Macrofauna-cenoses on Stratiotes plants in Dutch broads

ACADEMISCH PROEFSCHRIFT

ter verkrijging van de graad van doctor in de Wiskunde en Natuurwetenschappen aan de Universiteit van Amsterdam, op gezag van de Rector Magnificus Prof. Dr. G. den Boef, Hoogleraar in de Faculteit der Wiskunde en Natuurwetenschappen, in het openbaar te verdedigen in de Aula der Universiteit (tijdelijk in de Lutherse Kerk, ingang Singel 411, hoek Spui) op woensdag 14 september, des namiddags om 15.00 uur precies.

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1 INTRODUCTION

1.1. THE PURPOSE OF THE RESEARCH

The water soldier (**Stratiotes aloides** L.) is found in a number of Dutch broads, ditches and canals. The Aloë-like plants often grow together in great numbers, especially in broads, where they form an important stage in the terrestrialization. Most adult **Stratiotes** plants are emergent; the plants grow partly under the water surface and the tops of the leaves protrude out of the water. Adhering to the under-water parts of the plants and in between them, many species of macro-organisms are found, often in very high numbers (Gardeniers, 1971; Higler, 1966, 1968, 1969, 1971; Higler & Brantjes, 1970; Higler & Gardeniers, 1967; Karassowska & Mikulski, 1960; Mason & Bryant, 1974; Zimbalevskaya, 1972).
Marcro-organisms (or macrofauna) are those aquatic invertebrates, that are visible to the naked eye, such as triclads, leeches, snails, freshwater shrimps, water-insects and their larvae. A comparison between macrofauna lists out of samples of **Stratiotes** vegetations in different parts of The Netherlands shows a great similarity in fauna composition. Within the **Stratiotes** vegetation in a broad differences in the macrofauna distribution could be observed. Certain species were found near the open water and others in the heart of the vegetation or near the shore (Higler, 1969; Brantjes & Higler, 1970). We shall call the regularly occurring combinations of species ,,animal aggregations''. The term is derived from Allee (1931) and is used here for combinations of species, which are observed regularly under comparable conditions of a physico-chemical nature. Karassowska & Mikulski (1960) use this term in the same way.

The purpose of this research is to investigate animal aggregations in **Stratiotes** vegetations and to find correlations between the occurrence of these aggregations and characteristics of the environment.

1.2. MOTIVATION

a. **Stratiotes** plants are clearly defined unities in vegetations, which often consist of thousands of plants. Parts of these vegetations have a 100 % coverage of **Stratiotes** plants. For quantitative sampling of animals adhering to the plants, this phenomenon is of great practical advantage. The plants can be sampled as unities and besides there are often no alternatives for the macro-organisms which are being studied for attaching, hiding or feeding.
b. The broads with autochtonous swamp succession belong to the richest and most typical Dutch natural areas and the most important of them are nature reserves. The research on the macrofauna of **Stratiotes** vegetations contributes to the knowledge of the transitional stage from open water to firm land.
c. Most organisms, that were found on the **Stratiotes** plants, belong to the common species in eutrophic, stagnant waters.
A more precise description of their ecological demands and their mutual relationships is still largely lacking. Because of the factors mentioned under 1.2.a, an attempt can be made to study this problem, which would be much more difficult in mixed vegetations and in more divergent environments.

1.3. STRATIOTES VEGETATIONS FROM PLANTS-SOCIOLOGICAL VIEW

According to Westhoff & Den Held (1969) the autochtonous swamp succession with **Stratiotes** belongs to the Hydrocharito-Stratiotetum with **Hydrocharis morsus-ranae** and **Stratiotes aloides** as character taxa. The association belongs to the class of the Potametea.
Segal (1965) proposes a separate class of ,,Stratiotetea'' with seven associations, among which the association Hydrochareto-Stratiotetum. Segal (1965) indicates the role of **Stratiotes** in the autochtonous swamp succession. In both references it is stated, that **Stratiotes** plants die in winter. During our research, however, it became obvious that this does not happen

every winter. During the winter 1971-1972 a great part of the floating plants in the ,,Hol'' (Kortenhoef) did not sink to the bottom, nor decayed.
In the Dutch broads the terrestrialization often takes place on the sheltered side of the waterbody (western shore). The conditions for the development of **Stratiotes** are: shallow, eutrophic and quiet water with a sapropel layer on the bottom. It is a fast growing plant, that raises the sapropel layer every year by its decaying leaves. This process goes on until the water layer is too shallow for the development of the plant. By this time other plant species take over. The thickness of the sapropel layer increases from the centre of the broad to the shore. If the water layer measures 150 to about 60 centimeters, **Stratiotes** grows only submerged
These plants have large, flexible, slightly curled leaves. In the shallower water of about 60 centimeters and less, the plants emerge in summer. The leaves of these plants are straight and stiff and are generally shorter (20-40 cm long). If the conditions for **Stratiotes** are good, extensive fields of tens of square meters can be formed. On the shoreside of the vegetation, where the plants are smaller than near the open water, **Hydrocharis morsus-ranae** is found in high numbers. By the occurrence of rafts in this zone, the autochtonous swamp succession accelerates. At the open water side of the vegetation nympheids and elodeids occur, in clear water Characea and in polluted water **Ceratophyllum demersum.**
The plants that stay submerged through out the year grow far apart, the emersed plants grow near each other. The emersed plants near the open water are generally best developed, and often no other plant species grow in between them. A good description of the autochtonous swamp succession is found in Westhoff a.o. (1971).

1.4. PREVIOUS RESEARCH OF THE MACROFAUNA ON STRATIOTES PLANTS

Considering the previous research on the macrofauna on **Stratiotes** plants we shall distinguish between investigations that compare the macrofauna of the several plant species - among which **Stratiotes** - and investigations, that analyze the macrofauna inside **Stratiotes** vegetations.

a. A comparative research of the macrofauna on different plant species has always to face the problem of a quantitative comparison of the results. When a species occurs on different plants the comparison of numbers is difficult due to the different structure of the plants. In quantitative studies it is often neglected that the conditions within one type of monoculture vegetation can vary greatly, which influences the composition of the macrofauna in different parts of those vegetations. Nevertheless we shall examine the results of two investigations in which the macrofauna on different plant species is studied and where **Stratiotes** is included.

Karassowska & Mikulski (1960) compared the fauna on eight plant species in Lake Druzno, Poland. The species were: **Potamogeton crispus** L., **Ranunculus circinatus** Sibth., **Myriophyllum spicatum** L., **Ceratophyllum demersum** L., **Stratiotes aloides** L., **Nymphaea candida** Pres., **Nuphar luteum** L., and **Limnanthemum nymphaeoides** Hill.
For the first five plant species they mention the numbers of individuals per m^3 of plant material, based on the collection with a standard limnological sieve, loosely filled with plants. For the pleustonic plants numbers per m^2 of plant material are given, based on the collection of 50 leaves of each plant species. These methods are inadequate for quantitative comparison and therefore we calculated percentages of macrofauna groups per plant species from their tables. These figures are shown in table 1. The figures have been rounded off; + means less than 0.5%.

	Ceratop.	Ranuncul.	Stratiot.	Myriop.	Potam.	Nymphaea	Nuphar	Limnant.
Chironomidae	14	25	41	33	77	12		60
Mollusca	53	9	21	30	10	10	3	11
Hirudinea	2	15	9	5	2	74	25	54
Ephemeroptera	1	3	1	1	3	2		+
Isopoda	21	31	12	+	1	+		1
Trichoptera	10	13	16	30	7	2	3	11
Heteroptera		3		+	1		1	
Oligochaeta							8	1
Individ./m^3	4770	2899	10146	29888	12145			
Individ./m^2						4.27	19.22	18.75

Table 1. Distribution of macrofauna groups as percentages per plant species (derived from Karassowska & Mikulski, 1960).

The proportional occurrence of the main macrofauna groups differs for the said plant species, that grow in homogenous aggregations in one lake. If the species composition is compared, we can add qualitative differences between the plant species. The most abundant mollusc on **Stratiotes** for example is **Valvata piscinalis**, which does not occur on **Ranunculus** and **Potamogeton**. **Valvata cristata** was not observed on **Stratiotes**, but it was found on **Ranunculus** and **Potamogeton**. With the referred data it is possible to characterize the macrofauna composition of **Stratiotes** as compared to that of the other seven plant species under the defined conditions of Lake Druzno.
Pieczyński (1973) compared the macrofauna on **Elodea canadensis** Rich. and on **Stratiotes** in Lake Warniak, Poland. In his first table, he gives average percentages of the numbers of macrofauna groups in 1968 and 1969. We reproduce these figures in table 2, using the same sequence as used in table 1 for the corresponding groups.

	Elodea		**Stratiotes**	
	1968	1969	1968	1969
Chironomidae	61.4	54.0	68.7	81.8
Mollusca	1.1	0.5	2.0	0.6
Hirudinea	0.4	0.3	7.2	2.8
Ephemeroptera	6.5	10.5	4.0	3.0
Isopoda			0.1	< 0.1
Trichoptera	1.3	0.8	4.4	1.6
Heteroptera		< 0.1		< 0.1
Oligochaeta	25.1	27.3	8.0	1.8
other groups	4.2	6.6	5.6	8.4
Indiv./kg	5550	27840	2800	8410

Table 2. Distribution of macrofauna groups as percentages per plant species (derived from Pieczyński, 1973).

As no details on the species composition are mentioned, we can only compare the figures in the tables 1 and 2.
We cannot speak of a striking similarity between the proportions of the macrofauna groups in the case of **Stratiotes.** Apparently there are more factors that influence the fauna composition than the difference in species of host plant does.

In both publications discrepancies have been observed in the macrofauna on several plant species, but no successful effort is made to relate these differences to environmental and structural characteristics of the vegetations. In the present study we shall try to elucidate the relations between macrofauna composition and environmental factors of the Dutch **Stratiotes** vegetations.

b. We have been involved in comparative research of the macrofauna in different sections of **Stratiotes** vegetations in The Netherlands since the mid sixties. To start with we discovered qualitative and quantitative differences between the macrofauna on emersed and submerged plants (Higler, 1966; Higler & Gardeniers, 1967). We investigated **Stratiotes** vegetations in a number of broads and canals in many parts of the country and found, approximately the same species in about the same relative quantities. Certain differences could be related to environmental factors such as chemical composition of the water and management activities in the recent past. We also found regularities in species composition in different parts of a **Stratiotes** vegetation. On a line from open water to shore certain species showed a preference for certain sections on this line and it seemed reasonable to assume that the place in the vegetation with its specific characteristics is of importance for a number of elements of the macrofauna (Brantjes & Higler, 1970; Higler, 1968, 1969, 1971; Higler & Brantjes, 1970).
The mentioned investigations have been performed in summer, when **Stratiotes** vegetations are in maximal development. Most **Stratiotes** plants have emerged, only the plants in the deeper water (over 60 cm) stay submerged throughout the year. In this publication we shall mention emersed and submerged plants or emersed and submerged sections of the vegetation. This refers only to the summer situation.
Kuiper (1972) investigated the macrofauna on **Stratiotes** in the nature reserve the ,,Hol'' in Kortenhoef from January to June 1972. The plants from the emersed section of 1971 had not sunken very deep and could be sampled easily. He has shown that same species are found in summer and in winter.
There are some shiftings in quantitative respect and the total numbers per species are generally highest in summer.
The preliminary conclusions as mentioned above could be affirmed. In small broads, filled up with **Stratiotes**, Kuiper found the same species composition as we did in the emersed parts of vegetations and the species from the submerged parts were absent or only present in very small numbers.
We paid special attention to the larvae of Trichoptera and Ephemeroptera, because they showed a distinct overlapping in the different sections of the vegetation (Higler, 1969). **Caenis horaria** (Ephemeroptera, Caenidae) was found predominantly in the submerged part of the vegetation and **Caenis robusta** in the emersed part as well. The species of the genus **Cyrnus** (Trichoptera, Polycentropodidae) have been observed in the submerged parts and the emersed parts near the boundary zone with the ,,open water''. It turned out, that the two species **Cyrnus crenaticornis** and **C. flavidus** followed each other in the time. When small larvae of one species were found, the larvae of the other species were mature or pupating. The niches are therefore either separated in space or in time.

1.5. Physical and chemical research in stratiotes vegetations

In botanical literature some general remarks on the physical and chemical conditions in **Stratiotes** vegetations are given. They are sufficient for a rough characterization of the biotope.
Westhoff & Den Held (1969) mention: ,,shallow water, generally less than one meter deep, which is eutrophic or slightly polluted, quiet, sheltered, fresh or oligohalinic and standing over a thick, reduced sapropel layer on various soils. In mesotrophic and in very shallow water **Hydrocharis** dominates, in water deeper than one meter **Stratiotes** dominates''. They further mention an increase of the vegetation type until ,,recently'' by eutrophication and a decrease nowadays by herbicides.
Runge (1961) reports from Westfalen (B.R.D.) that the preferred biotope is formed by former river branches. Kurimo (1970) supposes that **Stratiotes** increases in numbers in Finland following pollution and that water, rich in phosphates in preferred.
In these references non-quantified terms are used to characterize the chemical conditions. The polluted waters in Finland are perhaps more oligotrophic than our ,,eutrophic'' broads. Without discussing these terms in detail, it is clear in what type of water we can expect **Stratiotes** vegetations.
For macro-organisms a number of parameters may be of importance because of the possible harmful effects of the variation of these factors during 24 hours. The circadian variation between the plants is greatest in summer. This refers to temperature, oxygen content and pH.
The folowing data on these parameters have been derived from Hogendijk (1969), Leentvaar (1967), Van Raam (1971) and Ulehlová (1970).

a) The temperature of the water in the surface layer of the emersed sections of the vegetation may rise in the summer until over 30 degrees.
   Under the plants the temperature is always some degrees lower and in the sapropel a fairly constant temperature of 15-16 degrees is observed.
b) The oxygen content of the water in the emersed part of the vegetation shows a great variation. In the summer, if there is no wind, oversaturation in the afternoon can be observed between the emersed plants growing closely together. In the night the oxygen content may fall to zero.
   In the waterlayer under the plants the oxygen content is considerably lower and in the sapropel layer there is no free oxygen at all. This means, that only in the upper thirty centimeters life for macro-organisms is possible. The oxygen drop under the plants often coincides with a temperature drop of 5-6 degrees.
c) The pH of the water between the emersed plants bordering the open water, is higher than the pH of the water in the broad outside the vegetation. Close to the shore the pH fluctuates round the values of the open water. Some minor differences of a half to one unit of pH have been observed close to the **Stratiotes** plants. At the lower side of the plants the pH is lower, at the sides around the plants the pH is higher than in the small pool in the middle of the plants. The pH range during 24 hours on one spot in the vegetation can amount to 4 or 5 pH-units (verbal communication by P.Schroevers).
   This process is well-known in Ca-rich waters, where an equilibrium exists between carbonates, hydrocarbonates and free CO_2. This equilibrium shifts in the direction of carbonates by the withdrawal of CO_2 by the assimilation activity of the plants. This causes a rise in pH and precipitation of $CaCO_3$.

1.6. RESEARCH OF MICRO-FLORA AND MICRO-FAUNA IN STRATIOTES VEGETATIONS

The research of the micro-flora and the micro-fauna demonstrates clear differences in species and numbers of the samples that were taken in the open water and in several zones of the **Stratiotes** vegetation.
Schroevers (1967) observed the greatest diversity in micro-flora species in between the **Stratiotes** plants. The richest zone was formed by the plants near the open water. Dresscher (1968) sampled a series from open water to shore in more detail and roughly confirmed the former observations. In his investigations the submerged zone turned out to be the richest one. The Chlorophyceae and Diatomeae preferred the open water and the submerged zone. The Euglenophyceae and the Chrysophyceae were predominantly found in the emersed zone bordering the open water and the Conjugatae were mainly found between the emersed plants.
Data on the micro-fauna can be found in Geelen & Salomé (1967), Geelen & Van der Heide (1968) and Davids & Dresscher (1971).
Cladocera are more numerous in the **Stratiotes** vegetation than in the open water. The dominating species are **Ceriodaphnia** spp. and **Polyphemus** sp. Copepoda prefer the open water. In Rotifera clear qualitative differences could be observed in the several samples that were representative of the several zones.

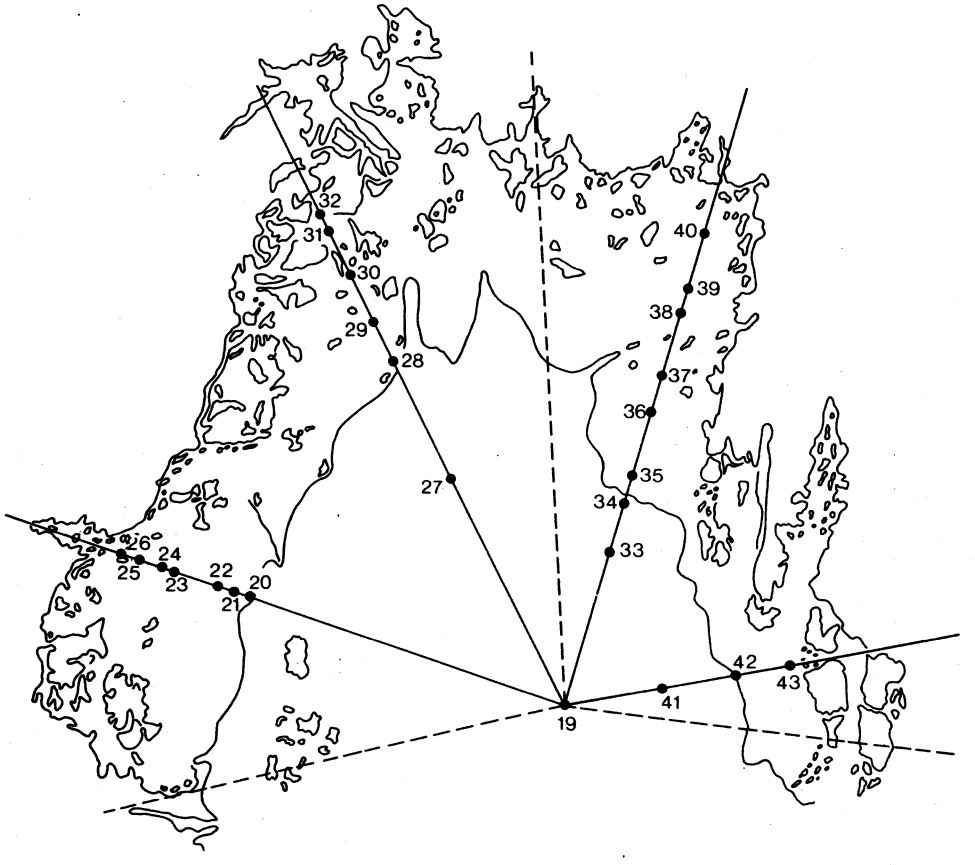


Fig. 1. View of the emersed part of the **Stratiotes** vegetation in the broad Venematen (from aerial photograph). The figures indicate sampling stations. The inner part shows open water with submerged plants (the stations 19, 27, 33, 34, 41). Outside the outer lines are the marsh and the shore.

2 MATERIAL AND METHODS

2.1. SAMPLING METHODS

In literature a number of methods for quantitative sampling of macrofauna on plants has been described. Most of them are unsatisfactory for our purpose.

a) The method of collecting a fixed volume of plant material does not take into account the density and the dimensions of **Stratiotes** plants. The method is highly inaccurate. The instruments used in this method are a hand net (Junk, 1973), a sieve (Karassowska & Mikulski, 1960) or a bucket (Kuflikowski, 1974). Hillbricht (1953, in Karassowska & Mikulski, 1960) uses a ,,handfull'' of plant material.
b) The same objectives as under a) apply to the method of sampling the plant mass growing over a surface unit of the bottom (Balkanovskaya, 1953, Gromov, 1960, Ščerbakov, 1967 and Sokolova, 1965 in Pieczyński, 1973; Beattie a.o., 1972; Macan, 1949 and 1965; McLachlan, 1969; Mörzer Bruyns, 1965).
c) The measuring of the length of the main stem (Krecker, 1939) is useless for our investigations, because all leaves arise from a very short stem.
d) The measuring of the weight of the sampled plants (wet or dry) has a number of disadvantages (Frost, 1942; Pieczyński, 1973; Zimbalevskaya, 1972). It does not take into account that the leaves can be thin or thick in plants of the same size, that the amount of water adhered to the plants is not always the same nor the amount of water within the plants and that some plants have many incrustations of lime, bryozoans etc. and others none.
e) In our own investigations before 1972 we used a fixed number of **Stratiotes** plants of about the same size (Brantjes & Higler, 1970; Gardeniers, 1971; Higler, 1968, 1969, 1971; Higler & Brantjes, 1970). This method is inaccurate, because the available plant surface of each plant for epiphytes and surface-bound animals is not the same.

In the method presented here, we measured the total amount of plant surface, available for sessile macro-organisms of the collected plants. This means that the method is only applicable if we restrict ourselves to the organisms adhering to the plants and to those that have a close relationship to the surface of the leaves because they are dependent upon shelter or prey on the leaves. The fast swimming animals are not captured quantitatively in this way, but only by accident. They play no role of importance in the calculations based on the quantitative sampling results.

A sample consists of one, two or three plants, carefully taken from the water with a large net or sieve. Animals that do not swim away fast or drop from the plants are included in the sample. These samples were put into large plastic bags or buckets with water and taken to the laboratory for examination.

The sampling stations have been chosen aselectively in known **Stratiotes** vegetations. In extensive vegetations the samples were taken on lines from open water to the shore. An example of this is given in Fig. 1. The starting point (19) which is the first sample, is fixed in the submerged part of the vegetation. The direction of the four lines has been chosen by using aselect numbers for the angles with regard to the dotted lines that border the vegetation. On each line the place of the sampling stations is fixed by aselect numbers.

From the adjacent water of every sampling station we collected water for chemical analysis and on the spot we measured: temperature, pH, electric conductivity, light intensity above the water and at several depths, distance from the surface of the water to the sapropel layer, thickness of the sapropel layer, depth of the heart of the plant, distance to the shore and distance to the border of the emersed and the submerged part of a **Stratiotes** vegetation. We carried out sketchings of the vegetation and counted the number of plants within a distance of one meter from the sampling plant (the density of the **Statiotes** plants). We measured from every sampling plant what part of the surface of the leaves was protruding from the water. This number had to be subtracted from the total surface of every sample, in order to estimate the available plant surface.

In the laboratory all organisms were picked from the leaves with a pair of pincers. Flatworms and leeches were identified alive and the length was measured. Watermites were stored in Koenike liquid. The remaining organisms were stored in alcohol 70%.
The surface of the leaves was measured carefully. For the sample surface we used the total surface of the leaves (both sides) of the plant(s) of every sample, subtracting the surface of the parts of the leaves that protruded out of the water (in the case of emersed plants). To check the error of the measurements which were made with marking gauge and ruler, a number of leaves were copied on millimeter-paper. These ,,paper leaves'' were weighed and that weight could be compared with the weight of a piece of millimeter paper of a known surface. The mean deviation of the measurements is 10 percent below the real surface. The surface was never overestimated. In the calculations we have neglected the deviations in the surface measurements. The sample surface ranged from 478 to 14252 cm^2 with an arithmetic mean of about 5000 cm^2.
The numbers of organisms per sample have been calculated as numbers per m^2 for every species. In this way the samples can be compared quantitatively. The method is very reliable, even if one is forced to disturb the situation of the sampling station by moving the boat and taking measurements. The reliability is achieved by the restriction to organisms that have a close relationship to the plants. The fast swimming fishes, beetles and some other insect species that frequently occur between **Stratiotes** plants, were caught occasionally, but they were not included in the studies.

2.2. PROCESSING OF THE RESULTS

The data resulting from the identification, counting, and measuring of the animals have been processed in a number of ways. The autecological approach of the material leads to a variety of interesting data, of which we only use those data that will contribute to the present research.

a. **Life cycles.** All specimens of the species that were collected in sufficient numbers, have been measured (Chironomidae and watermites excluded). The length of flatworms and leeches was measured from creeping animals in a water filled Petri-dish, which was placed over millimeter paper. From the snail houses we measured the greatest height or width (Planorbidae). The insect larvae have been measured without tails, cerci or distal prolegs. Prepupae, pupae and empty cases of Trichoptera are mentioned too.
   Using the measurements and the data on pupae we made reconstructions of the life cycles. These data are partly used in 5.2.
b. **Abundance and frequency.** The numbers per m^2 -sample of every species were put into graphs in sequence of increasing numbers. These graphs have a likeness to exponential curves. For this reason we used in the calculations ad c. the logarithms of the numbers per m^2. The average number per m^2 of the samples, when the species was present, has been calculated.
   Of most species a frequency distribution was made of the presence in increasing categories of abundance per sample. In this way the most frequently occurring numbers per m^2 are easily detected. The graph resembles a negative binomial distribution.
   The abundance and frequency data are given in 4.2 and used in the calculations of the cluster analysis.
c. **Cluster analysis.** This comprises the techniques that make divisions into groups, from a large number of objects (e.g. samples) based on a large number of data (measurements, animals). The starting point is the assumption that the set of objects is a stick probe from an unknown number of unknown populations, between which differences exist with regard to the data in question.

If a number of p data are known from n objects E_1, E_2,.....,E_n, the starting point for the cluster analysis is a matrix X_{nxp}. Most methods execute the analysis in two phases:

1) For each pair of objects the amount of similarity of the data is calculated. This is expressed in a distance or coefficient of (dis)similarity. The result is a symmetrical matrix D_{nxn}, in which d_{ij} represents the distance between the objects E_i and E_j,
2) Starting from the matrix D the clusters C_1,....., C_k are determined.

Our objects are the 73 samples and the data are the numbers per m^2 of the 82 most abundant species. As mentioned before (under b) we had to use the logarithms of the numbers per m^2. In the analysis the presence zero is used as well, so all numbers are increased by one and because of the differences in occurrence frequency of the species, this number is divided by the standard deviation of the frequency division. So the analysis is carried out for $\frac{\ln (N_{ij} + 1)}{\sigma_j}$. N_{ij} = the number of animals of species j in sample i

σ_j = the standard deviation of the frequency division of species j =

$$\left(\frac{\sum_{i=1}^{73} \left[\ln(N_{ij}+1) - \frac{\sum_{i=1}^{73} \ln (N_{ij}+1)}{73} \right]}{73 - 1} \right)^{1/2}$$

The clusters of the samples have a comparable species composition, qualitatively and quantitatively. To visualise the clustering, the data have been processed into dendrograms (Fig. 6 and 7). The calculations have been performed by I.W.I.S.-T.N.O., Wageningen on their computer. Seven different methods of cluster analysis have been applied, from which we use the results of the method of Ward for ease of survey.

2.3. EXPERIMENTS WITH ARTIFICIAL STRATIOTES PLANTS

In 1974 and 1975 we put 50 plastic **Stratiotes** plants into the broads Venematen and Loenert (north western part of the province of Overijssel) and in two broads in the ,,Hol" reserve (between Amsterdam and Utrecht). The artificial plants were placed in double rows between and outside **Stratiotes** vegetations and at several depths. Four to six times each year a number of the artificial plants and some living plants from the same sampling stations were investigated for macrofauna. The results of these experiments elucidate a number of problems, that arose during the processing of the data of the 1972 research. Under 4.5 some provisional results will be given, while a full account is to be published elsewhere.

3 DESCRIPTION AND CLASSIFICATION OF THE SAMPLING STATIONS

3.1. GEOGRAPHY AND CHARACTERIZATION OF THE INVESTIGATED WATER-BODIES

In table 3 a survey is given of the localities and dates of the 73 samples that were collected during 1972. More dedails on the sampling stations and the position of the sampled plants with regard to water depth and distances to the shore, the open water etc. are enumerated in table 4. These latter data can be measured precisely and will be used in the first instance in comparison with the results of the sampling of the macrofauna. Of course there are many factors - often difficult to measure - that influence the fauna composition. We shall describe a number of these factors from the sampling stations or sampled water-bodies. The water chemistry is dealt with in chapter 4. Literature, dealing with hydrobiological (or sometimes botanical) aspects of the water-bodies is mentioned at the end of the discussion per water-body.

nr	date	locality	municipality
1/2	19-IV	Het Hol, Kortenhoef	's-Graveland
3/5	25-IV	Het Hol, Kortenhoef	's-Graveland
6	26-IV	Suikerpot, Kortenhoef	's-Graveland
7/8	3 - V	Molenpolder	Maarssen
9	9 - V	Pond near Fort Ruigenhoek, Groenekan	Maartensdijk
10/12	16- V	Westbroekse Zodden, Westbroek	Maartensdijk
13	24- V	Tienhovense plas, Tienhoven	Maarssen
14	30- V	Oostkanaal, Griendtveen	Horst
15	30- V	Helenavaart, Helenaveen	Horst
16/18	6 -VII	Lindevallei, Wolvega	Weststellingwerf
19/32	12/18-VII	Venematen broad, St. Jansklooster	Vollenhove
33/43	29/31-VIII	Venematen broad, St. Jansklooster	Vollenhove
44	6 -IX	Nieuwkoopse plassen	Nieuwkoop
45/61	12/20-IX	Weerribben, Hogeweg	Oldemarkt
62/63	31- X	Junner Koeland	Ommen
64	31- X	Pond near Opheusden	Heteren
65	31- X	River backwater near Opheusden	Heteren
66/70	6 -XI	Het Hol, Kortenhoef	's-Graveland
71	8 -XI	Locality 65	Heteren
72	15-XI	Canal north of the village of Lekkerkerk	Lekkerkerk
73	20-XII	Botshol	Abcoude

Table 3. Date and locality of the sampling stations in 1972
nr = serialnumber of the samples.

nr.	origin sampling station	categ.	Type	depth	sap.	dist.b.	dist.s.	density
1	peat digging	II	em	77	88	-	20	43
2	,, ,,	IV	sub	62	163	-	1	17
3	,, ,,	III	em	69	161	10	30	14
4	,, ,,	III	em	57	143	40	2	29
5	,, ,,	II	em	75	118	10	10	15
6	,, ,,	II	em	45	95	-	10	8
7	,, ,,	III	em	44	82	-	5	28
8	,, ,,	I	em	44	75	-	3	5
9	pond	II	em	62	188	-	2	32
10	peat digging	II	em	44	72	-	4	48
11	,, ,, , ditchlike	I	em	53	61	1	1	43
12	,, ,,	II	em	38	106	15	5	42
13	,, ,, , broad	V	sub	61	55	-	2	16
14	peat-moor canal	I	sub	90	90	-	8	8
15	,, ,, ,,	II	sub	48	32	-	3	27
16	peat digging	I	em	41	190	5	10	64
17	,, ,,	I	em	46	159	10	5	35
18	,, ,, , ditchlike	IV	sub	65	84	- 3	12	3
19	,, ,, , broad	VII	sub	84	166	-20	40	4
20	,, ,, ,,	II	em	49	201	3	30	57
21	,, ,, ,,	II	em	52	198	6	27	34
22	,, ,, ,,	II	em	49	201	10	23	46
23	,, ,, ,,	II	em	42	168	18	15	34
24	,, ,, ,,	I	em	42	173	21	12	36
25	,, ,, ,,	II	em	45	200	26	7	38
26	,, ,, ,,	II	em	66	184	31	2	25
27	,, ,, ,,	IV	sub	73	177	- 8	50	3
28	,, ,, ,,	II	em	47	203	2	30	78
29	,, ,, ,,	II	em	39	211	8	20	76
30	,, ,, ,,	II	em	37	213	15	15	73
31	,, ,, ,,	II	em	32	218	25	5	63
32	,, ,, ,,	II	em	31	219	27	3	54
33	,, ,, ,,	IV	sub	86	164	-10	25	6
34	,, ,, ,,	IV	sub	72	178	- 1	19	18
35	,, ,, ,,	II	em	55	>200	2	12	40
36	,, ,, ,,	II	em	41	155	15	12	57
37	,, ,, ,,	II	em	52	142	16	12	49
38	,, ,, ,,	II	em	58	> 190	20	12	26
39	,, ,, ,,	II	em	39	> 210	24	10	51
40	,, ,, ,,	II	em	36	> 210	30	5	32
41	,, ,, ,,	I	em	93	> 160	-10	23	3
42	,, ,, ,,	III	sub	76	> 175	- 1	12	15
43	,, ,, ,,	III	em	51	> 200	10	3	42
44	canal in polder	II	em	72	154	2	2	2
45	peat digging	V	sub	94	>200	-30	5	3
46	,, ,,	IV	sub	67	> 180	- 5	4	5
47	,, ,,	III	em	54	> 200	½	2	28
48	,, ,,	III	em	56	> 185	1	1	49
49	,, ,,	IV	sub	58	> 190			12
50	,, ,,	IV	sub	58	> 190			27
51	,, ,,	II	em	53	> 200			35
52	,, ,,	II	em	55	> 195			20
53	,, ,,	II	em	60	> 190	3	3	59

nr.	origin sampling station	categ.	type	depth	sap.	dist.b.	dist.s.	density
54	peat digging	II	sub	54	>200	- ½	6	52
55	,, ,,	II	em	41	>210	5	1	33
56	,, ,,	II	em	47	>200	- 1	3	20
57	,, ,,	II	em	38	>210	½	2	78
58	,, ,,	I	sub	51	>200	-	3	4
59	,, ,,	II	em	48	>200	15	5	37
60	,, ,,	II	em	63	>190	30	5	52
61	,, ,,	IV	sub	69	>180	-	4	46
62	River oxbow	II	em	33	101	-	7	52
63	,, ,,	IV	em	50	115	-	10	26
64	pond in river forelands	III	em	45	>160	-	1	26
65	river backwater	III	em	40	38	-	1	25
66	peat digging cf nr 1	II	em	58	101	-	20	55
67	,, ,, cf nr 5	III	em	54	142	10	30	51
68	,, ,, cf nr 3	II	em	81	104	20	10	42
69	,, ,, cf nr 2	II	em	71	110	-	2	28
70	,, ,,	III	sub	74	89	-	2	22
71	river backwater cf 65	II	em	45	40	-	4	25
72	canal in polder	II	em	31	--	-	1	36
73	peat digging, broad	X	sub	95	155	-	5	1

Table 4. Some data on the sampling stations and the sampled plants.
category = code for the depth of the sample-plant(s)
I : distance watersurface-heart of the plant between 0 and 10 cm
II: ,, ,, ,, ,, ,, ,, 11 and 20 cm
etc.
type = condition of the plants
em type is strong with stiff leaves; mostly emersed
sub type is weaker with long, slender leaves; always submerged.
depth = distance from watersurface to sapropel layer in cm.
sapropel = thickness of the sapropel layer in cm.
distance b. = distance sampling plant to the boundary zone emersed-submerged in cm. With prefix - for plants outside the emersed part of the vegetation.
distance shore = distance sampling plant to shore or reeds forming the end of the emersed part of the vegetation in cm.
density = number of **Stratiotes** plants within a circle (r = 1 meter) with the sampling plant in the centre.

The samples 1/5 and 66/70 have been collected in the nature reserve the ,,Hol''. As the reserve is not accesssible to the public, the vegetations are seldom disturbed by boats. Hydrologically there is a certain isolation from the adjacent broad-and-swamp areas, where **Stratiotes** has disappeared in the last few decades. It is very probable, that water pollution and mechanical disturbance have caused this disappearance. In the south-eastern part of the reserve there is a clear indication of seepage. The water is milky coloured (iron phosphate and colloids of iron hydroxide) and the plants are covered with brown-reddish iron hydroxide. The sampling stations 1, 3, 5, 66, 67 and 68 are located in the seepage area in small broads that have been filled up with **Stratiotes**. This situation has not changed for the past 25 years (or longer) and still exists now (1977). The sampling station 70 has been chosen in the last plants of a **Stratiotes** vegetation that filled up parts of a broad before 1970. After 1972 no living **Stratiotes** plants have been observed here.
Lit: Higler, 1975, 1976; Hillebrand, 1973; Kuiper, 1972; Leentvaar, 1967 a; Meyer & De Wit, 1955.

The peat hole, where sample 6 has been collected, is connected with polluted water of a canal by an open ditch. The water looks very turbid. We found a few **Stratiotes** plants, although, until recent years, more than half of the surface had been overgrown by **Stratiotes**. After 1972 **Stratiotes** has disappeared. There is little water-traffic.
Lit: Higler, 1976; Leentvaar, 1967 a.

The samples 7 and 8 are from the nature reserve ,,Molenpolder'' that received water from the polluted river Vecht. Until recently a number of **Stratiotes** vegetations occurred in several places of the reserve. In 1972 we only found two poorly developed remnants of former vegetations. There is much boat-traffic. The water is turbid in most places (sampling station 7). A small area far from the water inlet has clear water (sampling station 8) but even here the **Stratiotes** plants were degenerating. The sapropel contained many remnants of **Stratiotes** plants from 1971.
Lit: Hadderingh, 1970; Leentvaar, 1969 a; Zwart, 1969.

Sampling station 9 is located in a small, round pond of about one quarter of an acre in grass-land, connected with a ditch on one side. The water is turbid. In 1972 and previous years the pond was full with **Stratiotes**, but after 1972 the plants had totally disappeared. No mechanical disturbance is possible.

The samples 10, 11 and 12 are originated from elongate peat digging holes in a well isolated area of grass-land and peat diggings. There is no mechanical disturbance and probably no inlet of polluted water. **Stratiotes** is growing here in patches between other plants or fills parts of the peat diggings. There is no plain zonation from open water to the shore. Sample 11 was part of an isolated group of **Stratiotes** plants in a ditch with no other emersed plants.

Sample 13 consists of a few small, submerged plants, growing near a narrow stretch of land in the ,,Tienhovense Plassen''. We were not able to find more plants in this area, although these were observed in several places in 1971. The water is turbid and there in an inlet of polluted water. In the area recreation takes place, there are summer cottages and there is some cattle-breeding. The managing authorities are planning to improve the water quality by letting in unpolluted water.
Lit: Leentvaar, 1969 a.

The samples 14 and 15 have been taken from canals in the ,,Peel'', an oligotrophic area in the southern part of The Netherlands. The supply of eutrophic water takes place via the canals, some of which were partly filled with **Stratiotes** in the sixties. In 1972 we found two small vegetations; one of small plants in a dense **Ceratophyllum demersum** growth (14) and one of plants of the same size (like big turions) in a dense **Potamogeton crispus** vegetation (15). Both samples were heavily overgrown by **Plumatella** colonies.
Lit: Higler, 1966; Schroevers, 1966.

The area of peat diggings and swamps known as the ,,Lindevallei'', from which the samples 16/18 originate, is in connection with the small river Linde in the south-western part of the province of Friesland. For the culture of reeds, a certain regime of water management was followed until recent years. A number of peat diggings were filled up with **Stratiotes**. In one of the peat diggings **Stratiotes** was taken away without removing the sapropel. Here **Stratiotes** did not return. In another one the plants returned within some years.
Sampling station 16 (from an abundant **Stratiotes** vegetation) was visited again in 1975. In that year the plants were gone and only 35-40 centimeters of water remained over the sapropel. Sampling station 17 was a typical terminal stage of the autochtonous swamp succession with many rafts near the shore. In the vicinity of station 18 we found during the visit in 1975 a floating layer of rootless emersed **Stratiotes** plants above relatively deep water (60 cm).
Lit: De Blok a.o., 1970; Boonman, 1970;Brantjes & Higler, 1970; Davids & Dresscher, 1971; Dvorak, 1972; Higler, 1971; Higler & Brantjes, 1970; Moed, 1971; Schroevers, 1970.

The broad ,,Venematen'' is the most important water-body of this study. The samples 19/43 were collected here in four ranges (Fig. 1). At the eastern side of the broad there is an open connection with polluted water, at the western side seepage water intrudes. In the sixties an extensive **Stratiotes** vegetation existed on the western side with an emersed part that reached over 80 meters from open water to the reeds near the shore. In 1974 a few plants were found and in 1975 none.
In 1972, fortunately enough, there was a well developed vegetation. In Fig. 1 the extension of the emersed part has been drawn, with, especially near the shore, small islands of rafts in between. Near the boundary emersed/submerged, nymphaeids and elodeids are found, and between the scattered submerged plants, especially **Ceratophyllum demersum.** In particular near the shore **Hydrocharis morsus-ranae** is found and in some places **Utricularia vulgaris.** The zone of emersed plants near the open water predominantly consists of **Stratiotes** and lemnids.
The reason for choosing the broad Venematen as a main object is the beautiful development of the vegetation from the plant-sociologists point of view and its great extension. By previous research it had become known that the macrofauna on the plants was extraordinary rich. Besides, a great deal of work had been done in this broad on water-chemistry, microfauna and microflora and higher plants.
Mechanical damage is caused by boats, especially those with outboard motors and by swans. In 1972, as in previous years, a swan's nest was found in the vegetation (near sampling station 26). The swans eat the leaves of the submerged plants and probably the tops of the emerged leaves as well just like coots do. The boats of fishermen make pathways through the vegetation that are used frequently. We observed those pathways also in previous years.
Lit: Davids, 1970; Gardeniers, 1971; Geelen, 1969; Higler, 1966 a, 1969; Higler & Gardeniers, 1967; Hogendijk, 1969; Keuning, 1971; Mol, 1974; Van der Perk & Smit, 1975; Van Raam, 1971; Schroevers, 1967, 1968; Ulehlová, 1970.

The plants of sampling station 44 were found in a waterway on the side of a road near a sewer drain. Much **Enteromorpha** was found there.

The sampling stations 45/61 are situated in the nature reserve ,,Weerribben''. The area is composed of peat holes, ditches and narrow stretches of land in between, covered with Alnetum. The samples have been taken from peat holes, two of which were fully filled with **Stratiotes** in the emersed stage (59/61). In some of the other peat holes there were larger or smaller fields of emersed plants with mostly scattered submerged plants outside these fields. The water from the peat hole in which the sampling stations 56/58 were situated, was very turbid and rowing brought much sapropel material to the surface as well as gas bubbles. In most peat diggings there is a regular boating. The influence of polluted water is manifest along the edges of the reserve and alongside the roads wih houses.
Lit: Higler & Tubbs, 1970; Leentvaar, 1958, 1959, 1960, 1965; Leys, 1972.

The samples 62 and 63 are from an oxbow of the river Vecht (province of Overijssel). There is an extended **Stratiotes** vegetation, where some polluted water from a park of summer cottages comes in. There is no mechanical disturbance.
Lit: Higler, 1970; Janssen, 1970; Leentvaar, 1969 b.

The sampling stations 64, 65 and 71 are in the forelands of the river Rhine. 64 has been taken from a small, circular pond, fully overgrown with **Stratiotes**, the samples 65 and 71 are from an old branch of the Rhine, where some small fields of **Stratiotes** grew.

Sampling station 72 is situated in a waterway alongside a road in the polder ,,Krimpenerwaard''.

The ,,Botshol'' where we gathered sample 73, is an area of peat diggings and broads with relatively much open water. The water is slightly brackish and in most places clear. In one place we found a number of scattered plants, lying on the bottom, and overgrown with threaded algae.
The localities where **Stratiotes** is found become fewer every year.
Lit: Hillebrand, 1973.

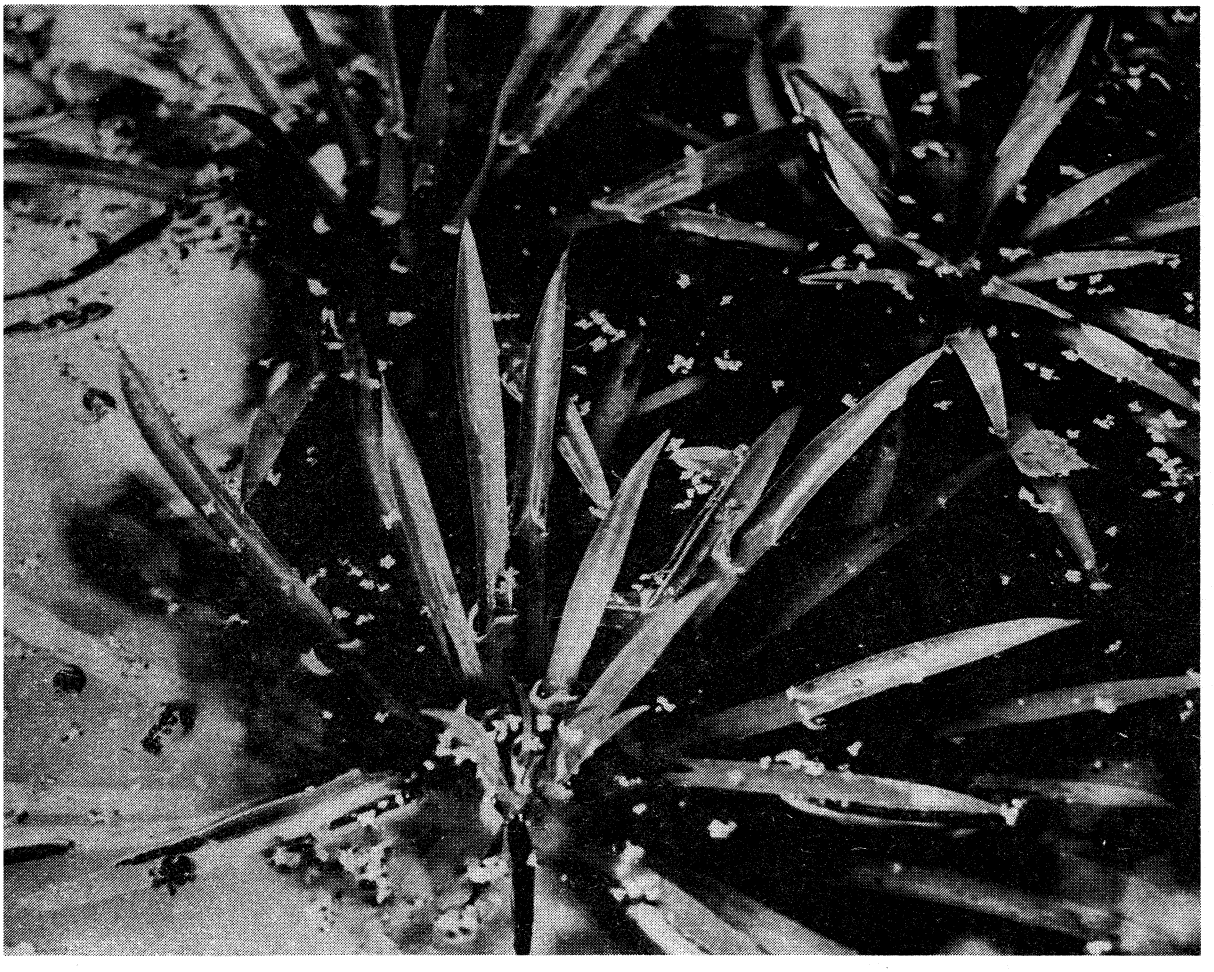
3.2. CLASSIFICATION OF THE SAMPLING STATIONS

In a previous research it has been shown, that a possible correlation exists between the occurrence of certain insect larvae and the position of the sampled plants in the vegetation (Higler, 1968, 1969). The factors, probably playing a role are: the emersed or submerged stage of **Stratiotes**, the plant density, the waterdepth, the sapropel thickness, the distance to the open water and the distance to the shore or reedmarsh. In a so called ideal terrestrialization with **Stratiotes** there is a distinct relation between these factors, which is depicted in Fig. 2 and summarized in table 5.
We have classified five possible combinations of factors, resulting in the groups A/E, in which some limitations are arbitrary.

	A	B	C	D	E
Type	emersed	emersed	emersed	submerged	submerged
Category	I-III	I-III	I-III	II-IV	IV-X
Density	20-60	20-80	45-80	10-30	1-10
Depth	30-50	40-60	50-70	50-70	55-100
Sapropel thickness	gradually decreasing				
Distance b		> 2 metr.	0-2 metr.	-(0-2) metr.	-(> 2) metr.
Distance shore	0-2 metr.	> 2 metr.	and gradually increasing		

Table 5. Classification of sampling stations on the base of physical characteristics. Explanation of terms as in table 4. The sign - in distance b. for the D - and E-groups means outside the emersed part of the vegetation. See also Fig. 2.

It is not difficult to classify most sampling stations from the ranges in the broad Venematen. Still there are a number of sampling stations, where the density or the depth does not fit well into the scheme. In other sampling stations outside the broad Venematen, it is often more difficult to decide in which group a sample fits. Problems arise in isolated fields of plants and in fully overgrown ponds. Nevertheless we shall try to classify the samples according to Fig. 2 and table 5 and provide additional remarks on deviations of this schematical presentation (table 6). In comparison with the results of the macrofauna investigation, we can decide whether the proposed classification makes sense or not.



The water soldier **(Stratiotes aloides)** in the emersed form.

nr.	group	remarks
1	B	broad filled up with Stratiotetum
2	D-E	group of submerged plants near the shore. No emersed plants
3		
4		
5		
6	B	a few plants; no vegetation succession; remnant of B
7	B	,, ,, ,,
8	B	,, ,, ,,
9	A-B	pond filled up with Stratiotetum
10	A-B	no real vegetation succession
11	C	isolated group of plants in a ditch
12	B	
13	E	isolated group of submerged plants near ,,reeds-shore''
14	E	small submerged plants in the upper water layer
15	B	small plants of the emersed type in the upper water layer
16	B	
17	B	
18	E	
19	E	
20	C	
21	B	
22	B	
23	B	
24	B	
25	A-B	
26	A	water is deep for A; swan's nest
27	E	
28	C-B	
29	B	
30	B	
31	B	
32	A	
33	E	
34	D	
35	C	
36	B	
37	B	
38	B	
39	B	
40	B	water is shallow for B
41	E	plants in the upper water layer
42	D	
43	B-A	
44	E?	floating emersed plants, but with density 2 and depth 72
45	E	
46	E	
47	D	density is too low for C
48	C	in the narrow emersed zone, no real B exists
49	E	

nr.	groups	remarks
50	D	
51	B?	no real emersed plants; very polluted looking water
52	A?	,, ,,
53	C	
54	B	the ,,open water'' is only a narrow fairway
55	A	
56	D	floating plants of the emersed type
57	C?	the waterdepth is too low for C
58	E	submerged plants in the upper water layer
59	B	
60	B	
61	D	density is rather high for D
62	B	very shallow water for B; no real vegetation succession
63	B	,, ,, ,,
64	A	pond filled up with Stratiotetum
65	A	no real vegetation succession
66	B	
67	B	
68	B	deep for B
69	B	
70	D	only submerged plants, remnant of Stratiotetum in previous years
71	B	cf nr 65
72	A	group of plants in a ditch
73	E	

Table 6. Classification of the sampling stations according to Fig. 2 and table 5.

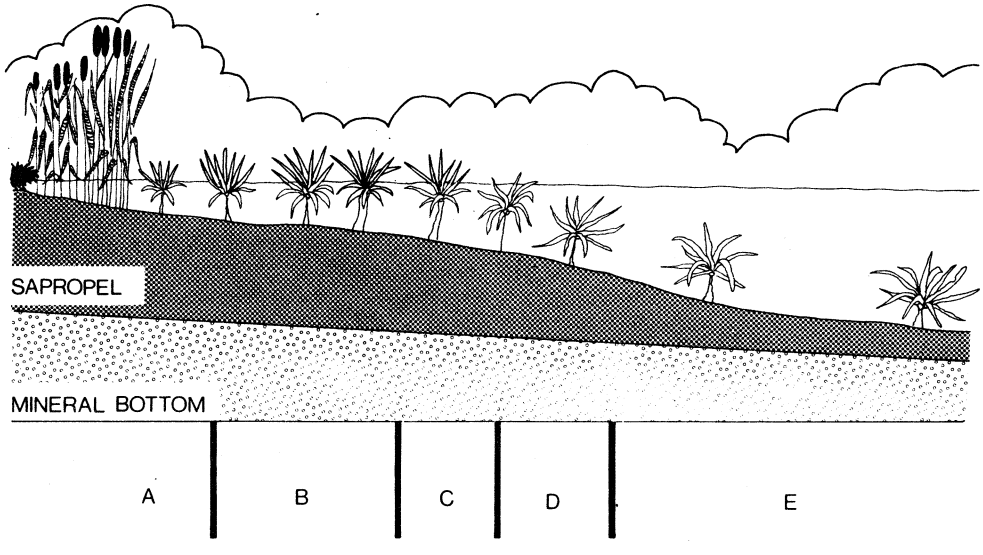


Fig. 2. Cross-section of the western part of a broad with an autochtonous swamp succession with **Stratiotes**. Explanation in the text and in table 5.

4. RESULTS

4.1. PHYSICAL AND CHEMICAL MEASUREMENTS

At the sampling stations water temperature, pH and electric conductivity were measured and three liters of water were collected for analysis of a number of parameters in the laboratory of Hugo de Vries Laboratories, University of Amsterdam. The results of this analysis are enumerated in table 7 and the main values are compiled in table 8. The analysis on P- and N-components has been carried out in filtrated water, the rest in non-filtrated water. The values of the pH in the water of the ,,Molenpolder'' are probably too low. For this reason the values for the samples 7 and 8 have been placed between brackets. The unusually low values must be due to the bad functioning of the pH-meter, as they are not in accordance with other pH-measurements in this area.

pH

At most sampling stations the pH was little over 7. The biggest part of the samples was taken in the afternoon in between dense plant masses. Under these conditions one would expect a higher value. Perhaps the presence of calcium bicarbonate prevents a strong rise. It is not likely, that the observed values of the pH can be limiting for the presence of the macro-organisms under consideration.

Bicarbonate (HCO_3^-)

The bicarbonate content was about 2 mgaeq./l at most sampling stations. In a number of samples from the ,,Weerribben'' and in one sample from the ,,Hol'' we found higher values (about 3.5.) and the waters in the river forelands contained 4.4. and 5.4. mgaeq./l (influence of the river Rhine). In the two samples from the oligotrophic area the ,,Peel'' we found lower values for bicarbonate as well as pH. Macro-organisms are not directly affected by bicarbonate, but sometimes indirectly by the combination bicarbonate, Ca^{++} and pH.

Calcium (Ca^{++}) and Magnesium (Mg^{++})

The observed values of calcium and magnesium are common in the Dutch eutrophic waters. The high magnesium content in sampling station 73 is connected with the degree of salinity in this area. The Ca^{++} content is also rather high and in accordance with the samples from the river forelands (64, 65, 71). The lowest values for calcium have been observed in the eastern part of the broad Venematen.

Electric conductivity (E.C.)

The E.C. is a measure for the ions in solution. In the eutrophic waters values over 200 µ-Siemens are found and in brackish waters (with high quantities of Cl^-) the E.C. may rise from 650 to several tens of thousands (sampling stations 44 and 73). The influence of Rhine water is seen in the rather high E.C. in sampling station 64. There is no direct relation to be expected between E.C. and fauna composition.

Chloride (Cl^-)

A number of ions are in their concentrations dependent on the presence and physiological qualities of plants and micro-organisms. The chloride content is not influenced by macro-organisms in the water, but reversed the organisms are highly dependent on the chloride content, especially in higher concentrations. Above 100 mg/l a certain influence starts on microfytes (diatoms), but as far the macrofauna is concerned, there are no effects before the concentration rises to 300 ‰ . (Higler, 1967) Therefore it is not probable, that chloride is an important eco-physiological factor at the sampling stations (except for no. 73).

Phosphorus (P)

The presence of phosphorus in the water can influence the occurrence of macro-organisms in an indirect way. Generally the growth of higher plants and algae is strongly stimulated by phosphates, which causes important changes in the environment. The investigated waters had high phosphate concentrations, as are found in eutrophic and hyper-trophic waters.
In some cases the water had become so turbid by algal bloom, that the visibility of preys for eye-hunters must be limited.
Most **Stratiotes** plants were overgrown with threaded algae, the growth of which is strongly stimulated by phosphate. In a number of cases these algae measured several centimeters, which forms a limitation for sessile organisms and a splendid dish for the specialized caddis larvae that eat threaded algae (fam. Hydroptilidae). High concentrations of phosphates are often found in polluted waters. Under such circumstances typical pollution-indicating organisms can become dominating features of the fauna composition.

Nitrogen (N)

Nitrogen has been measured as nitrate-N, nitrite-N and ammonia-N. Each of these compounds showed a great variance in the investigated waters. Nitrite is seldom found in measurable concentrations in natural waters. It is toxic to many organisms (several milligrams N per liter for fishes). NH_4OH dissociates into NH_3 if the pH is high, which is tonic as well. Much oxygen is needed for the nitrification of ammonia, so that under certain conditions the environment is unsuitable for organisms with a high need of oxygen.
At the majority of the sampling stations a thick sapropel layer is present with strongly reducing capacities. In most cases the organic matter content was high. In summer great differences in oxygen content exist between the upper water layer and the water just above the sapropel. The pH can vary accordingly. As a result one may expect high nitrate values in the upper water layer and under the plants at low oxygen contents, inhibition of the nitrification, and high values of nitrite and ammonia. The reduction processes can be intensified by the supply of ammonia-rich ground water or polluted water.
The observed values have been derived from one measurement at each station. We have not investigated the chemical processes during 24 hours and during the year, so no elucidation can be given of the complicated relationships with nitrogen at each sampling station. We know, that the values of nitrite and ammonia can be much higher than the observed ones. These phenomena are surely a limiting factor for macro-organisms in the shallow parts of **Stratiotes** vegetations.

Chemical oxygen demand (COD)

The COD is a good indication for organic substances in solution. The observed values are pretty high, which points to the great productivity of the investigated waters or pollution.

Sulphur (S)

Sulphate does not effect macro-organisms, but, in a reduced form (H_2S), it is tonic. The presence of H_2S and FeS in the sapropel could be demonstrated in many sampling stations. By its toxic and reducing capacities H_2S constitutes an extra limiting factor in and just above the sapropel.

Oxygen (O_2)

During our investigations we did not measure the oxygen content, because this makes only sense, if circadian registrations can be performed in a number of sites in the vegetation and on several depths. In the emersed part of the vegetation in summer, oversaturation has often been observed (Hogendijk, 1969; Van Raam, 1971). The oversaturation is caused by the

Stratiotes plants and the epiphyton and other microphytes. Immediately under the plants the oxygen concentration drops to values of 1 or 2 mg/l (Hogendijk, 1969; Leentvaar, 1967 a; Ulehlová, 1970) and in the sapropel no free oxygen is observed (Hogendijk, 1969). A similar vertical gradient was found by Junk (1973) in ,,floating meadows'' of water hyacinth during the night. Severe undersaturation can occur in the total water amount of the emersed sections (Van Raam, 1971).
This vertical gradient seldom occurs outside the emersed vegetation. The sapropel layer is much thinner or absent and mixing takes place by the action of the wind and the water (Hogendijk, 1969; Leentvaar, 1967 a, Ulehlová, 1970). As the oxygen content is of the greatest importance for the macrofauna, one can expect differences in species composition inside and outside the emersed part of the vegetation.

Temperature
The temperature of the surface water of all sampling stations has been measured at some time between 10.00 and 18.00 hours. In the case of measurements on one single day, differences in temperature exist at different sampling stations where the highest values are observed at the end of the afternoon. The shallow water in between the **Stratiotes** plants is warmed up soon and there is only little mixing of water between the plants, growing close together.
In Fig. 3 the temperatures found in 1972 (including Kuiper, 1972) are plotted. The fluctuations on one day or within one week can be considerable. The drawn curve shows the mean temperature during the year, which is of importance for the life cycles of a number of species. Davies & Reynoldson (1976) demonstrate the relation between the number of generations in a year of **Helobdella stagnalis** and the mean temperature.
The fluctuations in temperature decrease as the water becomes deeper. Ulehlová (1970) investigated the fluctuations of the water temperature during 24 hours in **Stratiotes** vegetations in the north-western part of the province of Overijssel. At 30 centimeters under the watersurface the temperatures were already the same as those in the sapropel. These values in the sapropel - in summer - were always between 15 and 17 degrees (Celsius). The circadian fluctuations in the surface layer ranged between 18 and 25 degrees. Our summer measurements are higher for the emersed parts of the vegetation (25°-36°), but measurements have only been performed by day. In the open water we found temperatures of about 22° in the same period. The differences in the main circadian temperature on several sites in one broad may be of importance for the distribution of the species and for differences in the rates of growth of populations of the same species.

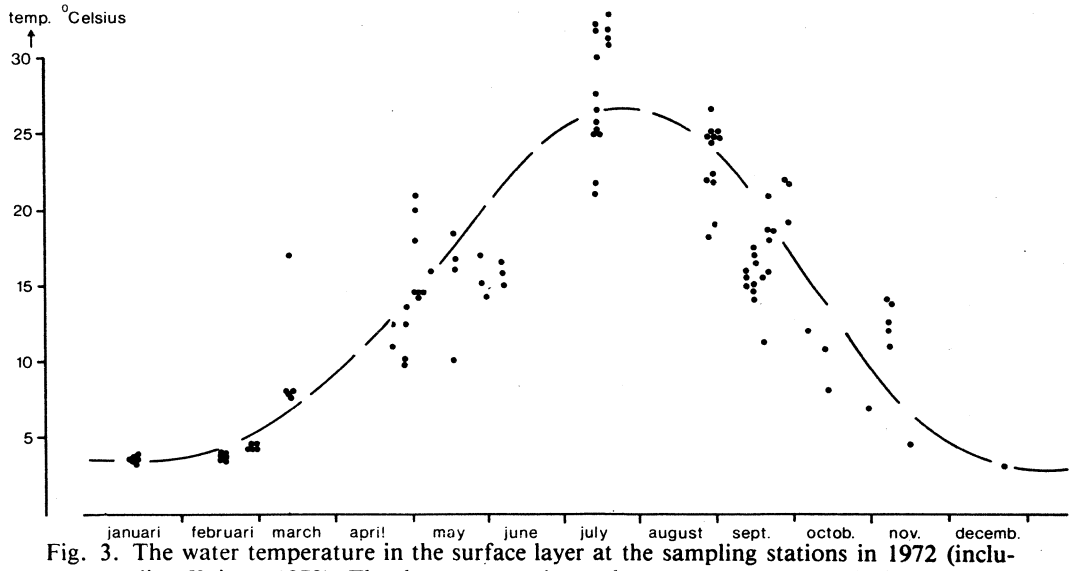


Fig. 3. The water temperature in the surface layer at the sampling stations in 1972 (including Kuiper, 1972). The drawn curve shows the mean temperature during the year on the basis of these measurements.

nr.	time	temp.	pH	E.C.	Cl^-	HCO_3^-	$P:PO_4^{3-}$	P-tot.	$N.NO_3$	N.NO2	$N.NH_4$	COD	$SO4^{--}$	$Ca++$	$Mg++$	$Na+$	$K+$	Fe
1	11.30	11.0	7.7	410	38	2.80	0,008	0.023	0.05	<0.005	0.23	34	29	53	6	17	3	
2	16.00	12.5	8.1	420	69	1.70	0.007	0.018	,,	,,	0.23	37	18	40	5	36	4	
3	11.50	10.0	7.4	427	64	1.95	0.160	0.160	,,	,,	1.60	35	20	46	6	34	4	
4	13.45	12.5	7.5	445	63	1.95	0.120	0.120	,,	,,	0.60	39	19	46	6	35	4	
5	14.30	13.8	7.2	434	64	1.95	0.012	0.016	,,	,,	0.36	39	16	45	6	34	3	
6	11.30	9.9	6.1	928	28	2.80	0.085	0.093	,,	,,	0.59	20	34	64	4	21	3	
7	12.00	18.0	4.7	622	78	2.70	0.410	0.410	,,	,,	0.64	38	50	60	7	44	9	
8	14.40	21.0	3.5	601	73	2.80	0.370	0.370	,,	,,	0.75	33	49	51	7	41	8	
9	15.30	16.2	5.7	729	106	3.00	0.120	0.130	0.1	,,	0.49	57	49	65	8	63	10	
10	12.00	18.5	6.9	357	18	2.80	0.046	0.160	<0.05	,,	0.91	31	20	67	6	11	<1	
11	14.30	16.0	6.7	357	16	2.70	0.017	0.022	0.10	0.11	<0.01	25	64	61	5	8	<1	
12	15.15	16.5	7.2	357	16	2.70	0.170	0.210	<0.05	0.021	,,	23	20	61	6	8	2	
13	15.00	17.0	7.0	686	39	1.90	0.026	0.026	,,	<0.005	,,	25	39	51	4	29	4	
14	14.30	15.0	6.6	555	47	1.50	0.039	0.041	,,	0.015	,,	23	62	48	6	31	6	
15	16.30	14.0	5.6	505	47	1.10	0.170	0.170	0.40	0.054	,,	24	65	43	6	51	8	
16	12.15	20.0	7.2	338	31	2.30	0.620	0.670	2.20	<0.005	0.04	39	9	30	4	15	1	4
17	13.40	20.5	6.9	260	27	2.10	0.042	0.130	<0.05	1.800	0.07	63	8	28	4	15	1	9
18	15.00	21.5	7.5	309	26	2.40	0.097	0.109	0.40	<0.005	0.04	31	7	47	4	13	<1	1
19	17.10	21.0	8.0		58	2.30	0.018	0.031	0.80	0.039	0.26	45	17	43	6	34	3	<1
20	17.20	25.0	8.0		60	2.10	<0.001	0.036	0.40	0.043	0.07	43	14	41	6	34	3	,,
21	18.20	25.0	8.3		58	2.10	0.011	0.050	0.40	<0.005	0.01	40	19	40	6	34	3	,,
22	15.15	30.0	8.1		59	2.10	0.025	0.048	0.30	,,	0.01	44	18	40	7	34	3	,,
23	17.30	27.5	7.5		60	2.10	0.009	0.031	0.10	,,	0.32	46	12	39	7	34	3	,,
24	11.40	21.5	7.1		57	2.10	0.059	0.067	0.10	,,	0.84	51	11	39	5	33	3	,,
25	13.05	25.0	7.3		56	2.20	0.027	0.029	0.40	0.081	0.18	49	11	40	5	32	3	,,
26	14.00	25.5	7.1		57	2.20	0.004	0.026	0.30	0.063	0.02	47	12	39	5	32	3	,,
27	13.45	26.5			59	2.40	0.004	0.033	0.10	0.063	0.07	46	17	42	4	34	3	,,
28	15.00	32.0			60	2.00	0.013	0.046	0.40	0.050	<0.01	44	14	37	6	35	3	,,
29	17.00	32.2		514	61	1.90	0.013	0.035	0.50	<0.005	0.01	48	14	34	6	35	3	,,
30	18.15	32.0			60	2.00	0.370	0.400	0.80	0.048	<0.01	42	13	36	6	35	3	,,
31	15.30	31.3		458	61	2.20	0.005	0.160	0.30	0.045	0.02	43	4	39	6	34	3	,,
32	16.30	32.9			58	2.20	0.007	0.064	0.30	<0.005	0.09	41	9	41	6	34	2	,,
33	11.00	18.0	7.6	380	58	2.10			0.30	0.038	<0.01	29	12	28	5	36	4	,,
34	15.00	22.0	7.7	380	56	2.20	0.008	0.019	0.40	<0.005	,,	28	25	26	5	35	4	,,
35	16.00	22.0	7.9	380	58	2.10	0.002	0.029	0.55	0.076	,,	30	19	24	5	36	4	,,
36	12.00	22.2	7.2	390	56	2.20	0.052	0.052	0.70	0.080	,,	33	22	25	5	35	4	,,
37	15.35	24.5	8.1	380	59	2.20	0.002	0.032	0.30	<0.005	,,	36	14	21	5	35	3	,,
38	17.00	26.5	8.1	370	58	2.10	0.005	0.023	0.40	0.036	,,	33	20	21	5	35	3	,,
39	18.00	25.0	7.7	380	59	3.30	<0.001	0.048	0.40	0.068	,,	31	16	24	5	35	3	,,
40	14.30	24.8	7.0	380	60	2.00	0.006	0.042	0.40	0.064	,,	34	14	23	5	35	1	,,
41	17.30	24.8	8.0	390	58	2.10	0.005	0.030	0.40	0.065	,,	31	14	34	6	35	5	,,
42	18.30	24.9	7.6	380	58	2.10	0.003	0.041	0.30	0.008	,,	34	19	23	6	35	4	,,
43	12.45	25.0	7.1	380	60	2.10	0.008	0.033	0.30	<0.005	,,	31	3	22	5	35	3	,,
44	14.30	19.0	7.6	880	194	2.30	0.023	0.085	0.40	,,	,,	58	56	33	15	104	7	,,
45	15.30	15.0	7.4	570	116	2.00	0.068	0.071	0.40	,,	0.20	26		40	9	36	2	,,
46	16.30	15.5	7.3	530	64	3.60	0.009	0.026	0.30	,,	0.01	26	55	38	8	32	2	,,
47	17.30	16.0	7.3	530	64	3.35	0.024	0.034	0.40	,,	,,	26	29	40	9	33	2	,,
48	16.30	14.0	7.3	530	65	3.40	0.029	0.069	0.20	,,	,,	26	32	40	8	33	2	,,
49	17.40	14.5	7.1	510	62	3.20	0.012	0.043	0.20	0.260	,,	24	29	35	8	33	2	,,
50	11.15	15.0	7.0	520	62	3.20	0.007	0.039	<0.05	<0.005	,,	38	39	35	8	31	2	,,
51	11.55	16.2	7.3	510	62	3.30	0.013	0.035	0.40	,,	,,	14	30	37	8	33	2	,,
52	13.00	17.0	7.2	540	66	3.40	0.005	0.048	0.20	0.016	0.16	26	29	44	8	34	2	,,
53	10.00	11.2	6.9	516	58	2.70	0.013	0.049	0.80	0.013	0.09	28	31	64	11	31	3	,,
54	13.10	15.5	7.3	512	58	2.80	0.008	0.052	0.40	<0.005	<0.01	24	31	64	10	31	2	,,
55	14.10	15.3	7.2	511	58	2.70	0.005	0.031	0.20	0.056	,,	29	29	61	10	31	2	,,
56	13.50	18.0	7.8	390	53	1.80	0.026	0.150	0.90	0.066	,,	48	24	41	10	31	4	,,
57	16.15	20.8	8.3	391	55	1.70	0.120	0.270	1.80	0.012	0.02	44	11	42	10	31	3	,,
58	17.40	18.5	7.5	392	52	1.70	0.075	0.370	2.40	0.045	<0.01	45	40	39	10	31	4	1
59	16.40	22.0	8.9	410	54	1.30	0.029	0.100	0.80	0.016	,,	41	18	22	10	31	5	<1
60	17.35	22.0	8.7	407	55	1.90	0.006	0.086	1.60	0.005	0.04	37	16	40	11	31	5	,,
61	18.45	19.0	7.5	435	55	2.10	0.006	0.054	0.90	0.038	0.01	45	9	41	11	31	6	,,
62	14.30	7.0	6.9	344	32	2.20	0.110	0.130	1.30	<0.005	0.07	25	10	46	3	16	3	,,
63	15.15	7.5	6.9	293	29	2.20	0.035	0.048	0.40	,,	0.02	66	12	44	2	14	2	,,
64	12.30		7.1	708	53	5.40	0.013	0.230	0.10	,,	0.01	55	0	89	10	34	4	1
65	14.45		7.4	569	36	4.40	0.020	0.340	0.20	0.025	<0.01	25	13	76	10	22	8	<1
66	11.20	11.0	7.1	418	52	2.70	0.008	0.026	0.30	0.021	,,	28	10	51	4	30	4	,,
67	12.50	12.0	7.4	563	103	3.60	0.017	0.022	0.10	0.022	0.06	65	31	53	5	54	5	,,
68	13.55	12.5	7.2	515	91	2.30	0.007	0.024	0.15	0.020	<0.01	27	14	51	5	47	4	,,
69	15.00	14.0	6.8	360	64	2.30	0.007	0.020	0.20	0.029	0.02	27	11	37	3	33	1	,,
70	15.55	14.0	7.2	424	68	1.60	0.039	0.042	0.40	0.085	0.01	31	16	44	4	37	4	,,
71	14.45		7.4	569	36	4.40	0.020	0.340	0.20	0.025	<0.01	25	13	76	10	22	8	,,
72	15.00	4.5	7.1	519	82	1.90	0.031	0.110	<0.05	<0.005	0.33	44	43	58	4			,,
73	15.15	3.0	8.2	2330	602	2.70	0.078	0.058	0.30	0.022	0.30	112	40	81	40	212	14	

Table 7. Time of the day, water temperature and some physical-chemical data of the sampling stations. All samples have been taken near the sampling-plant(s). Temp. in °C. Electric conductivity in u-Siemens. HCO_3^- in mgaeq. /1. COD in mg O_2/1. The other data are in mg/l (ppm.).

factor	number of obs.	$\bar{x}$	s	x_{max}	x_{min}
pH	67	7.27	0.81	8.9	(3.5) 5.7
E.C.	61	502	270	2330	260
Cl^-	73	66	68	602	16
HCO_3^-	73	2.43	0.72	5.40	1.10
$P{:}PO_3^-$	72	0.06	0.11	0.620	< 0.001
P-tot.	72	0.10	0.12	0.670	0.016
$N.NO_3$	73	0.39	0.47	2.40	< 0.05
$N.NO_2$	73	0.05	0.21	1.800	< 0.005
$N.NH_4$	73	0.13	0.28	1.60	< 0.01
COD	73	37.4	14.15	112	14
SO_4^{--}	72	23.08	15.17	65	0
Ca^{++}	73	43.68	14.65	89	21
Mg^{++}	73	7	4.59	40	2
Na^+	72	35.22	24.62	212	8
K^+	72	3.65	2.36	14	< 1

Table 8. The arithmetic mean ($\bar{x}$), standard deviation (s), maximum value (x_{max}) and minimum value (x_{min}) of a number of physical-chemical data of table 7.

4.2. MACROFAUNA

In the 1972 research we found over two hundred species of macro-invertebrates. It was impossible to identify all specimens to the species level, but for most groups we succeeded in doing this. The species list will be given in taxonomic units with eventually, comments on the identification or the distribution of species. For each species we mention the number of sampling stations where it was found (S), the percentage that S accounts for (out of 73 samples) (F), the total number of specimens (N) and the mean number per square meter plant surface ($\bar{n}/m^2$). In the last column the niche breadth is given, according to the formula $B = 1/\sum pi^2$ (Levins, 1968). Pi is the proportion of the species which is found in sample i. The maximal niche breadth is 73.

HYDROIDEA	S	F	N	$\bar{n}/m^2$	B
Hydra sp.	35	48	670	65	3.75

We did not identify the species. Relying on colour and morphology they seemed to belong to the same species. The numbers per plant are very variable (1 up to and including 184) and consequently the numbers per m^2 show a wide range (1-1306).

TURBELLARIA
Tricladida

	S	F	N	$\bar{n}/m^2$	B
Bdellocephala punctata (Pallas)	15	21	22	3.7	14.82
Dendrocoelum lacteum (O.F.M.)	51	70	354	20	31.69
Dugesia lugubris/polychroa	62	85	468	22	30.68
Planaria torva (O.F.M.)	36	49	155	11	11.23
Polycelis tenuis Ijima	32	44	66	5.8	21.33
Polycelis nigra (O.F.M.)	1	1	4	--	---

We did not separate **Dugesia lugubris** (O. Sch..) and **Dugesia polychroa** (O.Schm.), although both species do occur in The Netherlands (Den Hartog & van der Velde, 1973). Reynoldson & Bellamy (1970) showed the validity of both species.
The distribution of a number of lake-dwelling triclads in Britain is determined by the occurrence of the preferred prey according to the principle of competitive exclusion (Reynoldson & Bellamy, 1973). This leads to certain regular combinations of triclad-species. In fig. 4 we present the combinations of our triclad-findings. Most species are found together with two or more of the others. Only **Polycelis tenuis** and **Bdellocephala punctata** seem to live at different sampling stations. If we only look at the qualitative distribution over the sampling stations, we cannot confirm the referred data of the British research.

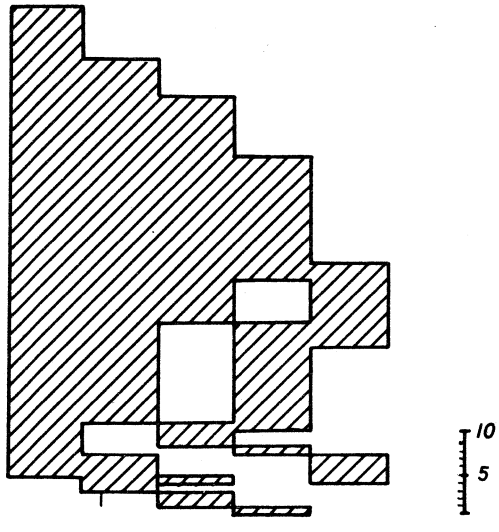


Fig. 4. The frequency of occurrence, together and separately, of triclads. The ordinate shows the number of sampling stations.

TURBELLARIA
Rhabdocoela

	S	F	N
Mesostoma tetragonum (Müll.)	1	1	2
Mesostoma ehrenbergi Focke	2	3	2
Bothromesostoma personatum O.Schm.	7	10	23
Microstoma sp.	6	8	10
Mesostoma sp. 1	5	7	10
Mesostoma sp. 2	1	1	1

The identification of the Rhabdocoela must be considered with some care. We found at least six clearly separable species (-groups). Three of these could be identified with reasonable certainty.

OLIGOCHAETA

	S	F	N	$\bar{n}/m^2$	B
Stylaria lacustris (L.)	63	86	3215	142.5	19.51
Lumbriculus variegatus (O.F.M.)	6	8	6		
Vejdovskyella comata Vejd.	1	1	1		
Nais cf elinguis (O.F.M.)	2	3	4		
Ophidonais serpentina (O.F.M.)	1	1	1		

The numbers of **Stylaria lacustris** varied greatly in the samples (1-several hundreds) and also as expressed in numbers per m^2 (1-1246)

HIRUDINEA

	S	F	N	$\bar{n}/m^2$	B
Glossiphonia complanata (L)	26	36	50	5	20.29
Glossiphonia heteroclita (L.)	67	92	839	15.7	
var. hyalina	60	80	478	23	17.68
var. papillosa	56	77	298	13.6	21.83
var. striata	30	41	63	6.7	6.82
Theromyzon tessulatum (O.müller)	11	15	15	3.5	7.15
Hemiclepsis marginata (O.Müller)	31	42	69	7.2	16.35
Haementeria costata (Fr. Müller)	1	1	3		
Helobdella stagnalis (L.)	54	74	610	29	28.05
Piscicola geometra (L.)	7	10	10	5.9	3.74
Erpobdella octoculata (L.)	41	56	192	9	18.49
Erpobdella testacea (Sav.)	19	26	54	7.2	10.98
Erpobdella nigricollis (Bran.)	45	62	196	11.2	22.34

Nearly 2000 leeches were collected. With a total sampled plant-surface of 34 m^2, this means an average of 59 leeches per m^2. Bennike (1943) mentions a maximum of 83/m^2, where square metres are meant as bottom-surface units. If we calculate on the same basis in the densest **Stratiotes**-vegetation, we find some thousands per square metre. We must conclude, that the investigated vegetations are extremely suitable for leeches. The most abundant species are

Glossiphonia heteroclita and **Helobdella stagnalis**, constituting 42% and 30% respectively of all leeches collected. In sampling station 16 we observed **Hirudo medicinalis** L. swimming between the plants.

BRYOZOA

Bryozoa have been observed in eleven samples. Once **Fredericella** sp. was concerned, the others were **Plumatella** sp. Statoblasts of **Cristatella** sp. were found in the samples, but no colonies have been observed. The bryozoans were not identified to the species-level.

GASTROPODA

	S	F	N	$\bar{n}/m^2$	B
Viviparus contectus (Mill.)	7	10	7	2.4	
Valvata cristata (Müll.)	27	37	97	9.6	7.10
Valvata piscinalis (Müll.)	4	5	8		
Bithynia leachi (Shepp.)	55	75	720	29.7	23.51
Bithynia tentaculata (L.)	64	88	927	38.4	26.73
Physa fontinalis (L.)	47	64	213	12.7	26.10
Lymnaea palustris (Müll.)	5	7	5		
Lymnaea auricularia (L.)	2	3	2		
Lymnaea peregra (Müll.)	36	49	237	13.8	21.86
Lymnaea stagnalis (L.)	14	20	14	2.1	11.54
Myxas glutinosa (Müll.)	27	37	102	10.8	5.34 (15.74)
Planorbis carinatus (Müll.)	8	11	14	7.4	4.86
Planorbis planorbis (L.)	15	21	78	25.1	2.32
Anisus vortex (L.)	31	42	141	9.2	10.76
Anisus vorticulus Trosch.	40	55	373	21.7	8.84 (21.94)
Bathyomphalus contortus (L.)	3	4	4		
Gyraulus albus (Müll.)	51	70	286	17.3	17.80
Armiger crista (L.)	17	23	54	6.9	6.48
Hippeutus complanatus (L.)	20	27	65	9.8	7.82
Segmentina nitida (Müll.)	7	10	19	6.9	5.43
Planorbarius corneus (L.)	14	20	54	8.9	6.18
Acroloxus lacustris (L.)	68	93	1256	44.7	29.39
(**Succinea** sp.	13	18	35)		

In total we collected 4712 water-snails, that is 139 per m^2 sampled plantsurface. **Stratiotes** appears to be very suitable for snails. They find food in filamentous algae, epiphytic diatoms and leaves dying off. The most abundant species are **Acroloxus lacustris, Bithynia tentaculata** and **Bithynia leachi**. They constitute respectively 27, 20 and 15% of the total number of snails.

Gyraulus albus, Anisus vorticulus, Physa fontinalis and **Lymnaea peregra** also have a high frequency of occurrence, but they are found in smaller numbers (together 24.5%). Another 7% is contributed by **Anisus vortex, Myxas glutinosa** and **Valvata cristata,** who are found in about 40% of the samples. The remaining 7% is constituted by 13 other species with a much lower frequency. The calculation of the niche breadth of **Myxas glutinosa** and **Anisus vorticulus** has been performed for 72 samples as well (between brackets). A large number of individuals in one sample, caused by many very young snails, has been left out.

LAMELLIBRANCHIATA	S	F	N	n̄/m²	B
Sphaerium corneum (L.)	8	11	29	10	3.14
Pisidium sp.	22	30	39	4.6	13.84

The **Pisidium** sp. have not been identified.

ARACHNOIDEA	S	F	N	n̄/m²	B
Araneida					
Argyroneta aquatica (Clerk)	19	26	48	6.5	9.24
Acarina					
Hydrozetes parisiensis Grandjean	1	1	1		
Arrenurus batillifer Koen	1	1	1		
Arrenurus bicuspidator Berl.	4	5	5		
Arrenurus bifidicodulus Piers	5	7	14		
Arrenurus buccinator (Müll.)	3	4	3		
Arrenurus claviger Koen	1	1	1		
Arrenunus crassicaudatus Kram.	3	4	3		
Arrenurus globator (Müll.)	7	10	19		
Arrenurus integrator (Müll.)	1	1	1		
Arrenurus knauthei Koen.	1	1	1		
Arrenurus maculator (Müll.)	14	20	32	5.6	5.92
Arrenurus medio-rotundatus Thor.	1	1	2		
Arrenurus perforatus George	4	5	4		
Arrenurus pugionifer Koen.	1	1	1		
Arrenurus schroederi Bess.	1	1	1		
Arrenurus securiformis Piers.	1	1	1		
Arrenurus sinuator (Müll.)	3	4	4		
Arrenurus tricuspidator (Müll.)	1	1	1		
Arrenurus truncatellus (Müll.)	1	1	3		
Brachypoda versicolor (Müll.)	1	1	1		
Hydrachna cruenta (Müll.)	1	1	1		
Hydrodroma despiciens (Müll.)	11	15	15		
Hygrobates longipalpis (Herm.)	1	1	2		
Limnesia fulgida Koch.	6	8	11		
Limnesia maculata (Müll.)	4	5	7		
Limnesia undulata (Müll.)	2	3	2		
Limnochares aquatica (L.)	1	1	1		
Midea orbiculata (Müll.)	1	1	1		
Mideopsis orbicularis (Müll.)	1	1	5		
Neumania deltoides Piers	1	1	2		
Neumania vernalis (Müll.)	2	3	3		
Piona alpicola (Neum)	1	1	1		
Piona coccinea coccinea (Koch)	1	1	1		
Piona coccinea stjördalensis (Thors)	3	4	8		
Piona conglobata (Koch)	1	1	1		
Piona nodata (Müll.)	1	1	1		
Piona variabilis (Koch)	2	3	4		
Pionopsis lutescens (Herm.)	1	1	2		
Tiphys ornatus Koch	3	4	22		
Unionicola crassipes (Müll.)	5	7	14		

The way animals were collected from the samples is not particularly suitable for collecting water mites. The list may therefore not be complete (certainly not quantitatively). In most samples we found many nymphs of water mites. These are difficult or impossible to identify. We found many specimens of **Hydrozetes** sp. in most of the samples. These oribatids are difficult to discover between the detritus. They have not been counted.
Not much is known of the distribution and ecology of water mites. Many of the observed species are mentioned by Besseling (1964) as very rare for The Netherlands, which, in many cases, is due rather to rare collection activities, than to rare circumstances (pers. communication of Dr. C. Davids, who is responsible for the identification of the Acari).

CRUSTACEA	S	F	N	$\bar{n}/m^2$	B
Asellus aquaticus L.	48	66	461	22	17.89
Asellus meridianus Rac.	57	78	820	43	16.30
Gammarus pulex Schell.	3	4	6		
Gammarus tigrinus Sext.	3	4	213		
Gammarus duebeni Lillj.	1	1	3		

The two **Asellus** species are abundant in the shallow, eutrophic waters in The Netherlands. They apparently occupy the same niche, but the tolerance of **Asellus aquaticus** to pollution is probably higher than that of the second species. (Hynes, 1960; Moller Pillot, 1971; Wolff, 1973).
In 42 of our samples both species occur together, but in many of those cases one species dominates. Dominating means that one species occurs about five times more than the other species average. In the next list the distribution of the **Asellus** species in our samples is summed up. The first column gives the number of samples (S), the second gives the same number expressed as percentage of the total number of samples (73) and in the last column the ratio **A. meridianus /A. aquaticus** is given. For this ratio we used the averages of the sums of the numbers per m^2.

	S	%	ratio
A.meridianus only	12	16	
A.meridianus dominating	18	25	4.9
both species equal	15	21	1.2
A.aquaticus dominating	9	12	0.2
A.aquaticus only	6	8	
no **Asellus** found	13	18	

A.meridianus is found more often and in higher numbers than **A.aquaticus.** The ratio **A.meridianus/A.aquaticus** can possibly serve (with other characteristics) for the estimation of waterquality.

INSECTA
The group of insects is richest in species (over 50% of the collected invertebrate species), of which the Chironomidae larvae constitute the main part, qualitatively as well as quantitatively. In the next table the orders are mentioned with the number of species and the number of specimens.

	species	specimens
Ephemeroptera	3	1095
Odonata	14	268
Heteroptera	12	234
Trichoptera	24	3773
Lepidoptera	3	13
Neuroptera	1	1
Coleoptera	14	158
Diptera	43	6453
Hymenoptera	2	?

Some chironomid species live as miners in holes in the leaves, although they also occur in constructed detritus funnels on the leaves. The numbers of tunnels, in most cases occupied, were estimated. We took samples from the mining larvae and did this at random, which means that the total number of Diptera present must amount to 15.000 - 20.000. Most species have more than two generations a year. No doubt chironomid larvae are very essential in the ecosystem studied.
Bugs as well as beetles need not leave the water in the adult stage, which is necessary for the other orders. In the paragraphs on these two orders adult as well as juvenile stages can be referred to, but we explicitly mention larvae or nymphs if the imago has not been observed or it is impossible to identify the larvae or nymphs to the species level.

Ephemeroptera

	S	F	N	$\bar{n}/m^2$	B
Cloeon dipterum (L.)	22	30	273	31	3
Caenis robusta Etn.	54	74	773	41	12,30
Caenis horaria (L.)	8	11	49	21	2

A fourth species, **Leptophlebia vespertina** (L.), has been found near sampling station 70 (Kuiper, 1972). As this part of the research has been carried out with another purpose and another sampling method, it cannot be added to the 73 samples.

Odonata

The identification of the Odonata nymphs has caused some problems. A number of them have been identified by Dr. B. Kiauta (Gen. Inst., Utrecht), but most nymphs were too small to identify. Odonata were always present in **Stratiotes** vegetations, nymphs as well as adults. The high numbers of adults in summer, belonging to more species than have been found in the juvenile stage, are probably important predators in the studied ecosystem. They prey abundantly on freshly emerged aquatic insects.

	S	F	N	$\bar{n}/m^2$	B
Lestes sponsa (Hans.)	2	3	2		
Ischnura elegans (v.d.L.)	29	40	76	7	18.07
Enallagma cyathigerum (Charp.)	2	3	3		
Coenagrion pulchellum (v.d.L.)	16	22	33	7	7.57
Coenagrion puella (L.)	2	3	2		

	S	F	N	n̄/m²	B
Erythromma najas (Hans.)	7	10	13	6	3.99
Zygoptera unidentified	33	45	123		
Zygoptera total	60	82	252	13	
Aeshna affinis (v.d.L.)	1	1	1		
Aeshna ? cyanea (Müll.)	1	1	1		
Aeshna ? grandis (L.)	1	1	1		
Aeshna mixta Latr.	1	1	1		
Aeshna viridis Eversm.	4	5	4		
Anaciaeshna isosceles (Müll)	1	1	1		
Aeshna sp. unidentified	3	4	5		
Cordulia aenea (L.)	1	1	1		
Sympetrum striolatum (Charp.)	1	1	1		
Anisoptera total	12	16	16	2.4	

The voracious Odonata nymphs must be considered as very important top predators in most **Stratiotes** vegetations, where fish are less abundant or lacking.

Lepidoptera

	S	F	N	n̄/m²	B
Paraponyx stratiotata L.	9	12	10	3.2	7.44
Nausinoe nymphaeata L.	1	1	1		
Nymphula ?stagnata Don.	1	1	2		

Heteroptera

	S	F	N	n̄/m²	B
Cymatia coleoptrata (Fab.)	33	45	159	15.6	12.72
Corixa punctata Ill.	1	1	1		
Hesperocorixa linnei (Fieb.)	3	4	4		
Sigara striata (L.)	14	20	33	7.8	8.98
Callicorixa praeusta (Fieb.)	1	1	2		
Corixinae (nymphs)	4	5	6		
Notonecta glauca L.	1	1	1		
Notonecta sp. (nymphs)	5	7	6		
Plea leachi MacGreg.	2	3	3		
Ilyocoris cimicoides (l.)	10	13	13	3.8	7.51
Ranatra linearis (L.)	1	1	1		
Microvelia reticulata (Burm.)	1	1	1		
Microvelia sp. (nymph)	1	1	1		
Mesovelia furcata (Muls, Rey.)	1	1	1		
Hydrometra gracilenta Horv.	1	1	1		
Hydrometra sp. (nymph)	1	1	1		

A number of species was captured only once or only a few times. This is partly due to the mobility of fast swimming predators, like **Notonecta**, partly to the unsuitability of the biotope

for certain species. **Gerris, Mesovelia** and **Hydrometra** are surface dwelling bugs, which are often observed, but captured only by accident. **Cymatia coleoptrata** is the only waterbug, that could be caught representatively. They do not swim away, but cling to the plants.

Trichoptera

	S	F	N	$\bar{n}/m^2$	B
Hydroptila pulchricornis Pict.	1	1	1		
Agraylea multipunctata Curt.	11	15	139	35.6	2.27
Agraylea sexmaculata Curt.	17	23	308	38.3	8.70
Orthotrichia costalis (Curt.)	5	7	12		
Oxyethira flavicornis (Pict.)	32	44	564	58.2	12.37
Tricholeiochiton fagesii (Guin.)	55	75	865	42.8	17.11
Cyrnus flavidus MacLachl.	17	23	64	10.8	7.20
Cyrnus insolutus MacLachl.	10	13	75	28.4	2.70
Cyrnus crenaticornis (Kol.)	7	10	28	12.1	5.06
Holocentropus picicornis (Steph.)	56	77	1311	61	14.25
Holocentropus dubius (Ramb.)	29	40	196	17.4	11.58
Ecnomus tenellus (Ramb.)	9	12	26	8.1	4.77
Phryganea grandis L.	3	4	3		
Phryganea bipunctata Retz.	1	1	1		
Agrypnia pagetana Curt.	2	3	4		
Limnephilus flavicornis (Fab.)	9	12	13	3.6	3.58
Oecetus furva (Ramb.)	34	47	102	10	13.75
Oecetus ?lacustris (Pict.)	1	1	1		
Athripsodes aterrimus (Steph.)	1	1	1		
Athripsodes senilis (Burm.)	2	3	2		
Leptocerus tineiformis Curt.	4	5	5		
Triaenodes bicolor (Curt.)	17	23	35	5.2	9.12
Mystacides longicornis (L.)	9	12	16	2.9	6.15
Mystacides ?nigra (L.)	1	1	1		

The first 6 species are exclusive feeders on filamentous algae, the second 6 species are carnivorous. The others feed on detritus and algae and smaller invertebrates and they can be considered as omnivorous. The caddis larvae form a very important part of the biocenosis by their high numbers and activities. They occur on all stations throughout the year, where species of one family alternate with each other in time and or space. In fig. 5 the combination of the Polycentropodidae and **Ecnomus** are depicted.

Neuroptera

We found **Sisyra fuscata** Fabr. twice.

Coleoptera

Many species of beetles are found among the plants, but only the larvae of some species are frequently captured with our method.

	S	F	N	n̄/m²
Haliplus sp. (larvae)	6	8	12	
Hyphydrus ovatus L. (larva)	2	3	2	
Hydroporus lineatus (F.)	1	1	1	
Hydroporini (larvae)	3	4	6	
Noterus crassicornis Müll.	1	1	1	
Agabus sp. & **Ilybius** sp. (larvae)	20	27	102	16.7
Colymbetes fuscus (L.)	1	1	1	
Dytiscus sp. (larva)	1	1	1	
Gyrinus marinus Gyll.	1	1	1	
Gyrinus sp. (larvae)	3	4	9	
Philhydrus testaceus F.	1	1	1	
?Helochares sp. (larva)	1	1	1	
Hydrobius fuscipes (L.)	2	3	2	
?Spercheus emarginatus Schall. (larvula)	1	1	1	
Scirtes sp./**Cyphon** sp. (larvae)	12	16	17	3.3

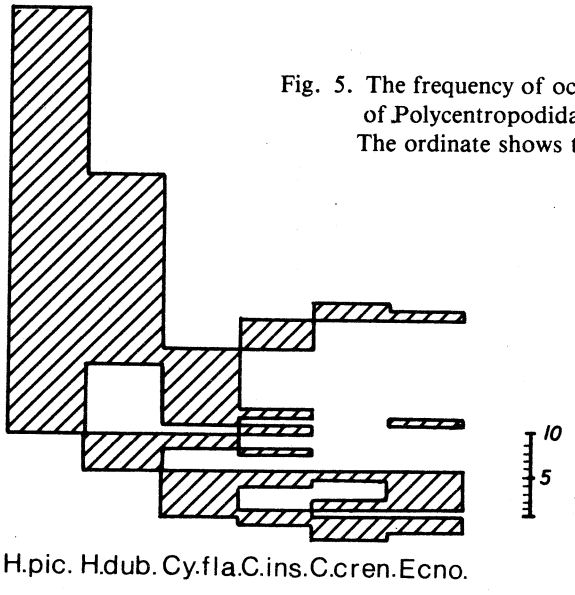


Fig. 5. The frequency of occurrence, together and separately, of Polycentropodidae larvae and **Ecnomus tenellus** larvae. The ordinate shows the number of sampling stations.

Diptera

	S	F	N	n̄/m²	B
of **Bezzia** sp.	50	69	215	12.7	22.02
Chaoborus pallidus (F.)	1	1	1		
Dixa sp.	5	7	11		
Psychoda sp.	1	1	1		
Pericoma sp.	1	1	1		
Hemerodromia sp.	1	1	1		
Eulalia sp.	5	7	6		
Stratiomyia sp.	1	1	3		
Tabanidae	3	4	4		
Not identified Diptera-pupa	Nearly in all samples with numbers from 2 to 10 per sample.				

Chironomidae

	S	F	N	$\bar{n}/m^2$	B
Glyptotendipes spp.	55	75	806	37.4	9.72
Glyptotendipes sp. B	50	69	550	32.4	17.54
Limnochironomus pulsus Walk.	30	41	714	52.3	10.64
Limnochironomus nervosus (Staeg.)	25	34	138	20.2	10.76
Endochironomus gr.**signaticornis**	10	13	64	27.8	5.25
Endochironomus spp.	49	67	410	19	13.13
Lenzia sp.	25	34	54	8.1	5.56
Polypedilum gr. **laetum**	8	11	94		4.56
Polypedilum ssp. (many **Pentapedilum exectum**)	44	60	227	13.7	20.73
Chironomus spp.	38	52	657	38	3.95
Parachironomus sp.	26	36	352	25	4.57
Stictochironomus sp.	2	3	4		
Microtendipes gr. **chloris**	13	18	38	7.5	4.68
cf **Cryptochironomus** sp.	1	1	1		
Harnischia viridula L.	1	1	1		
Tanytarsus sp.	32	44	175	16.2	14.43
Paratanytarsus sp.	37	51	408	29.8	7.45
Zavreliella marmorata (v.d. W.)	15	21	226	25.4	7.12
Lauterborniella agrayloides K.	4	5	43		
Cladotanytarsus sp.	3	4	4		
Cricotopus gr. **sylvestris**	22	30	370	42	11.33
Cricotopus sg. **Isocladius**	9	12	21		
Cricotopus spp. (-sg.Isoc.)	15	21	47	7.2	6.90
Microcricotopus gr. **bicolor**	4	5	5	9	2.56
Psectrocladius gr. **psilopterus**	37	51	286	20.4	7.36
Psectrocladius gr. **dilatatus**	16	22	55	7.8	5.81
Acricotopus lucens (Staeg.)	3	4	26		
Tanypus punctipennis (Meig.)	1	1	1		
Ablabesmyia sp.	31	42	132	20.8	7.02
Xenopelopia sp.	4	5	6		
Monopelopia tenuicalcar K.	10	13	66	24.9	2.96
Guttipelopia guttipennis (v.d. W.)	18	25	133	19.6	7.53
Anatopynia plumipes (Fries)	1	1	1		
Corynoneura sp.	29	40	100	10.7	13.28

The total number of Chironomidae is 6210. It must be stipulated, that the biggest part of the mining larvae has not been included (see page 33). This means that the miners from the genera **Glyptotendipes, Limnochironomus** and **Endochironomus** constitute much more than 40% of the total number of Chironomidae, as would be indicated by the list above.

Hymenoptera

In many of the Diptera pupae which were not identified, we found parasites of the family Braconidae. As they have not fully developed and coloured, it was not possible to identify them with certainty. Dr. van Achterberg (Museum of Natural History, Leiden) who kindly examined some of the parasites, recognized an **Ademon** species, probably **A.urinator** (De Stafani) and a specimen belonging to or related to **Chaenusa Ilopsi** Docavo Alberti.

Neither species is known from our country.
Parasites are an often neglected factor in this kind of ecosystem. Many Diptera suffer from them, as has been observed. It would be worth while, studying the relationships thoroughly.

4.3. GROUPING OF THE SAMPLING STATIONS

If we consider the most abundant macro-organisms in our research, it appears, that certain species frequently occur together and that others seem to avoid the same conditions. In the figures 4 and 5 this is demonstrated for flatworms and certain caddis larvae. By combining the data on presence and absence of the species, we can make a division of the sampling stations into groups with a more or less similar fauna composition. It is worth while looking for corresponding parameters within those groups and for differences between them.
In the cluster analysis method (2.2.c.) every sample is compared with every other sample on the basis of the numbers of every species per sample. We used 83 species that occurred abundantly or frequently in our 73 samples. The results of the cluster analysis have been represented in a dendrogram (fig. 6). The numbers on the ordinate are an expression of the degree of dissimilarity of the (groups of) samples. The horizontals connect two samples or groups of samples on a level, where a certain defined dissimilarity is ,,accepted''. On a higher level a greater dissimilarity has to be accepted and so the division into a few groups of samples arises. The division in the lower part of the dendrogram has been left out, because the differences among the samples in the smaller clusters are rather futile. Instead, the sample numbers have been written, placed into groups corresponding with the clusters.
The main division is into three clusters, represented by the roman figures I, II and III. Cluster III contains nearly all ,,D''- and ,,E''-samples, i.e. the submerged plants. In cluster II we find nearly all ermersed plants from the broad Venematen and two samples from the reserve ,,Weerribben'' (56 and 57). The remaining samples from emersed sections in cluster I are arranged according to geographical criteria.
From the results of the clustering we can conclude, that the submerged plants outside the dense, emersed vegetation accomodate another combination of animals as compared with the plants within the vegetation. Further we see, that the correspondence of ,,emersed'' samples from one waterbody is high. If there are characteristic features for samples of the A-zone, considering all A-samples and for the B- and C-zone, we must admit that these characteristics are suppressed by factors of local importance, such as water quality, for example.
The Venematen presents some interesting characteristics. The construction of the **Stratiotes** vegetation is in accordance with the model from the viewpoint of plant sociologists. The development of the vegetation is rich and extended. It is the only well developed vegetation of this type we were able to find. The samples have been taken within a relative short period and they seem to form a sufficiently homogenous cluster. We therefore used the same cluster analysis method with the 25 samples that have been taken from the broad Venematen. The resulting dendrogram is given in Fig. 7.
Here again we find a main division into three groups. The sampling stations of group III are ,,D''- and ,,E''-plants. Group I consists of plants from the southern part of the vegetation and group II of plants from the northern part plus some southern plants near the open water. It seems as if some influence from the south-western direction causes a reaction of the fauna in that part of the broad, that results in a clustering in regard to the northern part. It is worth mentioning that in the sampling stations of group I the variability in a number of chemical parameters in bigger than within the sampling stations of group II. It is very probable that liquid manure from fattening farms intrudes the broad in the southwestern part of the vegetation (Keuning, 1971). In the next paragraph we shall analyze the composition of the macrofauna in the clusters I and II.
From the tables 4 and 5 it can be concluded that there is a certain relationship between the plant density and the water depth. We have plotted this relationship in Fig. 8 for all sampling stations and in Fig. 11 for the Venematen sampling station. It has been shown in the figure whether the sampling stations belong to one of the three clusters. The possible relation of the plants of one cluster and the plant density is given in the figures 9 and 12 and in the same way the relation between plants of a cluster and water depth is given in Fig. 10 and Fig. 13.

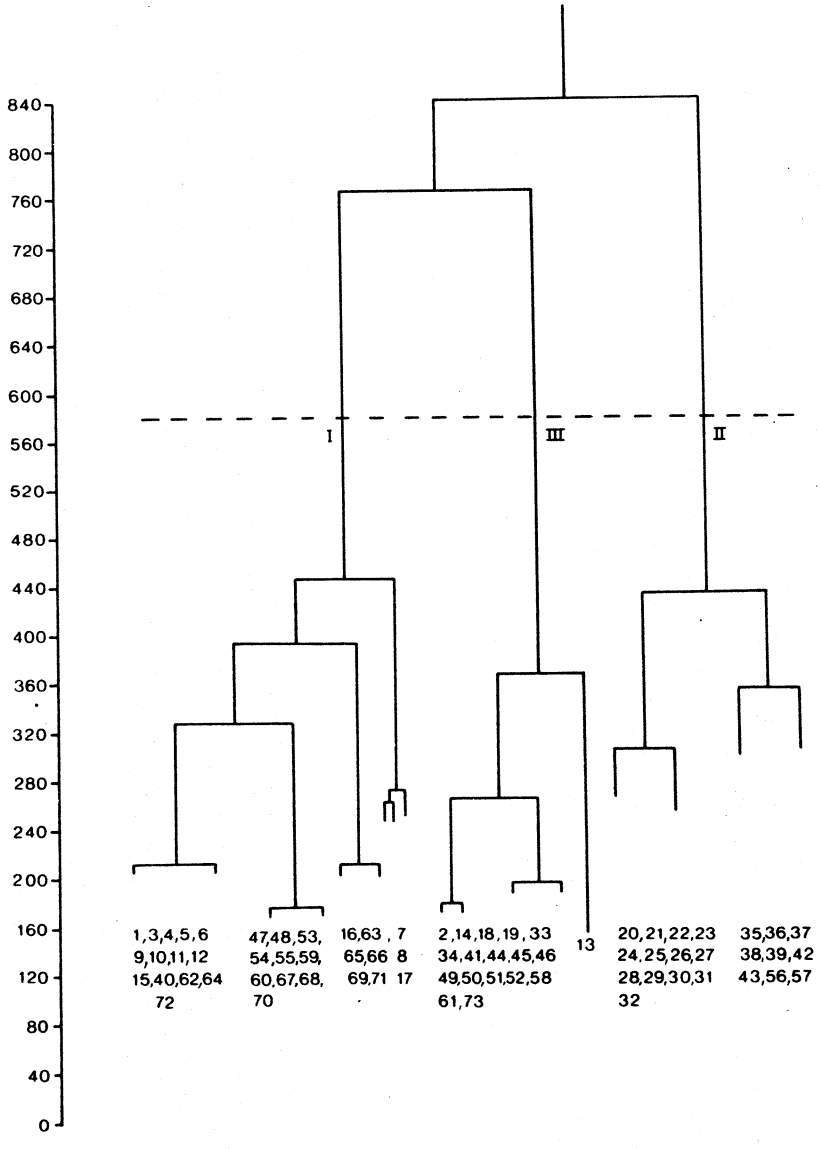


Fig. 6. Dendrogram, representing the grouping of all sampling stations on the basis of a cluster analysis. Explanation on page 38.

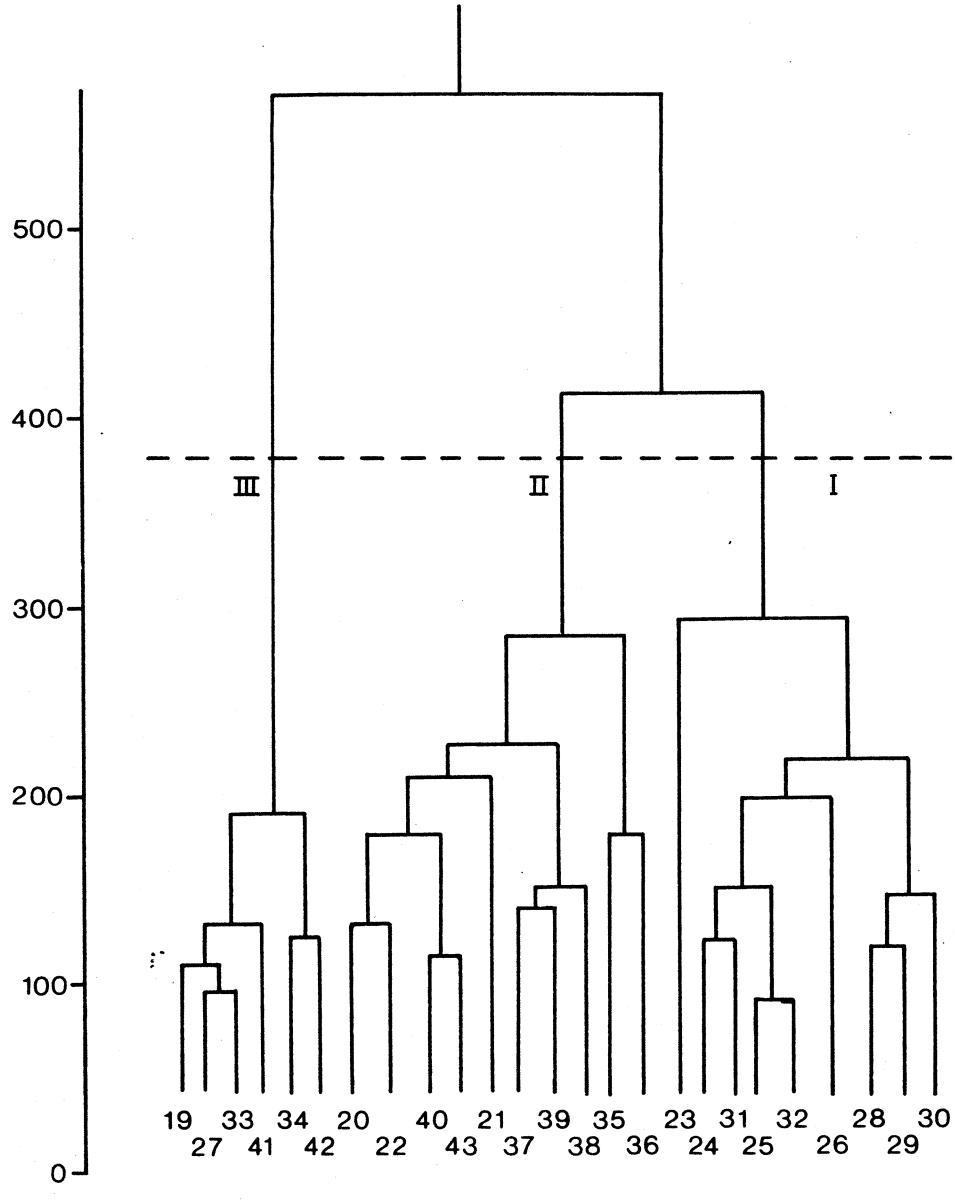


Fig. 7. Dendrogram, representing the grouping of the Venematen sampling stations on the basis of a cluster analysis. Explanation on page 38.

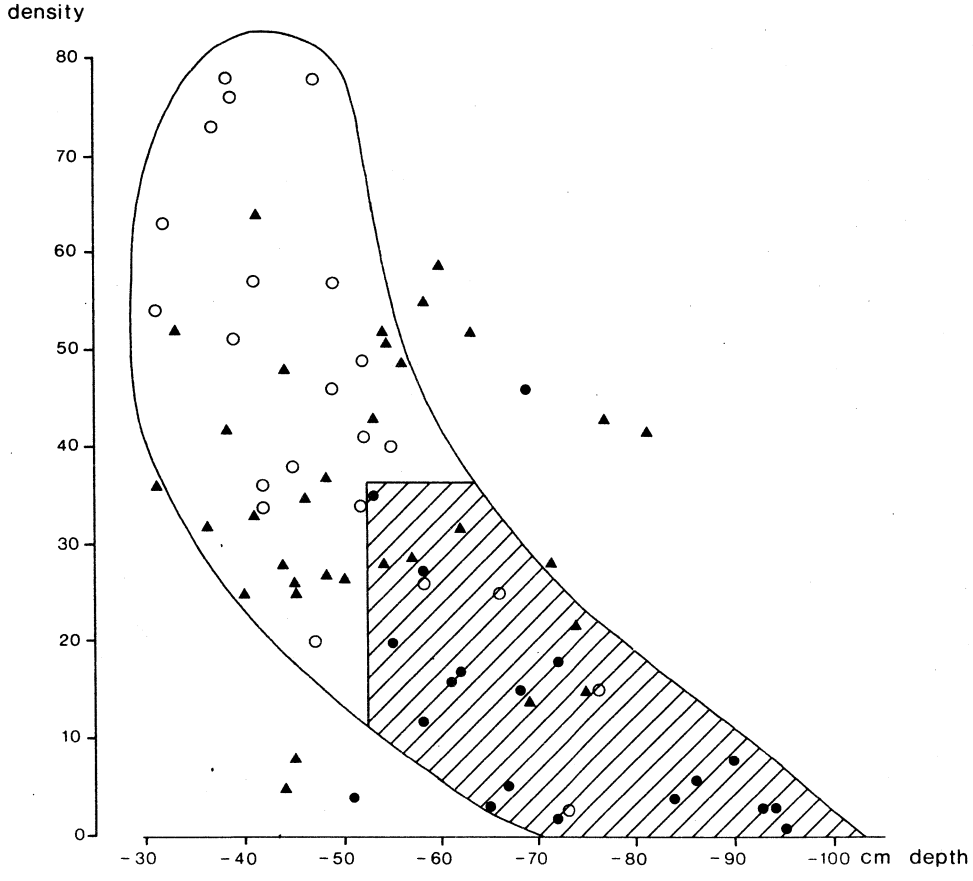


Fig. 8. The relation between the plant density and the water depth at all sampling stations. The density is the number of **Stratiotes** plants in a one meter ray circle.
▲ = the sampling stations of cluster I from Fig. 7
o = the sampling stations of cluster II from Fig. 7
● = the sampling stations of cluster III from Fig. 7
The shaded area comprises most stations of cluster III, the drawn line comprises most sampling stations according to a normal logarithm curve.

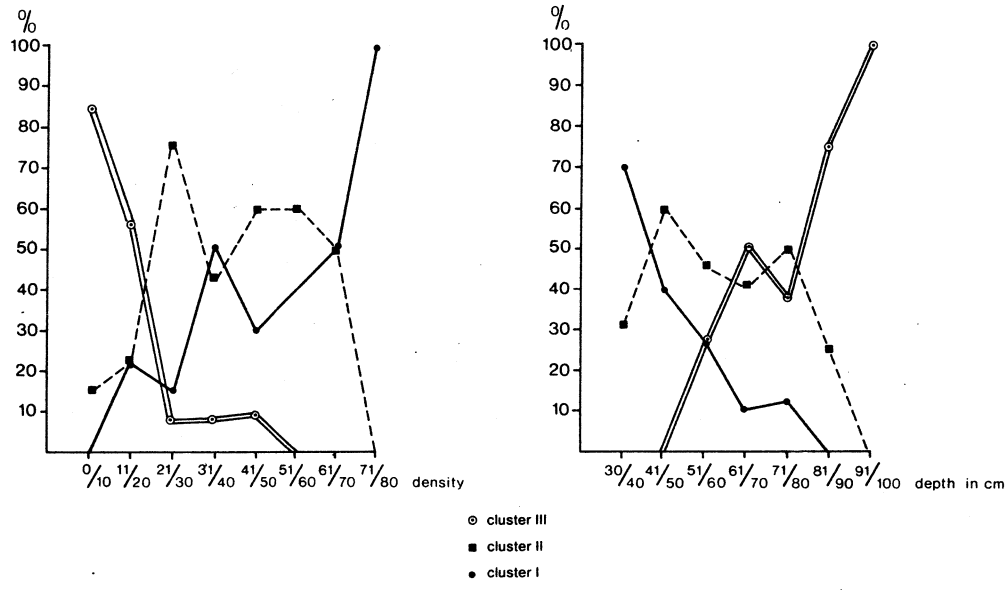


Fig. 9. The percentual division of all sampling stations per category of plant density for the three clusters.

Fig.10. The percentual division of all sampling stations per category of water depth for the three clusters.

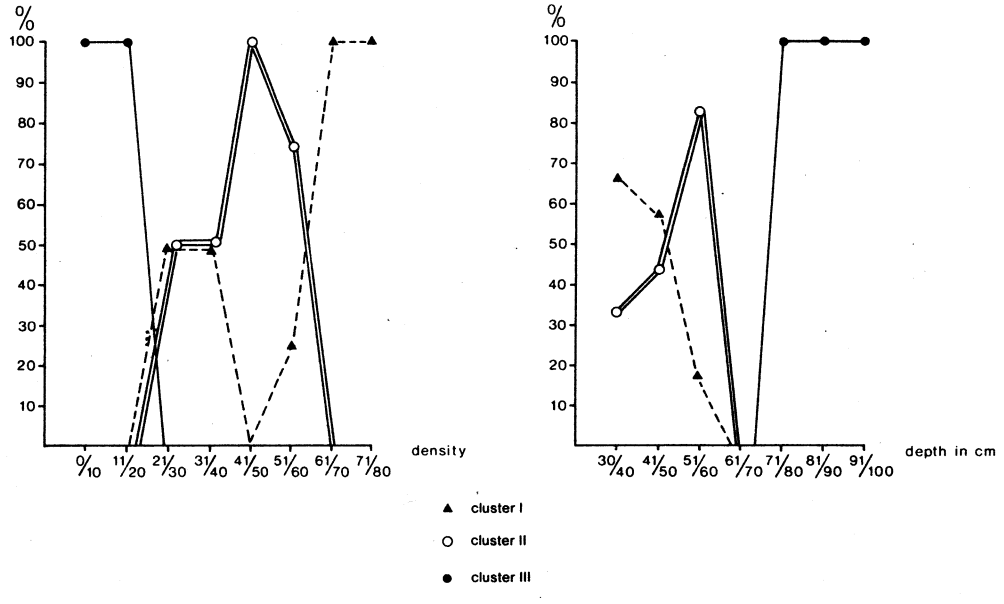


Fig.12. The percentual division of the Venematen sampling stations per category of plant density for the tree clusters.

Fig.13. The percentual division of the Venematen sampling stations per category of water depth for the three clusters.

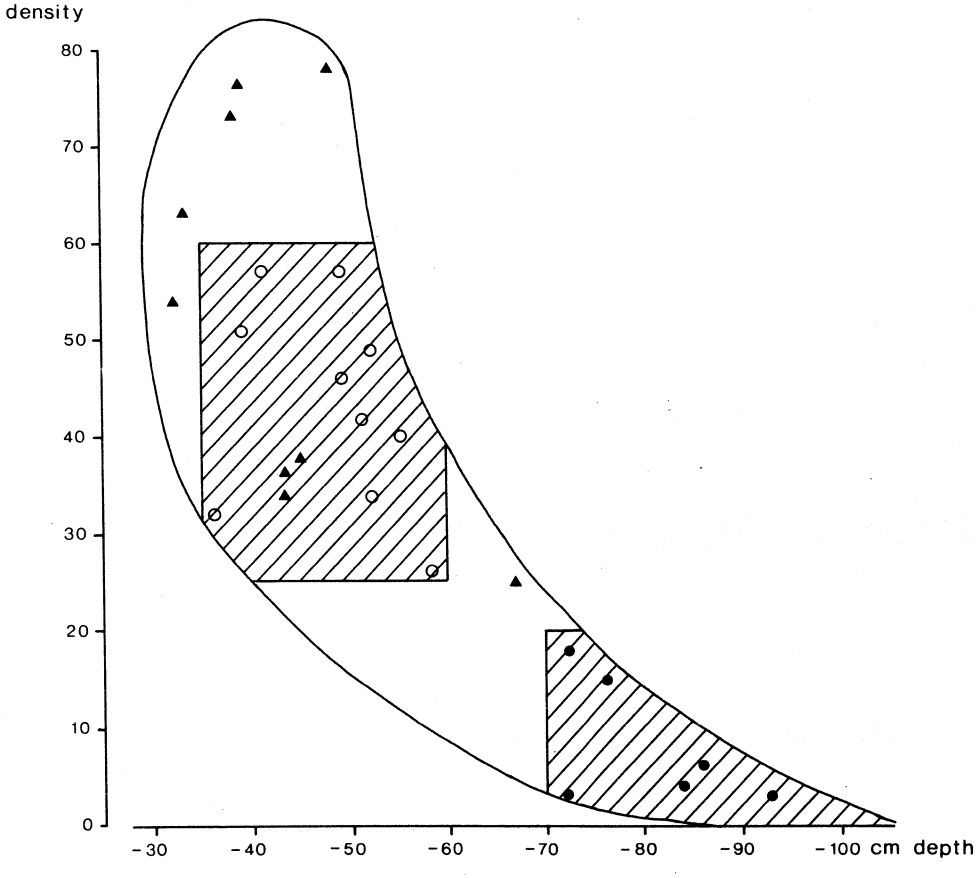


Fig.11. The relation between the plant density and the water depth at the Venematen sampling stations. Further explanation as with Fig.8.

In table 9 we listed the most important species in three groups. Within the groups the sequence of the taxonomic units of 4.2 is used.
The numbers have been rounded off. All numbers under 0.5 became zero. In 4.2 we used for numbers per m^2 only the samples where the species was observed. Here we used all the samples of a cluster, which lowers the arithmetic mean.

It is evident that the situation in the broad Venematen more satisfies the expectations from the vegetational point of view. Here we see an absolute division between the clusters I and II on the one side and cluster III on the other. An analysis of the macrofauna in relation to the zonation in the vegetation must start with the samples of this broad and can be interpreted for the other samples afterwards. In Fig. 8 nine sampling stations (most from cluster I) are not in accordance with the model of the relationship in a ,,standard" autochtonic swamp succession with **Stratiotes**. For most of these sampling stations the remarks in table 6 indicate aberrations in respect of the observed conditions in a **Stratiotes** vegetation. The stations 6 and 8, for example, are remnants of a disappearing **Stratiotes** vegetation in bad condition. Within cluster I we shall have to reckon with the influence of the seasons, the geographical position and those factors which are hard to judge, such as pollution, management and other alterations and disturbances.

4.4. GROUPING OF ANIMAL AGGREGATIONS

With the results obtained we can use three methods to divide the macrofauna into animal aggregations. These methods are;
a) cluster analysis,
b) grouping on the base of the clusters ad 4.3
c) grouping according to the code ad 3.2 (A.B.C.D and E).

a) The cluster analysis method for the construction of species groups has been used with 60 species. The chironomid larvae and the mite **Arrenurus maculator** were not included because they had not been identified at the time we applied this method. The results are given in a dendrogram, Fig. 14. The division into clusters has come into being by comparing each species with each of the other species. In the method used, the numbers per species are more important than the mere presence. In this way clusters are formed consisting of species with a high ,,affinity" to each other, and with a low one to other species from other clusters. Many of the observed animals are found together and the clustering is, of course, of only relative value. One of the problems in the difficult procedure of interpretation is formed by the differences in numbers per species. The main division into two groups is a result of this. In the left main cluster all species come together that occur in most sampling stations and in relatively high numbers, and in the right main cluster the species that have been found less frequently and in lower numbers. Within the two main clusters the affinity values are the result of various factors, such as place in the vegetation and external influences, as pollution for example. It must therefore be stated that the cluster analysis can only be a help and certainly not a starting point for faunal analysis.
b) The clustering of the sampling stations is based on the quantitative presence of 83 species of the macrofauna. In this procedure we are going to work in the opposite direction and try to analyze which species are responsible for the clustering of the sampling stations, taking the numbers as a starting point. From each species we list the arithmetic mean of the numbers per m^2 in each of the three main clusters of Fig. 6 and Fig. 7. In this way the quantitative share of each species to those clusters is expressed. This is a rather simplified approach, because the variation of numbers within one cluster is not taken into account. Nevertheless, with other methods, it brings us closer to a better understanding of the composition of the macrofauna. In a few cases it is evident that the obtained number is a result of one very high score in a cluster where most samples are without that species. The high score distorts the picture too much and we placed the number between brackets in those cases (tables 10 and 11).

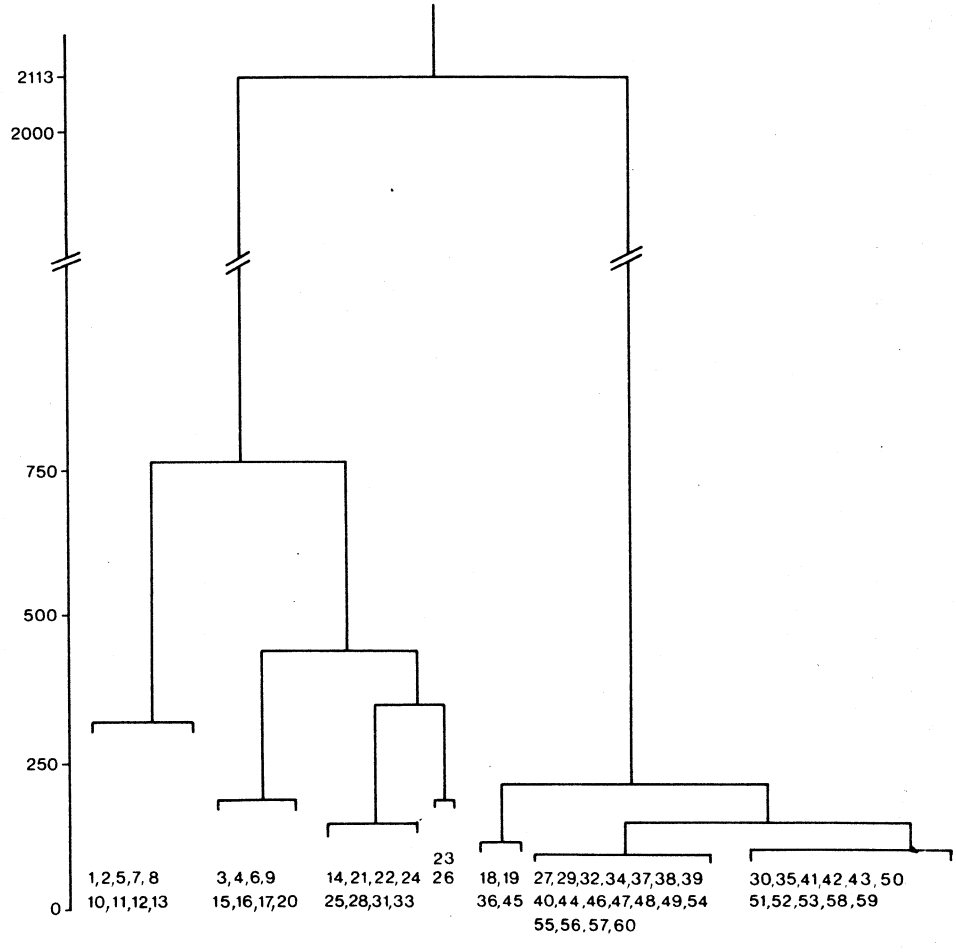


Fig.14. Dendrogram, representing the grouping of 60 species of the macrofauna. Explanation on page 48. The names of species have been represented by serial numbers; the corresponding names can be found in the tables 9 and 11.

In the first group we find the species with the highest arithmetic mean in cluster I (the emersed sampling stations outside the broad Venematen). As these sampling stations are scattered over the country and influenced by several different phenomena, the interpretation is difficult if not impossible. It gives no information on the sampling stations of a restricted area, so only the most general conclusions can be drawn.
The second group, which is the biggest one, consists of species with a high arithmetic mean in the emersed sampling stations of the broad Venematen and two from the reserve Weerribben. Since the zonation of the vegetation in the broad Venematen is the best example of the type we could examine, we take it for granted that the numbers of the species in the second column do represent a reasonably balanced macrofauna composition.
The third group, predominantly consisting of chironomid species, contains the species reaching their highest arithmetic mean in the cluster of the plants from deep water.

In the first three columns of table 10, the same procedure has been followed for the main clusters of the broad Venematen (Fig. 7). The sequence in this table is according to the third way of dividing the macrofauna (c). In this way a comparison is possible with the division on the basis of the position of the sampling stations in the vegetation. As we have stated before (under 4.3), we may expect a regular distribution pattern, dependent on the vegetation zonation, with superimposed on this, an influence from the southwestern part of the broad. Exponents of this influence are those species that dominate in I and surprisingly enough we find them for the greatest part at the top of the table. This shows a resemblance between the species of cluster I and the species of the A-situations, which confirms the assumption of a negative influence. As was expected, most species of the III-cluster can be found at the bottom of the table, where species in D and E situations are listed. The species of cluster II (the optimal situation in emersed sampling stations ?) can be found in the B-C-D-part of the table.

The most promising method for the division of the macrofauna is in accordance with the zonation in the vegetation. In the tables 10 and 11 the most important species have been listed in such a way that at the top of the tables we find those species that seem to prefer the A-zone and at the bottom the species preferring the E-zone. The numbers per m^2 are summed up. The best way of handling the results is starting from the data from table 10; with the help of the data from table 11 and data from literature and from other own research we can interpret the findings (next chapter).
There are several patterns of distribution to be observed. Some species seem to be restricted to one zone (**Endochironomus signaticornis, Argyroneta aquatica**), others prefer one zone and these are found in the adjacent zones in gradually decreasing numbers (**Chironomus** spp., **Tricholeiochiton fagesii, Corynoneura** sp.). The first pattern seems to be rather unnatural and is confined to the data of table 10. It turns out to change into the second pattern if more samples are taken into consideration (table 11). Nevertheless these patterns fit into the scheme of the vegetation zonation (Fig. 2).
A number of species is restricted to a few zones, that do not succeed each other (**Valvata cristata, Psectrocladius dilatatus**) and others are found in all zones without a clear preference for one of them (**Bithynia tentaculata, Acroloxus lacustris**). It is obvious that the arrangement of Fig. 2 gives us a good help for the interpretation of the distribution of most of the observed species, but that we have to reckon with secundary influences that disturb the picture for at least a number of species. The width of the zones A, C and D of two meters is a random choice to define borders, visible to the human eye. We must describe characteristics of the vegetation that are of importance to the macrofauna and therefore use our abstraction of the reality so far as it coincides with the observations on the basis of macrofauna data.

	I	II	III
26. Hydra sp.	41	16	41
37. Bdellocephala punctata	1	1	0
21. Planaria torva	5	2	1
34. Glossiphonia complanata	2	1	0
6. Gloss. het. papillosa	16	8	4
49. Theromyzon tessulatum	1	0	0
20. Anisus vorticulus	19	11	0
1. Acroloxus lacustris	61	34	14
45. Planorbis planorbis	11	0	0
54. Planorbis carinatus	1	1	0
55. Sphaerium corneum	2	1	0
48. Planorbarius corneus	2	1	1
38. Hippeutus complanatus	2	2	2
40. Argyroneta aquatica	3	1	0
83. Arrenurus maculatus	1	1	0
15. Asellus aquaticus	38	5	4
36. Cloeon dipterum	21	1	1
8. Holocentropus picicornis	70	29	22
74. Zavreliella marmorata	7	4	0
80. Monopelopia sp.	7	0	0
62. Limnochironomus pulsus	46	2	1
81. Guttipelopia sp.	9	2	1
67. Polypedilum sp.	7	6	6
75. Cricotopus spp.	2	1	0
9. Dendrocoelum lacteum	11	26	6
3. Dugesia lugubris/polychr.	20	21	6
27. Polycelis tenuis	1	4	2
11. Stylaria lacustris	71	217	103
29. Hemiclepsis marginata	2	4	1
17. Erpobdella nigricollis	8	9	1
30. Glossiph. het. striata	1	7	1
4. Glossiph. het. hyalina	19	28	6
39. Erpobdella testacea	2	3	1
10. Helobdella stagnalis	23	27	13
33. Myxas glutinosa	0	11	2
46. Pisidium sp.	1	2	1
28. Anisus vortex	4	7	0
22. Lymnaea peregra	8	11	1
16. Physa fontinalis	6	14	3
7. Bithynia leachi	23	30	12
2. Bithynia tentaculata	14	71	25
14. Gyraulus albus	6	24	9
5. Asellus meridianus	25	48	33
13. Caenis robusta	18	58	20
53. Caenis horaria	0	6	4
25. Cymatia coleoptrata	9	14	1
44. Triaenodes bicolor	1	2	0
12. Tricholeiochiton fagesii	27	51	20

	I	II	III
42. Agraylea sexmaculata	6	18	2
51. Agraylea multipunctata	0	17	0
24. Oecetis furva	2	12	1
31. Holocentropus dubius	5	13	2
23. Oxyethira flavicornis	4	50	36
35. Ischnura elegans	2	4	2
69. Chironomus spp.	16	22	4
19. Bezzia sp.	10	11	3
79. Ablabesmyia sp.	6	16	3
82. Corynoneura sp.	3	7	3
72. Tanytarsus sp.	2	12	11
64. Endochironomus spp.	2	12	11
61. Glyptotendipes sp.	17	36	34
60. Paraponyx stratiotata	0	1	0
18. Erpobdella octoculata	4	4	5
41. Armiger crista	1	2	3
32. Valvata cristata	3	5	6
56. Segmentina nitida	1	0	1
52. Ecnomus tenellus	0	1	2
43. Cyrnus flavidus	0	4	4
50. Cyrnus insolutus	1	1	13
73. Paratanytarsus sp.	5	20	28
63. Limnochironomus nervosus	1	11	13
76. Cricotopus gr. sylvestris	4	13	24
65. Endochironomus gr. signatic.	0	4	10
68. Glyptotendipes sp. B	15	0	27
78. Psectrocladius gr. dilatatus	2	1	3
66. Lenzia sp.	1	2	6
71. Microtendipes gr. chloris	1	1	3
77. Psectrocladius gr. psilopteris	6	7	24
70. Parachironomus sp.	6	6	14

Table 9. Distribution of the main species over the clusters of Fig. 6 (all sampling stations). The serial numbers of the species are given and the arithmetic means of the numbers per m^2 (the three columns).

Table 10	I	II	III	A	B	C	D	E
Chironomus spp.	46	3	0	80	10	7	0	0
Limnochironomus pulsus	4	1	0	8	1	2	0	1
Myxas glutinosa	18	8	1	33	5	10	2	1
Zavreliella marmorata	15	0	0	13	8	0	0	0
Holocentropus dubius	27	5	0	18	15	0	0	0
Valvata cristata	8	1	1	5	3	0	0	1
Asellus aquaticus	9	4	0	11	5	3	0	0
Hemiclepsis marginata	5	1	2	11	1	4	4	1
Pisidium sp.	5	1	0	3	3	0	0	0
Bdellocephala punctata	2	0	0	1	1	0	0	0
Helobdella stagnalis	49	9	5	37	28	12	6	5
Asellus meridianus	90	24	3	76	53	39	0	4
Gloss. het. hyalina	25	12	3	28	16	9	5	2
Planaria torva	16	7	3	14	9	7	5	2
Erpobdella nigricollis	12	8	2	11	9	7	3	1
Endochironomus spp.	10	2	6	13	5	3	4	7
Holocentropus picicornis	23	33	1	24	27	12	3	0
Argyroneta aquatica	3	0	0	0	2	0	0	0
Agraylea sexmaculata	0	39	1	0	24	7	4	0
Triaenodes bicolor	2	4	0	2	3	2	0	0
Dendrocoelum lacteum	28	18	5	20	27	24	4	5
Oecetis furva	12	7	4	5	10	5	4	0
Tricholeiochiton fagesii	35	78	7	16	60	37	17	3
Gyraulus albus	22	30	4	18	24	22	9	2
Anisus vorticulus	4	8	1	3	12	9	4	0
Cymatia coleoptrata	22	10	0	14	16	16	0	0
Anisus vortex	8	8	1	3	8	8	2	0
Acroloxus lacustris	25	30	13	16	27	19	11	14
Lymnaea peregra	11	11	2	6	11	9	5	1
Psectrocladius gr. psilopterus	3	10	3	4	8	0	6	2
Agraylea multipunctata	3	32	6	0	20	16	15	2
Bithynia tentaculata	93	49	68	33	61	93	56	74
Pentapedilum/Polypedilum	10	8	11	4	8	12	8	12
Polycelis tenuis	5	5	(6)	4	3	7	5	(6)
Gloss. het. striata	4	2	3	4	3	6	6	2
Physa fontinalis	15	9	8	5	12	13	9	7
Parachironomus sp.	9	4	3	8	6	8	3	3
Paratanytarsus sp.	1	34	73	3	4	95	67	77
Glyptotendipes sp.	3	15	41	8	3	41	32	46
of Bezzia sp.	7	14	10	10	9	16	11	0
Glossiphonia complanata	2	0	1	1	1	2	0	2
Armiger crista	1	4	2	2	2	3	0	2
Ablabesmyia sp.	8	26	9	8	15	40	15	7
Bithynia leachi	19	37	27	5	24	63	30	26
Hippeutus complanatus	5	5	1	2	2	4	0	1
Dugesia lugubr./polychroa	23	20	3	5	20	29	9	0
Ischnura elegans	5	4	2	1	5	8	3	0
Caenis horaria	0	(12)	7	0	0	(39)	16	2
Limnochironomus nervosus	4	16	33	0	8	34	93	29

	I	II	III	A	B	C	D	E
Tanytarsus sp.	2	15	24	8	7	24	35	19
Erpobdella octoculata	2	5	2	3	4	2	6	0
Caenis robusta	23	40	23	20	36	33	50	6
Stylaria lacustris	128	97	85	145	86	80	208	23
Gloss. het. papillosa	4	6	4	7	5	5	9	2
Oxyethira flavicornis	26	63	107	22	45	34	135	93
Hydra sp.	11	12	32	9	12	3	46	25
Cyrnus flavidus	0	4	15	0	0	9	21	12
Corynoneura sp.	0	11	5	0	6	12	14	0
Endochironomus gr. signaticornis	0	0	10	0	0	0	31	0
Cricotopus gr. sylvestris	0	1	35	0	1	0	104	0
Cyrnus insolutus	0	2	3	0	1	0	4	1
Erpobdella testacea	3	1	4	1	2	0	9	2
Glyptotendipes sp. B	39	30	57	30	32	39	12	80
Lenzia sp.	1	3	19	1	2	4	12	24
Polypedilum gr. laetum	0	1	23	0	0	3	20	24
Microcricotopus gr. bicolor	0	0	4	1	0	0	2	5
Psectrocladius gr. dilatatus	0	0	4	1	0	0	2	5

Table 10. Distribution of the main species in the broad Venematen in accordance with the clusters of Fig. 7 (first three columns) and the division in the sections A to E. The figures represent the arithmetic means of the numbers per m^2.

4.5. SOME PROVISIONAL RESULTS OF THE EXPERIMENTS WITH ARTIFICIAL PLANTS

The experiments with artificial plants were carried out during 1974 and 1975. Some provisional conclusions will be given briefly below.

- As compared to the living plants the artificial plants can accomodate comparable numbers and about 90% of the same species.
- This applies particularly to artificial plants amidst living plants and artificial plants against emersed shorevegetation (reeds, **Cicuta** etc.). The macrofauna shows a great resemblance with the macrofauna of living **Stratiotes**.
- Floating artificial plants above relatively deeper water (60-120 cm) separated from each other by one to more meters are inhabited by high numbers of caddis larvae and chironomid larvae from the D and E zone. Flatworms are absent; leeches and snails, **Asellus** and Odonata nymphs are scarce. Caenis nymphs, **Stylaria lacustris** and **Hydra** occur in ,,normal'' numbers. Bryozoans and sponges sometimes overgrow the plants in a way, that has not been observed in the living plants. A number of caddis larvae and chironomid larvae that were not or infrequently observed on the living plants were numerous.
- Colonization on relatively isolated plants shows the importance of mechanisms of dispersal in accordance with the successfulness of the species.

These experiments provide valuable information on the behaviour, the distribution and the life cycles of a number of species, that were not captured in high numbers in the 1972 research. The results will be processed and published as a continuation of this study.

	A	B	C	D	E	
40. Argyroneta aquatica	3	2	0	0	0	
69. Chironomus spp.	36	24	3	7	2	
36. Cloeon dipterum	15	11	2	4	2	
15. Asellus aquaticus	26	15	8	7	2	
44. Triaenodes bicolor	2	1	1	0	0	
33. Myxas glutinosa	11	3	4	1	1	
20. Anisus vorticulus	29	11	10	6	0	
1. Acroloxus lacustris	83	41	46	26	16	
29. Hemiclepsis marginata	5	3	4	3	3	
83. Arrenurus maculatus	0	2	0	0	0	
45. Planorbis planorbis	1	9	1	0	0	
54. Planorbis carinatus	0	1	0	0	0	
74. Zavreliella marmorata	5	8	0	0	0	
55. Sphaerium corneum	1	1	0	0	0	
37. Bdellocephala punctata	1	1	0	0	0	
46. Pisidium sp.	1	2	0	0	1	
25. Cymatia coleoptrata	5	10	4	0	1	
12. Tricholeiochiton fagesii	21	51	26	8	2	
80. Monopelopia tenuicalcar	0	6	0	3	1	
62. Limnochironomus pulsus	9	34	13	8	1	
42. Agraylea sexmaculata	0	14	10	1	2	
28. Anisus vortex	2	7	4	2	0	
22. Lymnaea peregra	2	10	5	4	0	
48. Planorbarius corneus	0	2	1	0	2	
38. Hippeutus complanatus	1	3	2	1	1	
17. Erpobdella nigricollis	8	9	3	2	1	
81. Guttipelopia guttipennis	5	7	4	0	1	
21. Planaria torva	6	7	3	2	1	
9. Dendrocoelum lacteum	11	20	17	1	8	
8. Holocentropus picicornis	46	64	27	50	3	
5. Asellus meridianus	29	41	20	17	33	
34. Glossiphonia complanata	1	2	1	1	1	
51. Agraylea multipunctata	0	8	7	4	1	
67. Polypedilum spp.	2	9	8	4	7	
19. cf Bezzia sp.	5	11	12	10	2	
11. Stylaria lacustris	70	87	260	260	82	
35. Ischnura elegans	2	3	4	2	2	
6. Glossiphonia heteroclita papillosa	10	12	17	8	4	
3. Dugesia lugubris/polychroa	22	19	28	6	5	
16. Physa fontinalis	6	8	11	4	5	
7. Bithynia leachi	14	25	46	16	17	3
73. Paratanytarsus sp.	7	5	42	24	26	
4. Glossiphonia heteroclita hyalina	17	20	37	13	5	
2. Bithynia tentaculata	20	36	75	20	31	
79. Ablabesmyia sp.	2	10	16	5	2	
24. Oecetis furva	3	6	11	4	0	
82. Corynoneura sp.	1	5	12	4	1	
13. Caenis robusta	15	19	107	25	24	
52. Ecnomus tenellus	1	0	4	0	3	

	A	B	C	D	E
30. Glossiphonia heteroclita striata	1	2	12	3	2
53. Caenis horaria	0	0	17	4	3
26. Hydra sp.	22	(40)	14	33	34
39. Erpobdella testacea	3	2	3	3	0
10. Helobdella stagnalis	16	26	19	31	5
14. Gyraulus albus	8	14	13	15	3
43. Cyrnus flavidus	0	0	5	5	5
63. Limnochironomus nervosus	1	3	14	17	11
31. Holocentropus dubius	8	7	3	13	1
72. Tanytarsus sp.	3	4	12	19	7
23. Oxyethira flavicornis	8	20	15	49	37
64. Endochironomus spp.	9	12	5	27	8
61. Glyptotendipes sp.	6	14	35	83	39
60. Paraponyx stratiotata	0	0	0	1	0
75. Cricotopus spp.	1	1	1	4	0
49. Theromyzon tessulatum	0	1	0	1	0
76. Cricotopus gr. sylvestris	7	3	3	58	19
65. Endochironomus gr. signaticornis	7	1	1	18	1
18. Erpobdella octoculata	5	4	3	4	6
27. Polycelis tenuis	4	2	4	3	6
68. Glyptotendipes sp. B	13	21	15	13	33
78. Psectrocladius gr. dilatatus	2	1	1	1	3
41. Armiger crista	1	1	2	0	3
66. Lenzia sp.	1	1	3	4	7
32. Valvata cristata	4	3	1	1	7
56. Segmentina nitida	0	1	0	0	1
50. Cyrnus insolutus	0	0	3	10	12
71. Microtendipes gr. chloris	0	0	0	2	3
77. Psectrocladius gr. psilopterus	1	8	2	5	29
70. Parachironomus sp.	3	6	3	1	22

Table 11. Distribution of the main species over the sections A to E in 73 sampling stations. The figures represent the arithmetic means of the numbers per m^2. The serial numbers of the species are placed before the names.

5. DISTRIBUTION AND RELATIONSHIPS OF THE MACROFAUNA

5.1. SPATIAL DISTRIBUTION

The results from chapter 4 support the hypothesis that the distribution of the macrofauna is closely related to the structural characteristics of the vegetation. The main parameters with respect to the macrofauna are the plant density and the water depth. The thickness of the sapropel layer is high at all sampling stations. Therefore differences in macrofauna distribution cannot be caused by differences in the sapropel thickness. In table 12 the arithmetic mean of the densities, water depths and thicknesses of the sapropel layer have been given for all sampling stations (T) and the stations of the broad Venematen (V); further the arthmetic mean of the numbers of species and of individuals per m^2 for the sections A to E have been mentioned as well.

		A	B	C	D	E
plant density	T	34	40	58	24	6
	V	40	49	58	17	4
water depth	T	47	51	51	64	74
	V	48	44	50	74	84
sapropel thickness	T	170	154	186	183	165
	V	203	196	204	179	169
number of species	T	40	44	50	39	33
	V	47	46	52	50	37
N/m^2	T	854	1002	1219	1103	663
	V	973	964	1308	1269	810

Table 12. Arithmetic mean of some values divided over the sections A to E. T comprises all sampling stations, V only the Venematen stations.

The plant density is highest in the emersed plants bordering the ,,open water''. The submerged plants grow further apart from each other than the emersed plants, and this phenomenon is observed from the point onwards where the D-section starts. The water depth decreases towards the shore (Fig. 2). The depth of 48 cm for the A-section in the Venematen is caused by the value of station 26, where the sapropel has been removed by the activity of swans. Without this station the figure should be 42 cm. The sapropel thickness is very high at all stations, but only slightly less in the area, where we find the submerged plants.

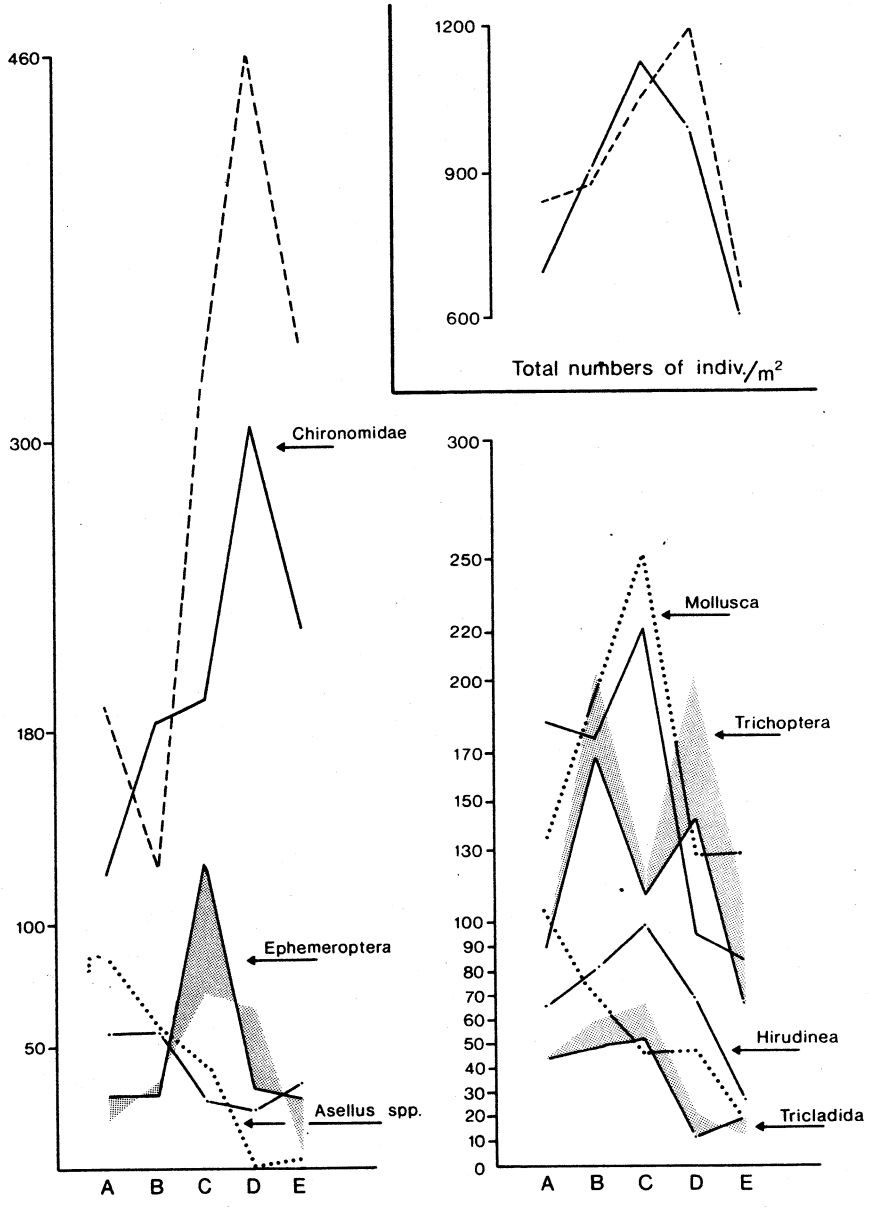


Fig.15. Total numbers of individuals per m² and numbers of individuals of the different groups for all sampling stations (_____) and for the Venematen sampling stations (.....). Only the data from table 13 have been used.

		Number of species					Individuals per m²				
		A	B	C	D	E	A	B	C	D	E
Tricladida	T	5	5	4	4	4	44	49	52	12	20
	V	5	5	4	4	3	44	60	67	23	13
Hirudinea	T	9	10	9	10	8	66	81	99	69	27
	V	9	9	8	8	8	103	69	47	48	17
Mollusca	T	15	17	14	11	11	184	177	221	96	85
	V	13	13	11	9	10	134	194	253	128	129
Asellus spp.	T	2	2	2	2	2	55	56	28	24	35
	V	2	2	2	0	1	87	58	42	0	4
Ephemeroptera	T	2	2	3	3	3	30	30	126	33	29
	V	1	1	2	2	2	20	36	72	66	8
Trichoptera	T	7	8	11	9	9	89	171	112	144	66
	V	6	9	8	8	5	87	205	122	203	111
Chironomidae	T	20	21	19	20	20	121	183	193	307	223
	V	15	16	14	17	15	190	124	324	460	341
Totals	T	66	72	67	63	62	696	904	1125	991	606
	V	56	61	54	52	46	844	876	1050	1196	671

Table 13. Numbers of species and of individuals per m² of the main groups derived from the tables 10 and 11, as divided over the sections A to E.
T = total number of samples (table 11)
V = Venematen samples (table 10)
The totals at the bottom of the table comprise all species of the tables 10 and 11. Further explanation in the text.

The highest number of species is found in the C-section, the lowest one in the E-section. The differences between the sections are not very high, due to the replacement of species by others that are more characteristic for that particular section. The highest numbers of individuals are to be found in the C- and D-sections, the lowest numbers in the E-section. Therefore the C-section is richest both in species and numbers. It has often been demonstrated, that the transition between two types of vegetation is attractive to more species than each of the vegetation types separately. The transition from submerged to emersed **Stratiotes** vegetation is a small ecotone in the larger scale ecotone from open water to marsh.

In order to get a better idea of the division of the main groups of macro-organisms over the different sections, we have presented the numbers of species per group and the numbers of individuals per m² per group in table 13. The data are based on the figures from the tables 10 and 11. This means that only the most abundant representatives of the groups are mentioned and not all species recorded. In Fig. 15 the numbers of individuals per m² in the different sections are shown, which gives us a good insight in the distribution of the main groups.

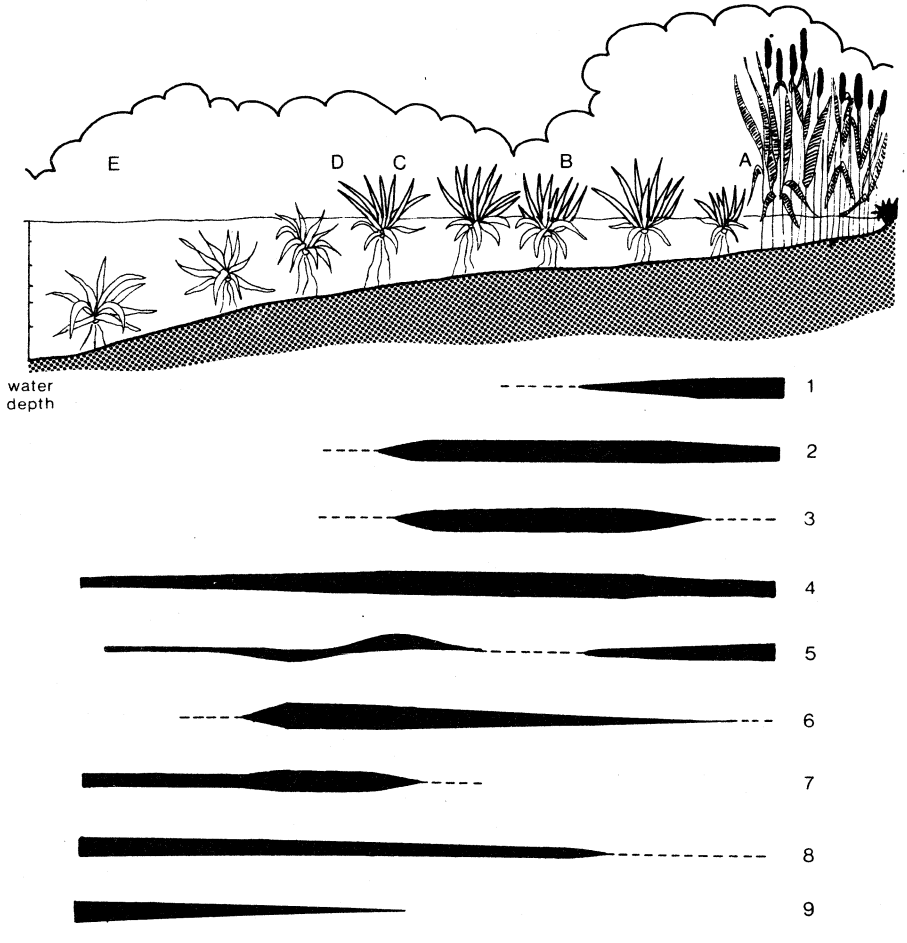


Fig.16. Spatial distribution of macro-organisms in **Stratiotes** vegetations. The groups of species, belonging to the distribution patterns 1 to 9 are listed in table 14. Further explanation in the text.

Several patterns of distribution can be recognized. The Tricladida, the **Asellus** species, and to some extend the Hirudinea attain their highest numbers in the A- and B-section and in some cases also in the C-section. Their numbers are low on the submerged plants. The Ephemeroptera and Mollusca reach the highest numbers in the C-section with a sub-optimum for Mollusca in the B-section and for Ephemeroptera (at least in the Venematen) in the D-section. The Chironomidae are most abundant in the D-section and the numbers in E are still rather high. The Trichoptera have two favourite sections, namely B and D. The Chironomidae are by far the most numerous group, followed by the Mollusca and the Trichoptera. Without identification on the species level, each section can be characterized by the quantitative distribution of the main groups. We come back to this in 5.5.

The best way to characterize the different sections is by means of the quantitative distribution of the species. We combined the data from the tables 9, 10 and 11 and constructed a model of the **Stratiotes** vegetation in a broad with the observed distribution patterns of the main species. This model (Fig. 16) with the corresponding species for each of the nine patterns (table 14) reflects the situation in a Dutch broad without much pollution. The primary criteria for grouping them into patterns are purely physical. The influence of pollution probably is manifest in the absence or presence of certain species and in the quantitative composition of certain groups of organisms.
In table 5 we defined the sections A to E, where the width of A, C, and D was chosen arbitrarely as a zone of 2 m. This facilitates the ascertainment of the type of the sampling plants, but must not be handled too rigidly in the processing of the data of the tables 10 and 11. The groups of Fig. 16 will be discussed briefly. The width of the lines indicates the preference for a section, and the dotted part of the lines the possible extension of certain members of the group into sections, where most of the other members are not or seldom observed. Table 15 summarizes the average niche breadth and the smallest and largest breadth as found in each group.

		average	minimal	maximal	niche breadth
group	1	11.49	3	17.89	
	2	16.90	7.53	31.69	
	3	6.53	2.27	10.76	
	4	21.22	13.13	29.39	
	5	7.62	5.25	10.98	
	6	17.64	6.82	30.68	
	7	7.23	2	14.43	
	8	9.10	4.57	17.54	
	9	4.10	2.56	5.81	

Table 15. The average, minimal and maximal niche breadth in each of the groups of table 14.

The sequence of the groups has been chosen in accordance with the affinity for certain sections, to start with A. The affinity only has been derived from the highest numbers per species, as found in the tables 10 and 11. The representation of the distribution patterns in Fig. 16 forms the visualization of the spatial component of the niche breadth. The data from table 15 elucidate the patterns in fig. 16.
Group 1 is confined to the shore-part of the vegetation. The highest numbers are observed in the A-section and part of the B-section. The species apparently do not avoid the conditions of very shallow water, thick sapropelium layer, often rather extreme temperature and oxygen ranges, but on the contrary seem to prefer this part of the vegetation. In the case of organic enrichment of the water, we can expect a further extension into the B-section for at least a number of the species of this group. The average niche breadth is relatively high; it could be

higher if **Cloeon dipterum** is omitted from the calculations because of its flight period in the main sampling months, and if the niche breadth of **Myxas glutinosa** is calculated without sample 26 with its mass of freshly hatched young.
Group 2 has been found in the emersed part of the vegetation from A to C with a decrease of numbers in the A-section. The average niche breadth is higher than in the first group, which is due to the adaptation of life conditions in the A-section as well in the C-section.
The species of group 3 are confined to the B-section proper, that is the part of the emersed vegetation with a dense growth of large **Stratiotes** plants and a water depth of 40 - 60 cm. They do not occur in section A. In most **Stratiotes** vegetations the B-section is by far the largest part of the vegetation. The surprisingly low niche breadth figures that have been calculated for the species in group 3, point to the homogenous nature of the B-section.
Group 4 consists of species that can be observed in all parts of the transect. Among this group the most abundant species are found. They do not show a particular preference but for the B-section, and the conditions in the A-section are not limiting. In deeper water the numbers are slightly lower. The niche breadth of the species in this group is very high, as could be expected.
The distribution pattern of group 5 causes some problems. The B-section seems to be avoided and the edges of the emersed vegetation (on both sides, A and C) are preferred. Some of the species occur regularly on the submerged plants too. The nearness of the bottom can be an important factor for **Valvata cristata** which is bottom-dwelling. The presence of birds in these particular areas can play a role for **Theromyzon tessulatum**. The niche breadth of the species in this group is generally low, which could be an indication of more specialized life conditions than is suggested by its distribution pattern. In fact, the species do not occur from A to E, and can be found in a restricted part of the transect like A and D for example.
The groups 6 and 7 show a clear preference for the edge of the emersed part of the vegetation. The numbers of group 6 are decreasing gradually in the direction of the shore, those in group 7 towards the open water. The average niche breadth for group 6 is much higher than for group 7. Apparently, the differences between submerged plants and emersed plants (or the respective sections D/C and C/B) are rather important and require a larger niche breadth for species, that occur in those sections. This is reflected by the results of the cluster analysis too, where a distinct separation between submerged and emersed plants is demonstrated.
Group 8 and group 9 consist of species predominantly found on the submerged plants. Group 9 is not found at emersed plants, group 8 only is small numbers. Apart from **Armiger crista** only chironomid larvae and caddis larvae are involved. In group 9 the smallest niche breadth figures are to be found. These species must be very specialized as far as **Stratiotes** vegetations are concerned. The species in group 8 have to cover a wider range in the transect (including emersed plants) and correspondingly their niche breadth is higher.
From the above considerations it is very probable, that the differences in conditions for the animals living in the submerged and the emersed area are most important in **Stratiotes** vegetations. This could be deduced also from the results of the cluster analysis. The second important influence is caused by the conditions near the shore that can be compared - roughly speaking - with influence of disturbance or pollution. The I, II, III division of the tables 9 and 10 points clearly in the same direction. In 5.4 we shall combine these data with some results from 5.2 and 5.3 in order to characterize the macrofauna-cenoses (or animal aggregations) in **Stratiotes** vegetations.

5.2. DISTRIBUTION IN TIME

There are several possibilities to be considered about distribution in time.

a) Many animals show diurnal rhythms in activity. If some have their activity period in day and others in night, the chance of meeting is considerably diminished. As most of the animals in this study are sessile, or only move, either by creeping or swimming over very short distances, this phenomenon can hardly influence the distribution patterns observed. It may play a more important role in food relationships.
b) Qualitative and quantitative changes in the fauna composition during the year are of much greater importance. This problem will be detailed further below.
c) Changes in fauna composition during a number of years in the same water can be caused

by natural conditions (terrestrialization in its different stages) or by artificial rejuvenation of the vegetation owing to the removal of **Stratiotes** plants. The first situation has not been studied, the second in previous research (Higler, 1971).

It goes without saying that considerable differences in fauna composition would be expected in different times of the year. The qualitative composition can be influenced by life cycles (resting stages in winter, eggs in winter or summer) and by change of habitat in relation with the differences in summer- and winter-appearance of the **Stratiotes** vegetation. Surprisingly enough we could hardly demonstrate examples of each of these possibilities. The species that occurred regularly, and that have been used for our analysis, were found throughout the year (we include the data of Kuiper, 1972). Bryozoans and sponges are not observed in some months, owing to the dying of the colonies in winter. Some species of water mites can only be found during two or three months of the year (personal communication of Dr. C. Davids). In winter and spring the sunken vegetation enables fishes to enter into parts that are impossible to penetrate in summer and autumn. Only small fishes such as young rudd (Scardinius erythrophtalmus) have been observed among the emersed plants. From our observations it can be stated that during the year there are no important changes in the qualitative composition, with regard to the species mentioned in this paper.
The quantitative composition of the fauna certainly must be influenced by the season. This can be one of the reasons for the difficulties we met in the interpretation of Fig. 6, where observations from April to December have been used, in qualitative, but also in quantitative ways. The reproduction of all groups considered does not start before spring or summer. In most cases the rising water temperature might initiate this, as has been demonstrated by Davies & Reynoldson (1976) for the leech **Helobdella stagnalis**. The numbers of most species have diminished gradually during winter, but by the time the young specimens have hatched (and can be recognized!), the highest numbers are found. For a number of the most occurring species we calculated the arithmetic means of the numbers per m^2 in each month. The expected course of the population, however, could not be demonstrated. In general the numbers are higher in summer and lower in winter, but the results were not very convincing. It is possible that the much smaller amounts of **Stratiotes** plants in winter, as compared to summer, do concentrate the animals, which results in comparatively high numbers per m^2.
Species with more than one generation a year start earlier than most of the others, but species with a very restricted flight period or reproduction period are generally found in highest numbers in midsummer. A complication is formed by insects with a flying adult stage in summer, but even here, during the flight period, we have found considerable numbers of young larvae or full grown larvae, due to differences in the growth. Only **Cloeon dipterum** was absent during its flight period at most of the sampling stations where it could be expected.

The group of flying water insects contains some very interesting examples of closely related species with more or less similar ecological demands, but with different life cycles. In previous studies (Higler, 1969) we assumed that the species in the caddis fly family Polycentropodidae are separated in space and time. The separation in time refers to species like **Cyrnus flavidus** and **C. crenaticornis**, which are found in the same part of the **Stratiotes** vegetation, but succeeding each other in flight period. From the data of the present research we are able to confirm this assumption for a number of species, such as **Holocentropus picicornis** and **H. dubius** (Fig. 17). We have depicted their larval lenght throughout the year. **Holocentropus picicornis** overwinters as a small larva, while **H. dubius** is about twice as big at that time. The difference in size is caused by a rapid growth of the young larvae of **H. dubius** in July/August. This species is univoltine. In July we found all sizes of larvae of **H. picicornis**, originating from the first as well as from the second generation. The young larvae of the second generation grow slowly. Although the two species are found together frequently (Fig. 5), the larvae are seldom of the same size. The same kind of distribution in time has been observed in the genus **Cyrnus**. In winter **Cyrnus flavidus** has large larvae and **C. insolutus** has small ones. The niche conception with its space and time component is demonstrated clearly in this family of caddis flies.

	Mollusca	Hirudinea	Chironomidae	Trichoptera	other groups
1	Myxas glutinosa Pisidium sp.	Hemiclepsis marginata	Chironomus spp. Zavreliella marmorata	Holocentropus dubius	Bdellocephala punctata Argyroneta aquatica Cloeon dipterum Asellus aquaticus
2	Anisus vorticulus Lymnaea peregra	Erpobdella nigricollis Gloss. heterocl ita hyalina	Guttipelopia guttipennis Limnochironomus pulsus	Holocentropus picicornis Oecetis furva Tricholeiochiton fagesii	Planaria torva Dendrocoelum lacteum Cymatia coleoptrata
3	Planorbis planorbis Planorbis carinatus Sphaerium corneum Anisus vortex Hippeutus complanatus		Monopelopia tenuicalcar	Triaenodes bicolor Agraylea sexmaculata Agraylea multipunctata	Arrenurus maculator
4	Acroloxus lacustris Bithynia tentaculata Gyraulus albus	Erpobdella octoculata Helobdella stagnalis Glossiphonia complanata	Polypedilum spp. Endochironomus spp.		Asellus meridianus
5	Valvata cristata	Erpobdella testacea Theromyzon tessulatum	Endochironomus signaticornis		
6	Bithynia leachi Physa fontinalis	Gloss. heterocl ita papillosa Gloss. heterocl ita striata	Ablabesmyia sp. Cricotopus spp. Corynoneura sp.		Polycelis tenuis Dugesia lugubris/polychroa cf Bezzia sp. Stylaria lacustris Ischnura elegans Caenis robusta
7		Piscicola geometra	Cricotopus gr. sylvestris Tanytarsus sp. Paratanytarsus sp. Limnochironomus nervosus	Cyrnus flavidus Economus tenellus	Caenis horaria Hydra sp.
8	Armiger crista		Parachironomus sp. Glyptotendipes spp. Glyptotendipes sp. B Psectrocladius gr. psilopterus Lenzia sp.	Oxyethira flavicornis	
9			Polypedilum gr. laetum Psectrocladius gr. dilatatus Microtendipes gr. chloris Microcricotopus bicolor	Cyrnus insolutus Orthotrichia costalis Hydroptila pulchricornis	

Table 14. Spatial distribution of macro-organisms in **Stratiotes** vegetations. The distribution patterns 1-9 are in accordance with Fig. 16.

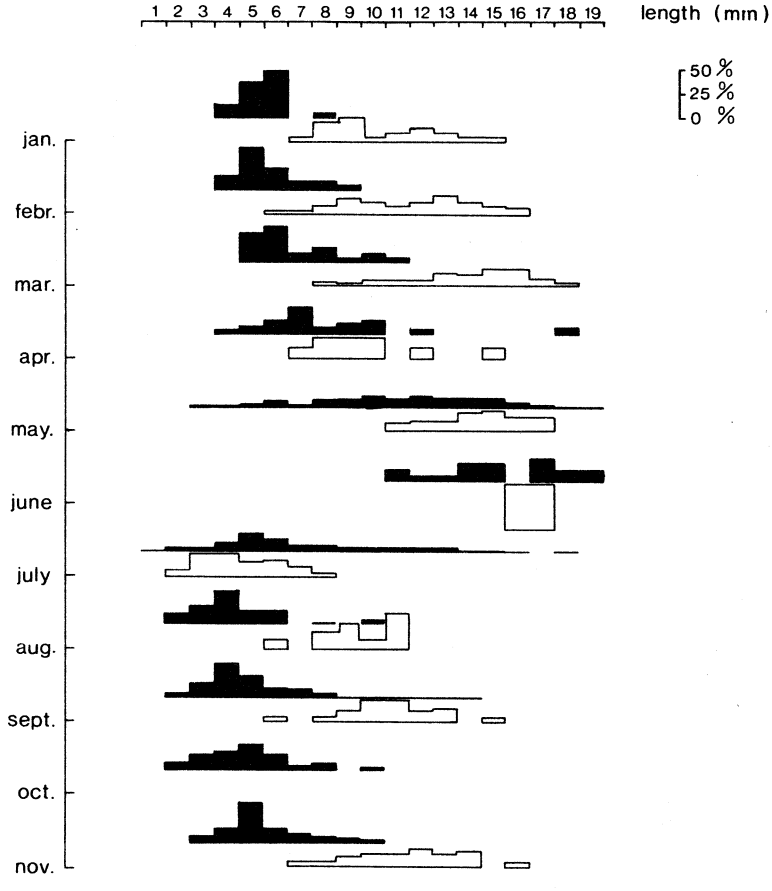


Fig. 17 Life cycles of Holocentropus picicornis (■) and Holocentropus dubius (▭)

Fig. 17. Percentual distribution of macrofauna groups on **Stratiotes** from investigations in Poland (Karassowska & Mikulski, 1960 and Pieczyński, 1973) and from table 10 and 11 is this paper.

5.3. FOOD RELATIONSHIPS

One of the ways to elucidate food relationships is the contruction of a food-wed, which, however, has limited significance. It is generally incomplete and often based on insufficient data; quantitative data are mostly absent. Besides, the relations change over the year and often apply only to very specific environmental circumstances. As far as the **Stratiotes** fauna is concerned, there is some information on predator-prey relations and food uptake of a number of species, but many observations have been carried out under laboratory conditions. It is clear that such data may be quite irrelevant for the normal life situation. In most cases remarks on the food preferred are vague and do not apply to single species, but to whole genera. Only few species seem to rely on a restricted and well defined kind of food, but in many cases there is hardly any specialization at all. According to Cummins (1973) most aquatic insects are best termed polyphagous or generalists. The availability, most frequently delineated by food particle size and texture, is the key to trophic relationships among aquatic insects. Rigler (1975) dealing with the problems of the trophic level concept in ecology, stresses that the only measurable trophic level is the first one of primary producers. The main food relationships in the **Stratiotes** fauna indicated here, are based on data from literature and from own observations. With these relationships we shall describe some of the differences in the fauna composition of different sections of the vegetation.

HYDRIDAE

The **Hydra** species are very voracious. They eat all kinds of small animals from tiny crustaceans to fish larvae. The main food components are Cladocera and Copepoda.
According to Wesenberg-Lund (1939) they have many enemies, among which a **Microstoma** species and the larvae of **Chaoborus** and Chironomidae. Lampert (1925) mentions **Lymnaea stagnalis** and Heimans & Thysse (1946) refer to **Lymnaea species**, some Coleoptera species (both larvae and adults) and some fishes, such as sticklebacks.
The **Hydra** species have been found in nearly 50% of the samples in all sections. The highest numbers were observed in the boundary zone of the vegetation, where the animal density was also the highest. Cladocera were present in large numbers in the emersed section and Copepoda in the submerged section (see 1.6), especially in eutrophic waters. The highest numbers of **Hydra** were found at the sampling stations 7, 58, 52, 47, and 49, which are all situated in waters very rich in nutrients, polluted or turbid. Under these circumstances the main food most probably consists of the abundantly present small crustaceans. It is possible that some of the listed predators are absent in the polluted or turbid waters, though we have no clear data on this.

TURBELLARIA

Flatworms consume living and dead animals, and can be cannibalistic. The small forms eat rotifers and small crustaceans, the bigger ones (Tricladida) arthropods, oligochaetes and snails. The elaborate studies of Davies & Rynoldson and collaborators suggest a certain specialization among the species that occur together (Bellamy & Reynoldson, 1974; Davies, 1969 a 1969 b; Davies & Reynoldson, 1969, 1971; Reynoldson & Bellamy, 1971, 1973, 1975; Reynoldson & Davies, 1970; Reynoldson & Young, 1963).
By serological techniques Davies & Reynoldson (1969) found predators to be salamanders, fishes, Odonata nymphs, Plecoptera nymphs, Trichoptera larvae, the leech **Erpobdella octoculata** and the snail **Lymnaea stagnalis**. Den hartog (1962) mentions certain parasites.
We found triclads at most sampling stations with an exception of those with the deep submerged plants. It is very improbable that food is a limiting factor in the sections of the emersed **Stratiotes** plants. The preference of **Dendrocoelum lacteum** for **Asellus** explains perhaps its distribution in the A- and B-section. **Polycelis tenuis** with a preference for Oligochaeta was found in the same group as **Stylaria lacustris. Dugesia lugubris/polychroa** probably eats molluscs as well as insect larvae, without a clear preference. **Planaria torva** prefers gastropods above **Asellus**, the second main food; Tubificidae and Chironomidae are

eaten seasonally and in small numbers (Reynoldson & Sefton, 1976). For **Bdellocephala punctata** no specific food is mentioned in the literature.

Stylaria lacustris

The food of this oligochaete worm consists of diatoms and unicellular algae (Ude, 1929; Wesenberg-Lund, 1939). Probably detritus and small animals are consumed as well.
Without any doubt **Stylaria** has many predators. We examined the stomach contents of caddis larvae (Polycentropodidae and **Ecnomus tenellus**) and found the remnants of **Stylaria** in all but one species. These investigations comprised larvae of all sizes and collections made over several months. Reynoldson & Bellamy (1973) state the preference of **Polycelis** species for oligochaetes. Most carnivorous insects and their larvae, the water spider and fishes are likely to be predators as well (Loden, 1974).
Stylaria was found at most sampling stations and seems to have no clear preference for any particular section in the vegetation. The highest numbers were observed in a turbid peat digging, but high numbers also occur in waters without pollution. The food cannot be a limiting factor in the distribution, nor the chemical composition of the water.

HIRUDINEA
The different genera of leeches have different preys. **Glossiphonia** species feed on molluscs. **Helobdella** takes molluscs as well as chironomid larvae and other small animals. **Theromyzon** is a parasite on birds, especially ducks; **Piscicola** is a fish parasite; **Hemiclepsis** is a parasite on amphibians and fish, but it also eats molluscs and worms. The **Erpobdella** species devour chironomid larvae and other small animals (Dresscher & Engel, 1960). Once we noticed an intact caddis larva including its case (**Tricholeiochiton fagesii**) in the stomach of **Erpobdella nigricollis**.
Birds, fishes, frogs, Odonata nymphs, Dytiscidae and waterbugs predate on leeches. The bigger species of the genera **Haemopis** and **Erpobdella** can eat other leeches as well (Dresscher & Engel, 1960).
Leeches have been found in high numbers on **Stratiotes** plants, which is not surprising from the point of view of food availability. The submerged plants have lower numbers than the emersed ones. The possibilities of resting between two leaves with dorsal as well as ventral side in contact with the plant material are much greater on the emersed plants, which means a better protection against predators. The fish parasite **Piscicola geometra** is found predominantly on the edge of the vegetation, where fishes from the open water can be attacked. **Erpobdella octoculata** and **E. testacea**, which are good swimmers, are found regularly on the submerged plants that grow widely apart. The presence of food or predators cannot be a limiting factor in the distribution of leeches in the **Stratiotes** vegetation.

GASTROPODA

The gastropods are mainly herbivorous and detritivorous, although they seem to eat carrion as well as living animals. Many authors mention higher plants, algae and detritus, but as far as we have observed there is no indication of consumption of live **Stratiotes** leaves, except perhaps the very young shoots. The main food source is formed by diatoms and filamentous algae on the plants. Detritus on the plants, containing many algae, is eaten without doubt. **Lymnaea peregra** prefers filamentous algae to diatoms (Calow, 1970). Pennak (1953) stamps **Lymnaea** and **Physa** as omnivores and carrion eaters; **Lymnaea** eats living and dead snails. **Lymnaea stagnalis** is known to take living animals (**Hydra**, Turbellaria). Further prey consists of fish eggs and egg cocoons of **Erpobdella** (Mann, 1953).
Fishes, birds, amphibians, leeches, beetle larvae, waterbugs and Odonata larvae predate on snails.
Gastropods were found at all sampling stations, with highest numbers in the C-section and lowest numbers in the open water on submerged plants. In the emersed part the possibilities of dispersal are better and fishes - as important predators in the submerged part - are absent. Leeches and Odonata nymphs are left to be the main predators. This seems a reasonable

explanation for the much lower numbers in the submerged samples, as the presence of food cannot be a limiting factor for gastropods.

Argyroneta aquatica

Young water spiders prey on Cladocera and Copepoda, adults on the larvae of Nematocera and on **Asellus** (Wesenberg-Lund, 1939), on water mites and insect larvae (Lampert, 1925). Among them caddis larvae are mentioned (Heimans & Thysse, 1946) and Clegg (1959) refers to ,,dead creatures''.
In the literature no mention is made of specific predators, but probably the spiders are eaten by birds, amphibians, fishes, Dytiscidae, waterbugs and Odonata nymphs.
Argyroneta was found especially near the shore-part of the emersed vegetation. Its prey consists of **Chironomus, Cloeon** and **Asellus** and probably also of young caddis larvae. Most of the expected predators are absent or scarce in this section.

ACARINA

Water mites are to be divided into predators, parasites, scavengers and perhaps herbivores, omnivores and detritivores (Böttger, 1970). The species recorded are nearly all predators. They feed upon Cladocera, Copepoda and insect larvae such as Chironomidae and Ephemeroptera. **Limnesia** species also predate on eggs of water insects and fishes.

Asellus

Water lice eat all kinds of decaying matter, but also algae (Clegg, 1959). Probably the main food source is decaying plant material (Wesenberg-Lund, 1939).
The **Asellus** species are preyed upon by many animals. As we saw before **Argyroneta** and flatworms are predators, but we can assume that most aquatic carnivores of some size prey upon Asellus.
Most of the observed water lice, especially **A. aquaticus**, are found near the shore where the amounts of decaying plant material are high. **A. meridianus**, the most numerous of the two, was found at all sections, but highest numbers were captured in the B-section. On the submerged plants the predation by fish must play an important role; on the emersed plants **Dendrocoelum lacteum**, Odonata nymphs, beetle larvae and water bugs must be the main predators.

EPHEMEROPTERA

The **Caenis** nymphs feed upon vegetable detritus (Redeke, 1948); the food of **Cloeon dipterum** consists of epiphyton, which Allanson (1973) demonstrated by scanning electron microscope photography.
All the larger carnivores among the Odonata, Coleoptera, Heteroptera etc. prey upon Ephemeroptera. **Cloeon** suffers especially from fishes (Pennak, 1953). In the literature specific predators of **Caenis** are not mentioned, but most of the aquatic carnivores could be involved.
Both **Caenis** species reach their highest numbers in the boundary zone of the sumberged and emersed vegetation. **C. robusta** is found on emersed plants, **C. horaria** seems to belong to the submerged part. There is some overlap of both species into their mutual zones. The free swimming nymphs of **Cloeon** only occur among and upon the emersed plants. Probably they are an easy prey for fishes in the submerged zone.

ODONATA

The nymphs of Odonata are carnivorous, and very voracious; even cannibalism in known (Corbet a.o., 1960). All aquatic animals, from small crustaceans to young fishes and tadpoles, are eaten. The Zygoptera prey upon Cladocera, Copepoda, Chironomid larvae,

Ephemeroptera nymphs (Jansen & Croes, 1971; Johnson, 1973; Lawton, 1971; Macan, 1974; Wesenberg-Lund, 1943) and even flatworms (Davies, 1969). The Anisoptera consume bigger animals as well and also prey upon zygopterids.
The following groups are mentioned as predators: fishes (Macan, 1974), big Anisoptera nymphs, birds, and spiders (**Dolomedes fimbriatus**) if the nymphs are defenseless just before emerging (Wesenberg-Lund, 1943).
The Odonata nymphs are important top-predators in the system, particularly in the emersed part of the vegetation. In the nymphal stage they do not meet many enemies (apart from the first instars) and they find food in abundant quantities. We found only few Anisoptera nymphs, and they seem to be confined to the B-section, while the Zygoptera occur in all sections.

LEPIDOPTERA

We did not find many caterpillars, but they are worth to be mentioned, because they belong to the few aquatic invertebrates that eat macrophytes. In our animal aggregations they play no role of importance.

HEMIPTERA

The Corixinae species in this research eat small animals, such as Oligochaeta, and detritus. The most abundant waterbug observed, **Cymatia coleoptrata**, preys upon Cladocera, chironomid larvae, and nymphs of other Corixidae and Ephemeroptera (Southwood & Leston, 1959). The larger waterbugs like **Notonecta** and **Ilyocoris** feed on all kinds of aquatic invertebrates and especially **Notonecta** is very voracious, seizing tadpoles, small fishes and large beetle larvae as well as smaller preys.
Many waterbugs are distasteful to fishes. Once captured, they are ejected immediately. Often one finds one or more water mite larvae attached to waterbugs; adult mites can eat the eggs of waterbugs (Davids, 1973).
Most waterbugs are only observed in the shallow water with dense vegetation, where they find plenty of food. Especially **Cymatia coleoptrata** does not swim away in the case of disturbance (e.g. sampling). The **Notonecta** species and some other bugs, which are present in the vegetation and probably also in the submerged part, are hardly captured, due to their swimming abilities. The larger carnivorous bugs are important predators and they must be included if food chains are considered.

TRICHOPTERA

The representatives of the family Hydroptilidae are specialized filamentous algae eaters (Nielsen, 1948). The larvae of the Polycentropodidae and **Ecnomus tenellus** eat cladocerans, ostracods, **Stylaria lacustris** and chironomid larvae. **Oecetis furva** is omnivorous and **Triaenodes bicolor** is probably herbivorous (Lepneva, 1963).
Caddis larvae are most vulnerable in the free swimming pupal stage. Fishes in particular are serious predators at that time. Caddis larvae are relatively safe in their cases. Water spiders are known to seize them, if they protrude too far out of the case and the small forms (Hydroptilidae) are swallowed as a whole by **Erpobdella**. The free living larvae of the family Polycentropodidae protect themselves in spun retreats and use their sharp jaws against predators and congeners. Perhaps they are preyed upon by large beetle larvae.
The group of Polycentropodidae larvae is very numerous in all sections of **Stratiotes** vegetations. In the end of this paragraph we shall describe the role of Polycentropodidae in more detail. The Hydroptilidae with a certain specialization on different genera and families of filamentous algae are distributed over all sections of the vegetation, probably in accordance with the distribution of those groups of algae. **Oecetis** and **Triaenodes** occur only in the emersed part of the vegetation.

COLEOPTERA

The Dytiscidae and Gyrinidae and their larvae are carnivorous. The other species that were captured, are herbivorous or detritivorous. The most abundant group of Coleoptera is formed by the larvae of **Agabus** sp. and/or **Ilybius** sp. They prey upon Cladocera and insect larvae and have been found predominantly on emersed plants. Together with other larger beetles and larvae they are very important top-predators. The larvae of the genera **Scirtes** and **Cyphon** eat vegetable detritus and parts from dead leaves. Some of them are microphagous or eat **Lemna** sp. (Bertrand, 1972).
As predators on beetle larvae we can expect fishes, Odonata nymphs, waterbugs and perhaps the water spider.
The Dytiscidae and their larvae are top-predators in the emersed part of the vegetation and perhaps also in the submerged part.

DIPTERA

The food of the Ceratopogonidae larvae seems to consist chiefly of chironomid larvae. The larvae of Chironomidae can be carnivorous, herbivorous or omnivorous. The Tanypodinae prey upon other chironomid larvae, on Cladocera and Oligochaeta. The Tanytarsini are detritivorous, just like most Orthocladiinae, but **Psectrocladius** sp. (Orthocladiinae) uses filamentous algae for food. The larvae of the Chironomini are omnivorous. Most of them eat detritus and many of the mining larvae belong to this subfamily. They filter small particles (vegetable and animal) through the tunnels. Especially the genera **Glyptotendipes** and **Endochironomus** out of this subfamily were found in high quantities.
As we have seen above, many carnivorous animals in the water are predators on Chironomidae. The most important among them are fishes; especially in winter the larvae are very vulnerable in absence of protecting vegetation. Nevertheless, the amounts of Chironomidae that reach the adult stage are enormous.
The chironomid larvae are the most numerous group in species as well as in total numbers. They are found in all sections with highest numbers on the submerged plants. The carnivorous species **Ablabesmyia** sp., **Guttipelopia guttipennis, Monopelopia** sp. and **Parachironomus** sp. are distributed over the groups 2, 3, 4 and 6 (table 14) and covering all sections of the vegetation as well.

The data presented in this paragraph show a number of existing and possible food relationships among the invertebrates in **Stratiotes** vegetations. During the life cycles of most species there will be a change in the food and in their predators, according to the size in the life stages. This will be demonstrated on the life history af a caddis fly from the family Polycentropodidae. The course of the offspring of one fertilized female is presented graphically in Fig. 18.

The cycle starts with an egg mass from one female. The highest possible number (N) within this cycle can be reduced by water mites, snails or by an infection with fungi (Pl). The freshly hatched larvulae are eaten by **Hydra, Chaoborus** larvae, water mites and **Cymatia coleoptrata** (P2). Their prey consists of microfauna like rotifers or small Cladocera (Fa). If the remaining larvae have become bigger, they eat Cladocera, Copepoda and Ostracoda (Fb). At that stage, however, they are eaten by water spiders, **Erpobdella** and **Ilyocoris** (P3). In the next stage predators like Odonata nymphs, beetle larvae and **Notonecta** (P4) are concerned, while fishes (P5) can be the main predators if their presence is allowed by the environment. In addition to small crustaceans more Oligochaeta are eaten and smaller chironomid larvae as well (Fc an Fd). The biggest larvae eat Cladocerans, **Stylaria lacustris** and chironomid larvae. Together with the larger aquatic carnivores, birds (**Chlidonias niger**) and amphibians (P6) can be predators. The pupal stage is rather safe, where probably only some parasites (P7) can be harmful, but the free swimming pupa (f) is a defenseless prey to invertebrate carnivores (P4), amphibians and birds (P6) and especially fishes (P5). Finally, the adult caddis fly is

eaten by birds and amphibians and sometimes by fishes (**Scardinius erythrophtalmus**). If one adult is left, the same cycle can start again. The energy gained by the use of F is transformed to food for P (with the well-known losses in food chains).
The changing of food and predators in the time applies to most of the animals observed. As a consequence, the reconstruction of food chains or food webs never can be performed in a detailed and complete way.

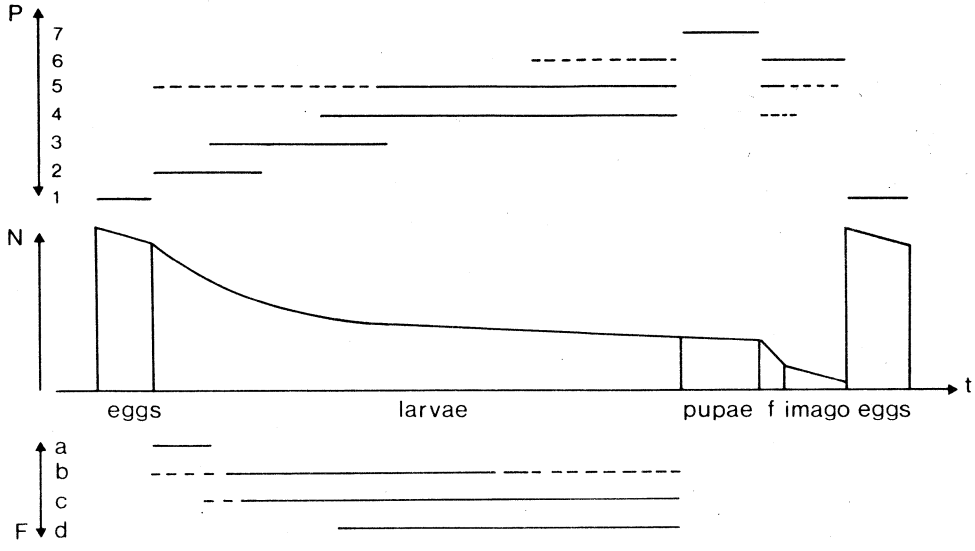


Fig.18. History of a caddis species (Fam. Polycentropodidae) with predators (P1 to P7) and food composition (Fa to Fd) during its life cycle. f = the free-swimming pupal stage. The values for N and t are chosen arbitrarely. Further explanation in the text.

5.4. ANIMAL AGGREGATIONS

In 1.1. we have described animal aggregations as regularly occurring combinations of species. We have seen that the distribution of the species under consideration is in accordance with the zonation in the vegetation in broads. Therefore, the animal aggregations have to be studied in every section separately. With help of the data in the preceding paragraphs, it is possible to reconstruct the outline of a food chain in **Stratiotes** vegetations and to indicate differences in the fauna composition in the various parts of the vegetation.

The primary food source is formed by
- epiphyton (in special diatoms and threaded algae)
- periphyton (free-floating micro-flora)
- decaying leaves
- detritus
- living plant tissues (to a very small extend)

Herbivores and detritivores are represented by
- Hydroptilid larvae
- Ephemeroptera nymphs
- **Asellus** species
- snails and bivalves
- Oligochaeta
- Chironomidae larvae (all species, except some carnivorous ones)
- Cladocera

Primary carnivores are
- **Hydra**
- Polycentropodidae larvae
- leeches consuming snails and worms
- cf **Bezzia** sp.
- **Cymatia coleoptrata**
- carnivorous Chironomidae larvae
- flatworms

Secondary carnivores, eating herbivores as well, are
- water spider
- dragonfly nymphs
- Dytiscidae (adults and larvae)
- larger waterbugs, such as **Notonecta** and **Ilyocoris**
- **Erpobdella** species

At the top of the food chains one finds amphibians, fishes and birds, and eventually man. This general picture is a rough outline indeed, and it fits into many freshwater habitats. The next step is to try and find more details of food chains in the various parts of the vegetation.

In the tables 10 and 11, the most important species in **Stratiotes** vegetations have been listed and the arithmetic means of their numbers in each section are given. These species have been divided into three trophic levels, and within those levels, they are divided into groups of taxa with about the same food demands and the same predators (table 16). We do not have the intention to describe a complete food web, but we use the data on food relations in order to make a more realistic division into groups, which can be studied in the different parts of the vegetation.

Consumers I	herbivorous detritivorous chironomid larvae
	Gastropoda
	Asellus spp.
	Ephemeroptera nymphs
	Leptocerid caddis larvae
	Stylaria lacustris
	Hydroptilid caddis larvae
Consumers II	carnivorous chironomid larvae
	leeches consuming snails and small invertebrates
	Hydra sp.
	cf **Bezzia** sp.
	Cymatia coleoptrata
	Polycentropodid caddis larvae
	Ecnomus tenellus
	Tricladida
Consumers III	**Argyroneta aquatica**
	Ischnura elegans
	Erpobdella spp.

Table 16. Groups of species with comparable food and predators.

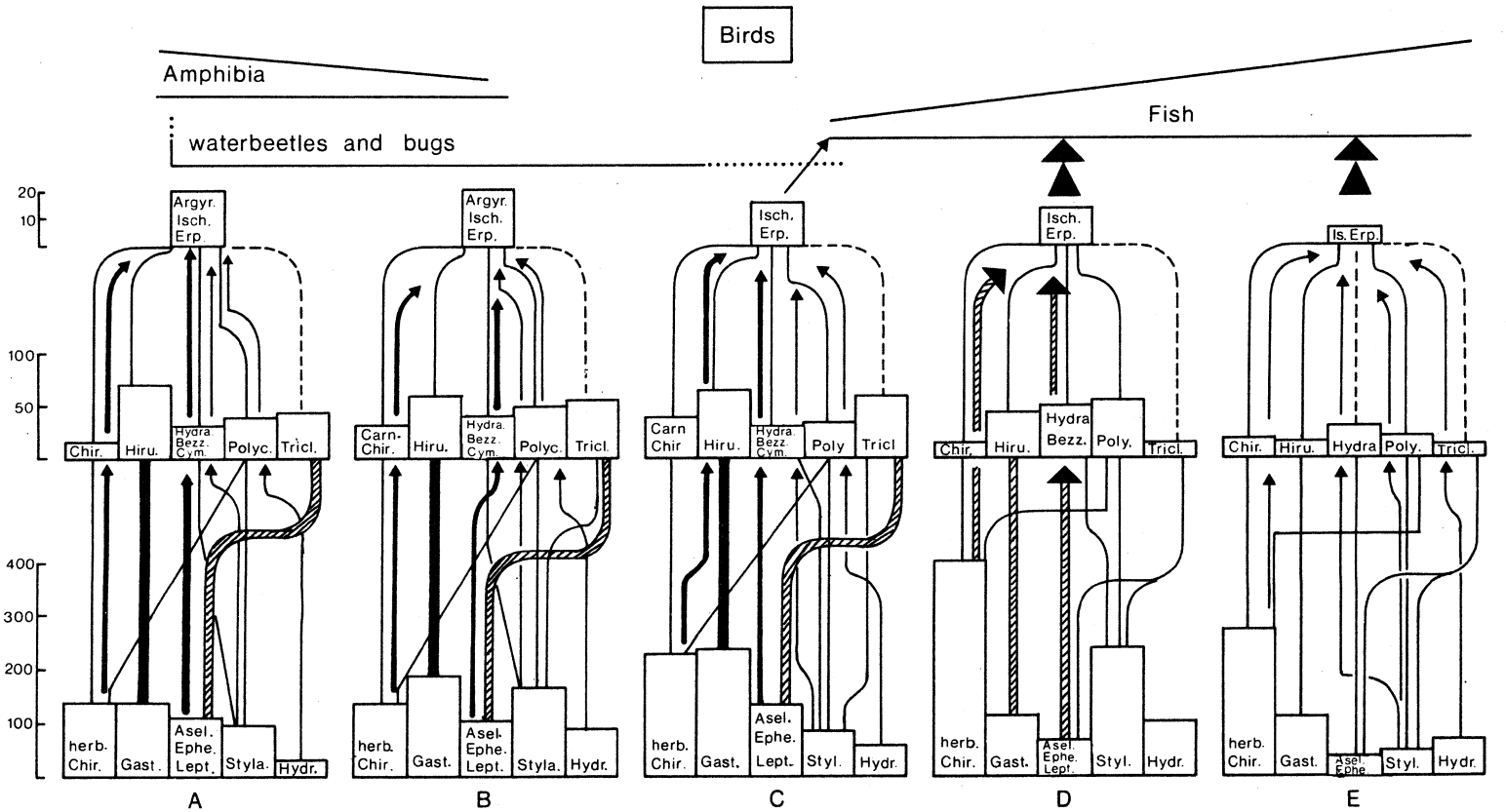


Fig.19. Animal aggregations in the sections A to E on the basis of food relationships. The height of the blocks corresponds with the number of individuals per m². The abbrevations in the blocks refer to the species names and names of taxonomic groups as listed in table 16. Further explanation in the text.

For each of the groups of table 16 we calculated the numbers per m^2 in the sections A to E. These numbers are derived from the tables 10 and 11. The percentual contribution of the carnivores gradually decreases from the shore to the open water. In section A it forms 30%, in B 27%, in C 24%, in D 17% and in E 16%.
There are two factors explaining this distribution. Within the emersed part of the vegetation huge masses of Cladocera are found, that form food for many predators; moreover the absence of larger carnivores like fishes guarantees a rich development of the invertebrate predators. In the sections D and E the numbers of Cladocera are much smaller and the pressure of fish is heavy.
In Fig. 19 the animal aggregations in the five sections have been depicted, on the basis of the groups from table 16. The numbers in each group are represented by blocks. The scale in the different levels had to be taken differently. The food relationships are indicated by lines from one level to the following and by lines with arrows from the first level to the third. The thick black lines are important relations from the point of view of energy flow, the striped lines are of smaller importance and the remaining, thin lines have a low contribution to biomass and energy flow. The numbers in this last category can be very high, but the organisms concerned are small, or they are not eaten by many of the depicted predators. The dotted lines represent incidental relationships. The abbrevations in the blocks correspond with the names of species and other taxonomic units in table 16. It will be clear that, in the light of the considerations of 5.3, only the main food relationships are given.
Fig 19 is more detailed than the picture of the graphs in Fig. 15, where only the quantitative presence of the main taxonomic units per section has been given. Nevertheless, no big differences between the first three figures A, B and C can be distinguished. In the figures D and E the contribution of the different blocks has changed considerably as compared to A, B and C and the lines are less distinct. It seems that the herbivores and detritivores in the emersed part of the vegetation are eaten predominantly by the depicted carnivores. In the sections D and E we found smaller numbers of these carnivores and some of the herbivores and detritivores, apparently not approachable to fishes, gain high numbers in these sections. Invertebrate predators such as leeches, triclads, Polycentropodidae larvae and damselfly nymphs, which are found in relatively high numbers in the first three sections, are favoured by the lack of large predators.

A closer look at the qualitative composition of the groups reveals the main differences between the sections. The animal aggregations from Fig. 19 have been represented in more detail in the figures 20 to 24. Each figure shows the main species from one of the five sections on a plant with a total available surface of $1m^2$. The underlined species reach their highest numbers in the section in question, the species with dotted lines reach their highest numbers but one. The sequence within the blocks has been chosen in such a way that species occurring in the sections A, B and C, but absent in D or E, are at the top, and species that are found only in D and E at the bottom of the blocks.

Section A is characterized by a high percentage of carnivores, especially leeches and caddis larvae of the genus **Holocentropus**. In the consumers I level we find detritivores in high numbers (**Chironomus** spp., both **Asellus** species, **Cloeon dipterum**). Most detritivores can stand low oxygen conditions and they are often found in the lists of indicator organisms for polluted waters. The shallow water with large amounts of decaying matter in section A provides suitable conditions for these organisms, while less tolerant species occur in low numbers or only in the other sections.

Section B froms the heart of the emersed vegetation and is generally richer in species and numbers than the preceding one. Among the carnivores many Cladocera-eaters are observed (**Holocentropus** species, **Cymatia**, cf **Bezzia**, flatworms) and the highest numbers of invertebrate top-predators are found in this section. The number of species is highest in section B (table 13). Detritivores and herbivores both find plenty of food and in particular the specialists eating threaded algae occur in high numbers (hydroptilid caddis larvae and **Lymnaea peregra**).

Section C is richest in numbers of individuals (tables 12 and 13). A relatively lower number of species occurs in high numbers of individuals; these species are generally the most abundant ones in **Stratiotes** vegetations. A difference in the fauna composition such as has been observed between section B and C, resulting in a decrease of the number of species and an increase in numbers of individuals, is often found in places where the stability is reduced by any form of disturbance. The C-section differs from the other sections in the exposure to wave-action, caused by wind or boats. This is a form of mechanical disturbance, obviously in disfavour of certain species (Trichoptera in general; Fig. 15). The plant density is highest in this section, probably as a result of wind action, which means that the possibilities for shelter and the presence of food per surface unit increase as compared to the sections A and B.
The Ephemeroptera nymphs **Caenis robusta** and **C. horaria**, snails (in particular **Bithynia tentaculata** and **B. leachi**) and the leeches of the species group **Glossiphonia heteroclita** are found in high numbers, and also **Ablabesmyia** sp. occurs in unusual high numbers. Other carnivores that prefer this section, are **Bezzia** larvae, damselfly nymphs **(Ischnura elegans)** and flatworms, among which **Dugusia lugubris/polychroa** reaches its highest number. The herbivorous/detritivorous chironomid larvae are more abundant than in the preceding sections. The **Cyrnus** species and **Ecnomus tenellus** join the other Polycentropodidae larvae in this section.

In **section D** the proportions of the various groups are different in respect of the situation in the preceding sections. Among the consumers I we find very high numbers of chironomid larvae, hydroptilid larvae and of **Stylaria lacustris**. The numbers of snails (species as well as individuals) and the numbers of water lice are much lower. The same decrease can be observed among carnivores such as leeches and flatworms. Polycentropodid larvae and **Hydra** have become the main invertebrate predators. It turns out to be that the visible boundary from emersed to submerged vegetation is reflected in the altered composition of the macrofauna community, and within a few meters. This might be due to the much lower plant density and the fact that fishes can enter into this part more easily. The dispersal possibilities for creeping animals and floating life stages have a sharp decrease. Swimming organisms and insects with aerial stages are more succesful in this section, unless they are eaten by fishes. Probably the influence of fishes is still restricted in this section, because of the low accessibility.

Finally **section E** shows a far different situation as compared to the emersed vegetation. The **Stratiotes** plants grow widely apart from each other and constitute only a part of the bottom covering vegetation. There is always a large amount of free water above the plants, or in some exceptional cases under and between the plants. Creeping animals have to move from one plant to another via the bottom or other plant species. They are vulnerable to fish. Among the carnivores we still find **Hydra** as an important predator; the caddis larvae are represented by **Cyrnus** species and **Ecnomus tenellus**. Numerically the most successful group is formed by chironomid larvae with seven species reaching their highest numbers in this section. The hydroptilid **Oxyethira flavicornis** is still found in high numbers and is joined here in some seasons by **Orthotrichia costalis** and **Hydroptila pulchricornis** from the same family, as we found in the experiments with artificial plants. So a number of species from the emersed sections are absent in section E, while other species are characteristic for this section, partly as ,,new'' species, partly as numerically important species.

In this chapter we studied the possibilities of characterization of the different sections in **Stratiotes** vegetations in broads with the help of macro-organisms. In 5.1 we showed the quantitative distribution of the main taxonomic units (Fig. 15) amongst the sections and the distribution patterns of species occurring together in comparable parts of the vegetation (Fig. 16). The data on food relations have been used to divide the species under study into functional units (Fig. 19) and these units have been filled in with species names and numbers per m^2 for each of the sections (Fig. 20 to 24).

It has become clear that one specific species list cannot be representative for the macrofauna on **Stratiotes** in general. It is necessary to define the qualitative and quantitative species composition in accordance with physico-chemical characteristics of the habitat. These characteristics are different from shore to open water. Near the shore the water is very shallow (20-40 cm), the sapropel layer is thick and the plant density is high. Therefore we can expect large changes in oxygen content and the presence of toxic substances such as ammonia, nitrite and hydrogen sulphide, especially in summer. The most offshore parts of the vegetation are situated in deeper water (100 cm) with a thinner sapropel layer and much room around the plants. These are the main differences between the extremes of the vegetation and the division of the macro-organisms reflects these differences. The **Stratiotes** plants act as mere substrate.

5.5. COMPARISON WITH THE FAUNA ON STRATIOTES IN POLAND

As we have seen in 1.4, the investigations on the macrofauna on **Stratiotes** plants in our research and those from the two Polish publications, can only be compared by considering whole groups (families, orders). The results for **Stratiotes** from the tables 1 and 2 are listed in table 17, together with data from our research, derived from the tables 10 and 11. Our data are given for the five sections from the broad Venematen and from the total number of samples.

	KAR.	PIEC.		table 10					table 11				
		68	69	A	B	C	D	E	A	B	C	D	E
Chiron.	41	68.7	81.8	22.6	14	30.9	39	50.9	17.4	20.2	17.1	31	36.8
Mollusca	21	2	0.6	16	22	24	10.9	19.3	26.4	19.6	19.6	9.7	14
Hirudinea	9	7.2	2.8	12.2	8	4.5	4	2.5	9.5	9	8.7	7	4.4
Ephemer.	1	4	3	2.4	4.1	7	5.6	1	4.3	3.3	11.2	3.3	4.8
Isopoda	12	0.1	< 0.1	10.4	6.6	4	-	0.5	8	6.2	2.5	2.4	5.8
Trichopt.	16	4.4	1.6	10.4	23.5	11.6	17	16.7	12.8	18.9	10	14.5	10.9
Heteropt.			< 0.1	1.7	1.8	1.5	-	-	0.7	1.1	0.4	-	0.1
Oligoch.		8	1.8	17.3	10	7.6	17.5	3.4	10	9.6	23.1	26.2	13.5
other groups		5.6	8.4	7	10	9	5.5	5.7	10.9	12	7.3	5.8	9.6

Table 17. Percentual distribution of macrofauna groups on **Stratiotes** from investigations in Poland (Karassowska & Mikulski, 1960 and Pieczyński, 1973) and from table 10 and 11 is this paper.

The similarity in the macrofauna composition in field of **Stratiotes** in Dutch broads gave rise to the hypothesis of animal aggregations, occurring at several places. We were able to confirm this, provided that the position of the sampling stations in the vegetation of the different waters compared, is the same (A-section has to be compared with A-section, etc.).
In table 17 we compare our findings with the Polish results. The differences between the data of Karassowka & Mikulski and Pieczyński are considerable. Apparently, the conditions in the two lakes differ greatly. The main differences between the results of these authors are the percentages for Chironomidae, Mollusca and Isopoda. These differences are of such an order, that the structure and the functioning of the macrofauna-cenoses in the **Stratiotes** of the two lakes must be fundamentally different.
Our data from the Dutch broads have shown, that one cannot speak in general of the macrofauna on **Stratiotes**. The Polish data are derived from samples from homogeneous vegetations, but without a more detailed knowledge of the position of their sampling stations and the way in which samples have been combined, it is very difficult to analyze their animal aggregations, that have led to the data of table 17.

Within the range of ecological possibilities for the occurrence of **Stratiotes** vegetations, we can expect a variety of physico-chemical and morphometrical factors, determining the distribution of the macrofauna. The organisms use the **Stratiotes** plants for substrate to attach themselves or their eggs, to find shelter or food or to build retreats on, in and between the leaves. The situations that we studied are obviously more favourable for molluscs than those in the sampling stations of Pieczyński, if we consider total numbers and percentages (table 17). Compared to the data of Karassowska & Mikulski we find about the same percentages of molluscs and leeches, but the number of species in these groups is much higher in our data. It seems more likely to conclude that the comparison between the Polish and Dutch data points to differences between Dutch broads and Polish lakes, more than to resemblance between the animal aggregation on **Stratiotes** plants in both areas.

Fig. 20. Animal aggregation in section A. Numbers per m².

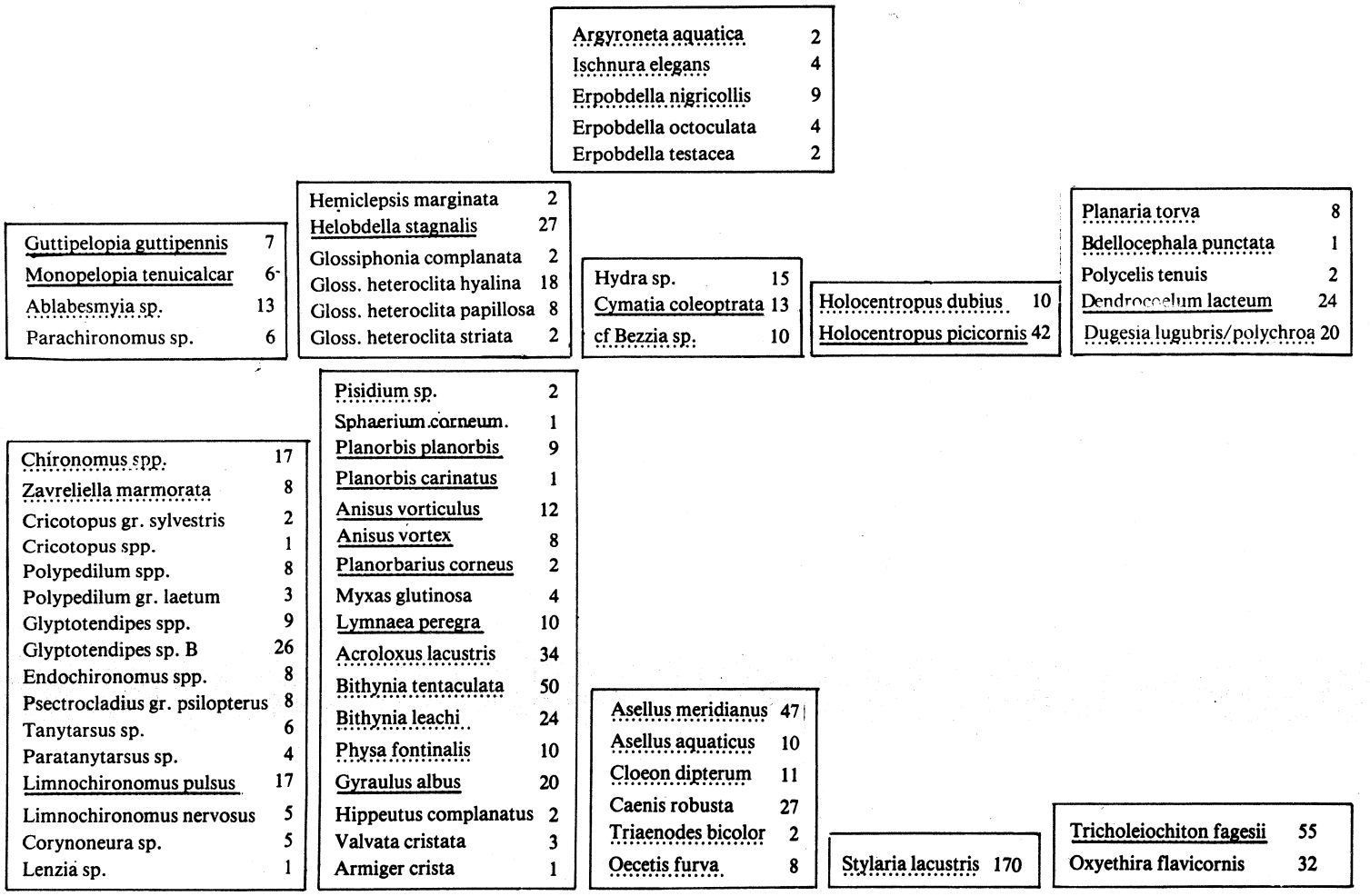


Fig. 21. Animal aggregation in section B. Numbers per m^2.

Fig. 22. Animal aggregation in section C. Numbers per m².

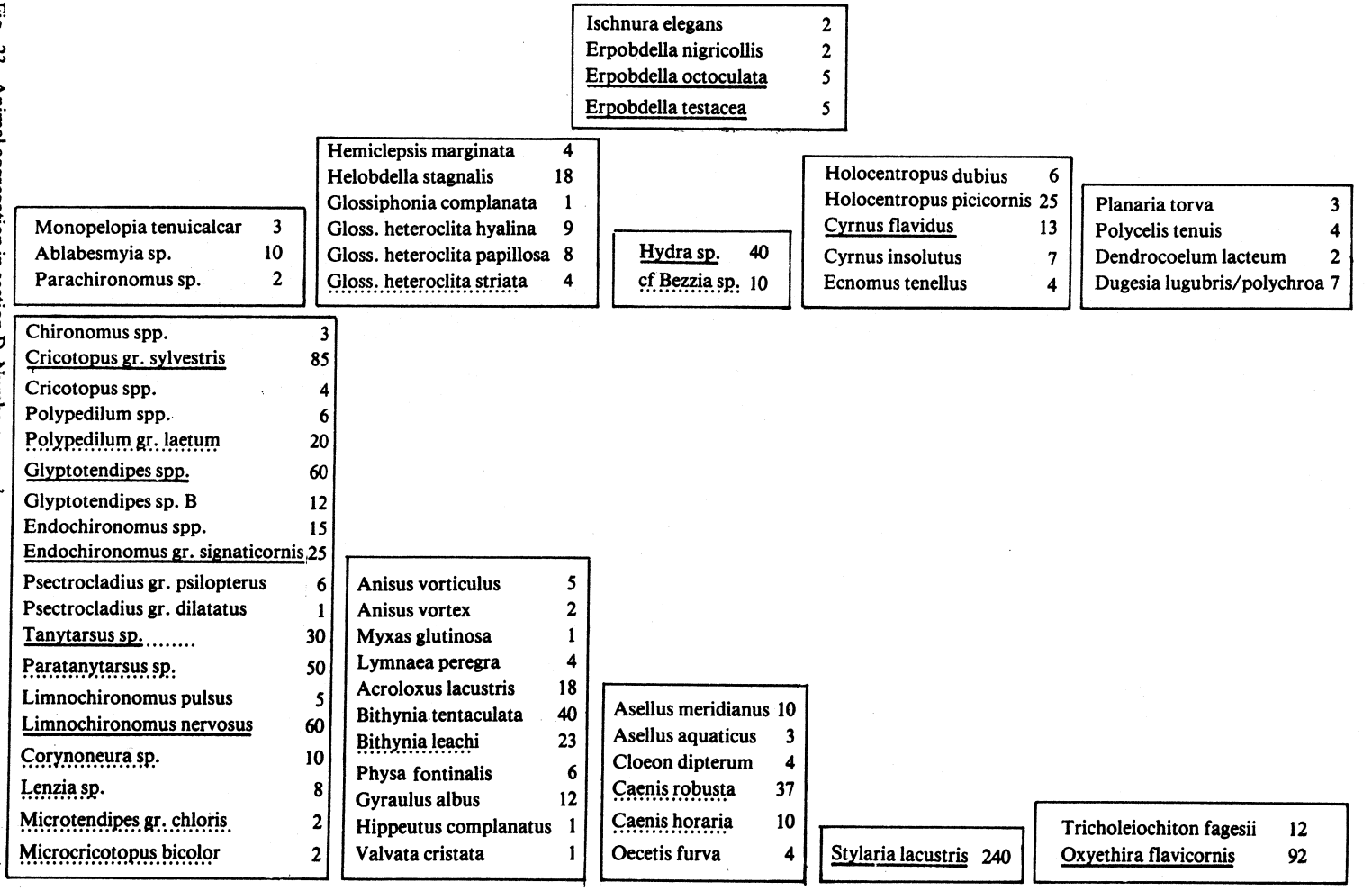


Fig. 23. Animal aggregation in section D. Numbers per m².

Fig. 24. Animal aggregation in section E. Numbers per m².

6. SAMENVATTING

De macrofauna op krabbescheerplanten (**Stratiotes aloides** L.) in Nederlandse laagveenplassen is bijzonder rijk aan soorten en individuen. Het doel van het hier beschreven onderzoek is het opsporen van regelmatig voorkomende soortencombinaties (animal aggregations) in krabbescheervegetaties en het leggen van correlaties tussen het optreden van dergelijke animal aggregations en milieufactoren. Gedurende 1972 werden 73 monsters verzameld uit laagveenplassen en enkele andere watertypen met krabbescheervegetaties. Ieder monster - dat aselect gekozen werd - bestond uit een, twee of drie krabbescheerplanten met de daarop voorkomende macro-organismen. Door deze bemonsteringsmethodiek wordt de macrofauna, die bestudeerd werd, beperkt tot sessiele en kruipende organismen en tot soorten, die een nauwe band met het bladoppervlak hebben vanwege hun prooi of schuilmogelijkheden. Het beschikbare bladoppervlak per monster werd nauwkeurig gemeten en de aantallen dieren in een monster werden omgerekend tot aantallen per m^2 beschikbaar bladoppervlak. Hierdoor is quantitatieve vergelijking tussen de monsters mogelijk. Bij de berekeningen van aantallen werden in dit proefschrift steeds de aantallen per m^2 gebruikt en wel van 83 meest voorkomende soorten.

Op grond van gegevens uit de vegetatiekunde kan een model van een verlanding met krabbescheer gemaakt worden, waarin de relatie wordt aangegeven tussen de positie van de planten in een reeks van open water naar oever en gegevens over de waterdiepte, de dikte van de sapropeliumlaag, de afstand tot open water en oever en de groeivorm van de planten. Met behulp van deze fysische en morfometrische gegevens werden vijf zones (A t/m E) in de verlandingsreeks onderscheiden. De 73 bemonsteringspunten werden ingedeeld in vijf groepen, overeenkomend met de zones, zoals deze gekarakteriseerd worden door de fysische en morfometrische kenmerken. Er blijkt een duidelijk verband te bestaan tussen de dichtheid der krabbescheerplanten en de waterdiepte. De zone, die het dichtst bij de oever wordt aangetroffen (A/B), wordt gekenmerkt door een geringe waterdiepte (30-60 cm) en een dikke, zuurstofloze sapropeliumlaag van meer dan anderhalve meter. In deze zone komen de meest extreme waarden van temperatuur, zuurstofgehalte en daardoor beïnvloede chemische parameters voor. In warme zomers treedt overdag dikwijls zuurstof-oververzadiging op, terwijl in de nacht het water tussen de planten praktisch zuurstofloos kan zijn. Gecombineerd met het optreden van NH_3, NO_2^- en H_2S betekent een dergelijke situatie voor veel organismen een ongeschikt milieu. Aan het andere uiterste van de reeks (D/E), waar de krabbescheerplanten niet boven water uitkomen en waar de plantendichtheid veel geringer is, komen dergelijke toestanden niet voor. Hier is de geringe plantendichtheid en daardoor de goede toegankelijkheid voor vissen een andere beperkende factor voor een aantal macro-organismen.

De 83 meest voorkomende soorten zijn gebruikt voor een cluster analyse (methode Ward), waarvan de resultaten in een dendrogram zijn gezet. Bij deze methode wordt een scheiding gemaakt in de bemonsteringspunten op grond van de soortencombinaties, waarbij de aantallen per soort eveneens in aanmerking genomen worden. De methode is toegepast op alle 73 bemonsteringspunten en eveneens op de 25 bemonsteringspunten, die in de uitgestrekte krabbescheerverlanding in de plas Venematen (N.W.-Overijssel) genomen werden. In beide gevallen is van een duidelijke driedeling sprake. Een van de drie ,,hoofdclusters'' van de dendrogrammen bevat bemonsteringspunten met minder dicht op elkaar groeiende planten in relatief diep water. Een tweede cluster bevat bemonsteringspunten uit de emerse zone met dicht op elkaar groeiende planten in ondiep water. Voor het derde cluster spelen vermoedelijk fysisch-chemische factoren een rol, zoals tijdelijk zuurstofgebrek en de aanwezigheid van toxische stoffen. Deze toestand komt vooral in de ondiepste gedeelten met een dikke sapro peliumlaag voor.

De regelmatig optredende soorten combinaties (animal aggregations) kunnen op verschillende manieren bepaald worden. Bij gebruik van de cluster analyse techniek blijken moeilijk interpreteerbare resultaten verkregen te worden. De hoofdindeling in twee groepen wordt bijvoorbeeld veroorzaakt door verschillen in aantallen en frequentie, zodat soorten van één animal aggregation in verschillende clusters terecht komen. De verdere indeling wordt veroorzaakt door een aantal factoren, zoals de plaats in de vegetatie en de chemische toestand van het water.
Een andere methode bestaat uit het berekenen van het quantitatieve aandeel van ieder der soorten aan de drie hoofdclusters van de bemonsteringspunten. In de monsters van beide clusters III komen bijvoorbeeld Chironomidae larven in grote aantallen voor. Deze monsters zijn alle afkomstig van de diepere gedeelten van de vegetaties. De monsters uit de Venematen, voorzover niet in cluster III van Fig. 6 voorkomend, worden in deze figuur allen teruggevonden in één cluster. De verlanding in de Venematen kon in 1972 als gaafste voorbeeld van een krabbescheerverlanding van een laagveenplas gelden. Daarom hebben wij aangenomen, dat de soorten, die in cluster II in hoge aantallen worden aangetroffen, het meest karakteristiek zijn voor een goed ontwikkelde krabbescheerverlanding, en werd dezelfde methode toegepast op de 25 monsters uit de Venematen (Fig. 7). In deze figuur wordt cluster II gevormd door emerse planten nabij het open water en de meer naar de oever gelegen planten uit het noordwestelijk deel van de verlanding. Cluster I bestaat uit A- en B-planten uit het zuidwestelijk deel van de verlanding, waar een verontreinigende invloed van bio-industrie wordt waargenomen. De soorten, die het best vertegenwoordigd zijn in de monsters van cluster II zullen derhalve de meest karakteristieke fauna elementen van het emerse deel van een krabbescheervegetatie vormen, zoals die in 1972 nog aangetroffen kon worden.
Bij de derde methode om regelmatigheden in de samenstelling van animal aggregations op te sporen wordt als uitgangspunt de zonering A t/m E genomen. Van iedere soort worden de gemiddelde aantallen per m^2 bemonsterd bladoppervlak in elke zone uitgerekend, zowel voor alle bemonsteringspunten, als voor de bemonsteringspunten van de Venematen. De resultaten van de berekeningen staan in de tabellen 10 en 11. De soorten, die in de grootste aantallen in zone A voor komen, staan boven aan in de tabellen en de soorten, die (bijna) uitsluitend in E aangetroffen zijn, onderaan. Deze volgorde vertoont vrij grote overeenkomst met de volgorde I, II, III uit de vorige methode.

De analyse van de ruimtelijke verdeling van de macrofauna in krabbescheervegetaties kan op verschillende manieren uitgevoerd worden. Als uitgangspunt is de zonering van de oever naar open water genomen, waarbij de waterdiepte en de plantendichtheid waarschijnlijk de belangrijkste factoren zijn, waardoor de verspreiding der organismen beïnvloed wordt. De hoogste aantallen soorten en individuen komen in de C-zone voor, de laagste in E. De verspreiding van de belangrijkste groepen - platwormen, bloedzuigers, slakken enz. - geeft enige informatie over de struktuur van de macrofauna-coenosen. Platwormen, bloedzuigers en de beide **Asellus** soorten komen met hoogste aantallen voor op de emerse planten van de A-, B- en C-zone. Haftelarven en slakken zijn in de C-zone het talrijkst. Chironomidae larven komen vooral in de D- en de E-zone voor in grote aantallen. Kokerjufferlarven vertonen een piek in de B-zone en een in de D-zone. De grote beperking van een indeling in groepen is, dat soorten uit één groep elkaar kunnen vervangen in verschillende zones, zonder dat het aantal soorten of het totaal aantal exemplaren verandert.
De gegevens van de tabellen 9/11 werden gecombineerd en herleid tot negen verspreidingspatronen (Fig. 16). Er is een grote overeenkomst tussen de lengte van de verspreidingspatronen en de niche-breedte van de soorten, die hierbij betrokken zijn. De verschillen in levensmogelijkheden voor de macrofauna tussen de emerse en submerse planten blijken tamelijk groot te zijn. De resultaten van de cluster analyse wezen hier ook op. Een tweede belangrijke scheiding wordt gevonden tussen de planten van de A-zone en van het eraan grenzende deel van de B-zone enerzijds en de overige emerse planten van de B- en C-zone. De oorzaak hiervan moet gezocht worden in de voor veel dieren moeilijke situatie nabij de oever, waar grote schommelingen in het zuurstofgehalte op kunnen treden.
De verspreiding in de tijd speelt nauwelijks een rol met betrekking tot de soortensamenstelling. Er werden interessante verschillen in de levenscycli gevonden tussen soorten uit één

geslacht, die dezelfde levenswijze en voedselkeuze vertonen. Bij de familie Polycentropodidae (kokerjuffers) worden nauwverwante soorten tesamen gevonden, waarbij de larven van de ene soort veel kleiner zijn (en ook ander voedsel gebruiken) dan de larven van een andere soort (Fig. 17).

De voedselrelaties in aquatische systemen zijn uitermate ingewikkeld. Het is eigenlijk niet mogelijk een eenvoudige voedselketen samen te stellen, zonder in te grove simplificaties te vervallen. Desondanks kunnen dergelijke simplificaties een aanduiding vormen van de struktuur van een levensgemeenschap, vooral in vergelijkende zin bij de verschillende zones in de krabbescheerverlanding bijvoorbeeld. We hebben derhalve een driedeling gemaakt in herbivoren en detritivoren, carnivoren I en carnivoren II. Met behulp van de gegevens over de verspreiding en voedselrelaties werd voor ieder der vijf zones een beeld van de animal aggregations gegeven, zoals die in de zomer op krabbescheer aangetroffen kunnen worden. In de figuren 20 t/m 24 is aangegeven wat het quantitatieve aandeel van ieder der soorten is en welke soorten in de betreffende zone hun maximale of submaximale aantallen bereiken.

Tot slot werden enkele onderzoekingen van poolse auteurs met betrekking tot de macrofauna op krabbescheer vergeleken met de resultaten van ons onderzoek. Een dergelijke vergelijking toont aan, dat het noodzakelijk is exacte gegevens over de aard der bemonsteringspunten te geven, zodat de gegevens, die vergeleken worden, inderdaad betrekking hebben op dezelfde situaties. Verder blijkt nog eens te meer, dat de krabbescheerplanten niet meer dan een oppervlak voor voedsel, kruipen en verbergen vormen, en dat de fysisch-chemische en morfometrische factoren van de bemonsteringspunten een belangrijker rol spelen voor het voorkomen van macro-organismen. Deze conclusie wordt ondersteund door de resultaten van proeven met kunstmatige krabbescheerplanten. Deze resultaten worden in dit proefschrift slechts summier behandeld, maar zullen elders uitvoeriger gepubliceerd worden.

7. REFERENCES

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ERRATA

I apologize to the reader for the following mistakes:

page	5	line 11	Marcro-organisms; read Macro-organisms
		41	plants-sociological; read plant-sociological
	11	49	Statiotes; read Stratiotes
	13	7	82; read 83
	14	6	dedails; read details
	24	18	tonic; read toxic
		38	,, ,, ,,
	38	45	in; read is
	41	3,4,5	Fig. 7; read Fig. 6
	45	2	48; read 44
	61		Fig. 17. Percentual ...; this paragraph must be left out
	62	44	Den hartog; read Den Hartog
	66	34	af; read of
	72	1	underneath Table 17 field; read fields
	82	6	Tjeukermeer; read Tjeuke meer
		7	Productivily; read Productivity
		16	Lindenvallei; read Lindevallei
		18	,, ,, ,,
		51	,, ,, ,,
	83	8	Hadderringh; read Hadderingh
	85	47	Segal, s.; read Segal, S.