax obscurus		15	1	
Sericostoma personatum	22	22		
Halesus radiatus	1	1		
Potamophylax rotundipennis	1	1		
Chaetopteryx villosa	1			
Micropterna sequax	4	5	2	
Agabus sp.	3		2	
Dryops sp.	1			
Elmis aenea	1	1	2	
Helodes minuta (larvae)		2	27	
Tipula sp.	2	2	1	
Limnophila sp.	2	5		
Bezzia sp.	1	1		
Palpomyia sp.	2	7		98
Hemerodromia sp.		1		
Macropelopia nebulosa	3			12
Apsectrotanypus trifascipennis	10			28
Procladius sp.	2			127
Conchapelopia melanops	9	4	8	
Zavrelimyia sp.	2		1	
Orthocladiinae			2	3
Chironomini	1		7	
Orthocladius sp.			1	
Corynoneura sp.	2	1	41	
Prodiamesa olivacea	8		1	3
Brillia modesta	1		57	
Brillia longifurca			5	
Diplocladius cultriger			24	
Rheocricotopus sp.	4	2	76	
Eukiefferiella gr. *discoloripes*	1	13	56	
Limnophyes sp.			2	
Micropsectra gr. *praecox*	105	3	102	67
Tanytarsus curticornis	3			
Rheotanytarsus sp.		10		
Paratanytarsus sp.			2	
Paratendipes sp.	1			
Stictochironomus sp.	4	7		
Polypedilum breviantennatum	15	5	2	
Polypedilum gr. *convictum*	1			358
Chironomidae pupae	1		12	
Pisidium sp.	5	1		1
Lepidoptera			1	1

Appendix 14 (continued)

Taxon	Section 6			Section 7
	S	G	L	S+FD
Somatochlora arctica				4
Caenis horaria				7
Corixidae larvae				3
Notonecta virides				1
Sigara striata				78
Sigara falleni				51
Sigara distincta				1
Sigara lateralis				13
Sigara falleni/longipalis				47
Hesperocorixa sahlbergi				4
Ilybius larvae				2
Laccophilus sp.				1
Stictotarsus duodecimpustulatus				2
Dicranota sp.				2
Cricotpus sp.				12
Psectrocladius sp.				3
Tanytarsus sp.				481
Cladotanytarsus sp.				119
Chironomus sp.				26
Glyptotendipes sp.				48
Cryptochironomus sp.				34
Microtendipes gr. *chloris*				21
Polypedilum nubeculosum				6
Lymnaea auricularia				33
Mystacides longicornis				1
Number of taxa	37	26	27	38

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Stellingen

1. De voor laaglandbeken karakteristieke kleinschalige afwisseling van substraattypen is van levensbelang voor de bodembewonende organismen.

2. De beschikbaarheid van voedsel is van grotere invloed op de habitatselectie door macro-evertebraten dan de substraatsamenstelling.

3. Het aangeven van substraatvoorkeuren door het procentuele aandeel van een soort binnen een monster te vergelijken met de substraatkarakteristieken is niet geoorloofd.

   L. Edwards, 1975. Doctoral thesis, Univ. Salford.

4. Het lijkt onvoldoende bekend te zijn dat beekregulatie leidt tot afname van de ruimtelijke en temporele afwisseling van substraattypen en daarmee tot uitroeiing van de voor beken karakteristieke benthische levensgemeenschappen.

5. Beken stromen.

6. Het verdient aanbeveling de term macrofauna niet te gebruiken voor macroevertebraten.

7. Het belang van beekbegeleidende bossen en houtwallen voor de benthische levensgemeenschappen bestaat niet alleen uit de levering van schaduw en voedsel.

8. Het verdient aanbeveling de beekkarakterindex verder te onderbouwen ten behoeve van milieueffectrapportage.

   J.J.P. Gardeniers & H.H. Tolkamp, 1976.

9. Dat volgens de 'Kaart van de biologische kwaliteit van de waterlopen in Belgie' beken met een goede kwaliteit slechts voorkomen in de Ardennen is niet uitsluitend een gevolg van waterverontreiniging in het overige deel van Belgie.

   'Kaart van de biologische kwaliteit van de
   waterlopen in Belgie'. Instituut voor Hygiëne
   en Epidemiologie, Brussel, 1979.

10. Standaardisatie van het determinatieniveau is geen voorwaarde voor harmonisatie van biologische waterkwaliteitsbeoordelingssystemen.

11. De mate waarmee men zich inzet voor het voortbestaan van een diersoort heeft minder te maken met zijn mate van bedreigd zijn dan met zijn aaibaarheidswaarde.

12. De overeenkomst tussen een promotieplechtigheid en de balts van kemphanen gaat verder dan het dragen van een prachtkleed.

Proefschrift van Harry H. Tolkamp
Organism-substrate relationships in lowland streams.
Wageningen, 6 februari 1981.