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The oligochaete fauna of running waters with special consideration of the relationships between the colonization by Tubificidae and the Substrate

by Bodo Wachs

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THE OLIGOCHAETE FAUNA OF RUNNING WATERS
WITH SPECIAL CONSIDERATION OF THE
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BY TUBIFICIDAE AND THE SUBSTRATE

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From the Bavarian Biological Research Institute
 (Demoll-Hofer Institute) Munich, Director: Prof. H. Liebmann

THE OLIGOCHAETA FAUNA OF
 RUNNING WATERS, WITH SPECIAL
 CONSIDERATION OF THE RELATIONSHIPS
 BETWEEN THE COLONIZATION BY
 TUBIFICIDAE AND THE SUBSTRATE*

By Bodo Wachs, Munich

With plates 4 to 5, 37 illustrations and 21 tables
 in the text and in 3 supplements.

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* Thesis from the University Munich

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1 . I N T R O D U C T I O N

The wealth of forms and the species-specific mass proliferation of the oligochaetes lead to the result that they have a considerable share in the formation of the benthos in running waters. The character of the substrate changes with increasing distance from the source, because the diminishing gradient results in a reduction of the stream velocity and a correspondingly greater sediment load in the stream.

Consequently, various life communities have developed that are characteristic for the diverse substrates in which their members must find optimum living conditions.

Since most of the oligochaetes are substrate feeders, those of their limnetic species that are prone to mass proliferation will also play a decisive role in the metabolism in the sediments.

Thus the problem presents itself to obtain on the one hand a comprehensive view of the existing species of an entire stream and of their ecological value by means of systematic and ecological studies and on the other to reach a causal understanding of the field observations through experimental investigations.

I thank Professor Liebmann for providing me with the theme, for his continued interest in the progress of the work and for valuable suggestions and counsel.

Thanks are due to Dr. K. Offhaus, who gave me special directions and put at my disposal a work place in his laboratory for conducting the carbon and nitrogen analyses of the muds.

2 . REVIEW OF THE LITERATURE

Except for a few papers, oligochaetes have always been ignored in the reports on the ecology of running waters. Thus they have not at all been included in the calculations of the abundance of the benthos in running water, and when it has been done, the values should be treated with skepticism. In the older literature that is generally oriented toward systematics, one finds only few ecological remarks among the descriptions of localities. On account of mistakes in systematics and ignorance of the possible range of variation of some species characteristics

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the species themselves and their total numbers collected must, unfortunately, be used with reservations.

Michaelsen (1903) has published the oligochaetes of the Elbe in the region around Hamburg together with remarks on their environments.

Wolf (1928) enlarged the very incomplete knowledge of the species of running waters through his investigations of the populations in the Moldavia around Prague. For the first time the annual cycle of an oligochaete fauna had been investigated through monthly observations at fixed sampling localities. The report contains not only remarks on morphology, but also on the substrate, mode of life and in part also on fluctuations in abundance.

The systematic investigations of Hrabě (1941) in May 1934 in the arms of the Danube delta at Čilistov were also confined to a short stretch of a river.

The oligochaete fauna of a longer stretch of a river or rather of a characteristic stream region attracted the interest of limnologists rather belatedly. Thus the ground-water researches of Noll and Stammer (1953) made known a few species (Phreoryctes gordioides and species of the families Aeolosomatidae, Naididae and Enchytraeidae) from springs of the region of the lower Main.

Dittmar (1955) found 12 species in various substrata of a meadow brook in the Sauerland (Westphalia).

Korn (1963) studied the oligochaete fauna in the greater part of the upper Danube (between Mähringen and Ulm) in order to clarify the relationships between the water quality and the inhabitants. A rather small number of species was found in the individual substrates along the length of the stream of about 170 km. It was stated that the main factors

regulating their distribution were "the sediment in the different small biosystems and the stream velocity".

The distributions of all oligochaetes in the substrates of the lower reaches of the Werra in relation to the effects of the waste waters of the potash industry were investigated by Wachs (1963).

As far as I know, Berg (1948) is the only one, who has considered a stream as an ecological system, including the consideration of its colonization by oligochaetes. Berg gives statements in regard to the preferred substrates for the 37 species reported for the Susaa (with neglecting the Enchytraeidae, which are very complicated systematically). In addition to this there are to be found for the first time remarks based on abundance figures about the distribution of the species along the course of the river that has been divided into upper, middle and lower reaches.

Wachs (1964) undertook the study of the entire oligochaete fauna of the about 340-km-long stretch of the Weser from Hann.-Münden to Bremen, which represents the so-called metapotamon of the Fulda according to the arrangement of ecosystems of Illies (1961 a). The results that are based mainly on single investigations demonstrate the occurrence of 30 species in the types of substrates present. The attempt has been made to include, on hand of the substrates mud, sand and gravel, the dependence on the substrate among the problems of ecological research by taking into account the number of the species and genera that can be present in a uniform environment and of their percentage distribution in it.

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However, not one of the authors of the papers mentioned has tested experimentally the relations observed in the natural waters and elaborated his conclusions. Comprehensive field observations are the prerequisite for the research into the dependence of the organisms on the

factors of their environment. At the same time such research should stimulate attempts to elucidate the causal relationships through experimental research, because only experiments provide the possibilities for a comprehensive explanation of the complex of ecological factors.

3 . C O L L E C T I N G L O C A L I T I E S A N D M E T H O D S

3 . 1 C o l l e c t i n g o f O l i g o c h a e t a

The investigations have been carried out in a stream of hilly country (Fulda) and one of the Alpine foothills (Isar), in each case during a full annual cycle.

The Fulda, the largest river of the Hessian hill country, has its source on the Wasserkuppe in the Hohe Rhön and it forms the Weser by confluence with the Werra at Hann.-Münden. Samples of the substrates were collected during the period January 1962 to January 1963 at intervals of two months at 14 stations (A to O) along the about 230-km-long river (see Fig. 2).

The Isar, of a length of 276 km, which rises in the Austrian part of the Karwendel Mountains, was investigated along its middle reaches and the first half of the lower reaches during the period from May 1963 to April 1964. Samples were collected once a month at the collecting stations in the natural stream bed of the Isar (stations P, R, U), three times at the storage lake¹ (station S) that is interposed in the Middle-Isar-Canal and once at each of the dams of the lower Isar

¹ I thank Dr. H. Schulte - Bayernwerk A.G., Munich - for making possible the investigations at the storage lake that were carried out from a motorboat.

(stations T, V to Y) (see Fig. 3).

At the periodically visited collecting localities the oligochaete fauna of all substrates that were present was sampled to a water depth of about 1 m, both qualitatively as well as quantitatively.

Because not much time was to be devoted to sampling, I used the following simple methods after having tried various devices and aids.

When the deposits had at least a thickness of about 15 cm, the sampling of mud and sand was carried out with the dredge after Ekman and Birge (15 X 15 X 15 cm³ and 10 X 10 X 11 cm³). At stations A to R and station U each sample consisted of a substrate amount of 225 cm² surface by 15 cm depth and at stations S, T, V to Y of a substrate amount of four times (100 cm² surface by 11 cm depth). Where the sedimentation was less I used a grocer's scoop of cast aluminium, which had a length of 16 cm, a width at the bottom of 5.5 cm and the bent-up sides of which had a greatest height of 5 cm. This was used to fill the mud, sand or gravel samples carefully into a plastic cup of 2.5 dm³ capacity containing 1 dm³ of water, until the fill reached the 1.5 or 2 dm³ mark (depending on the population density). In the case of gravel a sample was taken at each station that corresponded to a water volume of 1 dm³; the river water contained in the gravel sample was first drained off through a net of 0.2 mm mesh. Sand was collected in most instances in an amount of 0.5 dm³. During collecting precautions were always taken to ensure that the surface of the substrate sample in the stream bed with a volume of 0.5 dm³ was always equal to that of an Ekman dredge (15 X 15 cm²) for reasons of the subsequent statistical evaluation. [p. 314]

Rocks were brushed off carefully with a perlon brush in a water-filled plastic dish and their largest surface was measured afterward

(according to Schröder 1932). A sample consisted generally of about 1000 cm² rock surface.

Plants were detached from the substrate or cut off with scissors, collected in a net of 0.08 mm mesh and their volume measured in a beaker by means of their water displacement. Depending on abundance, an amount of either 0.5 or 1 dm³ of plant material was collected in each case.

Gastropods were collected singly in water-filled vials in order to demonstrate the presence of Chaetogaster limnaei.

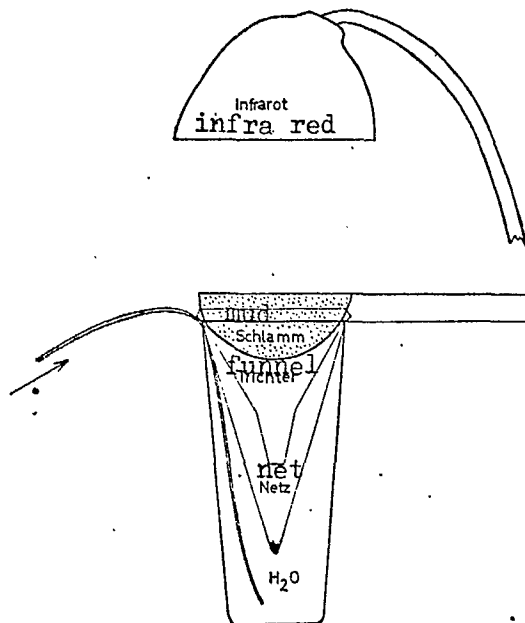


Fig. 1. Apparatus for the quantitative separation of tubicifides from mud samples.

A perlon net ("Monodur") of 0.45 mm mesh was used for sieving the mud samples at stations P to Y. Plant samples were sieved in a perlon net of 0.08 mm mesh. A perlon net with 0.20 mm mesh was used for all other substrates. Smallest amounts of sand, gravel and plants were washed repeatedly and sieved, so that near 100 per cent collecting efficiency was assured. The sieved-out sand material was transferred subsequently to watertight glass jars. For safe transport as well as for storing the

material for several days in a refrigerator it is absolutely necessary to leave only enough water in the glass jars as is required to keep the samples damp.

Only enough sieved material - thinned with water - was transferred under a binocular to Petri dishes to cover the bottom not deeper than 2 mm according to the transparency of the material. The animals collected were identified immediately under the microscope. [p. 315]

In order to obtain exact values for the abundance of the tubificids also for the mud and mud-sand substrates at stations F to O, the corresponding sieved samples were treated in the separating device shown in Fig. 1, which has already been described elsewhere (Wachs 1965). The heat generated by an infra-red lamp (150 w) causes a negative thermotactic reaction in the oligochaetes, which leads to their automatic, gentle separation. This efficient procedure provides an indication of the population density in muds without loss of time. After separation at least 100 tubificids of each sample were made into squash preparations and identified. The remaining specimens were counted and their numbers were distributed as percentages among the species according to the results of the identifications.

The photographs of characteristic organs of the oligochaetes were made from permanent mounts, for which were used living animals or body sections embedded in highly fluid "Celodal" (Bayer).

3 . 2 C h a r a c t e r i z a t i o n o f t h e C o l l e c t i n g L o c a l i t i e s

The topography of the collecting localities will be described briefly in the following. The papers by Schmitz (1949) and Scheele (1952)

give detailed descriptions of the geology and morphology of the Fulda region. The hydrology of the Isar has been reported on by v. Ammon and Stammer (1958).

The collecting localities of the Fulda (Fig. 2):

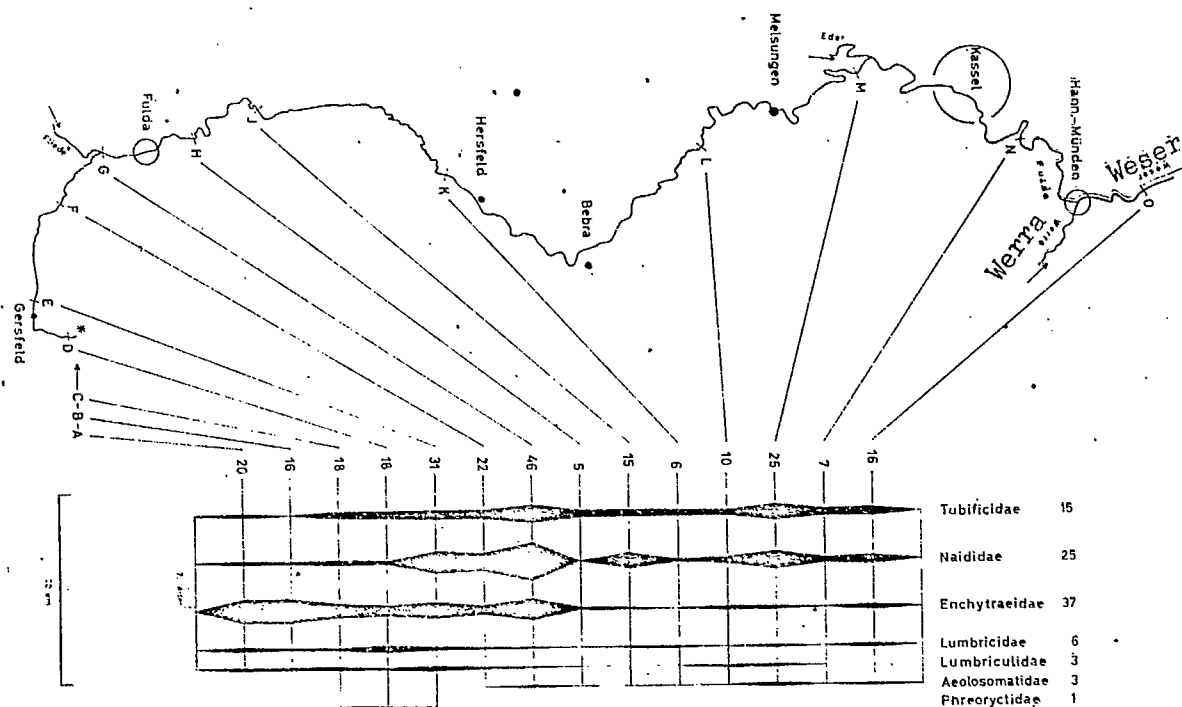


Fig. 2. Sketch map of the Fulda with collecting stations and the distribution of the species of the individual families of oligochaetes. Numbers at the stations indicate the sum of the species living there; The numbers following the families indicate the sums of their species that make up the fauna of the whole length of the stream.

Station A: Running source at an altitude of 820 m above sea-level with weakly acid and very soft water (see Table 4 and Fig. 17). Partial sedimentation of fine mud on subsoil consisting of calcareous sand. The source region of the Fulda lies on the south slope of the 950-m-high Wasserkuppe. In addition to a small number of boggy springs, the two running springs that have been investigated form the origin of the river.

Station B: Largest source at an altitude of 852 m above sea-level, whose

water issues from iron pipes and runs for a distance of 17 m over basaltic scree.

Station C: Situated 120 to 125 m below source B in a small boggy area that has been formed on the rather impervious Miocene basalt of the steppe-like slope of the Wasserkuppe. Sedimentation of fine mud, rich in plant remains.

Station D: Confluence of all source branches after 0.9 to 1.0 km in an alder thicket. Stream bed with a width of 1 to 2.2 m with basalt blocks and coarse rubble, between which small pools have formed. Rocks overgrown with Fontinalis antipyretica.

Station E: Below Gersfeld at about kilometre 7. Stream bed about 2.5 to 3 m wide, with basalt and sandstone rubble and predominant sand deposits. Already distinctly polluted with domestic effluents (see Figs. 18 and 19).

Station F: Near the community of Lütter at about kilometre 22. Stream bed 2.5 to 3.5 m wide with coarse and medium rubble. Regions of slow running water (mud sedimentation) are already becoming larger.

Station G: At about kilometre 34 between the mouth of the Fliede, which is rendered slightly salty through the effluents of the potash industry (doubling the water mass of the Fulda) and the village of Ziegel. The 13-m-wide stream bed is characterized by the variety of its substrata.

Station H: Extensive dammed up area near Kämmerzell near about kilometre 48. "secondary formation of sapropel" (according to Demoll and Liebmann 1952) caused by the dying of Sphaerotilus natans.

Station J: Near the village of Pfordt at about kilometre 63. The stream

is 30 m wide, with gravel as the predominant substrate.

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Station K: In the neighbourhood of Asbach at about kilometre 91. There are large deposits of sand in the quiet parts of the 55-m-wide gravelly stream bed.

Station L: Near kilometre 147 and the village of Neumorschen. Extensive deposits of sand on the 37-m-wide gravelly stream bed.

Station M: In Guxhagen near kilometre 181. Width of stream 58 m. Rocky-gravelly bottom predominant.

Station N: Near the village of Wahnhausen at about kilometre 216. Sedimentation of muddy sand in stretches of slow current on the approximately 60-m-wide stream bed.

Station O: Above the village of Vaake at about kilometre 238 (= Weser kilometre 9). Deposits of muddy sand behind the groynes of the 76-m-wide stream. The chemism of the Weser water (see Figs. 17 to 20 and Table 4) can be explained by the influx of the Werra, which is strongly salty on account of the effluents from the potash industry (see Wachs 1963, 1964).

The Isar stations (Fig. 3):

Station P: At Isar kilometre 117.9 in the neighbourhood of Grünwald.

Since the Alpine river has a higher waterlevel in summer than in winter and since its water power has been harnessed by numerous canals and dams, the water depth of the natural bed of the Isar is subject to considerable fluctuations (see also v. Ammon and Stammer 1958). The largest part of the gravelly, 50-m-wide stream bed is dry during almost the entire year. Mud samples were taken at the shore of the canal running

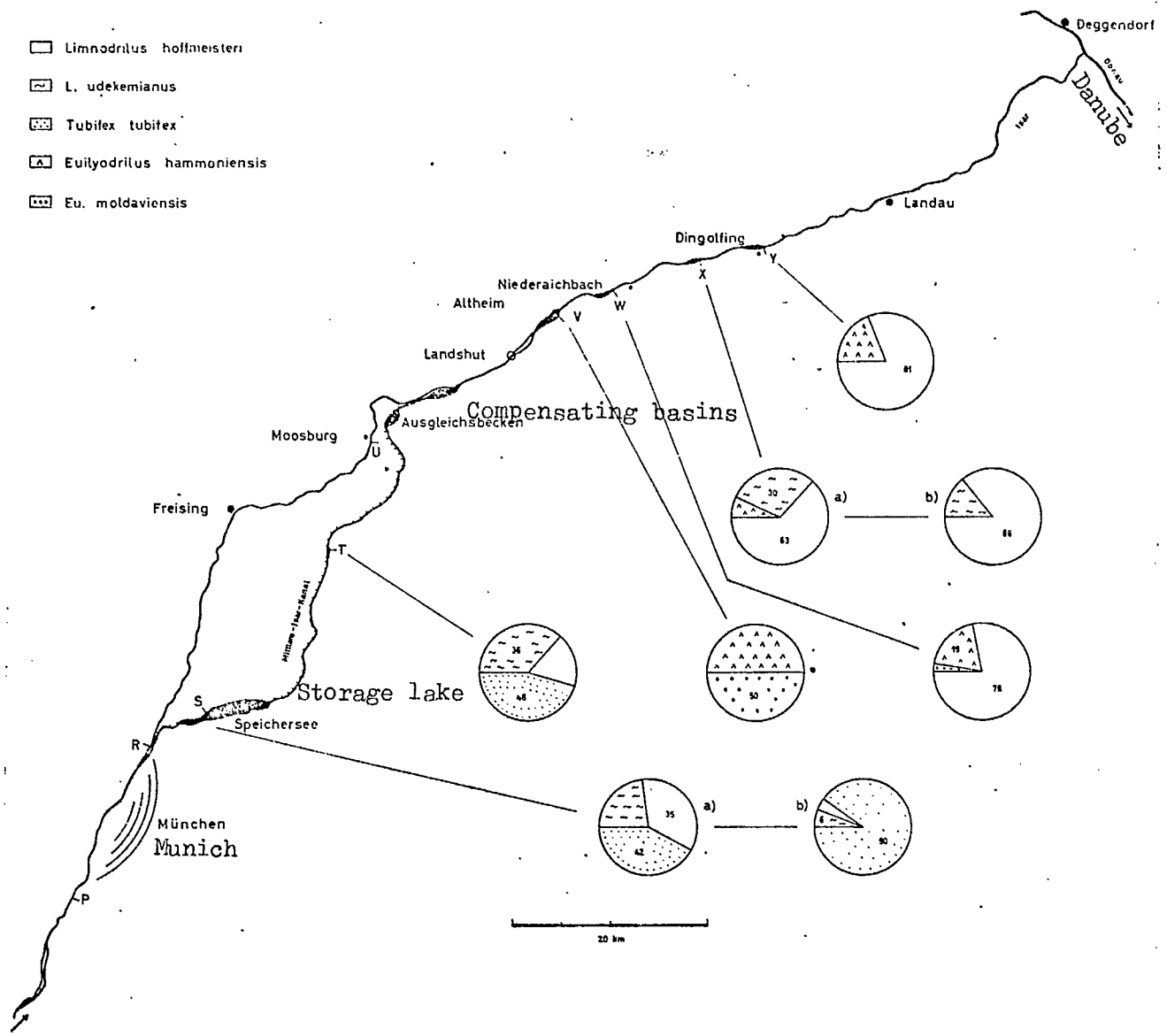


Fig. 3. Sketch map of the research area of the Isar and distribution of the species in the inlet of the storage lake and at the dams.

parallel to it.

Station R: Near the village of Unterföhring at kilometre 137.0. Stream bed is 56 m wide and has a gravelly bottom.

Station S: At the end of the first 10-km stretch of the Middle-Isar-Canal at the entrance into the storage lake, which receives the fully mechanically pre-cleaned sewerage of Munich, which is

further cleaned biologically in the sewerage fish-pond installation of the Bayernwerk A.G. (For details see Liebmann 1960 a, pp. 534-46). Deposits of sapropel.

Station T: At the dam of the power station Eitting at kilometre 35 of the Middle-Isar-Canal (= Isar kilometre 170). Investigated on May 15, 1963.

Station U: Near the village of Moosburg at kilometre 182.8. Stream bed 59 m wide, with gravelly bottom.

Station V: At the dam of power station Altheim (completed 1951) at kilometre 211. Investigated on August 12, 1963.

Station W: At the dam of the power station Niederaichbach, which came into use in 1951, at kilometre 217. Investigated on October 10, 1963.

Station X: Power station Gummering (completed 1957) at kilometre 225. Sample "a" taken 100 m above the dam, sample "b" taken 800 m above the dam. Investigated on July 15, 1963.

Station Y: At the dam of the power station Dingolfing that has been taken into use in 1957, at kilometre 232. Investigated on July 15, 1963.

3 . 3 A n a l y s e s o f S u b s t r a t e s

The samples for the chemical characterization and the determination of the grain composition of the muds were collected with the small Ekman bottom dredge (10 X 10 X 11 cm³). Sampling took place at stations A, C, E to H, K, N to R and U (April, August and December 1963) and at station S (May and August 1963 and April 1964) altogether three times each and at the Isar dams (V to Y) only at the time of the single

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investigations. After a thin surface layer had been removed, the mud was taken from a depth of 1 to 10 cm, sieved through a net with a mesh of about 1 mm and then dried in the incubator at 105°C. Amounts of 30 g each of dry substance of the muds at stations A to S and U were obtained and an amount of 90 g each of dry substance was collected from the muds of the dams. The dry substance was broken up in a mortar and then homogenized. There was thus available for each collecting station an amount of 90 g (approximately) of homogeneous starting material for the substrate analyses.

3 . 3 1 G r a i n s i z e o f t h e s u b s t r a t e s

An amount of 50 g each of dry substance was used for the separation of the grain sizes of the muds (between the limits of 0.1 to 0.001 mm). This was done by the sedimentation method after Bouyoucos-Casagrande that has been described as the hydrometer method by Schulte and Muhs (1950) and Köster (1960). The density of the suspension that changes according to the sedimentation process is measured with the hydrometer. During analysis 8 ml of a six-per cent solution of Na_2SiO_3 were added as anticoagulant. The specific weight of the river muds varied between 2.31 and 2.75; it was 1.97 g/cm³ for the kaolin used as artificial substrate. In order not to exceed the value of $R = \pm 0.2$ of the reading accuracy of the hydrometer at the beginning of each analysis, the measurements were carried out in quadruplicate during the period of 15 sec to 2 min. The grain distribution of the mixed-grain substrates (among others, of all river muds) had to be obtained through a combined analysis (hydrometric and sieving analysis).

The grain size of the sands found at the collecting stations

was determined twice a year for 500 cm³ each of dry sand with the test sieving machine "Lavib" (model ST 52), which works with batches. The values, given as volume per cent, represent the means of the two measurements.

The grain size of the gravels that are on the stream bottom always mixed with sand was determined once by means of 2 dm³ of substrate and has also been given as volume per cent. Hand-held sieves were used for processing the fractions of gravel from sand size to medium size gravel.

3.32 Chemical analyses of the muds

The following methods were used for the chemical characterization of the muds:

Water content: weighing before and after drying at 105°C (cf. Morgans 1956).

The values have been given as weight per cent of the wet mud.

For all following methods it was necessary to determine also the water loss of each starting substance. This was determined through a two-hour treatment in the drying pistol; it was lying in the different samples between the limits of 0 to 3 per cent. It was taken into consideration during the weighing before the start of the analyses.

Organic substance: glow loss at 500°C after 2 h (v. Ammon 1961).
Values given in per cent of dry substance.

Carbonates: difference between the glow loss at 500°C (2h) and at 800°C after a further 20 min (v. Ammon 1961). Given as per cent of the dry residue.

For the following procedures the dry substance that had been reduced to small pieces in the mortar, had to be reduced to a powder in a ball mill. Depending on the scatter of the results, two to four analyses were made for each sample and their mean value was calculated.

Organic carbon: method of Gertner and Iveković after the description by Offhaus (1959). Conduction of the wet oxidation with chromosulfuric acid and an $H_2SO_4 - H_3PO_4$ mixture. Gravimetric measurement of the absorbed CO_2 .

Total nitrogen: Kjeldahl decomposition with concentrated H_2SO_4 and selen reaction mixture. Titrimetric determination of the NH_3 that had distilled over.

3 . 4 C h e m i c a l A n a l y s e s o f t h e W a t e r

Chemical analyses were carried out during the period from January to September 1962 every eight to ten weeks in every case on the forenoon at the selected collecting station along the Fulda (near the substrate). The following methods were used:

pH value: electrical method.

Conductivity: conductometric.

Total hardness: chelatometric measurement with Titriplex B (or A).

Oxidizability: determination of the consumption of $KMnO_4$ (German standard methods, 1960).

Actual O_2 concentration: iodine-difference method after Ohle (German standard methods 1960).

Relative O_2 saturation: calculation with the O_2 calculator of Burkhard

(1955) and the nomogram of Mortimer (1956) with consideration of the water temperature and the mean local pressure according to the altitude above sea-level.

- Free CO₂: titrimetrically with NaOH (German standard methods 1960).
- Chloride: volumetric with silver nitrate (German standard methods 1960).
- Nitrite: qualitative proof with zinc-iodine-starch solution.
- * Nitrate: photometrically with brucine solution in the LEIFO-E.
- * Sulfate: iodometric with barium chromate.
- * Phosphate: photometrically with molybdenum-sulfuric acid in the LEIFO-E.
- * Total iron: photometrically with potassium thiocyanate in the LEIFO-E.
- * Na, K, Ca ions: flame photometer PF 5 by Carl Zeiss.
- * Mg ions: compensating photometer "LEIFO-E" by Leitz.

4 . S Y S T E M A T I C S O F T H E S P E C I E S D E T E R M I N E D

The oligochaetes were examined under the microscope or binocular only while they were alive. In order to be able to recognize the spermatheca in the rather opaque Enchytraeidae, a few drops of an orceine [p. 320]

* The analyses marked with an asterisk have kindly been carried out by Dr. Müller-Haeckel.

solution were added to the preparation (after Nielsen and Christensen 1959). It is necessary to examine most lumbricids with the binocular also after they have been fixed in 96 per cent alcohol for the better recognition of some morphological characteristics. It was possible to identify animals of all age classes, except for representatives of the families Tubificidae, Enchytraeidae, Lumbriculidae and Lumbricidae. In the families cited juvenile specimens could be identified as to species only in the genera Aulodrilus, Propappus, Cernosvitoviella and Cognettia.

The identification of species was carried out on hand of the systematic works by Ude (1929), Sperber (1948, 1950), Wilke (1949), Graff (1953), Nielsen and Christensen (1959, 1961, 1963) and Brinkhurst (1963), as well as with the aid of tables from two papers by Hrabě (1929, 1960). The systematic arrangement is based on that proposed for the oligochaetes by Michaelsen (1929) and by Kaestner (1955).

Only morphological characteristics that show considerable variation will be discussed in the list of the species collected.

Suborder: P l e s i o p o r a

A e o l o s o m a t i d a e :

1. Aeolosoma hemprichi Ehrenberg 1831.

Liquid globules in the epidermis mostly dark brownish yellow, seldom red or colourless, especially numerous at the ends of the body.

2. A. variegatum Vejdovsky 1884.

Liquid globules light green.

3. A. quaternarium Ehrenberg 1831.

Up to five hair bristles in the bundle.

N a i d i d a e :

4. Chaetogaster diastrophus (Gruithuisen) 1828.

In II at most seven bristles in the bundle.

5. Ch. langi Bretscher 1896.

In II (3)-5-7-(9) bristles in the bundle.

6. Ch. diaphanus (Gruithuisen) 1828.

Length of the duplet chains up to 11 mm.

7. Ch. cristallinus Vejdovský 1883.

8. Ch. limnaei von Baer 1827.

Mostly not more than ten bristles per bundle.

9. Specaria josinae (Vejdovský) 1883.

Coloration faint reddish.

10. Uncinaiis uncinata (Ørsted) 1842.

Anterior body as far as VIII-(X) strongly pigmented with yellow-brown and with large green spots; coloration changing to dark brown posteriorly.

11. Ophidonais serpentina (Müller) 1773.

Anterior body strongly dark yellow mostly as far as V, the following segments rusty brown or dark red. The mostly strong yellow colour of the gut is covered in the middle section by dark brown, crowded chloragogene cells. Dorsally 1-(2) bristles.

12. Nais communis Figuet 1906.

Coloration often light red or red. Eyes sometimes lacking; rarely only one eye present.

13. N. variabilis Figuet 1906.

Very rarely up to three needle-like bristles in the bundle.

14. N. simplex Piguët 1906.

15. N. alpina Sperber 1948.

Mostly colourless, rarely with yellow or red-brown pigmentation to VI. Eye spots very rarely absent.

16. N. barbata Müller 1773.

Yellowish brown coloration of the anterior body often with green pigment spots.

17. N. pseudobtusa Piguët 1906.

18. N. behningi Michaelsen 1928.

Colourless. Ventral bundles on II to V with 5-7 bristles. Proximal prong of these bristles at most half as long as the distal one.

19. N. bretscheri Michaelsen 1899.

Coloration yellow or heavily red-brown to V, from VI on dark brown. Ventral bristles from VII or VIII on mostly very thick (cf. Sperber 1948, p. 123, Fig. 13: H-L), the large bristles of type 2 occur less frequently (cf. Fig. 13: E-G, M).

20. N. pardalis Piguët 1906.

Ventral bristles from VI on of normal size and with forked prongs of equal length.

21. N. elinguis Müller 1773.

Anterior end reddish brown, yellowish or yellowish brown.

22. Slavina appendiculata (Udekem) 1855.

23. Vejdovskyaella comata (Vejdovský) 1883.

24. Stylaria lacustris (Linnaeus) 1767.

Anterior end mostly dark yellow with rust brown pigment spots, coloration of remaining segments dark brown. Ventrally 4-7-(10) bristles in the bundle as far as V.

25. Dero obtusa Udekem 1855.

26. Pristina rosea (Piguet) 1906.

Ventrally 2-7 bristles per bundle.

27. P. menoni (Aiyer) 1930.

Colourless, rarely faintly reddish.

28. P. amphibiotica Lastočkín 1927.

29. P. foreli (Piguet) 1906.

Coloration rarely pink.

T u b i f i c i d a e :

30. Tubifex tubifex (Müller) 1774.

31. T. ignotus (Stolc) 1886.

32. T. nerthus Michaelsen 1908.

At most three hair bristles in the dorsal bundle.

33. Psammoryctes barbatus (Grube) 1861.

Maximum length 8 cm. Ahead of the clitellum up to seven fan bristles in the bundle (Fig. 4). The proximal prong of the forked dorsal bristles is considerably wider and longer than the distal. The angle increases continuously with the rising segment number. Consequently the prongs of the bristles of the posterior end diverge by $\pm 90^\circ$ (Fig. 5). The shape of the dorsal bristles - of the fan bristles as well as of the forked bristles - is characteristic for the species also already in the immature stages (cf. v. Bülow 1957).

34. P. albicola (Michaelsen) 1901.

[p. 322]

35. Limnodrilus claparedeanus Ratzel 1868.

Maximum length 8 cm. Ahead of the clitellum 5-8-(9) bristles in the bundle. The exact description of the penis tube (Fig. 7 a), the maximum length of which was 1.42 mm, is to be found already in Wachs 1965).

36. L. hoffmeisteri Claparède

Greatest length 8 cm. Ahead of the clitellum up to 9 bristles in the bundle (Fig. 6). Penis tube (Fig. 7 b) not over 655 microns long.

37. L. udekemianus Claparède 1862.

Greatest length 11 cm. The last one-fourth of the body usually has yellow (brownish yellow) pigment spots, which appear rarely also in L. claparedeanus, but which are always lacking in L. hoffmeisteri and L. helveticus. Ahead of the clitellum up to 9 bristles in the bundle. Greatest length of penis tube (Fig. 7 d) 269 microns. Toward its outer end it has usually a more or less strong constriction, after which follows the broadly expanded cap.

38. L. helveticus Figuet 1913.

Greatest length 4.5 cm. Ahead of the clitellum up to 11 bristles in the bundle. The forked prongs of the bristles are of equal length (very rarely slightly longer distally) and always rounded off. The blunt prong ends are thus widely distributed also among specimens from running water (contrary to the concept of Figuet and Bretscher 1913 and Brinkhurst 1963) and they are not exclusively characteristic of lacustrine specimens. Penis tube (Fig. 7 c) in general about 10 microns longer than that of L. udekemianus and at the most 269 microns long. The cap of the tube that ends in two points is characteristic for the species.

39. Pelosclex ferox (Eisen) 1879.

40. Euliyodrillus hammoniensis (Michaelson) 1901.

Dorsal bundles ahead of clitellum with 3-6-(8) forked bristles and ventral bundles with 3-6-(9) forked bristles. Whereas the central

forked bristles resemble the ventral and dorsal ones of Tubifex tubifex and have a sigmoid shape, the dorsal bristles mostly are bent only above the nodulus into a sickle shape (Fig. 8). In addition their prongs include a smaller angle than those of the ventral ones. Spermathecal sex bristles at most 283 microns long (cf. Wachs 1965, Fig. 6).

41. E. moldaviensis (Vejdovský et Mráček) 1902.

Ahead of the clitellum up to 9-(12) bristles in the bundle.

42. Rhyacodrilus coccineus (Vejdovský) 1875.

The bundles ahead of the clitellum at the most with 6 dorsal and 8 ventral forked bristles. Two to five penial bristles in the bundle.

43. R. falciformis Bretscher 1901.

Bundles ahead of the clitellum with three to six bristles. Penial bristle at most 145 microns long.

44. Aulodrilus limnobius Bretscher 1899.

Coloration pale pink.

45. A. pluriseta (Piguet) 1906.

Coloration glowing (pink-) red.

E n c h y t r a e i d a e :

46. Propappus volki Michaelsen 1915.

Length to 9 mm. Number of segments 39 to 50. Coloration whitish, more rarely faintly reddish. Enlargement of gut in XII-XV possible.

Spermatheca extending from IV-X-(XII), with mostly pear-shaped ampulla and long excretory duct that contracts in V (Fig. 9).

47. Mesenchytraeus glandulosus (Levinsen) 1884.

48. M. armatus Levinsen 1884.

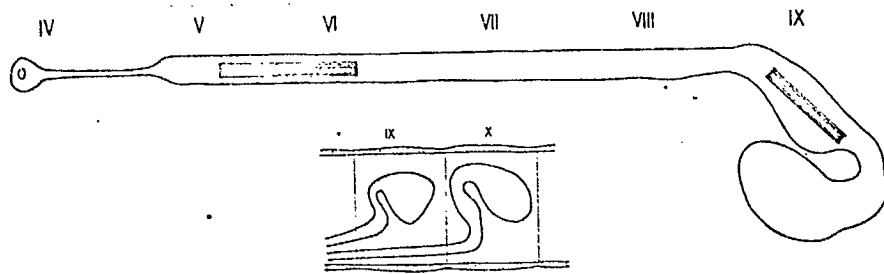


Fig. 9. Propappus volki. Spermatheca.

49. M. beumeri (Michaelson) 1886.

Ventral bristles number 5-7-(11) ahead of clitellum.

50. Cernosvitoviella atrata (Bretscher) 1903.

Blood very rarely reddish. Number of segments (18)-19-24-(28).

Ahead of the clitellum (3)-6-9-(15) bristles in the bundle. Temporarily up to three ripe eggs present. There are always three different shapes of spermatheca (Fig. 10) that differ in most cases only in the length of the excretory duct (shape in centre and at right in Fig. 10; cf. Nielsen and Christensen 1959, Figs. 15 and 16). The specimens investigated do not show a correlation between the number of segments and the length of the spermatheca. The specimens with a larger spermatheca have in general a greater body diameter and show a less dense arrangement of the lymphocytes.

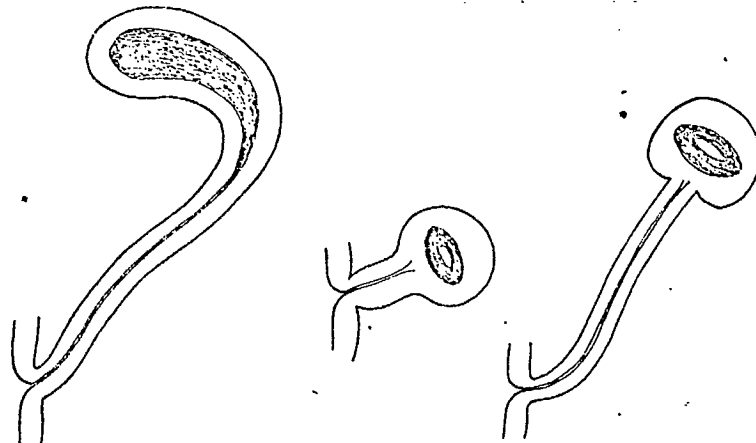


Fig. 10. Cernosvitoviella atrata. Various forms of the spermatheca.

51. Cognettia sphagnetorum Vejdovský 1877.

At most 81 segments.

It was hardly ever possible to make use of the spermatheca as an important characteristic for the identification of the two Cognettia species, because the specimens attain sexual maturity only extremely rarely. Christensen (1959) demonstrated asexual propagation through fragmentation.

52. *C. glandulosa* (MICHAELSEN), 1888.
53. *Achaeta bohémica* (VEJDOVSKÝ), 1879.
54. *Enchytronia parva* NIELSEN et CHRISTENSEN, 1959.
55. *Stercutus niveus* MICHAELSEN, 1888.
24—27 Segmente. (2)-3-(4) Borsten im Bündel.
56. *Henlea perpusilla* FRIEND, 1911, augm. CERNOSVITOV, 1937.
57. *H. nasuta* (EISEN), 1878.
58. *H. similis* NIELSEN et CHRISTENSEN, 1959.
Mindestens 37 Segmente.
59. *H. ventriculosa* (UDEKEN), 1854.
60. *Buchholzia appendiculata* (BUCHHOLZ), 1862.
61. *B. fallax* MICHAELSEN, 1887.
Mindestens 35 Segmente.
62. *Bryodrilus ehlersi* UDE, 1892.
63. *Fridericia bulbosa* (ROSA), 1887.
64. *F. bulboides* NIELSEN et CHRISTENSEN, 1959.
65. *F. callosa* (EISEN), 1878.
66. *F. bisetosa* (LEVINSEN), 1884.
67. *F. perrieri* (VEJDOVSKÝ), 1877.
68. *F. galba* (HOFFMEISTER), 1843.
69. *F. ratzei* (EISEN), 1872.
70. *F. hegemon* (VEJDOVSKÝ), 1877.
71. *Enchytracis albidus* HENLE, 1837.
72. *E. buchholzi* VEJDOVSKÝ, 1879.

[p. 324]

73. Lumbricillus rivalis Levinsen 1883, augm. Ditlevsen 1904.

It was possible to demonstrate through the investigation also of artificially salted running waters that a reduction in the salt content results in a continuous alteration of the body shape. Body length, number of segments, number of bristles per bundle and size of the sperm funnel become reduced. As can be seen from the following summary (Table 1), in specimens from

Table 1. Morphological changes in Lumbricillus rivalis in dependence on the salt content of the water.

Characteristic	Baltic Sea/ Denmark	Ulster 30 ‰	Werra 0,7—16 ‰	Weser 1,4—3,6 ‰	Fulda	Percolation filter
	NIELSEN & CHRISTENSEN, 1959	WACHS, 1963		WACHS, 1964	WACHS	
Bodylength (mm)	20—35	18—35	11—22	/	9—18	9—18
Number of segments	(50)—54—56—(60)	52—60	43—56	36—48	(30)—34—48	45—55
Bristles dorsal ahead of scutellum	6—9	/	4—7	/	3—7	3—7—(8)
Bristles ventral	7—12	/	(5)—6—7—(9)	/	4—8—(9)	4—9—(10)
Bristles dorsal back of scutellum	5—8	/	3—5—(6)	/	3—5	3—7
Bristles ventral	6—10	/	(4)—5—7—(8)	/	(4)—5—7	4—8—(9)
Sperm funnel (length : width)	ca. 10	/	ca. 4—6	/	ca. (3)—4	ca. 4

the (salt-free) medium of a lightly loaded percolation filter (on the sewerage test field of the Bavarian Biological Research Institute), which have been examined, only the number of segments was higher than in specimens from river water not polluted with salt.

[p. 326]

74. L. kaloensis Nielsen et Christensen 1959.

Length 10-12 mm. 28-34 segments. Spermatheca (Fig. 11) strongly narrowed toward the outside.

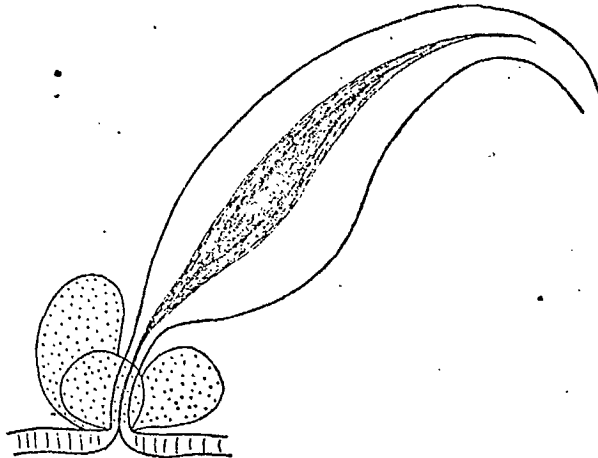


Fig. 11. Lumbricillus kaloensis. Spermatheca.

75. L. lineatus (Müller) 1774.

Greatest length 15 mm. (22)-24-26-(28) segments in contrast to the 38-42 of the marine specimens described by Nielsen and Christensen (1959).

76. L. pagenstecheri (Ratzel) 1869.

77. Marionina argentea (Michaelson) 1889.

At most 28 segments.

78. M. filiformis Nielsen et Christensen 1959.

At most 27 segments.

79. M. communis Nielsen et Christensen 1959.

80. M. tubifera Nielsen et Christensen 1959.

81. M. riparia Bretscher 1899, augm. Cernosvitov 1928.

23-38 segments.

82. M. appendiculata Nielsen et Christensen 1959.

II. Suborder: P r o s o p o r a

L u m b r i c u l i d a e :

83. Stylodrilus heringianus Claparède 1862.

84. Lumbriculus variegatus (Müller) 1774.

85. Trichodrillus tenuis Hrabě 1960².

Length up to 15 mm. At most 44 segments.

III. Suborder: O p i s t h o p o r a

P h r e o r y c t i d a e :

86. Phreorvctes gordioides (Hartmann) 1821.

L u m b r i c i d a e :

87. Dendrobaena octaedra (Savigny) 1826.

88. Eiseniella tetraedra (Savigny) 1826.

Different shapes of the cocoon of this species are shown in

Fig. 12.

89 a. Allolobophora caliginosa f. typica (Savigny) 1826.

89 b. A. caliginosa f. trapezoides Dugès 1828.

² I thank Prof. S. Hrabě for the determination of this species.

90. A. terrestris longa (Ude) 1885.

91. A. oculata (Hoffmeister) 1845

92. A. chlorotica (Savigny) 1826.

5. SEXUAL PERIOD OF THE OLIGOCHAETES

Exact statements about the time of sexual activity of aquatic oligochaetes are found only rarely in the literature. They are mostly restricted to occasional references to it.

5.1 Naididae

Stolte (1940) has demonstrated experimentally in the naidds "that a very definite combination of conditions (rich nourishment and optimum oxygen content of the water) leads to the development of sexual organs". The sexual condition is thus inaugurated solely through favourable external conditions and it can be "forced" experimentally at any time. [p. 327]

I found Stylaria lacustris to be sexually mature under natural conditions mainly from September to October, at a time that offers to the oligochaetes, according to Stolte, the optimum conditions in the waters.

Sexual and asexual propagation overlap (cf. Schuster 1915), however, in the naidds of the genera Nais and Pristina that are rich in individuals, which were investigated, the tendency to strong formation of chains is especially marked during the winter months. Schuster (1915) arrived at the opposite result and deduced from it for the naidds in general: "the slightly lower abundance in winter might be caused only by the asexual reproduction being less productive during the winter".

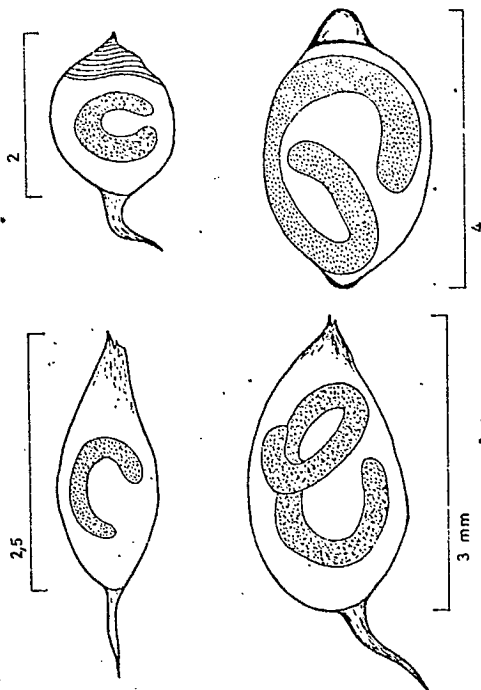


Fig. 12. Eiseniella tetraedra. Different forms of the cocoon.

Table 12 for the genus Nais shows that in my investigations the juveniles of many species of naidds appeared in greater numbers and caused greater population densities in the winter half-year (November - April).

5 . 2 E n c h y t r a e i d a e

It is very difficult to recognize a sexual period in the enchytraeids and it is only possible when not more than a single species of a characteristic genus occurs in the environment.

[p. 328]

According to Reynoldson (1939, 1947), the time of increased sexual activity in Lumbricillus lineatus (this probably applies to L. rivalis) and Enchytraeus albidus in percolation filters falls into the winter half-year, with a maximum from December to March.

I was able to demonstrate on 842 specimens of the species Propappus volki collected in the Fulda and Isar that the abundance values for this species are lower in the winter half-year and that a sexual period exists in the period from (March)-April-September-(October) (Fig. 13).

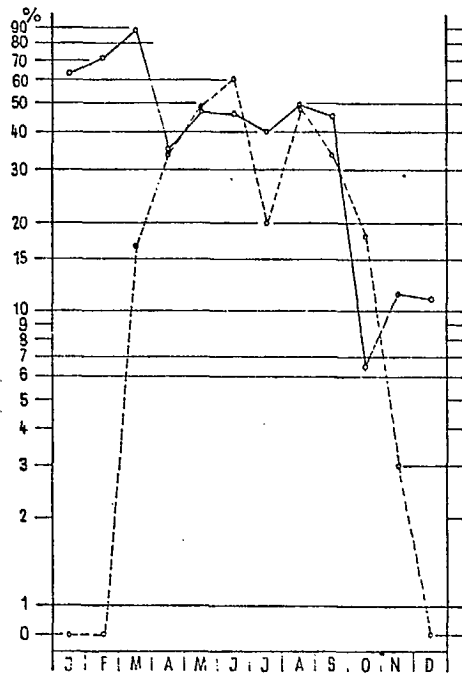


Fig. 13. Percentage share of sexually mature specimens of the species Propappus volki (---) and Stylodrilus heringianus (—).

5.3 Lumbriculidae

In the lumbriculid Stylodrilus heringianus sexually mature animals can be found at any time. It was possible to demonstrate an extended period of sexual activity from January to September through the examination of 2652 specimens (Fig. 13).

5.4 Tubificidae

It will be seen from the account of the seasonal fluctuations in abundance of the tubificids that are rich in individuals, that the population density diminishes noticeably during the cold season (cf. Tables 12 and 13). The cause for this must be looked for in the mode of propagation of these animals.

[p.329]

In the literature are to be found various opinions that are based on occasional observations, since sexually mature specimens can be found at all times. Exact statements about the existence and duration of

a sexual period have hitherto been made only by Poddubnaya (1959). On account of the ice cover on the Rybinsk Dam this author had to do without data for the winter months. She came to the conclusion that Tubifex newaensis, Limnodrilus hoffmeisteri and Euillyodrilus hammoniensis reproduce sexually once in the year from May till July and that the maximum in the number of individuals, combined with the appearance of a new generation, falls into the months July and August. This agrees in general with my results for Tubifex tubifex, Limnodrilus claparedeanus, L. hoffmeisteri and L. udekemianus.

In Fig. 14 the percentage share of sexually mature individuals per month has been given and arranged separately for the substrates mud, sand-mud and sand. The values have been obtained from a total of 26,531 tubificids that have been collected in the Fulda and separated in the apparatus shown in Fig. 1 (described in Wachs 1965). Since the three Limnodrilus species that are being discussed here are always living gregariously in the substrates treated and since they cannot be separated in the immature stages, the specimens collected were lumped together as a genus. The calculations for Tubifex tubifex have been based on specimens from substrates in which other species of this genus and Euillyodrilus hammoniensis and Rhyacodrilus coccineus are entirely or almost entirely absent. Sexually mature specimens of the species treated in Fig. 14 are to be found at all times. There is, however, no continuous transition to a sexual period, but the plainly recognizable maxima indicate a definite span of time. The graph does not show important differences in the propagation cycle between T. tubifex and the Limnodrilus species and the species furthermore show the same tendencies in the different substrates.

The sexual period of the tubificids in the Fulda that have been

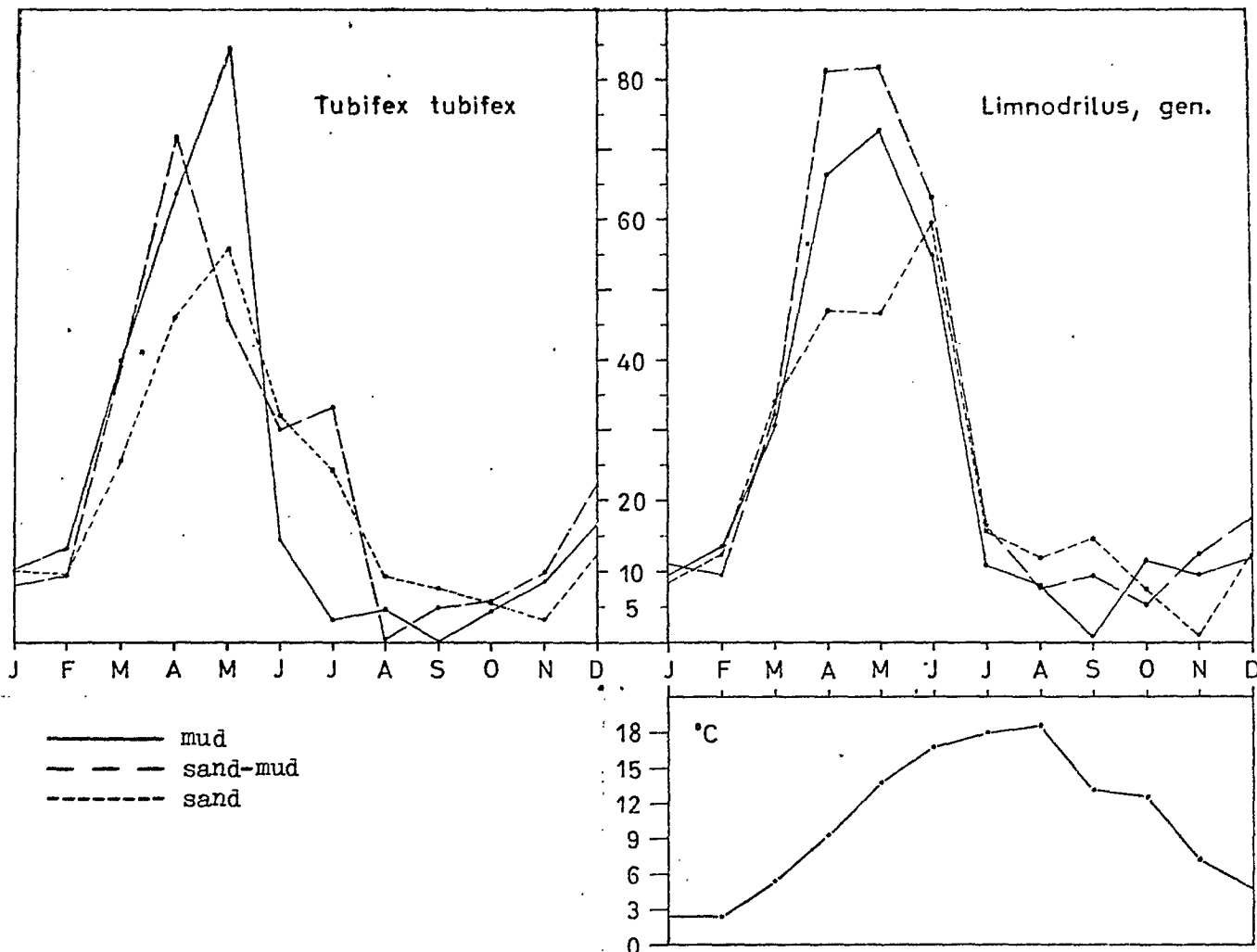


Fig. 14. Percentage share of sexually mature tubificids per month in the Fulda. The graph is based on the following numbers of individuals: in the mud 6,386 *Tubifex tubifex* and 1,369 of genus *Limnodrilus* (*claparedeanus*, *hoffmeisteri*, *udekemianus*); in the sand-mud 4,854 *T. tubifex* and 8,174 of genus *Limnodrilus*; in the sand 3,804 *T. tubifex* and 1,944 of genus *Limnodrilus*. Below right: mean monthly water temperature (January to December 1962 at all stations. The source region (as far as river kilometre 7) has not been taken into account.

taken into account was lying in 1962/63 unambiguously in the period from March to July (inclusively of July, because in this month the calculated values appear to be low on account of the great numbers of young individuals). Thus about 60 to 80 per cent of the individuals were sexually mature.

The curves drop abruptly in July/August and generally form a minimum during the months August to October. This coincides approximately with the point in time (cf. Poddubnaya 1962) at which the very young tubificids appear in greatest numbers: (June)-July-(August).

It was possible to demonstrate in 1962 the presence of tubificid cocoons with living eggs or embryos at stations H and K from January till October (Table 2). They were sieved from the mud at the two stations taken monthly in two Ekman dredgings (450 cm² by 15 cm height). According to the investigations of Poddubnaya (1962) in the Rybinsk Dam, the cocoons are deposited in the mud preferably at a depth of 5 to 10 cm. They were thus reached definitely by the dredge used. The results of this incidental investigation confirm the data for the occurrence of young tubificids that have been given above. [p. 330]

Table 2. Number of the tubificid cocoons per 100 cm² of mud.

Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sept.	Oct.
0.3	1.1	1.7	3.3	6.0	5.1	8.4	4.7	0.9	0.2

The number of eggs per cocoon varies considerably. Specimens of Tubifex tubifex obtained from dealers were kept - without substrate in running water - at a temperature of 10 to 13°C. Three thousand of the cocoons formed in the period from May 1962 to July 1964 were examined (Fig. 15). The cocoons of this species are semi-transparent and white

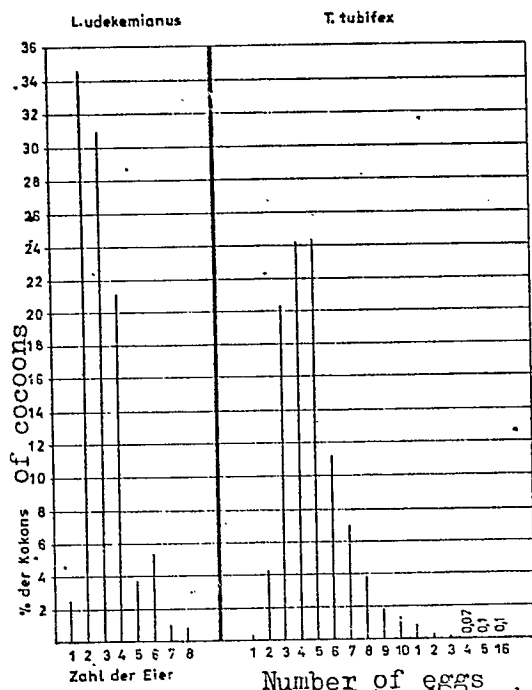


Fig. 15. Percentage share of the cocoons of T. tubifex and of Limnodrilus udekemianus in relation to the number of eggs contained in them.

in a clean medium. However, since they are imbedded under natural conditions in the sedimented substrate, their coloration varies, according to the degree of dirtiness from grey to blackish. The number of eggs per cocoon varies from 1 to 16 and thus shows still greater variability than the range of variation of 6 to 14 found by Penners (1933). In each case more than 1 per cent of the cocoons contain 2 to 10 eggs and more than 20 per cent contain 3, 4 or 5 eggs each. [p. 331]

The number of eggs in the larger cocoons of Limnodrilus udekemianus that are up to 3 mm long could be ascertained in 534 cocoons, which had been produced by worms that had been held in a pure culture (from April to September 1964) (Fig. 15). A maximum of eight eggs are contained in cocoons of this species (whereas Penners 1933 indicates five). Approximately 87 per cent of all cocoons examined contained two to four eggs; the most frequent number of eggs was two.

The very great difference in the number of eggs per cocoon in

the two species investigated allows the conclusion that T. tubifex has a higher potential rate of proliferation - under the assumption that the eggs of the two species have equal fertility. Reynoldson (1943) namely has demonstrated in the enchytraeids that a species-specific degree in sterility can have a compensating effect.

Poddubnaya (1959) conjectures that the duration of the propagation period in the tubificids is determined by temperature conditions. This statement prompted me to summarize the water temperatures that were measured during the period from January to December 1962 in the Fulda at the stations below river kilometre 7 (that is, without the source region) and thus obtain a mean monthly temperature (Fig. 14).

However, the course of the temperature curve does not show a plausible correlation between the point in time and the duration of the sexual activity. It is, however, striking that the majority of young animals appear exactly at the time when the river water has attained its maximum temperature. The biologically advantageous effect of this fact lies in the rapid increase in weight. The higher temperatures accelerate the post-embryonal growth through the increase in the intensity of the metabolism (see chapter 7) (cf. the papers on lumbricids by Michon 1946 et seq.).

The factor temperature also deserves attention in view of the general contention of Bornhauser (1913): "every seasonal effect on the animal community is lacking in springs on account of the constant low temperature". The author thus denies the existence of an annual propagation periodicity in the inhabitants of springs by marking the thermal environmental factor as the sole "timer" (see Aschoff 1958), which disappears as such on account of its constancy. For this reason, the

specimens collected from substrates within the source region were not taken into account when calculating the share of sexually mature tubificids (Fig. 14).

Bornhauser then continues: "the lack of periodicity in propagation has the result that the quantity of the fauna is always of the same size". It is possible that the behaviour of the oligochaetes (that manifests itself, however, periodically in sexuality and population density) is based on an innate rhythm, which could be synchronized to a certain extent with environmental factors and therefore allows local shifts in the time of the cyclic phases and variations in the duration of the periods. For example, Table 3 shows that there are considerable differences during the course of the year in the population density in the Fulda sources (5.5 to 8°C) of Nais communis and of the other oligochaetes. [p. 332]

Table 3. Population density of Nais communis and of the other oligochaetes in the sources of the Fulda (January 1962 to January 1963; abundance for 1 dm³).

Station	Month Substrate	<u>Nais communis</u>					Other oligochaetes						
		I	III	V	VII	IX	XI	I	III	V	VII	IX	XI
A	Sand-mud	14	0	10	36	34	39	32	24	174	142	104	73
B	Gravel a	150	0	39	10	668	997	4	16	13	11	18	23
B	Gravel b	132	3	40	197	192	196	3	10	69	10	2	7

6 . E C O L O G Y O F T H E O L I G O C H A E T E S

It will be attempted in what follows to define and separate as far as possible the ecological factors responsible for the density, composition and distribution of the oligochaete fauna - with special consideration of the tubificid population. The investigations will be based on field observations and on the results of experiments.

6 . 1 O c c u r r e n c e o f t h e O l i g o c h a e t e s
i n D e p e n d e n c e o n t h e C h e m i s m
o f t h e W a t e r

Korn (1963) deduced from his investigations of the importance of the oligochaetes as indicator organisms for the characteristics of the water in streams that "the chemism of the water affects the distribution of the oligochaetes only indirectly through the substrate". As regards the individual components, one should "in most cases not consider a direct relationship", but "this concerns rather more often only a coincidence" and the factors have to be "evaluated quite generally as indicators of the pollution and loading". In addition it appears questionable to deduce optimum living conditions and distribution maxima of the species from the variations of a single factor of the physico-chemical water condition. It is questionable in how far it is possible to use laboratory experiments for the clarification of the dependence on a chemical component of the water and to apply their results to the natural conditions in a feeder stream.

No unambiguously definable relations to the occurrence and distribution of the species were apparent from the water analyses carried out at the stations of the Fulda from January to September 1962. Therefore no conclusions will be drawn from the mean values obtained (Table 4 and Figs. 16 to 20) in regard to the oligochaete populations and the data will only be considered as contributions to the characterization of the stations.

It would be necessary to investigate through detailed experiments whether the oxygen content of the running waters is to be considered

as "an important factor regulating the distribution of most of the oligochaete species" (Korn 1963). For example, at station H the highest mean population density of T. tubifex for all stations of the Fulda coincides with the lowest mean value for the oxygen saturation and the most extended spectrum of the O₂ concentrations measured (cf. Fig. 16). As will be seen from the subsequent statements about the substrate, the cause for the better development (and the low O₂ concentration) can very well lie primarily in the state and composition of the sediment. According to Liebmann (1962), most oligochaetes are "rather indifferent" in regard to water pollution. Korn (1963) deduces from field observations that "the oligochaetes prove to be little suitable as guide forms for the classification [p. 333]

Table 4. Chemical data for the Fulda water in 1962.

		mg/l						
		pH	NO ₂ ⁻	freie CO ₂	Fe ²⁺ + Fe ³⁺	K ⁺	Ca ⁺⁺	Mg ⁺⁺
Mean value of n samples		5	3	3	1	1	1	1
Month of investigation		1,3, 5,7, 9	5,7, 9	5,7, 9	7	7	7	7
Station	km							
A	0,01	6,6	0	4,0	0,03	0	1,5	1,7
B	0	7,0	0	3,3	0,00	0	2,5	2,3
C	0,12	7,0	0	3,5	0,10	0	1,9	2,5
D	1	7,2	0	3,2	0,00	0	7,0	2,8
E	7	7,3	+	4,5	0,10	4,2	34,3	6,9
F	22	7,9	trace	1,6	0,17	4,9	25,0	6,9
G	34	7,3	+	5,6	0,24	7,8	16,3	12,3
H	48	7,7	+	8,7	0,51	8,0	34,0	11,3
J	63	7,1	+	8,9	0,38	8,8	30,5	11,0
K	91	7,3	++	7,1	0,32	7,8	30,5	11,0
L	147	7,7	++	6,5	0,20	7,6	50,0	13,0
M	181	7,5	++	6,4	0,14	6,8	51,3	12,0
N	216	7,3	++	10,3	0,16	7,4	43,2	12,0
O	238	7,6	++	5,2	0,15	35,0	88,0	102,5

of water quality". According to the investigations of Zimmermann (1962) the main reason for this fact is that in general "the current exerts a

stronger ecological effect on a number of organisms of running water than the load of wastes". The mutual effects of current and sediment on the one hand and for some species the resultant substrate on the other, will be of decisive importance for the occurrence of the oligochaetes.

In contrast, Goodnight and Whitley say that the tubificids are very well suited as indicators for the load in a body of water. It is claimed that if more than 80 per cent of the demonstrated fauna of a mud sample are tubificids, it means that the pollution is heavy, the presence of 60 to 80 per cent of tubificids indicates moderate pollution and when less than 60 per cent are found, it means that there is a return to normal conditions. Such an evaluation of the quality of the water has the advantage to make it possible to omit the determination of the species. However, I think that this division of the content on organic putrefiable substances in a river is too coarse. An experienced observer would be able to recognize it more simply and quickly and to carry out such an inventory would therefore be uneconomical in this regard. In addition, an investigation that is restricted to a small area might result in incorrect statements on account of the well-known non-uniform distribution of the tubificids (formation of "nests"). It will become apparent whether there is in the species of oligochaetes also an unobjectionable, statistically convincing reaction to pollution and a direct dependence on the load of waste only when - as has been demanded by Liebmann (1964) - the organisms that are characteristic for the evaluation of the water quality "have been investigated ecologically and physiologically better than hitherto". [p. 334]

It is usually not possible to determine the favouring factor solely from the ecological findings, even when there is a decided mass

proliferation. Thus Schuster (1915) calls Nais elinguis a "cold-water animal with a narrow tolerance for temperature fluctuations", although the species is independent of temperature as far as its distribution is concerned, which is indicated, for example, by its very sparse occurrence in the upper reaches of the Fulda. The halophilic tendency, shown by this naidid in the Weser and Werra and other streams (Wachs 1963, 1964), however, is striking. According to the investigations by Ax (1952), Nais elinguis is the most numerous oligochaete among the growth on posts in the Kiel Canal (8.8 to 15.2 per mil). Hagen (1951) classifies the species as a brackish-water oligochaete. An increase in the population density can parallel equally well an increase in current velocity (cf. Korn 1963). Nais elinguis thus attains mass proliferation among the algal growth on the concrete walls of the Middle Isar Canal (cf. the stream network of Fig. 3) and suppresses all growth of other naidid species.

The strong development of Lumbricillus rivalis does also not depend on salinity (cf. Wachs 1963). It can take place equally well in an entirely salt-free medium under an extremely high supply of organic substances. This is the explanation for the fact that the colonization by Tubifex tubifex and the Limnodrilus species of the mud of dam H is suddenly replaced by L. nivalis that grows in the thin and very loose deposits of mud below the dam that are formed by dying flakes of Sphaerotilus natans. In addition, I was able to demonstrate that the enchytraeid is the main representative of the macroscopic colonists of the filter rocks of a lightly loaded percolation filter in the sewerage test field of the Bavarian Biological Research Institute. L. rivalis obviously finds excellent living conditions in the biological sward on the lava

scoriae that are used as fill in the upper part of the percolation filters. These favourable conditions are created by the direct and indirect effects of the continuous influx of the mechanically cleaned sewage.

6 . 2 T h e S u b s t r a t e a s

E c o l o g i c a l F a c t o r

6 . 2 1 T y p e s o f s u b s t r a t e s

It was possible to make statements about the ecological spectrum of the species of oligochaetes rich in individuals as well as about the relationships between these forms and the substrate inhabited on the basis of the inventory made during a full year in a river of hilly country and in one of the Alpine foothills.

The sediments were investigated in regard to their mechanical and chemical composition. Plants and rocks in their role as environment were considered only during the one-year cycle of investigations in the Fulda (cf. Table 21).

6.211 Gastropods

Chaetogaster limnaei is restricted to the occurrence of gastropods. The members of this species live as commensals in the pulmonary sac of pulmonates and they have been found in investigations by Wagin [p. 335] (1931) in ponds with 100 per cent "infection" and with up to 900 individuals per mollusc (species of Lymnaea and Planorbis). The majority of the pulmonates examined by me did not harbour the oligochaete. Table 5 shows the small maximum number of Chaetogaster individuals in one gastropod, which was six for the species of Lymnaea, fourteen for Physa fontinalis

and twenty-one for Ancylus fluviatilis.

Table 5. Number of individuals of Chaetogaster limnaei as percentage of the snails examined.

Species	<i>Ancylus fluviatilis</i>	<i>Physa fontinalis</i>	<i>Lymnaea</i>	
			<i>auricularia</i>	<i>peregra</i>
Station	D, E, F, G, O, P	M, N, P	M	F, O
Number of gastropods examined	544	72	69	108
Number of Chaetogaster	Per cent of gastropod species			
0	73,9	25,0	56,5	61,1
1	8,0	16,7	4,4	13,9
2	4,7	1,4	13,0	8,3
3	2,2	8,3	2,9	5,6
4	2,5	4,2	17,4	8,3
5	2,2	2,7	2,9	1,9
6	0,4	1,4	2,9	0,9
7	0,4	4,2		
8	0,7	4,2		
9	0,4	8,3		
10	1,0	8,3		
11	0,4	2,7		
12	0,4	4,2		
13	0,4	4,2		
14	0,4	4,2		
15	0,4			
16	0			
17	0			
18	0,4			
19	0,4			
20	0,4			
21	0,4			

6.212 Plants

Naidids are the predominant colonists of plants - which are mainly species of Callitriche, Ranunculus fluitans and Chlorophyta. It can be seen from Fig. 21 that they constitute the dominant part of the oligochaete fauna of this section of the river environment. This figure [p. 336] gives the average percentage distribution of the dominant plant colonists among the oligochaetes at the individual stations. The exact percentages for the individual species on all substrates that have been found during

the cycle of a year can be taken from Table 21.

In the source region the enchytraeid Cernosvitoviella atrata occurs frequently besides the dominant Nais communis (83.9 per cent at station C). Chaetogaster diastrophus prefers the plant substrate, as does Ch. langi, whose proper environment is not the sandy and stony substrate, as has been assumed by Wolf (1928). The appearance of numerous individuals of Stylaria lacustris is unconditionally dependent on the river flora and increases strongly with the rising pollution of the water that is conditioned naturally by the increasing distance from the source. Thus is to be explained the occurrence of masses of this species in the Weser (Wachs 1964). The more favourable nutritional and oxygen conditions in the floating bundles of plants must be - according to species - of decisive importance for the existence of the naidids. Stylaria lacustris prefers probably only the plentiful supply of food. The grasses that become flooded during high water are colonized only by oligochaetes, as Nais communis and N. elinguis, with few exceptions (nematodes, gammarids).

6.213 Rocks

The naidids are as a rule dominant also on the rocks in beds of brooks and rivers (Fig. 22), that is, through the species Nais alpina, N. elinguis, N. communis, N. barbata, N. pardalis, Chaetogaster diastrophus and Ch. langi.

My statements about collecting localities for Nais alpina in the Isar and in the brook region of the Fulda, as well as those of Sperber (1950) and Hraběs (1960) lead to the assumption that this is a narrowly cold-tolerant species. Nais elinguis is absent from the Fulda sources and increases in numbers with increasing distance from there at

the expense of Nais communis (cf. its occurrence in the Weser, Wachs 1964). Nais elinguis therefore cannot be a narrowly tolerant cold-water form, as has been assumed by numerous authors (Schuster 1915 and others). This ecological assignment is in part also the consequence of systematic confusion, which has been pointed out also by Schuster (1915) and Stolte (1962).

At station 0 the average abundance of N. elinguis is 320 individuals per 100 cm² of rock surface. Rhyacodrilus falciformis (33.1 per cent), Cernosvitoviella atrata (16.7 per cent) and Marionina argentea (15.9 per cent) are frequent only in the source region. In the heavy coating by Sphaerotilus on the rocks below the dam at station H, the enchytraeid Lumbricillus rivalis occurs with an 87-per cent abundance (besides Tubifex tubifex) (cf. the statements about the chemism of the water, p. 40).

[p. 337]

6.214 Gravel

The composition of the grain sizes and thus, in dependence on the extent of the interstitial system and the current velocity, the intensity of the water exchange will be of decisive importance for the distribution of the species. Whether the dominance of the characteristic species that occur in the variable environment is determined mainly by the physiological significance of the current (cf. Ambühl 1959) or by the deposition of the fine organic substances that serve as food, is not well understood at present.

The characteristic species in the fast flowing regions of the brooks is the enchytraeid Propappus volki, which is dominant in the gravel of station F with 41.2 per cent of the individuals (and 66 per

cent when the juveniles also are included). As is shown by Figs. 18 and 19, the average load of organic substances is still rather small (mg/l):

KMnO ₄ consumption	11.6	SO ₄ ²⁻	11.4
PO ₄ ³⁻	0.31	NO ₃ ⁻	7.5

In addition, the highest values for O₂ in the whole Fulda were found here (relative O₂ saturation on average 108.5 per cent; Fig. 16). According to my observations - cf. also the investigations by Neisvestnova-Shadina (1937) in the sand (0.5 to 1 mm diameter) of the Oka and Volga - the determinative fraction of the preferred sandy freshwater environment is probably coarse sand (0.2 to 2.0 mm) and not large-grained gravel, which constitutes exactly at station F of all stations of the Fulda the largest proportion of the sediments (Table 6). Hitherto, this "characteristic enchytraeid" (Wachs 1964) has been found only at a few places so that it is not possible to deduce the decisive environmental factors from the incomplete knowledge of its life history.

Nais communis is dominant (95.4 per cent) in the gravelly bottom of the Fulda source (station B, a) and it is there very rich in individuals (a maximum of 222 individuals/100 cm²). The naidids Pristina rosea and P. foreli are dominant in the gravels of the middle reaches of the Fulda, farther downstream the tubificids Limnodrilus hoffmeisteri and Tubifex tubifex become dominant, until finally Psammoryctes barbatus is in the gravelly bottom of the Weser (Wachs 1964) the dominant species or the only representative of the oligochaetes.

The gravel deposits at the Isar station R (Fig. 24) are coloured black by iron sulfide. When they are being touched a very intensive development of gas takes place, thus only Tubifex tubifex occurs

here in numbers.

The investigations at the Isar stations P and U (Fig. 24 and Table 6) demonstrated unambiguously that the conditions for the development of large numbers of the lumbricolid Stylo-drilus heringianus are given by a grain size of the substrate between the limits of 0.063 and 15 mm. [p. 339]

6.215 Sand

The shape and the pore volume of the system of openings in the sand and above all the size of the capillary flow are of importance for the animal population in the sandy freshwater environment (Ruttner-Kolisko 1957, 1962). The intensity of the circulation in the pore spaces - which for the animal community of the capillary spaces is determined by the magnitude of the laminar flow, which here fulfills "at least approximately the function of the turbulent flow" (Ambühl 1962) - determines the exchange of water and substances. However, on account of the methodical difficulties in exact measurements, "little is known about the minimum magnitude of the water movement that is still effective physiologically" (Ruttner-Kolisko 1962). According to investigations by Stuart (1953) with the Pitot apparatus, the animals living under the peak of a sand hill obtain the greatest amount of oxygen, since interestingly the current is largest exactly at this point.

The enchytraeids Cernosvitoviella atrata and Marionina argentea occur most frequently in the sand (Fig. 25) of the source area. High values for the abundance of Stylo-drilus heringianus are the consequence of a specific grain distribution in the sand that corresponds exactly to the conditions that have already been discussed for the gravel in

Table 6. Distribution of the grain sizes of the gravel
at the stations (values in volume per cent).

\varnothing in mm \ Station	B, a	B, b	F	G	L	M	P, a	P, b	R	U
<0,063	/	/	/	/	/	/	/	/	/	0,5
0,063—0,1	1	0,08	0,02	0,05	0,1	0,8	0,08	/	/	5,2
0,1 — 0,2	4,84	0,21	0,18	3,8	4,5	3,94	0,22	/	1,6	15,8
0,2 — 0,63	22,76	0,66	1,55	9	9,44	16,6	0,4	/	0,2	4,9
0,63 — 1	13,1	0,45	0,75	9,05	9,06	14,2	1,6	0,08	0,2	7,1
1 — 2	16,1	0,9	1	5,8	5	15,4	0,7	0,12	1,2	4,5
2 — 6	30,12	6,5	3	9,4	9,3	20,3	3	5,7	13,8	15,5
6 — 15	/	11,5	14,5	18,5	26,25	/	90	20,1	27,5	34,5
6 — 20	12,08	/	/	/	/	28,76	/	/	/	/
15 — 20	/	/	/	16,2	15,8	/	4	/	22,5	/
15 — 25		38,5	/	/	/		/	67	/	9
15 — 30		/	35,7	/	/			/	28	/
20 — 45		/	/	28,2	20,55			7	/	3
25 — 50		41,2	/	/	/			/		/
30 — 45		/	43,3							

connection with this species (cf. station D of Table 7 and of Fig. 25). Optimum and tolerable living conditions for numerous (14) genera, among which Nais with six species, and Pristina with four species are predominant, are found in the pure sand of station G; of this about 63 volume per cent are lying in the region of medium fine sand. Going downstream, Nais elinguis, Tubifex tubifex, Limnodrilus hoffmeisteri and L. udekemianus increase steadily in numbers with increasing pollution. Individuals of L. hoffmeisteri appear here considerably more frequently than the other two species of tubificids mentioned. [p. 340]

Table 7. Distribution of the grain sizes of the sand at the stations (values in volume per cent).

Station \ Ø in mm	D	F	G	J	L
<0,063	/	0,02	0,2	0,01	0,1
0,063— 0,1	0,1	1,38	0,8	0,04	0,37
0,1 — 0,2	1,9	10,9	6,2	0,15	2,28
0,2 — 0,63	14,8	73,4	63,3	20,8	44,85
0,63 — 1	16,4	12,4	21,1	58,6	44,0
1 — 2	28	1,7	6,7	18,4	8,2
2 — 6	29,6	0,2	1,7	2	0,2
6 —15	9,2	/	/	/	/

6.216 Sand-mud

The evaluation of the grain-size analyses of the muddy sediments showed that it is logical and, from an ecological point of view, even necessary to subdivide them into the substrate types sand-mud and mud. The deposits that have been called sand-mud in what follows have either still a grain size of less than 0.5 mm or they lie between the limits 0.5 and 0.005 mm. In addition, their main fraction lies between 0.2 mm and 0.5 mm. Only the curve for the grain distribution of the sediment at station P shows an insignificant deviation.

The sand-mud (Figs. 26 and 28) of the source and brook region is poor in organic deposits and is colonized mainly by Cernosvitoviella atrata or by Nais elinguis. Downstream three species of tubificids dominate the faunal picture at an increasing rate with the increasing degree of putrefaction processes in the substrate. Limnodrilus hoffmeisteri is always the most abundant species, followed by Tubifex tubifex and L. udekemianus with noticeably smaller abundance values. In contrast, L. helveticus is the dominant form in the sandy-muddy sediment of station P (Figs. 24 and 28). In my investigations of several river systems I could record this Limnodrilus species only in the Alpine region (Isar).

6.217 Mud

The grain distribution of the mud in a river (main fraction in the region of 0.08)-0.1-0.2 mm; cf. Figs. 29 - 31) that differs from that of sand-mud, results also in a different percentage composition of the oligochaete fauna (Fig. 3 with stations S and T; Figs. 24 and 27).

The muddy substrate, in which Cernosvitoviella atrata and Nais communis are still dominant in the source region, becomes poorer in species and richer in individuals with increasing pollution farther downstream. Wolf (1928) was able to demonstrate "a strong dependence" of the number of species "on the oxygen content of the water adjacent to the mud".

In the typical mud of a river (that is, not including that of the brook section), which corresponds to the statements about the grain sizes given above, only the tubificids of the order Oligochaeta are still finding favourable environmental conditions. In the river mud - with the exception of that in dams of large area, the natural self-cleaning of

which has been altered forcibly (about the effects of dams see Liebmann 1960 b) - the dominant member of the oligochaete fauna is always [p. 341]

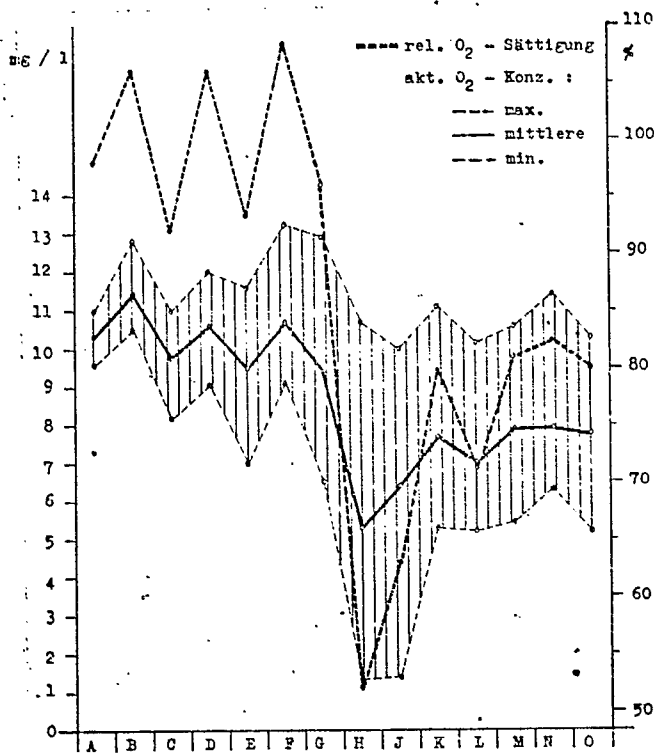


Fig. 16. Actual oxygen concentration and relative oxygen saturation in the Fulda in the period from March to September 1961.

==== rel. O₂ saturation
 actual O₂ concentration:
 --- maximum
 — mean
 --- minimum

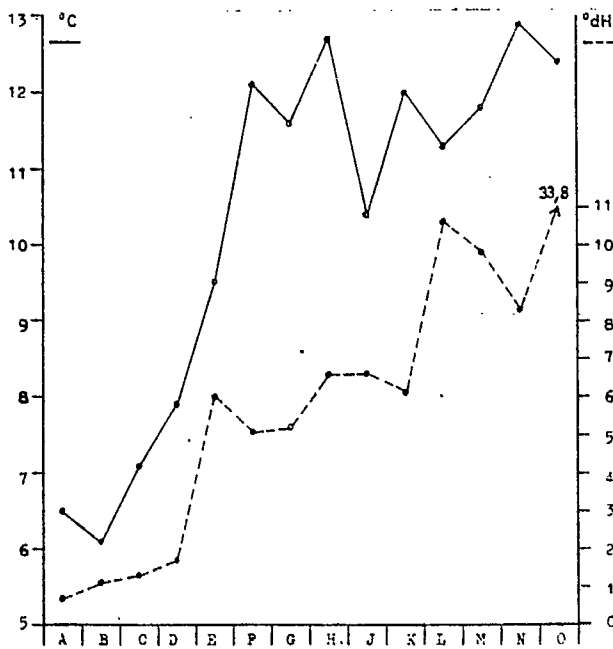


Fig. 17. Water temperature and total hardness of the Fulda in the period from January to September 1962.

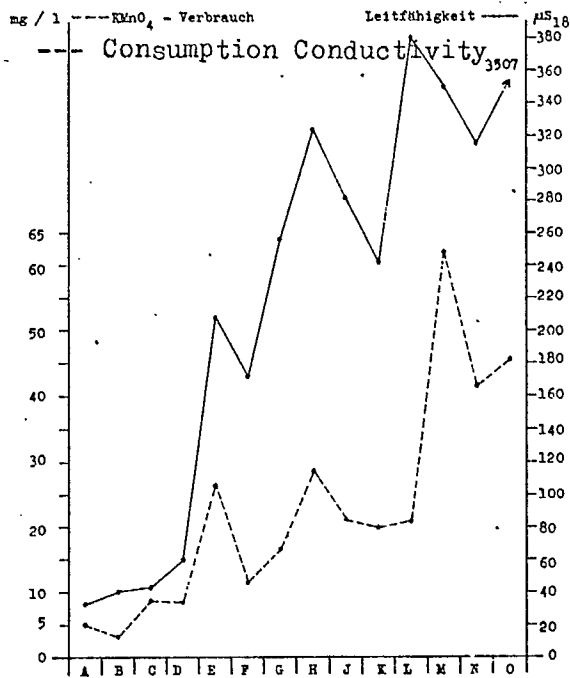


Fig. 18. Conductivity and oxidizability of the Fulda water during the period from January or March, respectively to September 1962.

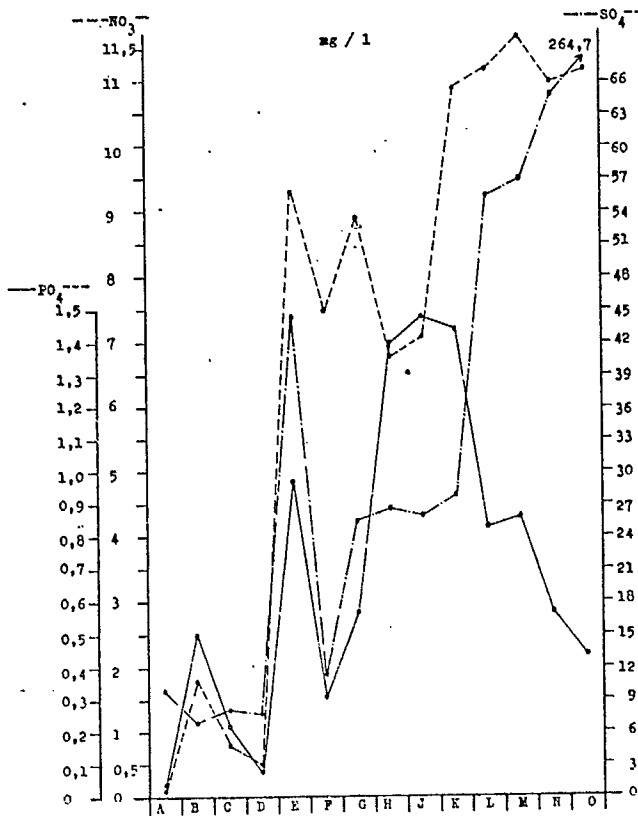


Fig. 19. Content of nitrate, sulfate and phosphate of the Fulda during the period from March to September 1962.

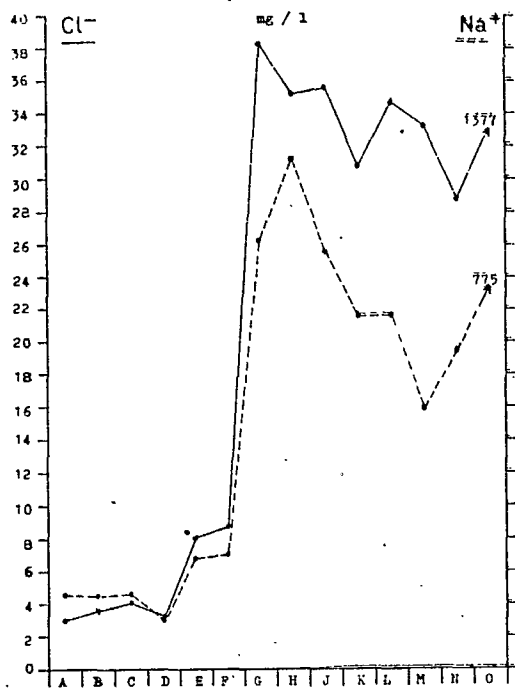


Fig. 20. Content of chlorine ions (from January to September 1962) and of sodium ions (July 1962) of the Fulda water.

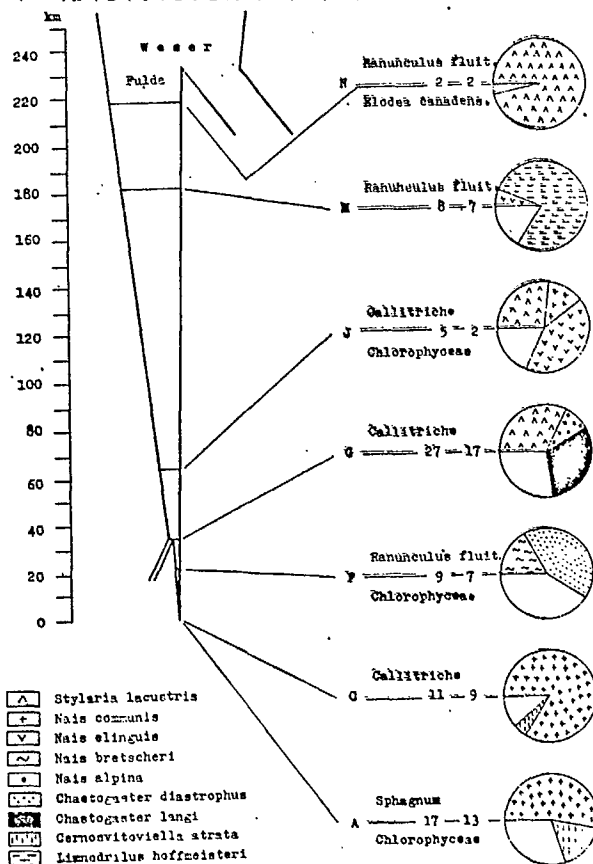


Fig. 21. Percentage distribution of dominant inhabitants of plants. The figures at the distributional diagrams give the number of species present (left) and genera (right). This applies also to the following illustrations.

- ▲ Stylaria lacustris
- Nais communis
- ▽ Nais elinguis
- ~ Nais bretscheri
- Nais alpina
- ⊠ Chaetogaster diastrophus
- ⊞ Chaetogaster langi
- ⊡ Cermonovitiella atrata
- ⊞ Limnodrilus hoffmeisteri

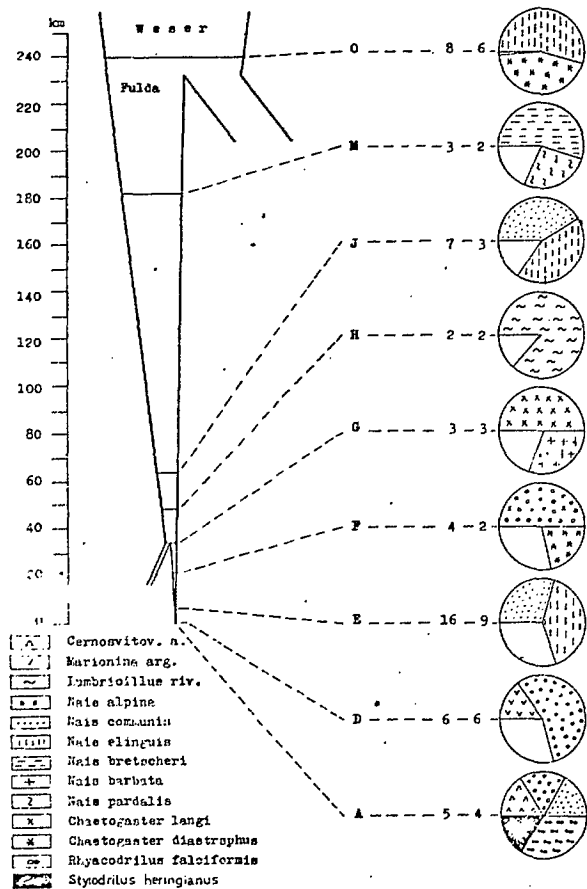


Fig. 22. Percentage distribution of dominant inhabitants of rocks.

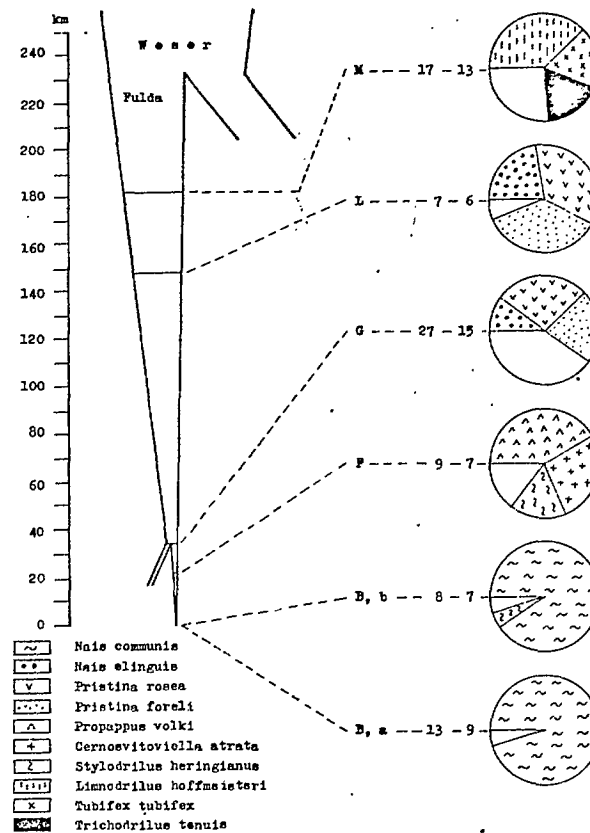


Fig. 23. Percentage distribution of dominant inhabitants of gravel.

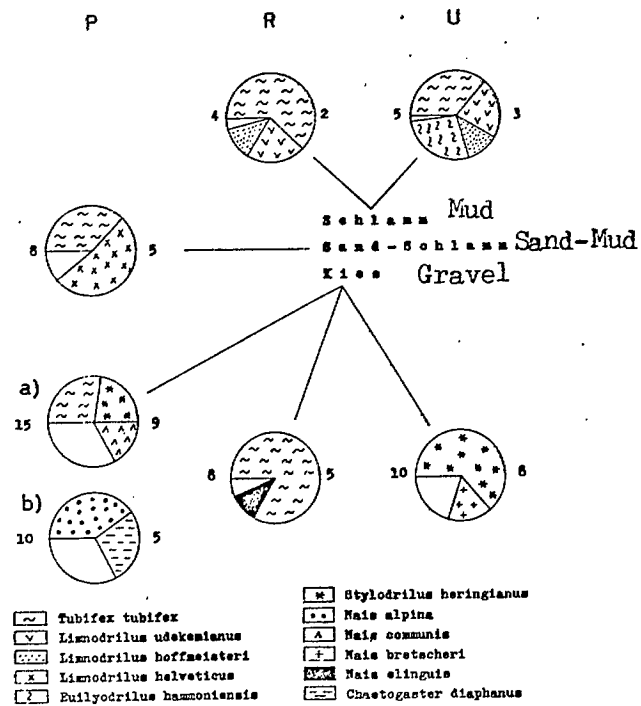


Fig. 24. Percentage distribution of dominant inhabitants of the substrates at stations P, R and U of the Isar.

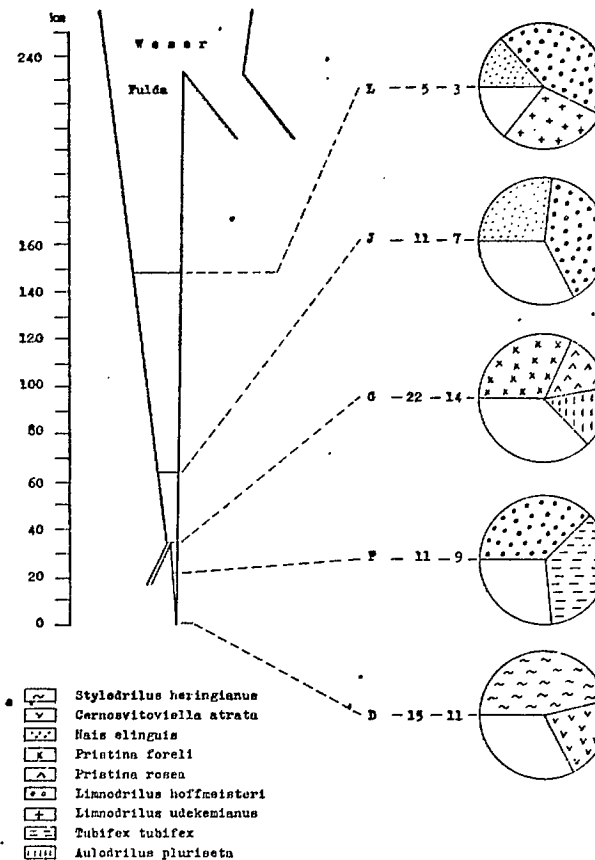


Fig. 25. Percentage distribution of dominant inhabitants of sand.

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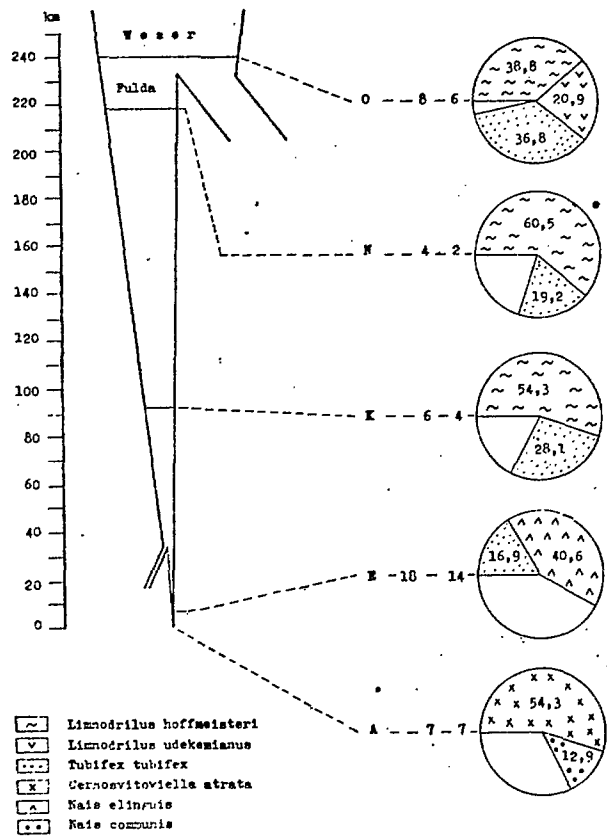


Fig. 26. Percentage distribution of dominant inhabitants of sand-mud.

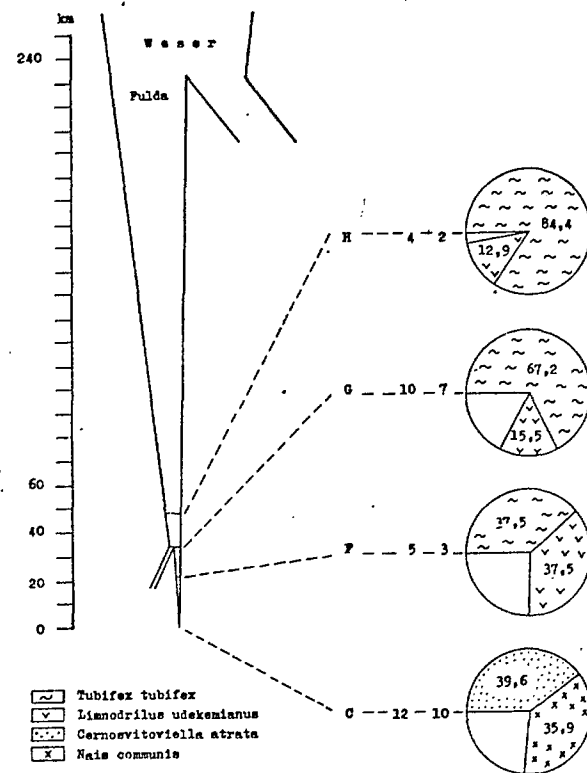


Fig. 27. Percentage distribution of dominant inhabitants of mud.

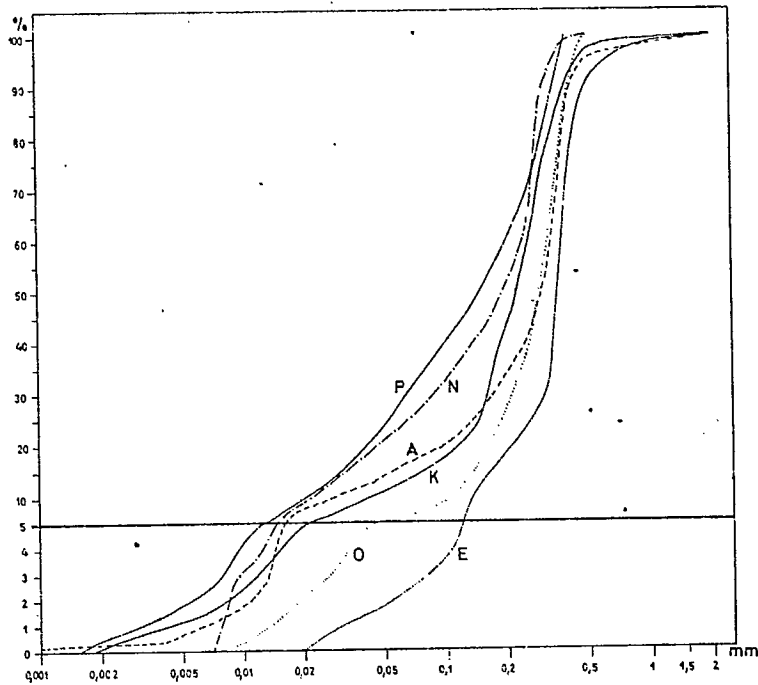


Fig. 28. Curves of the distribution of grain sizes of the sand-mud at stations A, E, K, N, O and P. Logarithmic abscissa scale for all accumulative curves. Values in weight per cent.

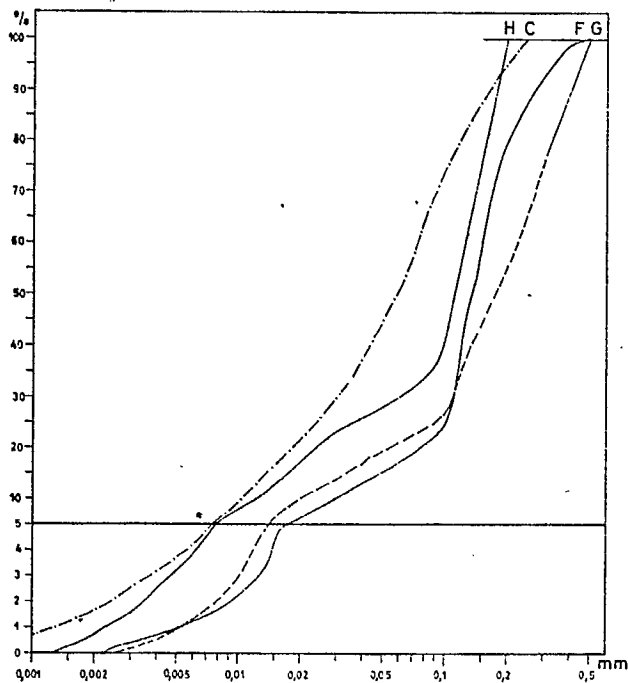


Fig. 29. Curves of the distribution of grain sizes of the mud at stations C, F, G and H.

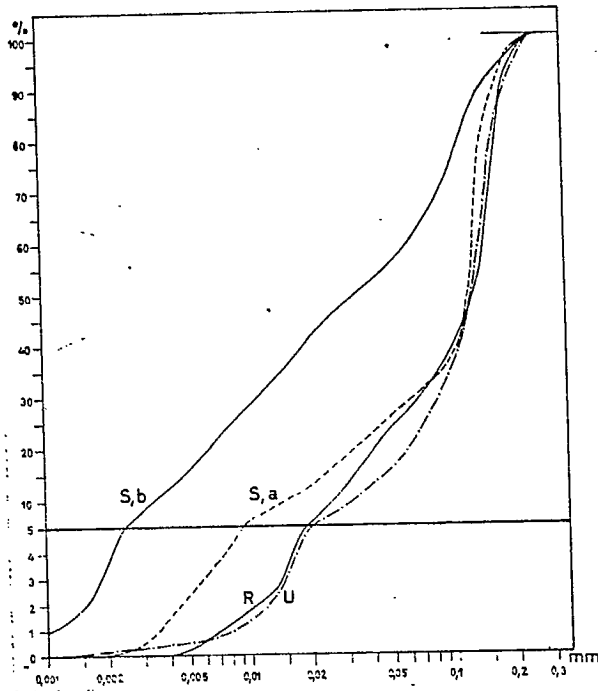


Fig. 30. Curves of the distribution of grain sizes of the mud at stations R, S and U.

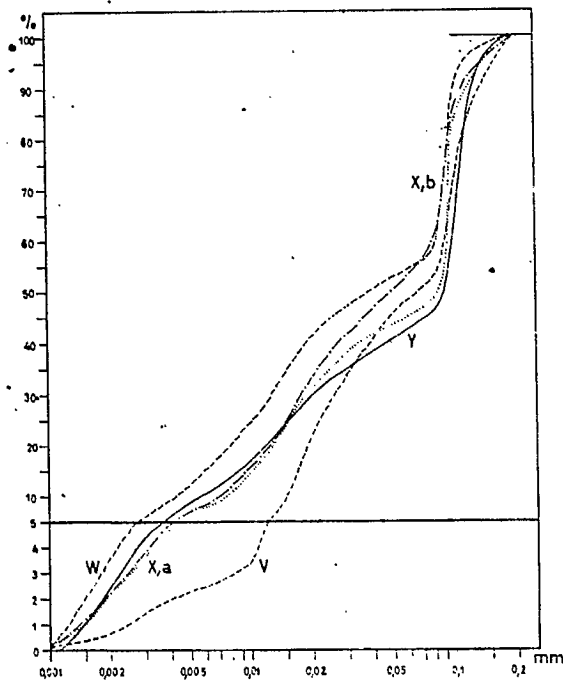


Fig. 31. Curves for the distribution of grain sizes of the mud at the Isar dams investigated.

Tubifex tubifex. This ubiquitous species also lives in pure water with a constantly low temperature, as soon as there takes place locally an accumulation of organic material in the form of small pools (cf. Korn 1963). Thus it is present already, to the extent of 10.5 per cent, in the oligochaete fauna in the micro environments of one of the running sources of the Fulda (station A). Only Limnodrilus udekemianus among the three species of Limnodrilus (L. udekemianus, claparedeanus, hoffmeisteri), which also inhabit mud, occurs in a notable number of individuals (cf. Fig. 32).

Strange to say, the quantitative composition of the oligochaete fauna of the mud of larger dams shows marked differences from that of the environments treated above. In the barrages of the Isar (Fig. 3, stations V to Y) I did not find Tubifex tubifex at all and I could find it only very rarely in those of the middle reaches of the Weser (Wachs 1964). In contrast, individuals of Limnodrilus were dominant in the barrages of

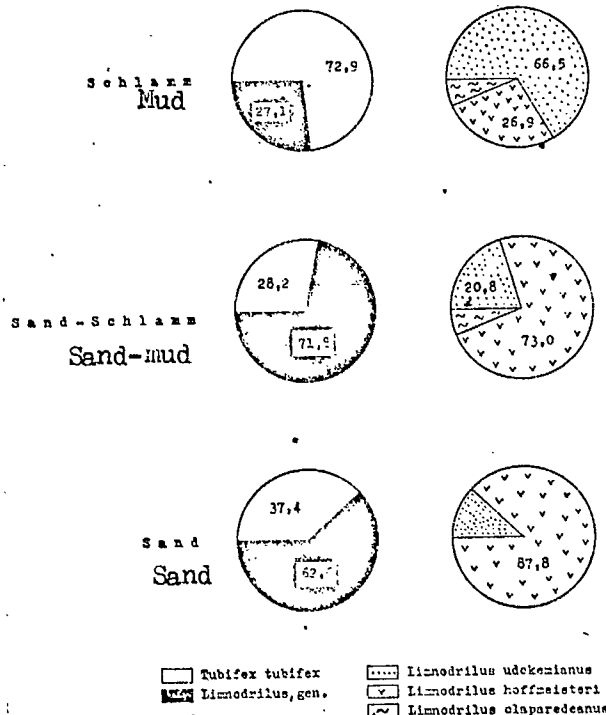


Fig. 32. Percentage distribution of Tubifex tubifex and of three species of Limnodrilus in the mud (based on 3389 individuals), sand-mud (7451 individuals) and sand (666 individuals), - On the right side of the graph the share of the genus Limnodrilus has been set = 100 per cent.

both river systems. Whereas L. claparedeanus forms the majority in the Weser, L. hoffmeisteri furnishes the main percentage share in the Isar. The kind of distribution of the grain sizes cannot provide the explanation for these different phenomena in the benthos of natural river stretches and that of large artificially dammed up barrages.

[p. 350]

By way of summary, Fig. 32 is intended to show the unambiguously different dependence on the grain size of the substrate of dammed up running water by means of the percentage distribution in three types of substrate - in mud (0.5 to <0.005 mm), in sand-mud (either >0.5 mm or between 0.5 and 0.005 mm) and in sand (>2 mm) - of Tubifex tubifex and the genus Limnodrilus in general and then especially of three species of Limnodrilus. It is not at all true that the dominance of one form in one environment can be recognized unambiguously through the taking of one sample; rather, there can be great variation in the dominance. Only the statistical evaluation of numerous samples, taken over an extended period of time provides a clear picture of the composition of the fauna. According to this, Tubifex tubifex dominates in the mud with an average share among oligochaetes of about 73 per cent. In contrast, the genus Limnodrilus dominates in the sand-mud with about 72 per cent and in the sand with about 63 per cent.

When one examines the ecological demands of Limnodrilus separately according to species, one finds again clear differences. Whereas L. udekemianus predominates in the mud with a share of about 67 per cent of the genus, L. hoffmeisteri inhabits with 73 per cent the sand-mud and with about 88 per cent the sand. L. claparedeanus is absent from the sandy substrate. The percentage of the number of individuals of L. hoffmeisteri increases with increasing grain size (up to 2 mm), whereas the percentages

of Tubifex tubifex, L. udekemianus and L. claparedeanus decline sharply.

According to my investigations, Tubifex tubifex will always dominate in the mud of a not dammed up stream when the substrate has a minimum share of 45 weight per cent in the region <0.15 mm diameter; when the share is less, the Limnodrilus populations will dominate.

When one takes into consideration also samples from barrages, then one must add that the fraction between the limits 0.08 and 0.1 must be greater than 13 weight per cent, if the conditions for the grain size distribution in the sediment are to be met that lead to the dominance of Tubifex tubifex.

6 . 2 2 C h e m i s m o f t h e M u d s

The specific grain distribution of the sediments is of great importance for the presence and dominance of the various species of oligochaetes, but this does not preclude the dependence of these species on other factors. Above all, it has still to be clarified, which components determine the population density of the tubificids.

It must be the goal of a biological analysis of a locality to define it exactly, that is, by numerical values. The presence of a species does not define an environment, but the frequency of this species does. [p. 351]

Since the curves for the grain distribution of the substrate types did not show any correlation with the mean values for the abundance of the tubificids, it was obvious to investigate the influence of the chemism of the sediments. Some components of the complex of chemical factors (Tables 8 to 10) - as organic substance, organic carbon and total nitrogen - were analyzed and considered in relation to the quantitative occurrence of the tubificids (mean value of the results obtained in each case during the annual cycle).

There is considerable parallelism between the water capacity of sediments and their content of organic substances (cf. Ungemach 1960). It is precisely the values of these factors that are especially high in the muds of barrages (Table 8, stations V to Y). This is perhaps - for reasons that are not yet very well understood - connected with the absence or the very scarce occurrence of Tubifex tubifex in the benthos of the large barrages. Whereas the water content of the sediments in the barrages is constant at about 80 per cent and whereas the values for the organic substances always are more than 11 per cent, the corresponding figures for the muds of natural stream sections are lying between 50 and 68 per cent and in the range of (2)-4-7-(11.5) per cent.

A "considerable parallelism between organic carbon and total nitrogen" that has been confirmed by Ungemach (1960) for the gyttjas of European lakes, does not exist in the muddy sediments of running waters according to the present results. There is no correlation between the content of organic substances, organic carbon and total nitrogen. This peculiarity of river sediments eliminates all possibility to infer the approximate content of organic carbon from the proportion of organic substances and indicates a high variability of its chemical composition. The influx of carbohydrates and proteins in running waters must be able to shift so far in favour of one of the constituents that there is no possibility for the establishment of an approximate constancy or of even a narrow range for the C : N ratio. Instead, the value C : N shows astonishing differences (in mud 1.6 to 18.7). It is therefore only too evident that no unambiguous relations to the density of tubificids can be obtained from this inhomogeneity (in regard to chemical composition). It is true that in general the abundance values increase with rising content of

Table 8. Chemical data for the muds at the entrance into the storage lake and at the dams of the Isar.

Chemism	Environment	Storage Lake		Dams				
	Station	S, a	S, b	V	W	X, a	X, b	Y
Water content, per cent		62,0	49,8	78,8	81,1	81,8	81,1	81,1
Carbonates, per cent		8,66	3,58	7,00	6,08	6,81	3,24	10,02
Organ. subst., per cent		6,21	6,00	11,63	15,88	17,43	16,40	15,36
Organ. carbon, per cent		5,23	2,03	3,43	9,47	9,68	2,03	6,80
Tot. nitrogen, per cent		0,49	0,31	0,52	0,62	0,65	0,63	0,62
C : N		10,7	6,6	6,6	15,3	14,9	3,2	11,0

Table 9. Chemical data for the river muds and the mean abundance (per 100 cm²) of the tubificids.

Chemism Abundance	Station	C	F	G	H	R	U
	Source						
Water content, per cent		89,7	56,4	62,1	63,5	67,9	56,1
Carbonates, per cent		2,03	0,33	0,41	2,80	2,62	7,02
Organ. substances, per cent		24,39	2,18	6,33	11,48	6,56	4,26
Organ. carbon, per cent		7,02	1,66	0,67	2,18	5,20	2,91
Tot. nitrogen, per cent		0,70	0,21	0,42	0,59	0,28	0,26
C : N		10,0	7,9	1,6	3,7	18,7	11,2
Tubificids, adults + juv.		10	319	129	417	—	—
Tubificids, adults		0,8	20	40	72	24	5
<u>Tubifex tubifex</u> , adults		0,2	8	28	61	15	2

Table 10. Chemical data for the sand-muds and the mean abundance (per 100 cm²) of the tubificids.

Chemism Abundance	Station	A	E	K	N	O	P
	Source						
Water content, per cent		53,1	41,9	38,0	45,9	38,4	42,3
Carbonates, per cent		1,42	0,31	0,52	1,65	1,64	7,21
Organ. substances, per cent		6,36	2,98	3,49	6,56	2,38	3,31
Organ. carbon, per cent		0,82	1,00	1,73	1,63	1,62	3,97
Tot. nitrogen, per cent		0,15	0,17	0,19	0,33	0,14	0,19
C : N		5,5	5,9	9,1	4,9	11,6	20,9
Tubificids, adults + juv.		8	33	230	434	234	—
Tubificids, adults		4	14	113	143	135	48
<u>Tubifex tubifex</u> , adults		4	10	32	27	51	19

organic substances, organic carbon and total nitrogen (Tables 9 to 10). However, there is by no means a mathematical dependence that would provide the possibility to infer from the density of individuals the magnitude of any of the chemical components or vice versa.

[p. 353]

It is true, there is an exception in the colonization of the mud of the Fulda (without the source region) at the stations F, G and H. There is found a very clear correlation between the content of organic carbon - in the region between 0.67 per cent and 2.18 per cent of the dry weight - and the mean density of tubificids of all ages that consists in a linear dependence of the two values. To the muds of these three stations applies the rule that to a content of exactly 0.52 per cent of organic carbon correspond as colonists 100 tubificids of all ages per 100 cm² of substrate.

The comparative investigations in the Isar show that different conditions obtain in every river system, which do not allow final unobjectionable conclusions to be drawn. In view of "the individual development of the running waters themselves in nature, there simply are no absolute equalities" (Illies 1955). The widely held opinion that "the density of colonization in tubificids depends in the very first instance on the content of organic substances in the bottom sediments" (Meschkat 1937) is valid only to a limited extent. The optimum development of the tubificids in a substrate depends obviously on a specific co-operation between mechanical, chemical and other components of the comprehensive complex of factors.

6.23 Selection of the substrate in the experiments

In the following the evaluation and explanation of the field observations will be examined by means of experiments.

Exploratory experiments were carried out by placing different substrates into glass troughs of 7 mm inner width that had water flowing through them. Large Petri dishes with a diameter of 18 cm and a height of 3 cm were used for the numerical evaluation of the substrate selection tests. A plexiglas tube was fastened to the centre of each dish and surrounding this at a distance of 2 cm was a plastic ring with sieve-like perforations. Radial inserts of plastic sieve plates were used to subdivide each Petri dish into nine (eight) sectors of equal size. The sectors could be filled to the rim of the dish with different substrates, always three times three (four times two, two times four) - alternating in each case (Fig. 33). The dish filled with substrates was placed into

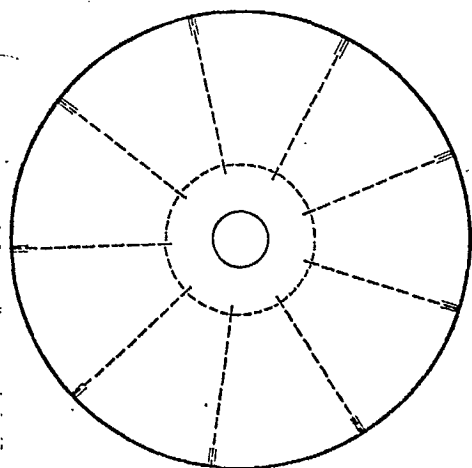


Fig. 33. Plan view of the Petri dish used for the experiments for the selection of substrate.

a bowl through which flowed Munich tapwater of 10 to 14°C that was filtered through activated charcoal. The adult test animals could then be

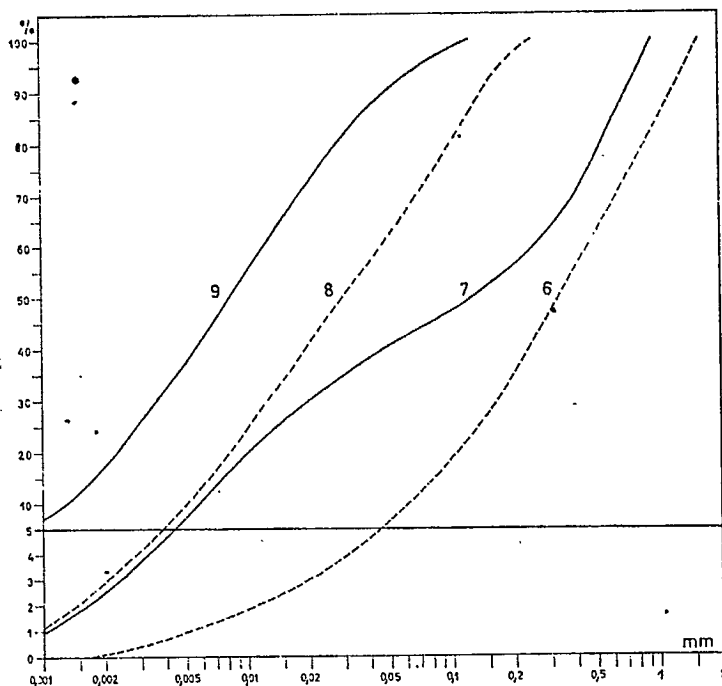


Fig. 34. Curves for the distribution of grain sizes of the synthetic substrates 6 to 9 as used in the experiments for the selection of substrate.

placed into the space between the two inner rings. The sole purpose of the centre space was to prevent the animals from forming into a tight ball on account of the pronounced contact sense of the species of tubificids that were used. The worms (in each case individuals of only a single species) thus had the opportunity to travel over the entire space of the dish and to select actively the environment that was the most favourable for them. Each experiment was terminated after five days. The individuals were sieved out from the different substrates and counted. The selection experiments with the mineral substrates - in which it is assured that the composition remains the same - were carried out several times in order to avoid working with a number of individuals that might be too large temporarily.

[p. 354]

In order to arrive at well founded conclusions in spite of the variability of the results of the individual selection experiments, Petri dishes with nine sectors and three different substrates were used, except

for the initial experiments, when two different substrates were used alternately in eight sectors. On account of this subdivision each selection experiment consists actually of three experiments. Fourteen series of experiments (I to XIV) with a total of 25 types of substrates (1 to 25) [p. 355] in different combinations were carried out (Figs. 35 to 37). The composition of the different synthetic substrates that are indicated by arabic numerals in the figures was as follows:

(a) Mineral substrates:

- 1: gravel of 7- to 5-mm diameter (limit between fine-medium gravel and small gravel);
- 2: sand of 2.5- to 1.5-mm diameter (limit between small gravel and gravelly sand);
- 3: sand of 0.5- to 0.3-mm diameter (macro-coarse-medium sand);
- 4: sand of 0.2- to 0.07-mm diameter (main fraction at 0.12 mm; fine-medium sand);
- 5: mud of 0.25- to <0.001 -mm diameter with main fraction at 0.07 mm; obtained from pulverized dry substance of river muds through igniting at 800°C for 20 min.
- 6: sand-mud of 1.5- to 0.0017-mm diameter (curve for grain distribution in Fig. 34);
- 7: substrate of 1- to <0.001 -mm diameter (curve for grain distribution in Fig. 34); obtained through mixing quartz sand, substrate of type 5 and kaolin;
- 8: substrate of 0.25- to <0.001 -mm diameter (curve for grain distribution in Fig. 34); obtained through mixing substrate type 5 with kaolin.
- 9: kaolin of 0.13- to <0.001 -mm diameter (curve for grain

distribution in Fig. 34);

10: substrate of 0.32- to <0.001 -mm diameter, with main fraction at 0.06 mm;

11: substrate of 0.32- to <0.001 -mm diameter; obtained through mixing of substrate types 9 and 10 in the proportion 1 : 1.

(b) Organic substrates:

The organic substrate types 12 to 23 were obtained by mixing the substrate 5 with animated mud (sieved through a net with 0.2-mm mesh) from the oxidizing ditch of the Munich sewage test field. The distribution of grain sizes was constant between the limits of 0.25 and <0.001 mm.

Substrate type	In per cent of dry substance	
	Organic C	Total N
12	4,56	0,39
13	17,15	2,26
14	3,50	0,31
15	7,21	0,72
16	1,43	0,16
17	2,76	0,30
18	5,42	0,61
19	0,67	0,07
20	2,75	0,28
21	0,27	0,04
22	0,82	0,10
23	0,13	0,015

24: 5.96 per cent organic carbon; 0.66 per cent total nitrogen;

0.5- to <0.001 -mm diameter. Obtained through mixing substrate types 3 and 5 + animated mud in the ratio 1 : 1.

25: 7.04 per cent organic carbon; 0.73 per cent total nitrogen;

1.5- to 0.0017-mm diameter. Obtained through mixing quartz sand and substrate 6 + animated mud in the ratio 1 : 1.

6.231 Different grain sizes

Since the selection tests are, of course, reproducible only to a certain extent on account of the great variability of the individual results, only the unambiguous tendency will be documented in the evaluations (Figs. 35 to 37) by means of the percentage distribution.

When the Limnodrilus species are provided with the possibility of choice between mineral substrates - from small gravel to fine sand - they always move into that substrate, the particles of which have the smallest diameter (Fig. 35, tests I and II).

When only sand and mud are available, the finer sediment is again preferred (test III).

Within the genus Limnodrilus the ecological demands differ when only mud and sand-mud are available (tests IV to V).

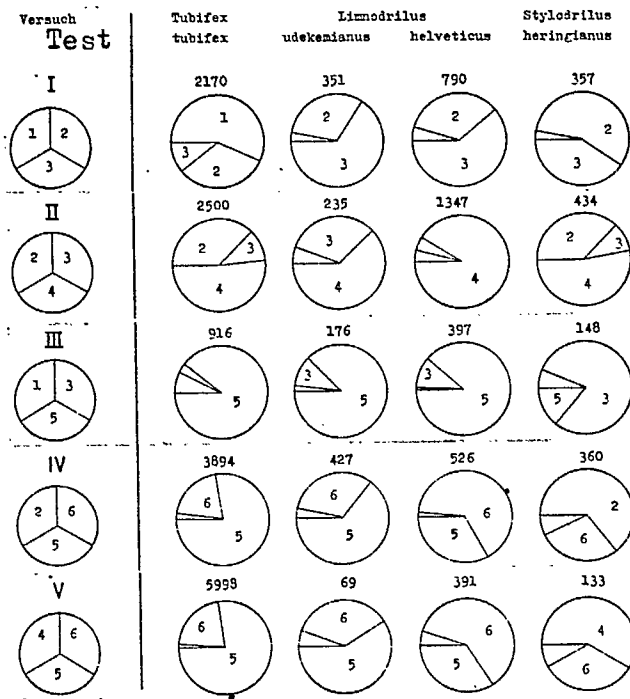


Fig. 35. Selection tests in substrates with different grain sizes for four species. In Figs. 35 to 37 the combination of the numbered substrates is shown on the left side. The sectors of the other circles represent the percentage distribution of the animals and the figures above the circles give the numbers of individuals on which the test results are based.

As had already been found in field observations, L. udekemianus selects the muddy substrate, L. helveticus (tests IV to VII), in contrast selects the substrate with a greater share in the sandy region, it avoids, however, the grain sizes above about 0.3 mm (tests II and III). The

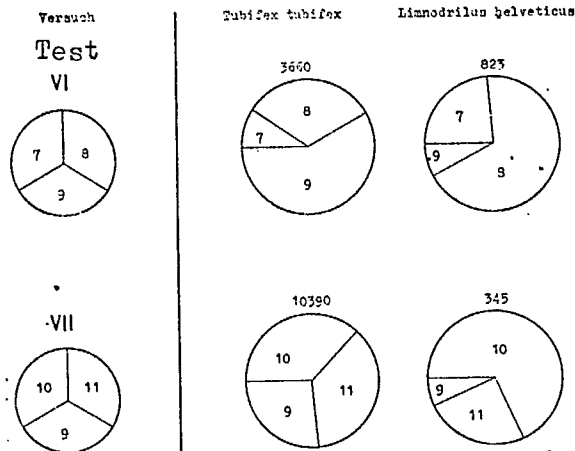


Fig. 36. Selection tests in substrates of different grain sizes with two species.

ecological valency thus corresponds to that of L. hoffmeisteri.

The reaction of Tubifex tubifex in test I (preference for the coarser grain sizes) can be explained perhaps most easily as a sustained search attitude for a smaller grained environment (than 7- to 0.3-mm diameter). Within the three substrates offered the individuals of this species are able to move fastest without mechanical injuries in substrate 1. However, when the diameter of the particles is smaller, T. tubifex moves predominantly into the fine-grained substrate (tests II to IV). In this substrate, particle sizes above 0.2 are being avoided and fractions below 0.001 are being strongly preferred (tests V and VI). The preferences of T. tubifex for muds with fractions below 0.001 mm disappear when the main region lies below the limit of about 0.06 mm (test VII).

The significance of the grain size of the substrate has been examined also in tests with the lumbriculid Stylodrilus heringianus (Fig. 35). Mud and sand-mud are definitely avoided. The animals seldom enter substrates between the limits gravel and coarse medium sand. The unambiguous preference for the fraction 0.2 to 0.07 mm in the selection tests proved that the frequent occurrence of St. heringianus in gravels and sands is related mainly to the share of the fine fractions.

6.232 Different chemism

The selection tests with muds of the same grain size distribution and different content of nutrients - defined by the content of organically bound carbon and nitrogen - (Fig. 37, tests VIII to XII) show that Tubifex tubifex and the Limnodrilus species can sense differences in the chemism of the substrate (tests VIII and IX). The worms avoid the pure mineral mud and prefer the sediment with the highest nutritional content.

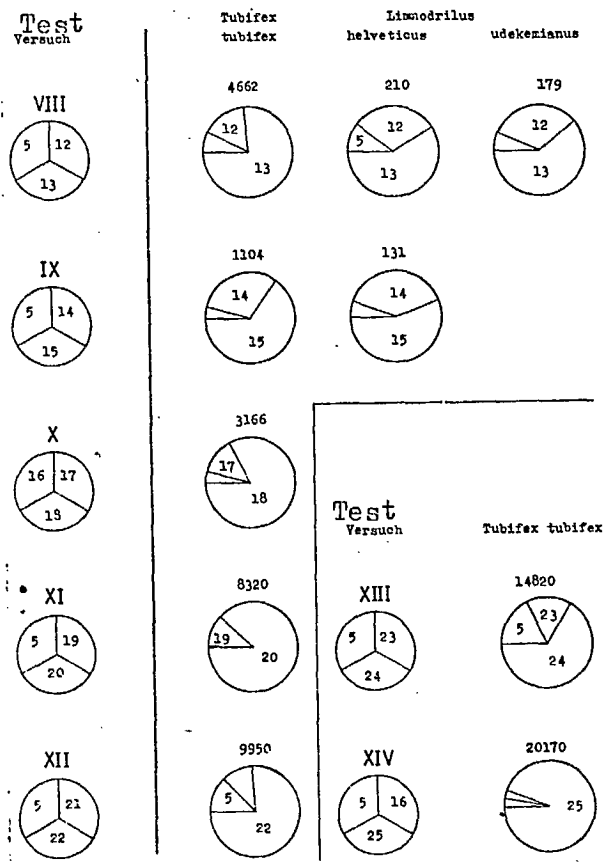


Fig. 37. Selection tests in substrates with different carbon content and nitrogen content (tests VIII to XII) and with differences in the grain size and in the chemism (tests XIII and XIV).

T. tubifex is able to indicate small differences in the carbon content (and in the nitrogen content, respectively) (tests X to XII). According to test XII the individuals react in muds with a carbon content of less than 1 per cent (and a nitrogen content of about 0.1 per cent,

respectively) very clearly (with a sevenfold number) to a difference of 0.55 per cent carbon (and 0.06 per cent nitrogen, respectively), but not at all any more to one of 0.27 per cent carbon (and 0.04 per cent nitrogen). [p. 359]

When finally T. tubifex is being offered the choice between fine-grained substrates (muds) without nutrients or with a low content of them and a coarse-grained substrate with a high content of nutrients, the animals do not move into the mud, but into the medium containing carbon and nitrogen, in spite of the high share in the grain sizes in the region of the fine sand and coarse sand (Fig. 37, tests XIII and XIV). Although in test XIV the sand-mud (substrate 25) does not contain grain sizes below 0.0017 mm, 94 per cent of the individuals have here preferred the carbon content of 7 per cent over the nutrient-poor (1.43 per cent C) mineral mud.

Therefore, the nutrient content of the sediment is of primary importance for the frequency of T. tubifex and not the fineness of the grains. However, this artificial distribution of the mechanical and chemical values that is running oppositely does not exist in the sediments of running waters. For these reasons the development of T. tubifex and of the Limnodrilus species will depend on that combination of factors that has been established through field observations and that is fixed by the course of the curve for the distribution of grain sizes.

6 . 3 M a x i m u m C o l o n i z a t i o n D e n s i t y a n d S e a s o n a l A b u n d a n c e F l u c t u a t i o n s

It is well known that the colonization density of every species is dependent on the effects of the ecological conditions and on the season.

In addition, it can show noticeable differences within a small area in one and the same substrate, especially in the case of oligochaete species that are rich in individuals (especially in tubificids).

In order to obtain a concept of the frequency of individual forms, the maximum abundance values of common species have been assembled in Table 11. The data include also the juvenile individuals of the colonists. Among other things, this representation shows clearly also the approximate centres of distribution in the Fulda of the species cited.

[p. 360]

Table 11. Greatest abundance of species rich in individuals.
(Unit of measurement for plants: 100 cm³,
for other substrates: 100 cm²).

Species	Station (Fulda)	Date (1962)	Substrate	Total individuals
<i>Chaetogaster diastrophus</i>	O	21. 8.	Stones	130
<i>Ch. langi</i>	G	7. 12.	<u>Callitriche</u>	26
<i>Nais communis</i>	B, a	2. 11.	Gravel	222
<i>N. alpina</i>	G	7. 12.	<u>Callitriche</u>	7
<i>N. bretscheri</i>	G	7. 12.	Gravel	11
<i>N. pardalis</i>	E	13. 9.	Stones	7
<i>N. elinguis</i>	O	30. 4.	Stones	660
<i>Stylaria lacustris</i>	N	15. 10.	<u>Elodea</u>	19
<i>Pristina rosea</i>	G	30. 9.	Gravel	58
<i>P. foreli</i>	G	30. 9.	Gravel	67
<i>Propappus volki</i>	F	23. 7.	Gravel	49
<i>Cernosvitoviella atrata</i>	A	14. 5.	Sand-mud	24
<i>Tubifex tubifex</i>	H	1. 6.	Mud	1916
<i>Aulodrilus plurisetia</i>	G	3. 8.	Sand	35
<i>Stylodrilus heringianus</i>	C	4. 9.	Mud	36

Furthermore, the high colonization density in the running springs and in the upper reaches of the genera Nais, Pristina, Propappus, Cernosvitoviella and Stylodrilus suggests very strongly that it is hardly justifiable to ascribe, according to Illies (1952), "an unimportant role" to the oligochaetes "in the manifestation of the brook fauna".

Knowledge of the season and of the duration of the sexual

maturity of the animals is of great importance for ecological research, because the structure of the biotic community changes with this periodicity. Seasonal differences of abundance are shown in Table 12. Individuals of all ages have been taken into account for the two Nais forms, but only adult individuals have been considered for the remaining species. The [p. 361]

Table 12. Average population density in a half-year per 100 cm² substrate.
(Sch = mud, S-Sch = sand-mud, S = sand, K = gravel)

Species	Summer (May-Oct.)	Winter (Nov.-Apr.)	Substrate
<i>Nais communis</i>	16,4	28,3	S-Sch, S, K
<i>N. elinguis</i>	88,1	162,5	S-Sch, S, K
<i>Cernoscitoviella atrata</i>	2,9	3,3	S-Sch, S, K
<i>Stylodrilus heringianus</i>	3,5	2,3	Sch, S-Sch, S, K
<i>Tubifex tubifex</i>	21,2	23,4	Sch, S-Sch
<i>Limnodrilus helveticus</i>	22,7	22,4	S-Sch
<i>L. hoffmeisteri</i>	24,8	25,5	Sch, S-Sch
<i>L. udekemianus</i>	10,3	8,8	Sch, S-Sch
<i>L.</i> , genus	46,1	44,4	Sch, S-Sch
<i>L.</i> , genus (einschl. juv. Ind.) (incl. juv. ind.)	162,6	96,5	Sch, S-Sch

Nais species show marked fluctuations in abundance on account of the greater number of juveniles during the winter half-year, whereas in the other oligochaetes the relations are rather better equalized. Seasonal differences, however, appear again very clearly, when the data are based on the individuals of all age classes - as it has been done for the genus Limnodrilus. One can deduce from this compilation that a monthly sampling (in the same biotic community!) during half a year (according to the classification used in Table 12) is entirely sufficient and provides reliable results, when one intends to establish the population density of adult tubificids of running waters that is to be valid as the annual average. Because the inclemency of the winter (ice formation etc.)

impedes ecological work, it is best to chose the period from May to October as the working time.

Table 13. Average number of individuals of the oligochaete fauna per 100 cm² mud or sand-mud, respectively.

Period	Station								
	A	C	E	F	G	H	K	N	O
Summer	29	21	108	446	226	746	472	849	530
Winter	30	38	120	251	100	68	45	267	247

Table 13 is intended only to support by means of a summary representation the unambiguous demonstration that in contrast the abundance values of the tubificids of every age are considerably lower during the winter months. Below station F the muddy substrate is inhabited almost exclusively by tubificids and exactly there the differences in colonization begin to increase enormously.

6 . 4 C l a s s i f i c a t i o n o f t h e R u n n i n g W a t e r s A c c o r d i n g t o S u b s t r a t e s

As conclusion it is intended to consider the ecology of the oligochaetes living in running water from the point of view of the existence and the distribution of the species of this animal order in the entire course of a stream. Geological circumstances make it impossible to carry out such an investigation in an Alpine stream (almost exclusively a gravel bottom, no large areas of sediments). On account of this, it is not possible to compare the ecological system of a river of hilly country with that of a river of the Alpine foothills, when one intends to use the substrate types as the starting point for the observations. The distribution of the species (cf. Table 21) of the individual oligochaete families has therefore been presented only for the river system

of the Fulda (Fig. 2). This is eminently suitable for this purpose on account of its hydrology. In addition, the Fulda is of special interest in this connection, because it has been better investigated than most other German rivers and has provided a decisive contribution to the limnological zonation of running waters (Illies 1949, 1950, 1953, 1954, 1958, 1961a; Müller 1950, 1952; Scheele 1952; Stave 1953; Schmitz 1957).

The oligochaetes develop an abundance of species in running water, the size of which was unknown until recently. It was possible to demonstrate the presence of altogether 90 species in 7 families in the Fulda (see Table 21 for the percentage distribution in the substrates of the sampling stations). If one takes into account also the Weser (Wachs [p. 362] 1964) as the natural continuation of the Fulda, then the oligochaete fauna of this river system - without the brackish estuarine region of the outer Weser - consists with Pristina aquiseta and Octolasion lacteum of 92 species and 40 genera (the occurrence of Paranais litoralis that is bound to the small salt content of the Weser has not been taken into consideration).

In the source region the Enchytraeidae constitute the family richest in species (within the oligochaetes), but not richest in individuals, as the statements have shown. Since the majority of the 37 enchytraeid species reported from the Fulda actually represent amphibious or terrestrial organisms, their number must become positively reduced downstream on account of the changes in the river bed. Representatives of the two most important limnic families, the naidids and tubificids (25 and 15 species respectively in the Fulda), occur frequently in the entire course of the river. The maximum number of species (46) in the upper reaches (station G) is due to the great variety of the substrates,

that has come into existence there shortly after the entrance of the first large tributary. After another stretch of about 150-km length (station M), there is found another increase in species (25), because the selected environment again shows a number of micro habitats. The sudden decrease in the number of forms at station H indicates the impoverishment of the substrate types that has taken place.

Of the species of the oligochaete fauna typical for running waters that have been reported, there are only four that can be considered to have only a narrow temperature tolerance. Nais alpina colonizes rocks, gravel, sand and plants in cold water with a small temperature amplitude. Rhyacodrilus falciformis and Tubifex nerthus only occur on stones and in the mud of the source region. It is possible that these three species with narrow temperature tolerances are relicts of the glacial fauna, which chose the locality in question as a refugium. Phreoryctes gordioides also occurs in the source region in the substrates and under stones. However, the proper environment of this species is subterranean, but not in the ground-water, it is rather represented "by the moisture saturated layer between ground-water and soil" (Noll and Stammer 1953, cf. Thienemann 1912).

The occurrence of the other species that have been found here, as far as they are not amphibious or live in the border layer of the shore, is connected in the first instance with the substrate. Numerous species of the recorded (terricolous) enchytraeids are able to live amphibiously, as well as the lumbricids Dendrobaena octaedra, Octolasion lacteum and the Allolobophora forms. They are therefore found mostly only in the brook region of the streams (as strays or aliens), although this region is not their proper environment. Thus Enchytraeus albidus,

which is frequently cited in the literature (by Illies 1961b, among others), must be considered as a "stray" only in the animal community of the mountain brooks. On the other hand, there are at least 50 species of oligochaetes - mainly naidids - that live regularly in the region of the brooks. The occurrence of the lumbricids Eiseniella tetraedra and Allolobophora chlorotica is characteristic of a region near the shore of running waters (cf. Fuller 1953). [p. 363]

The ecological investigations of the oligochaete fauna of the entire course of a river has resulted in the knowledge that the kind and composition of the substrate are the decisive factors in the formation of the animal communities concerned. The majority of the typical limnic species occur everywhere along the course of the river (Table 21). If one should represent these ecological findings graphically in the manner of the representation of the "species structure"³ (Illies 1953, 1954) (this is here not possible on account of the large number of curves with very irregular courses), one would obtain a tangle of curves that vary continuously in their extension in height. The marked peaks always coincided with a large number of types that were present, or that had been taken into account. However, it is required that the curves drop roof-like laterally, because "the steepness of the slope of the curves from station to station (that is, the steepness of all curves, taken as a sum)" forms "a criterion for the intensity of the change in species" (Schmitz 1957). The confusing picture of such an elaboration can be traced back

³ This kind of representation that has been developed by Illies (1953) in regard to four orders of insects has been defined thus: "to begin with the number of species found there was established for each individual sampling station. Furthermore, at each sampling station was ascertained how many species of the other sampling stations are still present there".

unambiguously to the occurrence of the oligochaetes in different environments in the running waters. Consequently, such a method of analyzing the group of animals according to biotic communities must be based on one substrate only. The "species structure" of the oligochaetes in the river has been presented in Table 14 and Fig. 38, based on only the mud substrates at ten stations. The curves do not slope down roof-like, but fluctuate in their height, they run in part horizontally and in parts of their courses they coincide. Consequently, the course of the individual curves can be seen only in Table 14, the total picture of Fig. 38 hardly allows a separation into only the following three main parts of the course:

- A - C source region (or krenon, after Illies 1962),
- C - G salmonid region (or rhithron, after Illies 1951a),
- G - O ciprinid region (or epipotamon, after Illies 1961a).

Although the river sections can be defined physiographically and although the ecological systems contain biotic communities that can be defined generally and that are characteristic, it must be emphasized:

[p. 364]

in general "there are no sharp boundaries between the individual regions" (Liebmann 1962) and

specifically the order Oligochaeta has proved to be absolutely unsuitable for an analysis of the stock of the benthic fauna, when it is intended to be used as the basis for the division of the running waters into regional types.

Table 14. Numerical representation of the "species structure" of the oligochaetes in the course of a river with regard to the muddy environments only.

Station	A	C	E	F	G	H	K	M	N	O
A	7	6	4	2	2	1	1	1	1	1
C	6	12	5	2	2	1	1	1	1	1
E	4	5	18	5	5	4	5	3	4	6
F	2	2	5	5	4	4	4	3	4	4
G	2	2	5	4	10	4	4	3	4	4
H	1	1	4	4	4	4	4	3	4	4
K	1	1	5	4	4	4	6	3	4	6
M	1	1	3	3	3	3	3	5	3	3
N	1	1	4	4	4	4	4	3	4	4
O	1	1	6	4	4	4	6	3	4	8

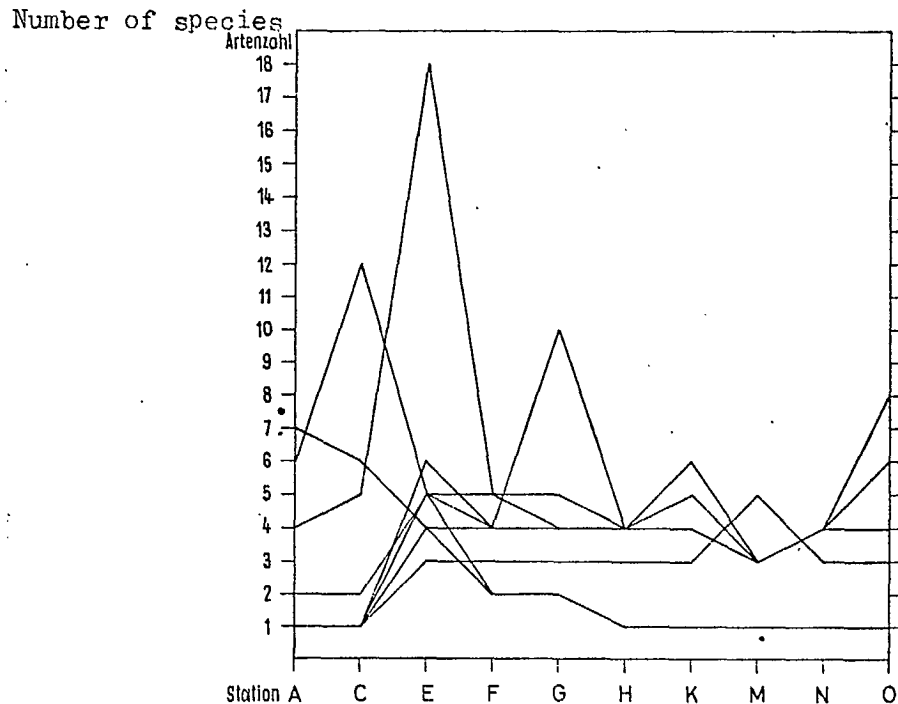


Fig. 38. Graphic representation of the "species structure" of the oligochaetes in the course of a river according to the results in Table 14.

Even when one takes account of the phenomenon that the boundaries between the animal communities are obtained "only through summary observation of the change in all animal species present" (Schmitz 1957), it is useless to fit the order of animals treated here into this method. The results obtained have shown that there exist no characteristic and easily recognizable benthos associations that are directly dependent on the distance from the source. Rather, the great ecological differences in small areas lead already to the formation of a mosaic of animal communities (cf. Ambühl 1959, among others). The statement by Schmitz (1957), which he applies to running water, however, only with the beginning of the ciprinid region, namely, that the animal communities appear side by side or alternately, mainly bound to certain substrates, thus applies generally to the distribution of the oligochaete fauna. The benthic animal communities formed by it can occur either side by side in the cross-section of the river or they can repeat themselves along its length. At the same time the communities "can change more or less distinctly from one into the other through common mediating species" (Illies 1949). This can happen in communities at the borders of the sedimentary mosaics or in substrates with a grain spectrum that has a greater than average diversity. These two ecological phenomena were demonstrated by Illies (1949) also for the occurrence of Coleoptera in running waters. It is, of course, essential that the analysis of the running water benthos takes into account the community mosaics of all the existing micro environments. Accordingly, the types of substrates present must also be treated separately, because only then is it possible to make statements about the limits of distribution of the organisms. It is not possible to speak either of a continuity in the sequence of species, nor of an abrupt change in the

fauna in the course of the river. One can therefore not discern a regional distribution of the oligochaetes, since the change in the fauna parallels the change in substrates, which results directly from the changes in the current speed. Most of the species are living everywhere in running water, as long as the preferred substrate is present (cf. Berg 1948). As has already been emphasized, Tubifex tubifex is found also in the mud of the source (cf. Bornhauser 1913, Beyer 1932). In the treatment of the oligochaete fauna, the running waters can thus not be classified according "to zones" nor "as a whole", but only according "to substrates" (see Illies and Botosaneanu 1963). Behning (1928), Nietzsche (1937), Illies (1949) and Szczepanski (1953), for example, also arrived at the mosaic division through their investigations of the individual typical benthos communities of the substrates. The characteristic species of the spatially fixed mosaics have been described in the chapter on the substrate types.

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In Table 15 have been assembled the maximum colonization densities for seven of the substrate types investigated, based on the number of the forms demonstrated at each station. These statements thus do not represent the sums of the possible species in a type of substrate, but they refer in each case to the bottom layer of one station. When one considers the sedimentary substrates (that is, except the plants) one finds a continuous increase in the number of species in the following direction:

mud to stones to sand-mud to sand to gravel.

Furthermore, there exists in all substrates, that is, in every environment with the same structure and with the same ecological conditions, a marked coexistence of closely related species (cf. Wachs 1964).

Table 15. Greatest number of species, genera and families in different types of substrates.

Station	Substrate	Grain size (mm)	Number of		
			Species	Genera	Families
G	<i>Callitriche spec.</i>	/	27	17	6
M	<i>Ranunculus fluitans</i>	/	8	7	3
E	Stones	/	16	9	3
G	Gravel	45 — 0,063	27	15	5
G	Sand	6 — <0,063	22	14	3
E	Sand-mud	2 — 0,02	18	14	5
C	Mud	0,25 — <0,001	12	10	4

7 . SEDIMENT TRANSPORT BY TUBIFICIDS

By analogy with the activities of the lumbricids in solid ground, the tubificids "are able", according to observations by Alsterberg (1925), "to transport unheard-of amounts of material in an unexpectedly short span of time". Accordingly, a worm of the genus *Tubifex* or *Limnodrilus* is supposed to transport four times its own weight (live weight) of so-called detritus (calculated as dry substance) to the surface of the mud within 24 h (at about 12°C!).

The significance of tubificids as movers of sediment has been investigated by means of comprehensive experiments with *Limnodrilus hoffmeisteri* and *L. udekemianus* once again by Poddubnaya (1961). In these the author could demonstrate a great increase in metabolism that took place first with increasing temperature (in the region 0.5 to 22°C) and second with increasing mud content of the substrate (on the example of the three sediments clay-sand, clay-sand-mud, mud). Investigations by Ravera (1955) in Lago Maggiore have shown that the amount of mud taken up by oligochaetes

depends also on the depth at which the worms live. This bathymetric effect that does not apply to running waters and the different mud content of the environment were not taken into consideration in my investigations.

In my experiments I treated the water temperature as the only variable under otherwise constant conditions. Mud from the Isar at stations R and S that had been sieved through a net of 0.2 mm mesh was filled into a glass vessel of 5-cm height. After about 150 to 250 adults of Tubifex tubifex had been transferred to the mud, the surface was covered with a loose layer of absorbent cotton and then tightly closed with a transparent sheet of plastic. This thin sheet of plastic was perforated with holes arranged in parallel rows. The holes are of such a size that about four worms lying closely appressed to one another can reach through them at the same time. The glass vessel was then put into a beaker with running tap water. After the animals had pushed the posterior end of the body through the cotton and the holes into the open water, the vessel was suspended upside-down in an Imhoff funnel (1000 ml), which was supplied with a stream of tapwater from above through a rubber hose (Fig. 39). The principle of this inverted arrangement of the tubificids had been given by Alsterberg (1925) in his classical experiment. After one to three days the worms had become "accustomed" to the new conditions and had oriented themselves accordingly in the water of the funnel with the posterior end of the body pointing down. The cause of this movement that finally becomes necessary for survival, which, however, is never required in nature, is the existence in tubificids (Tubifex tubifex and Limnodrilus hoffmeisteri) of two important senses that have been investigated in detail by Alsterberg (1924). The negative geotaxis changes finally into a positive one

due to the positive reaction of the very keenly developed air perception.

The Imhoff funnel that was provided with a stopcock at the bottom was standing in a deep plastic pail filled with water. The water temperatures (measured in the funnel in the zone of the worms) of 3 to 12°C were obtained and kept constant by cooling coils hung in the pail - or in addition also in the funnel - that were connected to an automatic refrigerator operated with methylalcohol. A thermostatic stirrer ("Thermomix") working in the pail served to obtain the required temperature and keep

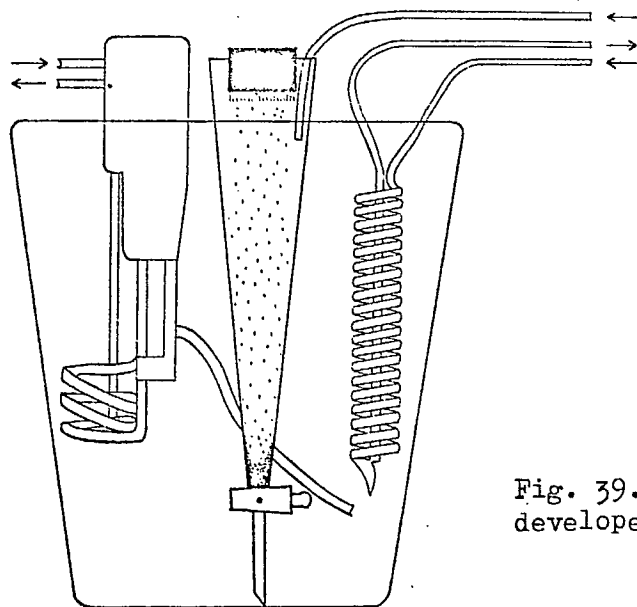


Fig. 39. The experimental arrangement developed for the measurement of the metabolic activity.

[p. 368]

it constant (Fig. 39). The experiment was started as soon as the animals protruding from the mud container made regular undulating movements in the water. The worms were counted four times daily and the calculated mean was considered to be the representative number of Tubifex individuals taking part in the experiment on the day in question. The experiment was interrupted or terminated after one or several days. The amount of faeces that had accumulated in the Imhoff funnel was drained into a graduated tube and measured in cm^3 after a settling period of six hours. The mud

volume obtained in this manner was recalculated for 100 worms and 24 h. Whereas Poddubnaya (1961) obtained the amount of animals (Limnodrilus) and of faeces gravimetrically after drying on filter paper, I have used the number of worms and - on account of the different specific weights of the substrates - the volume of the mud.

In order to discover whether it would be possible to ascertain the amount of excrement also with a normal arrangement of the mud vessel, I covered some containers that were standing in running water with the opening uppermost with very finely perforated plastic sheet. However, the worms immediately began to form tubes on the sheet.

Often the experiments were running in a satisfactory manner for only a few days, after which they had to be started anew. The results - among them also the means of several experiments - are very variable and they have been assembled in Table 16. The mean values from Table 16 are presented graphically in Fig. 40 and show plainly the enormous differences in the intensity of the metabolism in tubificids in the temperature range 10 to 18°C that usually prevails in running waters. In the winter the worms ingest only very small amounts of substrate. In contrast, they require the thirteenfold to seventeenfold amount of nourishment during the summer. However, since at the time of the greatest increase in water temperature the number of adult tubificids is only small and since the juvenile animals as a rule take up less material, the amount of substrate moved in a biotic environment is bound to increase less rapidly than is shown in Fig. 40.

In order to obtain an approximate idea of the amounts of excrements that are moved to the surface of the sediments in a river, the number of adult tubificids per m² was ascertained for May and as an

Table 16. Experimental results regarding the amount (in cm³) of faeces produced by 100 individuals of Tubifex tubifex within 24 h.

After n days	Temperature in °C	3	6	10	12	15	18	20	22	25
		1				1.57	2.56	5.64	5.88	
2		0.36		1.37		2.48			6.02	6.79
3			0.62		1.64			5.95		
4		0.42			1.89	2.97	5.19	6.24	6.79	8.10
5				1.60		2.41	6.08		7.51	
6			0.76				5.18	6.87	5.76	6.83
7						2.06		5.64		7.81
8				1.42	1.78		5.01	6.75	7.57	
9			0.84			3.01	5.05			
10							4.54	4.51	6.73	
11				1.21		2.79	4.90	6.03	6.96	
12					1.67	2.93	5.14			
Mean value for 24 h		0.39	0.74	1.40	1.71	2.65	5.19	5.98	6.76	7.28

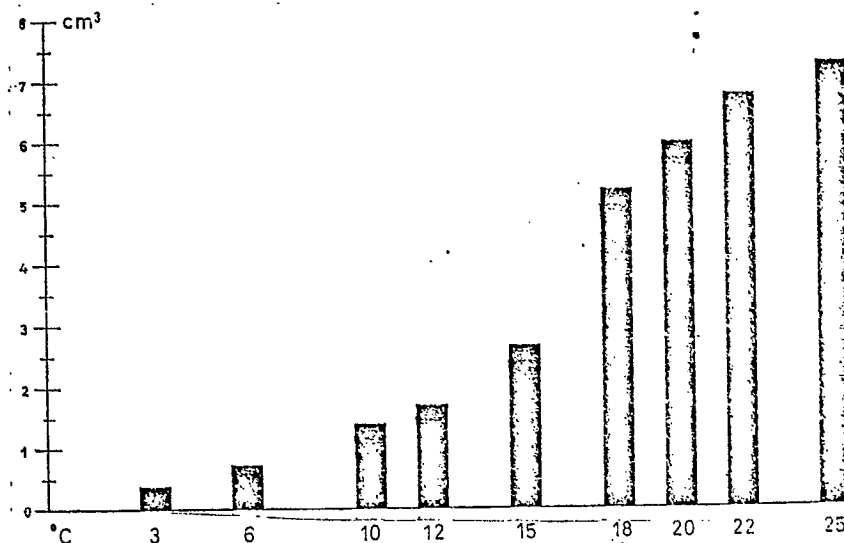


Fig. 40. The amount of faeces (in cm³) produced per day by 100 individuals of Tubifex tubifex in relation to water temperature.

annual average at two stations. The experimental results were introduced into the calculations with regard to the temperature measured. They are assembled in Table 17. In the calculations the metabolic intensity for the Limnodrilus species has been equated with that for Tubifex tubifex. Since the juvenile worms have not been taken into account, the figures

for the amounts of faeces are minimum values. Thus, for example, the tubificids at station H (27,173 adults/m²) transported in the month of May at least 43.7 dm³ of mud per m² and thus made it accessible to aerobic micro-organisms for mineralization. It is hardly probable that greater amounts would be transported in another month in this biotic environment, since in May the greatest number of adult worms is present and the water temperature is relatively high. The amount of faeces found for the period of a year is, according to Table 17, only slightly different from that in May. It is therefore not possible to calculate the amount of excrements for this long period on the basis of the mean values of two quantities (temperature and number of individuals) that vary strongly. Consequently, the values for one year are lying below the actual figures and therefore have been put in parantheses as being theoretical. [p. 369] [p. 371]

8 . F E E D I N G O F O L I G O C H A E T E S

8 . 1 S p e c i e s R i c h i n I n d i v i d u a l s o f A e o l o s o m a t i d a e , N a i d i d a e , E n c h y t r a e i d a e a n d L u m b r i c u l i d a e

Hardly anything is known about the food of limnic oligochaetes.

Table 18 gives a review of the food (except bacteria and protozoa) of species that are observed frequently. The greater number of marks (/) as indicators for a species are intended to indicate a greater share of the food in the gut; a quantitative comparison may therefore be made only in a horizontal direction.

Lehmann (1933) established in a biotic environment rich in tubificids that Chaetogaster diaphanus, a predator of small animals, had taken, besides its main food consisting of Cladocera, also single chironomids

Table 17. The amount of substrate transported at two biotic environments by adult tubificids in May (and during one year).

Station	Substrate type	Organic substance per cent	Period	Water temperature	Adults	Individuals per m ²	Faeces (dm ³)
P (Isar)	Sand-mud	3.31	May 1 - 31	12°C	<u>T. tubifex</u>	710	0.376
					Tubificids	8880	4.707
			1 year	10°C	<u>T. tubifex</u>	1900	(9.709)
					Tubificids	4800	(24.528)
H (Fulda)	Mud	11.48	May 1 - 31	18°C	<u>T. tubifex</u>	22644	36.432
					Tubificids	27173	43.721
			1 year	12°C	<u>T. tubifex</u>	6100	(38.073)
					Tubificids	7200	(44.939)

Table 18. Gut content of species observed frequently.

Species	Gut content		Plants				Animals						
	Sand grains		Fine detritus	Diatomaceae	Chlorophyceae	Desmidiaceae	Plant remains	Rotatoria	Naididae	Propappus volki	Cladocera	Copepoda	Ephemeroptera
	Coarse	Fine											
<i>Aeolosoma hemprichi</i>													
<i>A. variegatum</i>													
<i>Chaetogaster diastrophus</i>													
<i>Ch. langi</i>													
<i>Ch. diaphanus</i>													
<i>Ch. cristallinus</i>													
<i>Ch. limnaei</i>													
<i>Uncinatis uncinata</i>													
<i>Ophidonais serpentina</i>													
<i>Nais-Spezies</i>													
<i>Stylaria lacustris</i>													
<i>Pristina-Spezies</i>													
<i>Propappus volki</i>													
<i>Mesenchytraeus beumeri</i>													
<i>Cernosvitoviella atrata</i>													
<i>Cognettia glandulosa,</i> <i>sphagnetorum</i>													
<i>Henlea nasuta</i>													
<i>Marionina argentea</i>													
<i>Stylodrilus heringianus</i>													
<i>Lumbriculus variegatus</i>													

[p. 372]

and tubificids. I found only plant remains in the gut of Chaetogaster diastrophus, which is frequently designated as carnivorous in the scientific physiological literature. I was never able to demonstrate cercariae in the gut of Ch. limnaei (cf. Berg 1948); according to Krasnodebski (1936) they form as a rule the most important part of its "fundamentally animal food". When trematodes are present, Wagin (1932) and Beyer (1955) also see an important destroyer of cercariae in Ch. limnaei.

The findings of Rehbronn (1937) in Stylaria lacustris also differ from the present results. When there is available a rich supply



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of food of diverse composition, the fine detritus does not constitute the main food, but Chlorophyceae and coarse sand particles are taken up preferentially.

8 . 2 T u b i f i c i d s

Doubtlessly, there exist relations in qualitative and quantitative respect between the fauna of the substrate-feeding tubificids and the "nutritional content" that is always being cited in the literature, but which is characterized at the most by the share of organic substances. This, however, does not yet prove in how far the complex of the "detritus" (decaying material) can be used as an energy source or can be converted into body substance.

The tubificids restrict their feeding to the "nutritive layer", which, according to Alsterberg (1925), has a height of at least 6 cm and follows after the thinner upper layer; but defecation takes place at the surface of the substrate. Interestingly, the transportation of the substrate is restricted to the fine fraction, so that the coarse-grained sediments remain lying untouched in their layer. Alsterberg (1925) had already made this observation, which was confirmed experimentally by Poddubnaya (1961). This author demonstrated by means of investigations of faeces that were conducted separately for the species Limnodrilus hoffmeisteri, L. udekemianus and Tubifex newaensis that the dominant spectrum of grain sizes of the mineral components is 0.1-0.05-(0.01) mm. Substrate particles larger than 0.2 mm are practically no longer ingested. The selective sediment transportation that takes place continuously in this manner provides the means for the aerobical degradation of the loose material that has been brought to the surface within a certain period of time within

this cycle.

The following experimental contribution concerns the importance of the tubificids that occur in large numbers of individuals for the mineralization of the sedimented mud. While investigating the energy exchange, Ivlev (1937, 1939) made experiments with Tubifex tubifex at 16 to 18°C. He obtained the result that the value of assimilation ("corresponds to the difference between the utilized energy and that eliminated as excrement") "amounts on an average to 50.37 per cent of the total amount of the energy utilized" (Ivlev 1937). This utilization value is high and therefore provided the inducement to express the processing for obtaining energy, including the synthesis of body substance (assimilation), as the content of carbon and nitrogen of the ingested mud, but not by the change in the content of calories in mud, animal substance and excrements.

[p. 373]

The feeding experiments were carried out with Tubifex tubifex. A homogeneous mixture of river mud and animated mud served as food for the animals. The animated mud is deposited in an oxidation ditch (on the sewage test field of the Bavarian Biological Research Institute) into which are fed the sewage waters of Munich. Both kinds of mud were collected on the day on which the experiments were started, sieved through a net of 0.2-mm mesh, mixed and filled into two or three large Petri dishes (diameter 18 cm, height 4 cm). The dishes were placed into a water basin through which flowed Munich tap water (filtered through activated charcoal) with a temperature of $12^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$. After the substrates had settled, adult and juvenile worms that had been starved for several days were added. After 13 to 14 h the animals were isolated by sieving, freed from adhering mud particles through careful and effective washing, transferred to dishes and placed under fast dripping water. The faeces were

pipetted off continuously during the next five hours and separated from cocoon hulls, eggs and very small individuals. About 66,000 organisms were used for each of the majority of the experiments (\bar{A} about 150 mg dry substance of faeces). About 88,000 individuals had to be fed when the analyses for C and N were intended to be made simultaneously. The material for the analyses of the starting substance was obtained by mixing equal amounts of mud samples that had been collected at the beginning and end of the experiment.

The results of the chemical examinations of the mud before and after its passage through the gut of the worms (50 analyses each of C and 35 each of N) are shown in Figs. 41 and 42. The scatter of the points is considerable for the very small amounts of data; however, a linear dependence is recognizable (straight line b) on the basis of the numerous analyses. The gentler slope of the straight line obtained through the arithmetical means ($\bar{=}$ $\bar{=}$ $\bar{=}$) indicates a better utilization (proportion as far as the straight line a) of the nutrients and will not be taken into account. Thus Tubifex tubifex utilizes on an average 21 per cent of organic carbon (Fig. 41) and 34 per cent of the total nitrogen (Fig. 42) of the muddy food. However, here it is not known in how far symbiotic gut bacteria alter the chemism of the food.

If there existed in nature a direct circulation of food and excrements without a change in the chemism that takes place outside the body of the tubificids, then the starting food with a content of 2 per cent C and 0.3 per cent N (the averages of the river mud) would have to pass through the gut of T. tubifex about five times (in respect to N) to fifteen times (in respect to C) if a nearly complete mineralization were to be achieved.

After passage through the gut of the worms the ratio between C and N changes according to Figs. 41 and 42 on an average in favour of C. The results of the 15 experiments, in which food and faeces were analyzed simultaneously for their content of C and N (Table 19) demonstrate a change that is often considerable in the value C/N in both directions. The increase in the ratio C/N that takes place generally can, however, not be seen from the mean of the 15 random samples on account of the large scatter.

[p. 375]

Table 19. Feeding experiments with Tubifex tubifex with analyses for C and N of the food and faeces.

No.	C		N		C/N	
	Food	Faeces	Food	Faeces	Food	Faeces
1	1,92	1,88	0,50	0,20	3,8	9,4
2	2,52	1,41	0,48	0,44	5,2	3,2
3	3,87	1,98	0,17	0,14	22,8	14,1
4	5,19	1,09	0,43	0,40	12,1	2,7
5	6,99	1,85	2,05	1,08	3,4	1,7
6	7,86	3,25	0,71	0,05	11,1	65,0
7	8,60	5,61	5,07	3,11	1,7	1,8
8	8,78	6,92	1,13	1,24	7,8	5,6
9	9,19	5,55	0,46	0,21	19,9	26,4
10	12,22	9,33	3,77	4,10	3,3	2,3
11	12,56	11,19	2,09	2,04	6,0	5,5
12	14,09	12,40	2,66	1,88	5,3	6,6
13	19,57	14,98	2,84	2,28	6,9	6,5
14	22,19	20,21	2,98	3,07	7,4	6,6
15	23,79	17,71	4,36	1,74	5,4	10,2

On account of their continuous selective ingestion of substrate amounts with a grain size under (0.2)-0.1 mm (Poddubnaya 1961) that lie at greater depths, the tubificids accomplish a progressive and additional degradation of the mud and they prepare the way for the aerobic degradation of the organic proportion of the sediments by providing the loose deposition of coprogenic material on the surface of the mud. Although

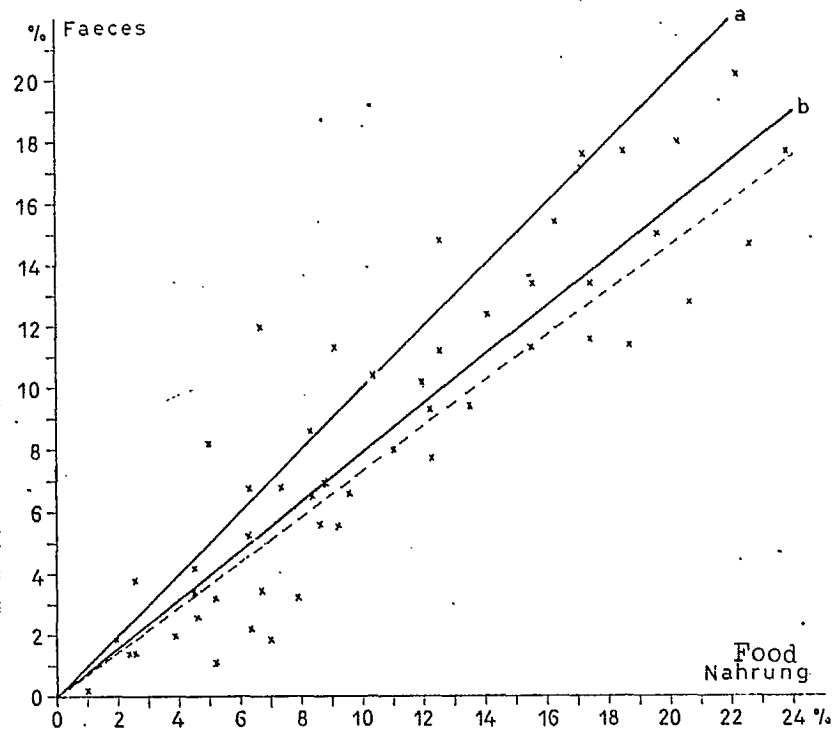


Fig. 41. Utilization of the organic carbon of the food by Tubifex tubifex.

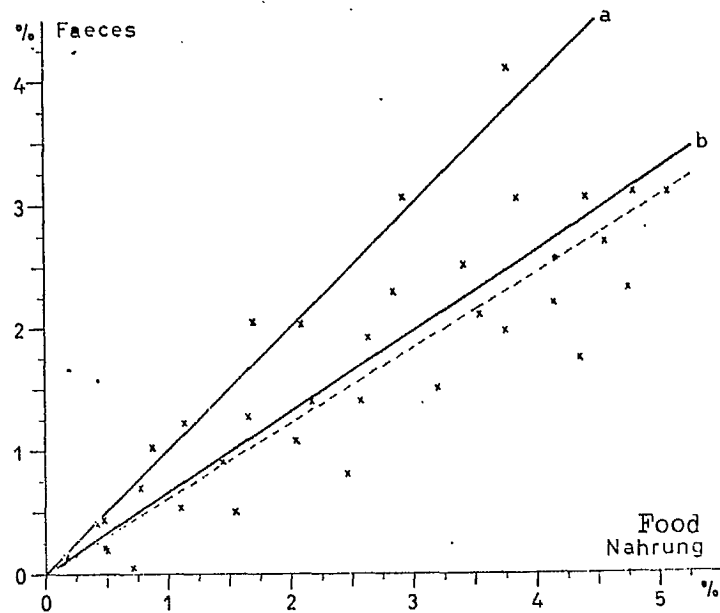


Fig. 42. Utilization of the total nitrogen of the food by Tubifex tubifex.

mineralization takes place "mainly by bacteria" (Ungemach 1960), "the tubificids have to be considered as important biological links in the natural self-purification" (Liebmann 1960a), since they regulate the "processes leading to biological self-purification" (Soloviev 1924).

It is intended to show by means of an example in Table 20 the order of magnitude of the elimination of organic substances from the river sediments that is accomplished by the metabolic processes in the tubificids. According to this, the adult tubificids alone at station H did consume per m² about 47 g of organic carbon and about 20 g of total nitrogen during the month of May.

9 . D I S C U S S I O N A N D S U M M A R Y O F T H E R E S U L T S

The oligochaete fauna of running waters serves as the starting point for the examinations in only a few systematic-ecological investigations. The statements in the older literature cannot be used at all, or only with reservations on account of taxonomic mistakes. The dependence of the limnic oligochaetes on the substrate has only recently been considered in ecological river investigations (Berg 1948, Korn 1963, Wachs 1963, 1964). The available field observations gave, to begin with, an overview of the existing stock of species and their ecological importance. Above all, they provided fundamental indications for the planning of the experimental investigations, which were intended to clarify the causal relations between environment and organisms. [p. 376]

The qualitative and quantitative composition of the oligochaete fauna in a river of hilly country (Fulda) and in a river of the Alpine foothills (Isar) each were investigated by means of systematic and ecological

studies during an annual cycle. The various substrates along the course of the Fulda of about 230-km length have a total of 90 species, belonging to 39 genera and 7 families.

It was established that there is present in running waters a wealth of species. The extent of this was not at all indicated by the meagre statements in the literature. Partial descriptions have been given of morphological characteristics that are decisive for the identification of species and our previous knowledge of them has been examined critically.

There can be found in the literature only occasional remarks about the time of sexual maturity in limnic oligochaetes. However, they do not give any information about the duration of a sexual period, since mature individuals appear in every season. Exact statements about the existence of a sexual period has been available hitherto only through the investigations by Poddubnaya (1959) in the Rybinsk Dam. It was possible to confirm them in general and to amplify them. The exact knowledge of the reproductive cycle is absolutely necessary for the correct evaluation of random catches that were not made rhythmically. Wrong explanations of extremes of abundance values and incorrect evaluations of the quality status of a stream can be avoided in this manner.

Table 20. Weight of the organic carbon and total nitrogen per m² that has been utilized by tubificid adults during the month of May at station H.

Station	H	
Period	May 1 to 31	
Water temperature	18°C	
Adult tubificids per m ²	27,173 individuals	
Volume of mud transported	43.721 dm ³	
Dry weight of this mud	10.165 kg	
Weight of organic C and of the total N	in the food utilized by tubificids	221.60 g C 59.97 g N 46.54 g C 20.39 g N

Stylaria lacustris attains sexual maturity mainly from September to October.

The sexual period of Propappus volki extends from (March) to April to (October).

Stylodrilus heringianus has an extended period of sexual activity from January to September.

The sexual period of Tubifex tubifex, Limnodrilus claparedeanus, L. hoffmeisteri and L. udekemianus falls into the time from March to July. During the months of April and May about 60 to 80 per cent of the individuals present are sexually mature.

The numbers of very young tubificids are greatest from (June) to July to (August).

The number of eggs per cocoon in Tubifex tubifex is one to sixteen (as a rule four to five) and only one to eight (mostly two) in Limnodrilus udekemianus.

The population density in species of naidids and tubificids that occur in large numbers is subject to large seasonal fluctuations. The density in species of the genus Nais is greater during the winter (November to April). Tubifex tubifex and the Limnodrilus species are considerably more numerous in summer. The monthly sampling during the summer from May to October is, however, sufficient for the establishment of the abundance of adult tubificids that is to serve as an annual average. If several streams are to be compared in respect to the abundance of tubificids, statements in the literature are meaningful only if they have been obtained by considering only adult individuals (as reference values). It is useless to attempt to establish high densities when their size depends in the final analysis -subjectively - on the method of

sieving and on the exactness of the counting.

There are no unambiguous correlations between the chemism of the water and the occurrence and distribution of the species (cf. Korn 1963). Thus neither Tubifex tubifex nor the species of Limnodrilus are specific indicators of pollution (contrary to the deductions of Kolkwitz and Marson 1909); they are not "sewerage worms, but mud worms" (Hentschel 1917, cf. Alsterberg 1922). Since the content of nutrients in the muddy substrate increases with it becoming more saprogenic, so increases also the population density of the tubificid species that are prone to mass proliferation (cf. Zahner 1964). They must therefore be considered to be "sewerage dominants", "since they live not only in pure water, but also in polluted water" (Liebmann 1962, p. 239). however, they develop best in a substrate that is rich in organic substances (cf. Steinmann and Surbeck 1918).

[p. 378]

The decisive factors for the existence and for the distribution of almost all typical limnic oligochaete species are the kind and the composition of the substrate. Seven types of substrates have been distinguished and the qualitative and percentage distribution of the oligochaete fauna in them has been ascertained. Preferences for the different types of substrates have been developed among the species. In all sediments are to be found correlations between the spectrum of grain sizes or certain fractions and the characteristic species in each case. This phenomenon has been established at the individual stations by means of the dominant colonizers of plants, stones and certain grain sizes of the sediments. The species then represent the indicator organisms for a definite substrate type by virtue of their percentage value. In practice it is necessary to proceed in the reverse direction. Thus, when kind and

composition of the substrate are known, one can infer the most common species and their approximate percentage in the oligochaete fauna with the aid of the illustrations and tables.

The majority of the gastropods in running water does not contain the commensal Chaetogaster limnaei.

Aquatic plants are colonized mainly by naidids. Chaetogaster diastrophus, Ch. langi and Stylaria lacustris prefer plants as substrate.

As a rule, the naidids are dominant on stones with the following species: Nais alpina (with a narrow cold tolerance), N. communis, N. barbata and N. pardalis (richer in individuals in the upper reaches), N. elinguis (richer in individuals in the lower reaches), Chaetogaster diastrophus and Ch. langi.

The following occur in numbers in clean gravel: Propappus volki, Stylodrilus heringianus, Nais communis, Pristina rosea and P. foreli. However, large numbers of the enchytraeid Propappus volki are not directly associated with this type of substrate, but with the extensive fraction of coarse sand that is contained in it. A requisite for a high frequency of the lumbricolid Stylodrilus heringianus is a sandy or gravelly substrate that contains grain sizes between 0.07 and 0.2 mm.

The sand is inhabited predominantly by six species of Nais, four of Pristina and by Stylodrilus heringianus. In the source region Cernosvitoviella atrata and Marionina argentea are dominant. Increases in the populations of Nais elinguis, Limnodrilus hoffmeisteri, L. udekemianus and Tubifex tubifex run parallel with rising pollution.

A specific combination of factors could be established by means of measurements of the grain sizes of the muddy substrates for the species of tubificids that occur in large numbers of individuals in running water.

This combination cannot be analysed on account of the complex effects of all components that take place under natural conditions; it is, however, exactly represented by the course of the curves for the distribution of grain sizes.

[p. 379]

The sediment designated as sand-mud contains either a share in the grain sizes over 0.5 mm or it lies between the limits 0.5 and 0.005 mm with a main fraction of 0.2 to 0.5 mm. Limnodrilus hoffmeisteri is dominant in this substrate, but it is replaced by L. helveticus in the Alpine river.

The muddy substrate - with a main fraction of (0.08)-0.1-0.2 mm - in which Cernosvitoviella atrata and Nais communis are still predominant in the source region, farther downstream becomes poorer in species and richer in individuals. Tubifex tubifex is dominant in the mud of rivers that are not dammed up, when at least 45 weight per cent are lying in the region of < 0.15 mm diameter, otherwise populations of Limnodrilus preponderate. When larger dammed-up areas are taken into account, the dominance of Tubifex tubifex is dependent in addition on a share of less than 13 weight per cent in the region from 0.08 to 0.1 mm. In barrages of large dimensions Limnodrilus species are generally dominant. The dominant occurrence of Tubifex tubifex is thus the result of subtle demands on the grain size of the substrate. It can therefore not be caused by a considerable influx of organic substances or through heavy loading with sewage in every random sedimentation area of the stream.

It was possible to differentiate exactly the ecological requirements of the most important species by means of the granulation of the substrates. Tubifex tubifex is the most numerous species in the mud, with

a mean proportion of about 73 per cent of the oligochaetes. On the other hand, the genus Limnodrilus predominates in the sand-mud with about 72 per cent and in the sand with about 63 per cent. When only the Limnodrilus species are taken into account, L. udekemianus predominates in the mud with about 67 per cent, L. hoffmeisteri is the most frequent in sand-mud with 73 per cent and in the sand with about 88 per cent.

River muds show a great variability in their chemical composition, but there is no correlation between the content of organic substance; organic carbon and total nitrogen. In general, the mean density of the tubificid populations in the mud increases with rising content of these three chemical components. As regards the individual constitution of the various running waters, the conditions are different in each river system.

The interpretation of the field observations was checked by means of selection experiments with tubificid species and with Stylodrilus heringianus in 25 synthetic substrates. These demonstrated that oligochaetes will move preferably into the environment that is most suitable for them - when they have the opportunity. Tubifex tubifex does no longer prefer muds with fractions below 0.001 mm, when the main fraction lies below the limit of about 0.06 mm.

Tubifex tubifex is able to perceive small differences in the contents of carbon (and of nitrogen, respectively) in the sediments. In experiments it prefers a high content of nutrients in the mud - defined by the proportion of organically bound carbon and nitrogen - to a fine granulation. [p. 380]

The examination of the colonization by oligochaetes reveals a mosaic-like structure of the animal communities (cf. Korn 1963) that may

be repeated everywhere in the cross-section and along the length of the stream. This mosaic structure is exclusively the result of the number and spatial extent of the substrate types. There is thus no regionally-limnological colonization by oligochaetes. The number of species in a sediment substrate type decreases from gravel through sand, sand-mud to stones. In the final analysis, the change in the substrate types and their mechanical and chemical composition are responsible for the limits of distribution, for the existence and the optimum development of the limnic oligochaetes.

The percentage distribution of the tubificid species in the benthos of natural river courses and that of large-scale barrages is remarkably different. The differences, however, are not caused by the kind of grain distribution of the sediments; the cause may possibly be found in the different conditions of depth and currents.

Almost all the typical limnic species that have been found are living everywhere in the course of the rivers. Only four insignificant species may be considered to be intolerant of large temperature fluctuations: Nais alpina, Rhyacodrilus falciformis, Tubifex nerthus and Phreorvctes gordioides.

There is found in all substrates the coexistence of several species of the same genus. This phenomenon is especially striking in respect to species of naidids and tubificids (cf. Wachs 1964).

The observations of Alsterberg (1925) have provided some indications that the tubificids are of great importance for the biological cycles in streams on account of their transportation of sediments. Comprehensive experiments by Poddubnaya (1961) have demonstrated that the metabolism increases greatly with rising temperature and growing content

of mud in the sediments. According to Ravera (1955) the depth of water in lakes also has some influence on the amount of food required. My own experiments with Tubifex tubifex - at a water temperature of 3° to 25°C - make obvious the enormous rise in the metabolic processes between the limits of 10° and 18°C that obtain usually in running waters. Our present knowledge of the propagation cycle in tubificids and of the temperature regime in the rivers indicates that the sediment transportation per unit area by tubificids in the running waters in Central Europe attains its maximum in May or thereabouts.

[p. 381]

The observations of Alsterberg (1925) and the experimental results of Poddubnaya (1961) demonstrate the transport of the substrate is confined to the fine fractions, so that the coarse-grained portions of the sediments remain lying in their layers. To what extent are the tubificids capable to process the ingested amount of mud for the production of energy? Feeding experiments with Tubifex tubifex have shown that the individuals of this species utilize on an average 21 per cent of organic carbon and 34 per cent of total nitrogen of the muddy food, at a water temperature of 12°C. In general, the C : N ratio of the excrements (that are deposited on the sediment surface) is greater than that of the ingested mud. The continuous selective sediment transport by the tubificids results thus in an additional mineralization that is not negligible and above all progressive and that thus makes it possible for the aerobic degradation to take place in the first place. Accordingly, the individuals of the tubificid species that are prone to mass proliferation regulate as indispensable members the processes that lead to biological self purification (cf. Soloviev 1924, Liebmann 1960a).

The kind of food used by the frequently observed species -

except species of tubificids - has been tabled on the basis of the gut content.

A B S T R A C T

The qualitative and quantitative composition of the oligochaete fauna of running waters has been investigated by systematic ecological studies. The research has been carried out along the Fulda, a river of hilly country, and along the Isar, a river of the Alpine foothills, during a full year. The different substrates along a stretch of about 230 km of the Fulda are inhabited by a total of 90 species, belonging to 39 genera and 7 families. The colonization density of the species of the genus Nais is greatest during the winter half-year (November to April). Tubifex tubifex and the species of Limnodrilus, on the other hand, are found in greatest numbers during the summer.

In order to determine the mean population density of adult tubificids in the running waters, it suffices to take monthly samples during the summer half-year (May to October). Sexually mature aquatic oligochaetes are found at all seasons. However, a definite reproductive period exists, the duration of which has been determined for a few species.

The oligochaete fauna does not depend directly on the chemical composition of the running waters. The decisive factors for the existence and the distribution of almost all typical species of aquatic oligochaetes are the type and composition of the substrate. Consequently, animal communities are formed in the running waters that are mosaic-like and that can repeat themselves across the whole width of a stream as

well as along the entire length of its course.

Seven types of substrates have been distinguished and it has been determined how the oligochaete fauna is divided between these diverse types. Certain species have acquired a preference for a particular type of substrate. By means of the accompanying illustrations and tables one can determine the characteristic species and their approximate average percentages in the oligochaete fauna, when one knows the type and mechanical structure of the substrate. It has been possible to differentiate especially the ecological demands of Tubifex tubifex and of the species of Limnodrilus as function of the grain sizes of the substrate. [p. 382]

The river muds present a great variability in their chemical composition, but there is no correlation between contents of organic substances, of organic carbon and of total nitrogen. The interpretation of the results of the field observations has been checked by experiments in 25 synthetic substrates on species of tubificids and on Stylodrilus heringianus.

The significance of the tubificids as organisms moving sediments has been demonstrated experimentally in Tubifex tubifex in relation to temperature (3° to 25°C). The manner of feeding of the species observed most often (except the species of tubificids) has been obtained in the form of a synoptic table through investigating the gut contents. Controlled feeding experiments with Tubifex tubifex have shown that the individuals of this species consume on an average 21 per cent of organic carbon and 34 per cent of total nitrogen of the mud offered at a temperature of 12°C.

Table 21. Mean percentage share of the individual oligochaete species stations in the Fulda and in the Isar. Individuals of all ages were Phreoryctes and the species of naidds; in all other species only adu in alphabetical order.

Abbreviations: Sch = mud, SS = sand-mud, G = gastropods, juv.

River	F U L D A																															
	Substrate					Mud					Sand-mud					Sand					Gravel					Stones						
	C	F	G	H	A	E	K	M	N	O	D	F	G	J	L	B ₁	B ₂	F	G	L	M	A	D	E	F	G	H	J	M	O	A	C

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Translations of
Foreign Language Titles

- 1 The quantitative investigation of the bottom fauna of running water.
- 2 The respiratory mechanism of the tubificids.
- 3 The sensory physiology of the tubificids.
- 4 The food circulation in some types of inland lakes.
- 5 The importance of currents as an ecological factor.
- 6 The peculiarities of water currents in physical, chemical and biological respects.
- 7 Chemical evaluation of settling tank mud and stream muds.
- 8 Chemical-biological investigations for the mapping of the Isar with special consideration of the sewage disposal of Munich.
- 9 Animal periodicity under the influence of timers.
- 10 A biotic community in brackish water on wooden piles of the Kiel Canal.
- 11 Life in the Volga.
- 12 The animal communities of the springs and brooks of the region of the Baumberge.
- 13 The animal communities of the springs in the environs of Basle.
- 14 Systematic-ecological studies in littoral oligochaetes of the Jutland Peninsula.
- 15 On the determination of the relative oxygen saturation of water.
- 16 On the distribution of Sphaerotilus natans in the river.
- 17 German standard methods for the investigation of water, sewage and mud.
- 18 A brook in the Sauerland [SE Westphalia].

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- 19 Zoogeographical-ecological investigations of the lumbricids of the valley of the middle Saale.
- 20 The earthworms of Germany.
- 21 Comparative ecological and systematical investigations of the littoral oligochaete fauna in freshwater, brackish water and oceanic regions of Schleswig-Holstein.
- 22 Results of biological investigations of the pollution of the Elbe at Hamburg.
- 23 Two new species of lumbriculids and some remarks on the systematics of a few species already described.
- 24 To the knowledge of the oligochaetes of the Danube.
- 25 The communities of aquatic beetles in the Fulda.
- 26 To the ecological divisions of the Fulda.
- 27 The Mölle. Faunistic-ecological investigations of a trout brook in the Lippe mountains.
- 28 The colonization of the Fulda (especially the benthos of the salmonid region) according to the present status of the investigations.
- 29 Aquatic mites (Hydrachnellae) of the upper Fulda.
- 30 The biological aspect of the limnological typing of running waters.
- 31 The ciprinid region of Central European running waters.
- 32 Attempt of a general ecological division of running waters.
- 33 The life community of the mountain brook.
- 34 The significance of the current for the biotic community in the salmonid region and in the ciprinid region. [p. 384]
- 35 Problems and methods of the classification and ecological zonation of running waters, considered especially from the faunistic point of view.

- 36 Energy exchange in aquatic animals. IVth communication. Utilization coefficient and assimilation of energy in Tubifex tubifex (O.F.M.).
- 37 Textbook of special zoology.
- 38 Ecology of animal saprophiles.
- 39 Studies of the ecology of the oligochaetes in the upper Danube with consideration of the effects of sewage.
- 40 Mechanical analysis of rocks and soils. Manual of granulometry and morphometry
- 41 Investigations of the food of the oligochaete Chaetogaster limnaei K.E.v.B.
- 42 Food investigations in Chaetogaster diaphanus.
- 43 Handbook of the biology of freshwater and sewerage, II.
- 44 Investigations of the influence of barrages on the natural self purification.
- 45 Handbook of the biology of freshwater and sewerage, I.
- 46 Outstanding tasks of natural sciences in water economy.
- 47 Biological sewerage investigations in a groyne field downstream from Hamburg.
- 48 Hamburg. Elbe investigations. IV. Oligochaeta.
- 49 On the phylogeny of the oligochaetes.
- 50 The phases of the growth in weight of the lumbricoid Eisenia foetida.
- 51 Fishes and fish regions of the Fulda.
- 52 Biological fishery investigations in the Fulda.
- 53 (Distribution and seasonal dynamics of the biotic communities of the stream bed and methods for their study) [in Russian, cited after Albrecht 1959].

- 54 The Kossau. Hydrobiological-faunistical investigations in running waters of Schleswig-Holstein.
- 55 The ground-water fauna of the lower Main region from Hanau to Würzburg, including the Spessart.
- 56 Contribution to the determination of the organic substance in effluents from the viscose-fibre industry.
- 57 On the differences in the cocoons of some tubificids.
- 58 Catalogue of Swiss invertebrates.
- 59 (On the seasonal changes in the tubificid population in the Rybinsk Dam) [in Russian].
- 60 (Material on the nutrition of the most common species of tubificids in the Rybinsk Dam) [in Russian].
- 61 (On the vertical distribution of Limnodrilus newaensis Mich. and L. hoffmeisteri Clap. in the benthos of the Rybinsk Dam) [in Russian].
- 62 Contributions to the fishery biology of Brandenburg lakes. II. The natural food supply, especially the nutrition of animals serving as fish food in the littoral region of a eutrophic lake.
- 63 The biotic environment of the limnic sand.
- 64 Pore space and capillary water flow in the limnic sand, an example of the significance of retarded flow.
- 65 Systematic-ecological investigations of the diatomaceous flora of the Fulda.
- 66 The chemism of the water of the Fulda with special consideration of the geological influences.
- 67 The biotic environment of the mountain brook and its delimitation, represented by the example of the upper Fulda.

- 68 On the possibility of the quantitative investigation of the bottom and shore fauna of running waters, at the same time: biological fishery investigations in the region of the Weser. I.
- 69 Soil investigations for engineering structures.
- 70 Morphological and biological studies in Naidae in Saxony and Bohemia.
- 71 On the role of Tubifex tubifex in the generation of mud.
- 72 Botanical contribution to the limnological classification of the upper Fulda.
- 73 The effects of organic pollution on the fauna of Swiss running waters.
- 74 Oligochaeta - Bronn's classes and orders of the animals.
- 75 The mountain brook of the Sauerland [SE Westphalia].
- 76 Oligochaeta - Dahl: the animals of Germany.
- 77 Chemism of sediments and its relation to the metabolism in 40 European lakes.
- 78 To the knowledge of the oligochaetes of the Werra.
- 79 Contribution to the oligochaete fauna of a navigable river.
- 80 Occurrence and distribution of oligochaetes in the Eder Barrage.
- 81 Chaetogaster limnaei K. Baer as predator of cercariae.
- 82 Key to the native lumbricids.
- 83 On the bottom fauna of the Moldavia in the region of Prague in the annual cycle. Oligochaeta.
- 84 Relations between the occurrence of tubificids and the supply of organic substances in Lake Constance.
- 85 The effects of currents on the composition of biotic communities in experiments.

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PLATE 4



Fig. 4. Psammoryctes barbatus. Dorsal bundle of bristles on IV with six fan bristles (195 microns) and two hair bristles.

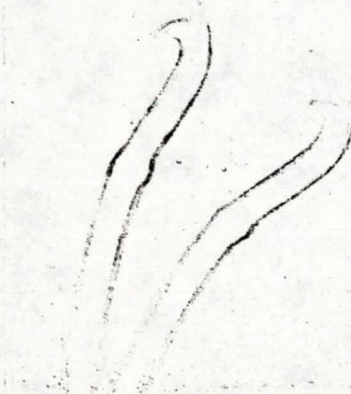


Fig. 5. Psammoryctes barbatus. Dorsal bundle of bristles from the posterior end of the body (221 microns).

PLATE 5



Fig. 6. Limnodrilus hoffmeisteri. the four bundles of bristles from III.

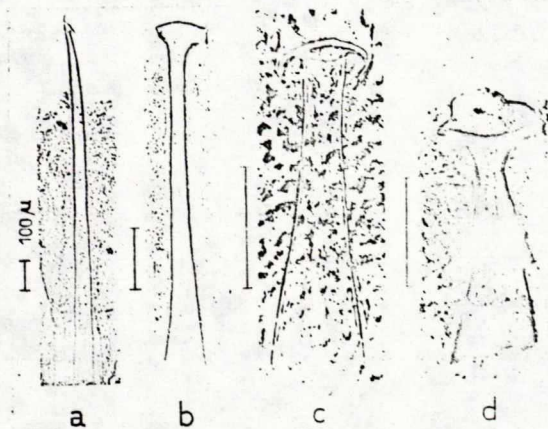


Fig. 7. Penis tube of Limnodrilus claparedeanus (a), L. hoffmeisteri (b), L. helveticus (c) and L. udekerianus (d).

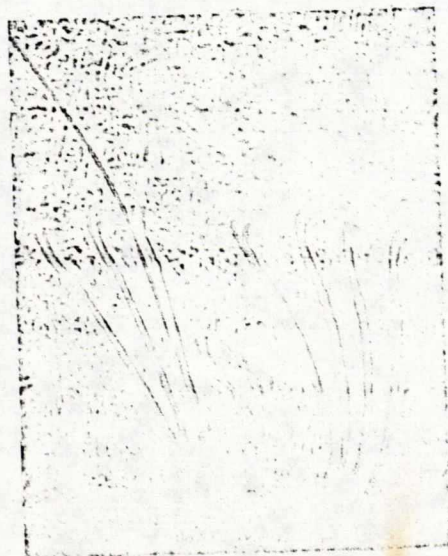


Fig. 8. Eulyodrilus hammoniensis. Dorsal (left) and ventral (right) bundle of bristles (segment VII).