On the Vertical Distribution of Oligochaetes in Lake Sediments

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I. INTRODUCTION

The availability of bottom invertebrates as food for fish has long been a question of primary interest to fishery biologists. To what extent are deep-burrowing animals like worms and some chironomid larvae available in this context? There is no doubt, however, that fish will readily take worms if they are offered.

The vertical distribution of the benthos is also of great importance in relation to its influence upon the circulation of matter in the body of water (*cf.* TESSENOW, 1964; EDMONDSON and WINBERG, 1971). The activities of benthic organisms have not often been thought of in terms of regeneration of material and energy from the sediments (BRINKHURST, 1972).

In order to get better information on the vertical distribution of oligochaetes and to a lesser extent other invertebrates, in lake sediments the author once found it necessary to construct a new sampling device adopting a new technique, *i.e.* thin metal slides which instantly devided an unbroken mud-water core into thin layers once the sampler had reached the desired depth in the sediments (MILBRINK, 1968).

In this way very mobile animals like several crustaceans, chironomid larvae, *Chaoborus* larvae, some oligochaetes etc. are prevented from making any larger vertical movement after sampling. The whole process is a matter of tenths of a second, provided the release wire is tight enough.

Vertical displacement of the more motile species can not be determined unless the sectioning of the core commences immediately after collection (COLE, 1953, *cf.* also LENZ, 1931; BERG, 1938; BRINKHURST and KENNEDY, 1965; SÄRKKÄ and PAASIVIRTA, 1972).

The author is not aware of the existence of any similar bottom sampler. In the author's opinion the vertical distribution of the entire bottom community is worth closer study. Physical-chemical measurements have also been made in addition to the different zoological data given by this technique (MILBRINK, 1969).

This micro-stratification technique has successfully been transferred to potentiometric measurements, to studies of bacteria and organic matter in the mud etc. by Dr. J. OLÁH and Dr. A. FRANKO, Hungary (unpublished material; some results kindly put at the author's disposal. Results will shortly be published in Annal. Biol. Tihany, Hungary).

The purpose of the present paper is, in first hand, to illustrate and discuss the vertical distribution of oligochaetes with reference to a selected area in Hovgårdsfjärden in central Lake Mälaren.

II. GENERAL BACKGROUND

The Lenz-Ekman sampler was an important means towards the understanding of the vertical distribution of the fauna in lake sediments. Metal shelves were inserted through slots in an ordinary, but tall, Ekman-sampler thereby dividing the mud-water core into strata. However, the very insertion was not made until the filled sampler had reached the water surface again. Naturally, there is always some chance that mobile animals have already been able to displace themselves vertically, a fact which would make such samples more or less useless for this purpose (*cf.* LENZ, 1931; BERG, 1938; SÄRKKÄ and PAASIVIRTA, 1972).

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It is also difficult to avoid compression or expansion or other displacement of the sediments if the core is fetched from some depth (*cf.* EDMONDSON and WINBERG, 1971). Of course, the effects of such changes of the core are largely reduced if the core is already divided before the changes commence i.e. before the sampler is removed from the sediments.

LENZ' sampling technique was later adopted by BERG (1938) and BORUTSKY (1935, 1940) with minor modifications, mostly concerning the distance between the shelves. The recommendations in EDMONDSON and WINBERG (1971) are evidence that the technique is still widely used.

These samplers have been used for different purposes, for instance, by DEKSBACH (1939), KIRPICENKO (1940), PODDUBNAYA (1961), PODDUBNAYA and SOROKIN (1961), PATARIDZE (1967), KJÄLLMAN and GRIMÅS (1967), and SÄRKKÄ and PAASIVIRTA (1972).

Another box sampler constructed on much the same working principle is the Digerfeldt-Lettevall sampler (DIGERFELDT and LETTEVALL, 1969). Accordingly the shelves are inserted after the sampler returns to the water surface. The sampler is tall which is an advantage on very loose bottom material and it is transparent for a better localization of the different sediment strata and in particular the mud-water interface. Special varieties of the above are the hand directed samplers by FORD (1962) and FAGER (1966).

Modern core samplers with transparent tubes of plexiglass like the Kajak sampler, the simplified corer described by the author (MILBRINK, 1971) and several others, provide fairly undisturbed mud-water cores which can be subdivided with the piston technique designed for the well-known Jenkin sampler (MORTIMER, 1941/1942). The Elgmork sampler is also a useful device on very loose bottom material (ELGMORK, 1962).

A great number of corers and samplers, some of them suitable for microstratification studies, are presented in HOPKINS (1964), EDMONDSON and WINBERG (1971), and to some extent in MILBRINK (1971). Most corers with narrow openings seem to be designed primarily for micro-fauna studies, for which purpose they operate quite satisfactorily.

At the moment there is also a growing interest in hand-taken cores (the SCUBA technique). Tube samplers are recommended for microstratification studies by BRINKHURST and JAMIESON (1971).

The coring technique, however, must be handled very carefully since if the tube is not wide enough the friction of the core against the walls may be considerable. Accordingly there will always be a risk that the sediment strata get partly mixed (*cf.* EDMONDSON and WINBERG, 1971).

Some of the above works have been more or less focused upon the vertical distribution of oligochaetes, *i.e.* PODDUBNAYA (1961), PODDUBNAYA and SOROKIN (1961), BRINKHURST and KENNEDY (1965), PATARIDZE (1967), BRINKHURST *et al.* (1969), and SÄRKKÄ and PAASIVIRTA (1972).

III. MATERIAL AND METHODS

The ultimate aim of the study presented first (Fig. 2) was to acquire thorough information on the vertical as well as the horizontal distribution of oligochaetes — and other invertebrates — referring to the particular date of sampling. The area selected was Hovgårdsfjärden in the central — *i.e.* the cleanest — parts of Lake Mälaren, the bottom fauna of which is well-known to the author.

The area was visited by G. ALM in 1915—1916, by S. VALLIN in 1933, by T. WIEDERHOLM in 1969—1970, and by the present author in 1970 and 1971. The oligochaete material of these surveys has remained preserved to the present-day. A paper on the oligochaete fauna of Lake Mälaren covering this material is in preparation.

The bottom area selected is absolutely flat and sheltered and considered homogeneous in most respects, for instance in texture, bottom fauna composition (MILBRINK, 1972), exposure to wave actions, streams etc. Thus it is among the best possible areas for the purpose. The depth is 32 m and the width about 2×6 km². The time of sampling was August 1970.

In order to obtain enough information on both the vertical and the horizontal aspects several parallel microstratification samples had to be taken. Since each sample of this kind means the necessary acquirement of a great number of subsamples and much labour is involved preparing the sampler for each core, it is generally not realistic to take more than two or three parallel samples a day, which is naturally a drawback in terms of representativity. In combination with 5—10 Ekman samples or some 10—20 tube samples, however, a fairly accurate picture of the horizontal aspect is usually secured.

In Hovgårdsfjärden seven microstratification samples and one Ekman sample — all obtained in one day — were spread radomly in the grid measuring 100×50 m². The same grid was later used (in March 1971) in a special study on the horizontal distribution of the bottom fauna (MILBRINK, 1972), when 48 samples were similarly spread in the net.

Each of the other four examples given below describes the results from 2 or 3 microstratification samples in combination with ordinary Ekman samples and has been selected because here the oligochaete material was analysed in detail. Such analyses are generally extremely time-consuming, since the majority of worms are immature. The selected samples primarily serve as examples of the vertical distribution of oligochaetes from various habitats and will to some extent modify the general picture obtained in Hovgårdsfjärden.

The second example given below is from Norra Björkfjärden — also in central Lake Mälaren. The samples were obtained from a depth of 30 meters in September 1967. The third example is from Ekoln, a much enriched basin in northern Lake Mälaren — the depth being 32 meters and the time of year February 1968; the fourth from Lake Erken, a eutrophic lake to the east of Uppsala near the Baltic — the depth being 18 meters and the time of year June 1968; the fifth and last also from Lake Erken and the time of year August 1968.

It must be emphasized that the above examples merely represent the momentary distributions of organisms.

The bottom material was generally very lightly sieved through a 0.3 mm sieve, while the water-containing chambers were tapped through bags of nylon gauze with 0.06 mm meshes. All sediment residues were examined as soon as possible without foregoing preservation. In the first test described below, however, preservation liquids were added to the residues of four samples.

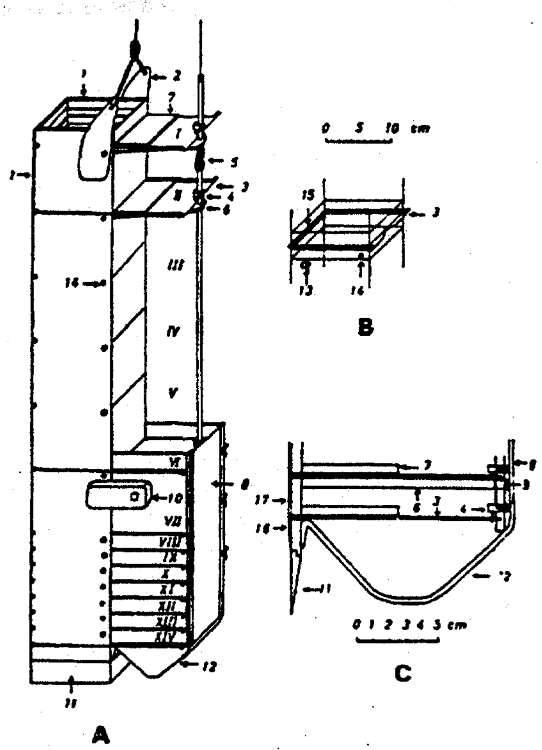

Fig. 1 A and B scale roughly 1 : 11, Fig. 1 C scale roughly 1 : 4. The slide mechanisms for Nos. III, IV, and V and most of the springs are omitted from the drawings. Fig. 1 B is a more detailed sketch of the fitting of the slide between runners of plexiglass. At the bottom is a shock absorber of 1 mm brass (15). Fig. 1 C a transverse section through the lower part of the "slide-box". 1. The tube of 6 mm plexiglass 2. the suspensions, brass plates and steel wire. 3. slide of 1.5 mm duraluminium 4. movable hooks on a rod (of 9 mm brass) which is spring-loaded (5). 6 and 7. supports of 6 mm plexiglass with brass bearings (9) for the rod 8. hinged lid to the "slide-box" 10 exchangeable lead weights 11. exchangeable brass edge 12. streamline protection cone made of plexiglass 13. spout of plexiglass 14. hole with a plug for the chamber 15. brass plate for shock absorbtion 16. bevelled runner of plexiglass 17. runner of plexiglass (2 mm).

The results are illustrated in a manner which may need some explanation. The diagrams (Figs. 2—6) are composed of smaller units each representing the abundance of a group (or other entity of bottom invertebrates) or individual species per vertical centimetre of the core.

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IV. RESULTS

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These intervals of precision are the natural consequences of the chosen distance between parallel slides of the microstratification sampler (2.5 cm) and the number of samples obtained. Accordingly the obvious lack of continuity in the vertical distribution of some species (or other entities of animals) is not necessarily real.

Brief description of the sampler (see Fig. 1)

The sampler is built of 6-mm plexiglass, the tube has a square cross-section measuring exactly $^{1}/_{60}$ m² (167 cm²) — in order to simplify the estimation of specimens per square metre unit.

The slide box and the protection cone built of plexiglass of varying thickness are considered necessary to reduce turbulence in front of the device. The slide box is easily dismantled in the field which facilitates the changing of slides.

The slides are made of 1.5 mm duraluminium, a hard, elastic, and very light material. They are loaded with slender springs of stainless steel placed outside the tube.

For the purpose of these studies a distance of 2.5 cm was chosen on empirical grounds to separate the lower slides, while further up 10 cm was considered appropriate.

The closing mechanism is operated from the water surface by means of a thin wire. As mentioned before the whole releasing procedure takes a matter of a few tenths of a second, a fact which makes it difficult even for mobile animals to move much vertically.

For further details the reader is referred to MILBRINK (1968).

IV. RESULTS

Horizontal distribution

The microstratification samples from Hovgårdsfjärden also gave information on the horizontal distribution. It emerges from Tables 1 and 2 that

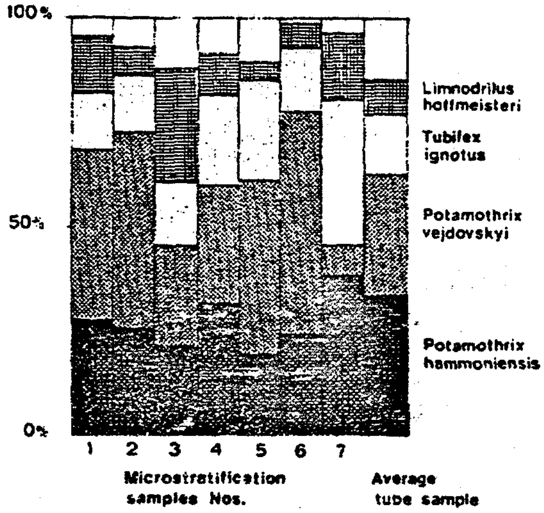


Table 1. *The composition (in per cent) of Tubificidae in bottom samples obtained in Hovgårdsfjärden, Lake Mälaren, in August 1970 (separate microstratification samples) and in March 1971 (an average tube sample).*

the qualitative composition of tubificids had not changed markedly from August 1970 to March 1971. The same species dominated in approximately the same proportions. The only tubificid having changed notably was *Tubifex tubifex*, which had increased from 1 to 11 per cent. This "change", however, is not necessarily real as *T. tubifex* and *T. ignotus* may be very difficult to separate properly from each other in their youngest stages. At the same time *T. ignotus* had actually decreased from 20 to 14 per cent.

Ten tubificid species were common to both studies; only *Limnodrilus udekemianus* having been replaced by the closely related *L. claparedeanus*.

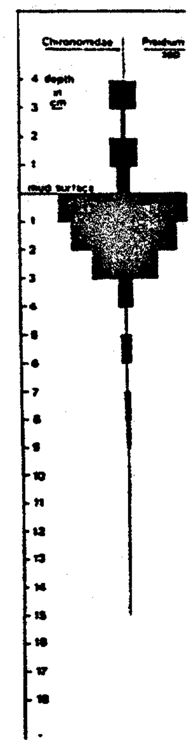
In each microstratification sample the four major components made up at least 88 % of the whole tubificid population (see Table 1). The study in March revealed that the same four dominating species made up 84.5 % of all tubificids. When looking more closely at the contents of oligochaetes of different species in each sample (Ekman or microstratification sample) it must be remembered that an ordinary Ekman sampler takes 1.3—1.5 times more bottom material than the other sampler *i.e.* in proportion to its larger aperture (Table 3).

Table 2 *The composition (in per cent) of Tubificidae in bottom samples obtained in Hovgårdsfjärden, Lake Mälaren, in August 1970 (separate microstratification samples) and in March 1971 (an average tube sample).*

	Microstratification samples 1	2	3	4	5	6	7	mean	Average tube sample
P. hammoniensis	27.3	25.3	21.2	31.5	19.5	24.7	38.4	26.8	34.0
P. vejdovskyi	40.9	47.0	24.2	28.3	41.5	52.8	7.4	34.6	28.0
P. ferox	2.3	—	6.2	1.1	—	—	—	1.4	2.0
P. barbatus	—	—	3.0	—	—	1.0	—	0.6	1.0
L. hoffmeisteri	13.6	6.9	27.2	9.8	3.7	5.4	16.0	11.8	8.5
T. ignotus	13.6	13.8	15.2	21.7	24.3	15.0	34.5	19.7	14.0
T. tubifex	—	—	3.0	—	3.7	1.1	—	1.1	11.5
B. vejdovskyanum	2.3	3.9	—	7.6	4.9	—	3.7	3.2	<1
A. pluriseta	—	3.1	—	—	—	—	—	0.4	<1
P. bedoti	—	—	—	—	1.2	—	—	0.2	<1
L. udekemianus	—	—	—	—	1.2	—	—	0.2	<1
	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 3. *Relative abundance of different Oligochaeta in eight bottom samples from Hovgårdsfjärden, Lake Mälaren, in August 1970. Single specimens are indicated with one X. More than 4 specimens/sample are marked with XX.*

	Ekman sample	Microstratification samples Nos. 1	2	3	4	5	6	7	Frequency
TUBIFICIDAE									
Potamothrix hammoniensis	XX	XX	XX	XX	XX	XX	XX	XX	in all samples
Potamothrix vejdovskyi	XX	XX	XX	XX	XX	XX	XX	XX	in all samples
Peloscolex ferox	X	X	—	X	X	—	—	—	
Psammoryctides barbatus	—	—	—	X	—	—	X	—	
Limnodrilus hoffmeisteri	XX	XX	XX	XX	XX	XX	XX	XX	in all samples
Tubifex ignotus	XX	XX	XX	XX	XX	XX	XX	XX	in all samples
Tubifex tubifex	—	—	—	X	—	X (X)	X	—	
Bothrioneurum vejdovskyanum	XX	X	XX	—	XX	XX	XX	XX	in all samples but one
Aulodrilus pluriseta	XX	—	X	—	—	—	—	—	
Potamothrix bedoti	—	—	—	—	—	X	—	—	
Limnodrilus udekemianus	—	—	—	—	—	X	—	—	
Total number of species	7	6	6	7	6	8	7	5	
NAIDIDAE									
Vejdovskyella comata	XX	XX	XX	XX	XX	XX	XX	XX	in all samples
Speciaria josinae	XX	XX	XX	XX	XX	XX	XX	XX	in all samples
Stylaria lacustris	X	X	XX	XX	XX	XX	X	X	in all samples
Piguetiella blanci	X	—	X	X	—	X	X	X	
Uncinais uncinata	XX	XX	XX	X	XX	—	XX	X	in all samples but one
Nais sp.	X	—	—	—	X	—	—	X	
Arcteonais lomondi	X	—	—	—	X	—	XX	—	
Pristina sp.	X	—	—	—	—	—	—	—	
Vejdovskyella intermedia	—	X	—	—	—	—	X	—	
Chaetogaster cristallinus	—	—	—	—	—	—	X	—	
AELOSOMATIDAE									
Aelosoma sp.	—	—	—	—	X	—	—	—	
Total number of species:	8	5	5	5	7	4	8	6	



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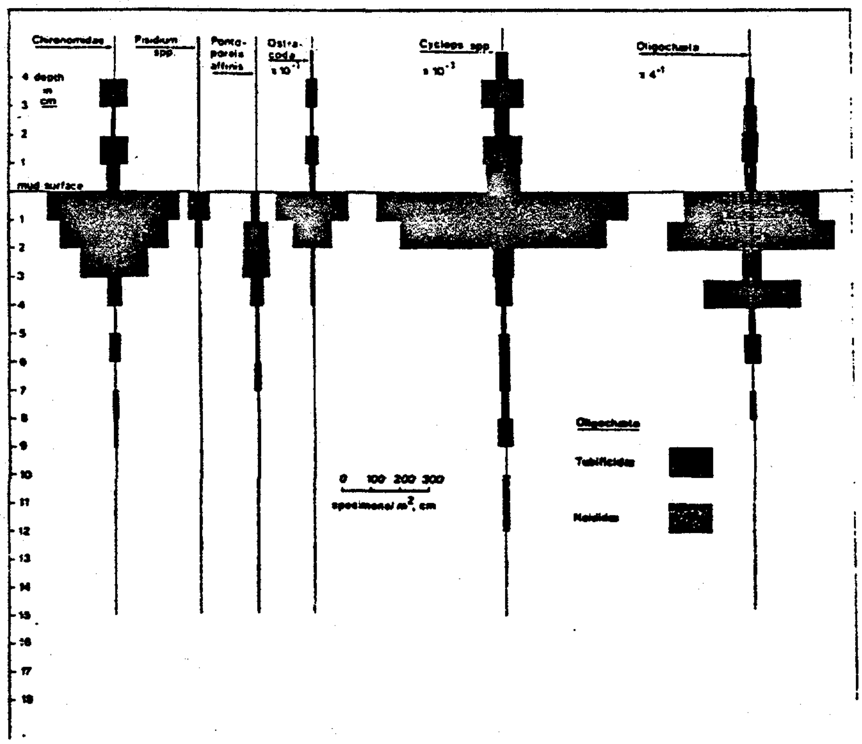


Fig. 2: 1. (Hovgårdsfjärden).

The Ekman collected 7 tubificid species, while none of the m-samples (microstratification samples) contained less than 5. The mean value was 6.4. Similarly the Ekman took 8 naidid (and aelosomatid) species. The m-samples varied between 4 and 8 with a mean value of 6.

The four dominating tubificid species were represented — even well-represented — in all samples. A fifth species was represented in all samples but one. Similarly two naidid species were well-represented in all samples, a third species was represented in all samples, and a fourth in all but one. Of a total number of 22 oligochaete species the Ekman took 15 and the m-sampler between 11 and 15, with a mean value of 12.

In fact, most bottom fauna constituents were rather evenly spread over the grid judging from these comparatively few samples, *e.g.* chironomid larvae had a mean value ($\pm$standard deviation) of specimens/m^2 of 1584($\pm$420), *Pontoporeia affinis* (264$\pm$108), and oligochaetes 6660($\pm$1776).

Vertical distribution

Even if stress here has been laid upon the vertical distribution of oligochaetes in general — and the Hovgårdsfjärden material in particular — the author has considered it desirable to illustrate the distributions of the other main constituents as well.

An adverse relationship between numbers of chironomid larvae and tubificid oligochaetes has, for instance, been presumed by Brinkhurst and Kennedy (1965) and Jonasson (1972).

Hovgårdsfjärden

Important bottom fauna constituents in the Hovgårdsfjärden material (Fig. 2) were chironomid larvae, oligochaetes, pisiids, *P. affinis*, nematodes, and small crustaceans like ostracods and copepods. Naturally, several other groups were represented as well, such as Hydracarina, Ephemerida, *Corethra* larvae, hydras etc., even if all those groups are not illustrated in the diagrams. Most of the last-

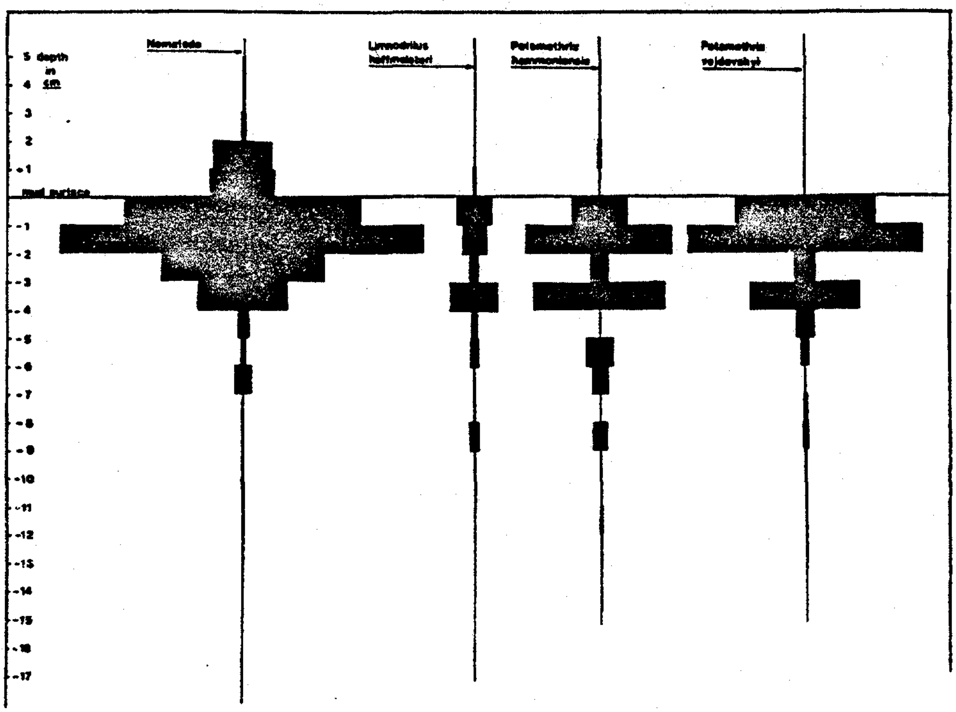


Fig. 2: 2. (Hovgårdsfjärden, continued).

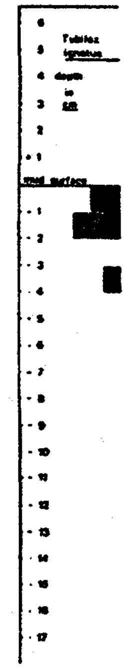
mentioned animals were concentrated at the mud-water interface, or even above it, either as a consequence of undue turbulence acting upon very light organisms at the moment of sampling or as a consequence of spontaneous, swimming movements.

Most chironomid larvae (Fig. 2) were concentrated in the top centimetres of the mud core — some obviously dwelling in funnels of clay at the interface; a minority of larvae were found deeper, and some even above the interface (mostly belonging to the family Tanypodinae).

Pisidium spp. were also recorded at the interface and so were most ostracods. *Pontoporeia affinis*, on the other hand, was most numerous at depths varying between 1 and 3 cm in the sediments, which is in good agreement with the author's experience. The species may be dwelling there out of nutritional reasons, but it is also quite plausible that it is an avoidance reaction against the approaching sampler (*cf.* discussion below). Similarly, one *Corethra* larva was found between 4 and 6.5 cm in the mud (*cf.* discussion). *Cyclops* spp. were, as usual, the deepest burrowing organisms, even if — as here — the bulk of organisms were found at the interface.

On the whole, naidids were well separated from tubificids vertically. Some species of Tubificidae were also well separated from others (see below). Sapkarev (1959) and Brinkhurst *et.al.* (1969), for instance, found few, if any, indices of a vertical separation of different tubificid species (see discussion below). Judging from the samples from Hovgårdsfjärden and the other m-samples, *Limnodrilus hoffmeisteri* and *Potamothrix hammoniensis* are generally the deepest burrowing tubificids (see further text). In the author's experience *Potamothrix vejdovskyi*, *T. tubifex*, and *Potamothrix heuscheri* (see below) also burrow deeply. *L. hoffmeisteri* is generally fairly evenly spread through the mud column with rather undistinct maxima of abundance.

In the Hovgårdsfjärden samples *L. hoffmeisteri*, *P. hammoniensis*, and *P. vejdovskyi* were recorded deepest in the mud (to a depth of about 10 cm).



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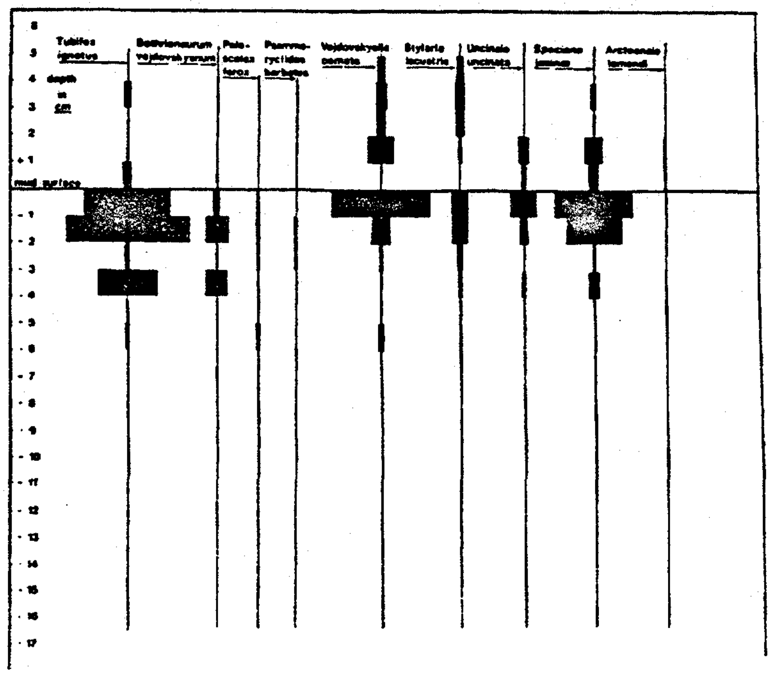


Fig 2: 3. (Hovgårdsfjärden, continued).

The two former species, however, seemed to have their maxima of abundance slightly lower than the latter species and *Tubifex ignotus*. The remaining tubificid species, *i.e. Bothrioneurum vejdovskyanum*, *Peloscolex ferox*, *Psammoryctides barbatus*, *Potamothrix bedoti*, and *Aulodrilus piuriseta* were all recorded in the topmost sediment layers, but since the number of specimens obtained of each species was rather limited it is hardly possible here to say anything definite about the vertical preferences of those species.

On the whole there were very few naidids recorded below a mud depth of about 2 centimetres. The deepest recorded species were the ones illustrated in Fig. 2: 3. The remaining six naidid species were all found superficially in the mud or immediately above it.

The composition of tubificids confirms the general opinion that the water in Hovgårdsfjärden is of good quality. *P. ferox* and *P. barbatus* do not appear at all in polluted areas of Lake Mälaren, i.e. in waters with decreased concentrations of oxygen in water strata close to the bottom. Accordingly the species are confined to the central basins of the lake (*cf.* Milbrink, 1973).

Norra Björkfjärden

The second example on the vertical distribution of oligochaetes was also fetched from the central basins of Lake Mälaren, *i.e.* Norra Björkfjärden (see above). This material was also used as an example in Milbrink, 1968 and 1969. The general picture of distribution of the fauna sketched for Hovgårdsfjärden is also valid here (Fig. 3).

Chironomid larvae were concentrated at the mud-water interface, most of the larvae being *Micropsectra* sp. Pisiids, nematodes and weakly built crustaceans like cladocerans and ostracods were all found superficially in the mud, while most *Cyclops* spp. were recorded deeper, *i.e.* between 4 and 9 cm.

Tardigrada is only one example of a category of bottom invertebrates more or less bound to the interface.

Two tubificid species, *P. hammoniensis* and *L.*

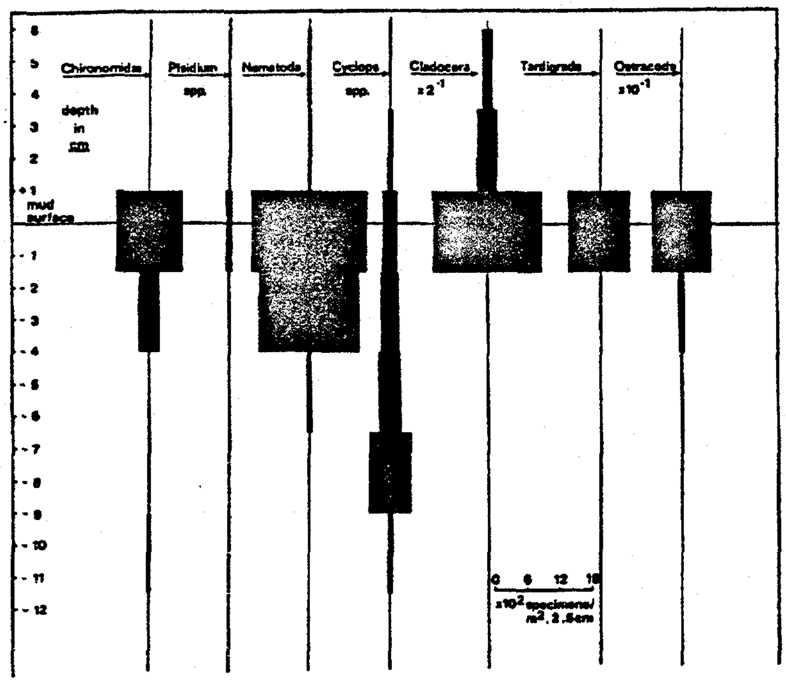
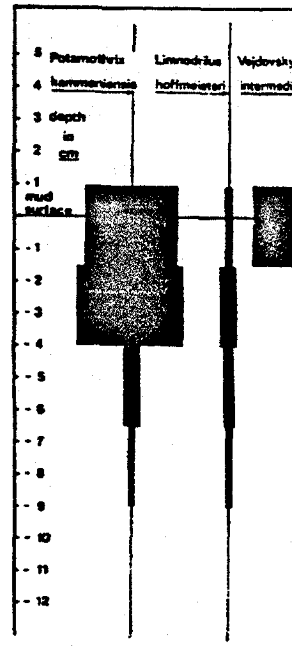


Fig. 3:1. (Norra Björkfjärden).



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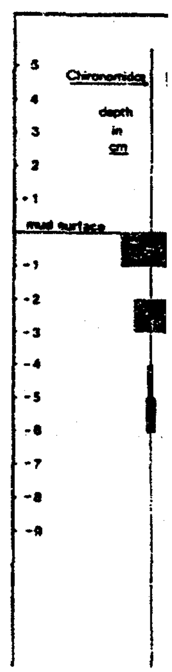

hoffmeisteri, and seven naidid species, two of which, *Vejdovskyella intermedia* and *V. comata*, are illustrated in Fig. 3 were well separated vertically with naidids (without exception) occurring in the topmost centimetres of the core and tubificids burrowing deeper (*cf.* Milbrink, 1969). Here, too, *L. hoffmeisteri* was rather evenly spread through the column in contrast to *P. hammoniensis* (*cf.* also Fig. 2).

Ekoln

A winter situation from the Ekoln basin, Lake Mälaren, is the third example (Fig. 4). Larvae of *Chironomus anthracinus* were spread from the surface down to depths of about 5 cm, *i.e.* about as deep as the deepest penetrating tubificids. Pisiids and ostracods were concentrated at the mud surface, while *Cyclops* spp. were the deepest penetrating organisms (at least 7—8 cm deep), possibly in dormant stages (*cf.* Elgmork, 1959).

Tubificids were the almost totally dominating bottom inhabitants. Naidids (*i.e. Pristina* sp.) were few, possibly depending upon the time of the year. There seems to be little doubt that the tubificid species here were separated vertically. The top layers of the sediments were largely dominated by *P. heuscheri*, the next few centimetres rather equally inhabited by *P. heuscheri*, *P. hammoniensis*, and *T. tubifex*. Strata between 4 and 6 cm were in their turn dominated by *P. hammoniensis*. Characteristically enough, *L. hoffmeisteri* was rather equally distributed through the entire column. The vertical preferences of *P. bedoti* and *T. ignotus* seem here to be vague. The specimens of *A. pluriseta* were distributed superficially in the mud, which is in accordance with earlier statements about the species.

Both the specific compositions of oligochaetes and chironomid larvae and the quite superficial distribution pattern of most bottom animals except copepods suggest a rather poor oxygen situation at the interface. The Ekoln basin is one of the most polluted basins of Lake Mälaren.

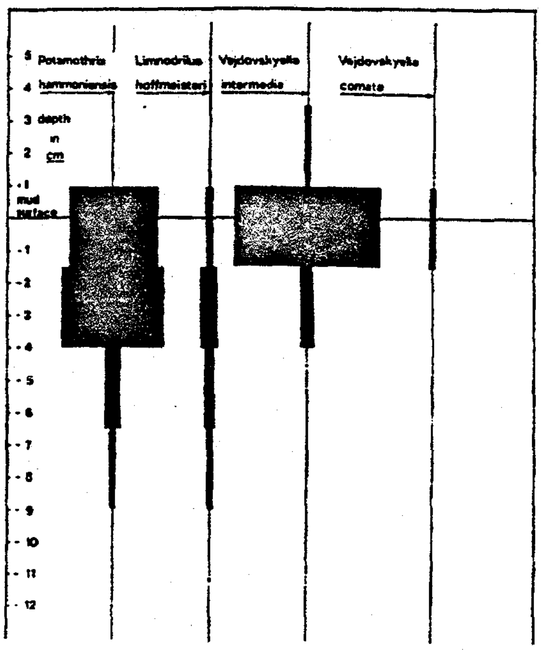

Fig. 3: 2. (Norra Björkfjärden, continued).

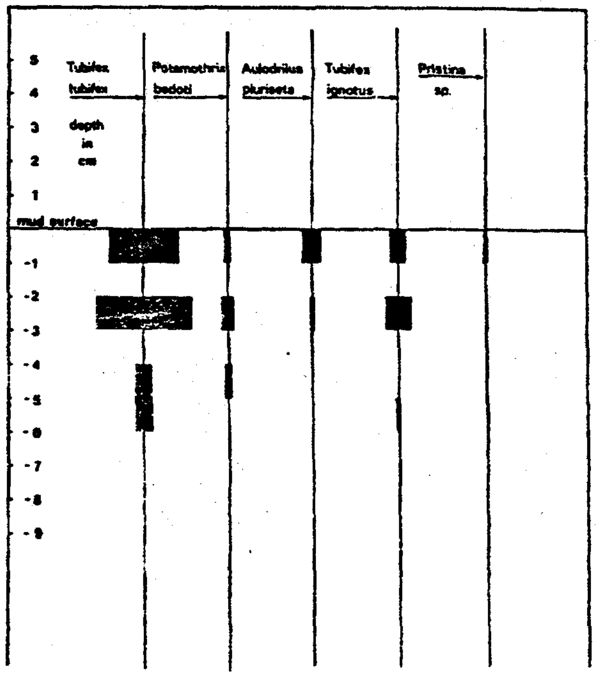

Fig. 4: 2. (Ekoln, continued).

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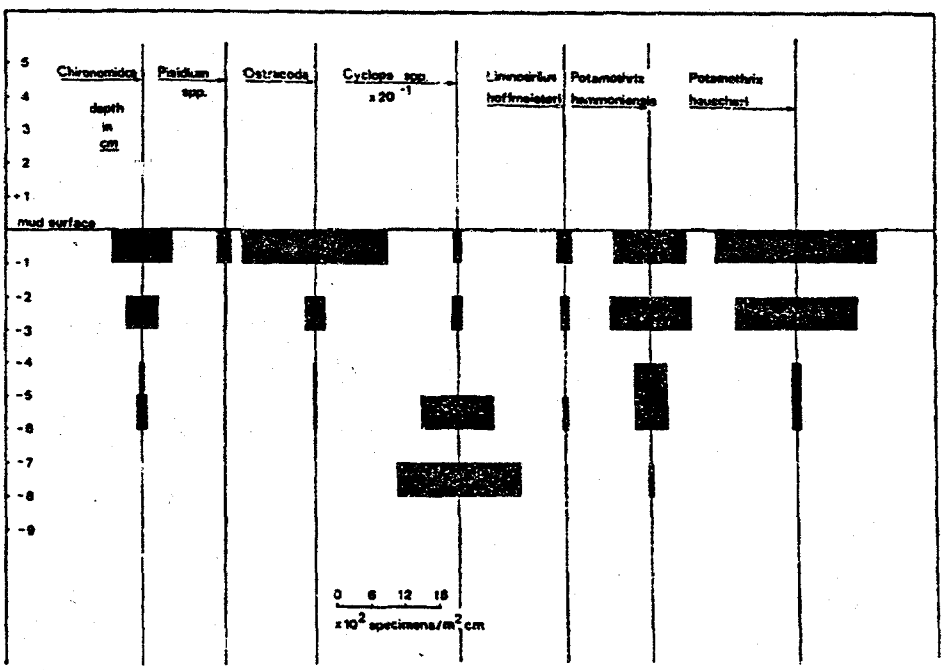


Fig. 4: 1. (Ekoln).

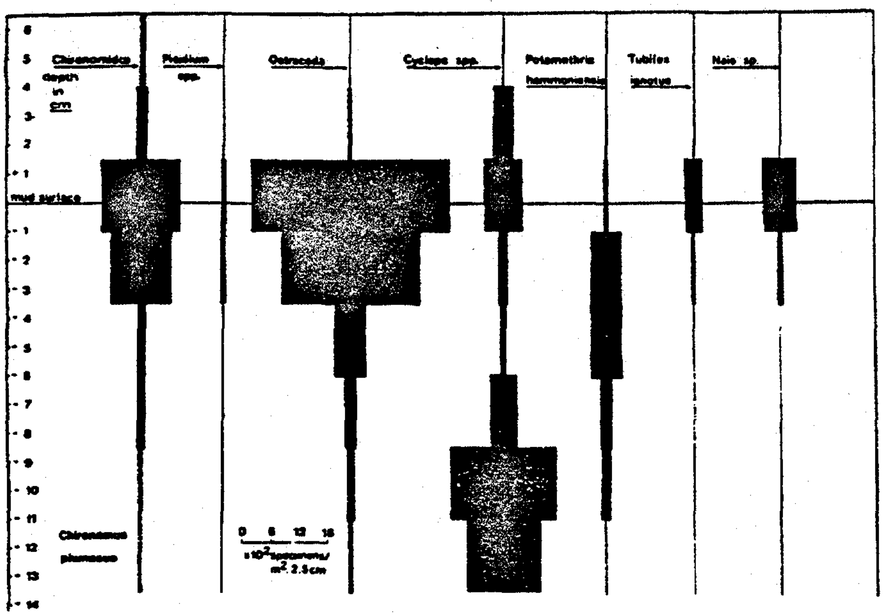


Fig. 5. (Lake Erken, June 1968).

Lake Erken

The last two examples are fetched from the same locality in Lake Erken, the first from June and the last from August 1968. The vertical distribution pattern was almost the same both times (Figs. 5 and 6).

Chironomid larvae were here easily separable into two groups, *i.e.* big larvae of *Chironomus plumosus* dwelling between 5 and 15 cm in the mud and the rest with a maximum of abundance close to the interface.

In August pisiids were located much deeper in the sediments than is generally the case. As a rule most pisiids are found close to the interface (cf. above), but BERG (1938), on the other hand, recorded them very deep in the loose sediments of Lake Esrom.

On both occasions ostracods were spread deeper than usual in the mud (*cf.* above) and *Cyclops* spp. displayed maxima of abundance at depths of about 10 cm. Numbers of specimens were found even at depths of about 15 cm.

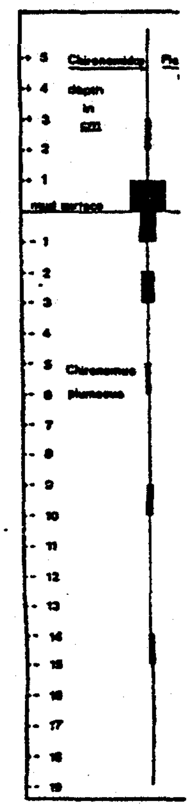
P. hammoniensis had slightly dissimilar distribution patterns on the two occasions. In August great concentrations of mostly young stages of the species were concentrated at the interface, while in June the maximum of abundance lay between 2 and 6 cm.

On both occasions *T. ignotus* and *Nais* sp. were limited to the interface and so was *Aulodrilus pigueti* in August.

Three of the dominating tubificid species from Hovgårdsfjärden were tested as to the proportions of mature and immature worms above and below a mud depth of about 3—4.5 cm (*cf.* Fig. 7 and discussion below).

There is no doubt that there were considerably more adult worms below that level than above it. The proportion of sexually mature specimens of *P. hammoniensis* below that level were on an average (seven m-samples) 23 % compared to 7 % above it. Similarly, the relations for *P. vejdovskyi* were 48 % and 26 % respectively and for *L. hoffmeisteri* 70 % and 15 % respectively. Accordingly there were at least about twice as many adult worms of each species below that level as above it.

Similar results, although sometimes less obvious, have been obtained by the author in previous tests with this technique in different waters.



V. DISCUSSION

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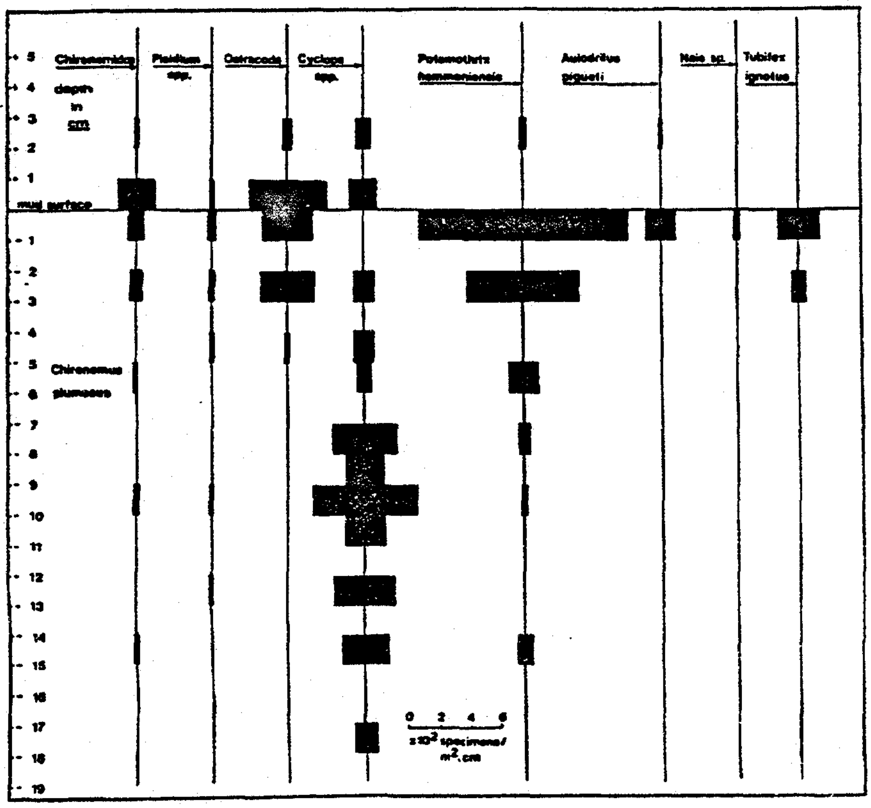

Fig. 6. (Lake Erken, August 1968).

V. DISCUSSION

The extent to which oligochaetes are available to fish is a question which never seems to get a definite answer. East-European authors like Poddubnaja (1961), Popchenko (1971), Galinsky and Nikitin (1972), and Yarochenko *et.al.* (1972) present evidence that a great number of species of fish, esp. "coarse fish", actively feed on oligochaetes. There is little doubt that "suckers" like bream (*Abramis brama* (L.)), dace (*Leuciscus leuciscus* (L.)), and carp feed most intensively upon tubificids. Kennedy (1969) and Kennedy and Walker (1969) come to the same conclusions from a parasitological approach.

Grimås (1963) discusses the availability of the bottom fauna to fish, especially salmonids. Similar considerations were previously made by Naumann (1930), Allen (1942), Ricker (1952), and Hayne and Ball (1956). Grimås concluded that salmonids in general are poor consumers of oligochaetes.

Nevertheless there are exceptions. Recently brown trout turned out to be an important predator upon the lumbricid *Eiseniella tetraedra* Savigny in impounded lakes in Norway (Aarefjord *et al.*, 1973). *Coregonus lavaretus* fed most intensively and unselectively upon tubificids in pulp mill fibre banks at depths of about 100 metres in Lake Mjösa, Norway (P. Aass kindly put material at the author's disposal) etc.

The question seems to focus upon the extent to which the worms are exposed to predators like fish. Very agile animals or even swimming ones are certainly of the greatest interest to most fish. *E. tetraedra*, for instance, is a tremendous swimmer when threatened as is evident from aquarium experiments performed by the author (unpubl. material). Its former name *Lumbricus agilis* Hoff-

Fig. 7. Proportions (in per cent) of mature worms of three of the dominating tubificid species in Hovgårdsfjärden above and below a mud depth of about 3—4.5 cm.

mud depth	P. hammoniensis	P. vejdovskyi	L. hoffmeisteri
	dominating tubificid species		
topmost 3—4.5 cm	7	26	15
below a depth of 4—4.5 cm	23	48	70

meister, 1843 is further evidence of the rapid movements of the species.

Naidids are not seldom encountered in stomachs of various fish especially in fish with littoral feeding habits, which may be linked to the fact that naidids sometimes tend to appear in swarms litorally, thereby being more accessible to fish. *Stylaria lacustris*, *Uncinais uncinata* and other naidids are sometimes identified in stomach contents of whitefish and other fish in Sweden. *Paranais litoralis* is at times an important food item for flounders and plaice in Danish estuaries (Muus, 1967) etc. Most naidids, however, are very inconspicuous and easily overlooked in an ordinary stomach analysis.

Several naidids (*e.g. Stylaria lacustris*) are good swimmers (cf. Sperber, 1948), but also immature tubificid worms (*e.g. Potamothrix heuscheri*) are definitely capable of swimming freely for short distances if compelled (Milbrink, unpubl. material). Brinkhurst (1969) denies this capacity of tubificids.

Grigelis (1966) presents evidence that proteins are particularly concentrated in the tails of tubificid worms. If oxygen conditions are poor the worms are more or less compelled to expose more of their rear ends than needed for normal purposes (Alsterberg, 1925), thereby being more exposed to fish. This means that if fish snap the rear ends of the worms they will get a highly concentrated source of nourishment (*cf.* Poddubnaja, 1962). Accordingly it is not surprising that cyprinid fish in particular snap the respiring ends of tubificids.

The distribution of oligochaetes and other invertebrates in the sediments may very well be a function of nutritional preferences, but the deep migrations by some tubificid species may also be related to their specific state of maturity according to Poddubnaja and Sorokin (1961) and Sorokin (1966).

In Brinkhurst and Chua (1969), Brinkhurst and Jamieson (1971), Wavre and Brinkhurst (1971), Brinkhurst (1972) and other works produced by Brinkhurst much attention is focused upon the role of micro-organisms in the diet of tubificids. Different tubificid species can co-exist both vertically and horizontally probably because they feed selectively upon specific micro-organisms. Brinkhurst (1972) has even found mixed tubificid cultures thriving better than pure cultures in laboratory experiments.

Estimations of correlations between different characteristics of the bottom substrate and bottom invertebrates of all kinds have long been of the greatest interest to bottom fauna investigators. There is little need to mention any particular works, but already Ekman (1915) and Alm (1922) thoroughly discussed such relationships.

Burrowing animals like tubificids and lumbriculids, some chironomid larvae, some amphipods, and copepods are on good grounds supposed to evoke a tremendous effect upon the circulation and irrigation of superficial layers of the sediments. A certain amount of transportation and dislocation of different sediment strata is also most evident, naturally with unknown consequences to palaeobiological investigations (cf. Stockner and Lund, 1970).

Under experimental conditions the rate of biochemical oxidation of organic matter in the sediments increased 1.5—2 times in the presence of tubificids according to Zvetkova (1972), but Solowiev (1924), Ravera (1955), Kuznetzow (1959), Schumacher (1963), Wachs (1967), Zahner (1967), and Brinkhurst (1972) also found a strong dependence between the burrowing activities of tubificids in high densities and the circulation of salts, dissolved gases, organic compounds etc. The additional irrigating properties of communities of some chironomid larvae are also of the greatest importance (*cf.* Tessenow, 1964; Hargrave, 1972; Jónasson, 1972).

When macroorganisms are absent, deposits of inorganic mercury in the upper few centimetres of

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the sediment are responsible for almost the whole amount of released methyl mercury. If Tubificidae or *Anodonta* are present in high densities, deposits down to 2.5 or 9 cm from the mud surface respectively are effective (JERNELÖV, 1970).

ALSTERBERG (1925) described the active transport of material by tubificid worms in the form of faeces from a depth of feeding of about 2—4 cm in the mud to the surface, but he doubted that tubificids could help ventilating the top sediment layers to any considerable extent. Similar points of view were presented by WAGNER (1968).

Depending upon the season and the actual state of maturity, tubificid worms may be found quite deep in the mud and, according to Russian works, obviously irrespective of where their specific sources of nourishment are concentrated (see above). The obvious vertical separation of adult and juvenile forms of three of the dominating tubificid species in Hovgårdsfjärden are further evidence (see above).

Since all oligochaetes need access to the interface for respiration even normally very deep-burrowing specimens spend much time in the top few centimetres. For that reason it may seem difficult to separate the true vertical preferences from other elementary needs (*cf.* BRINKHURST *et.al.*, 1969). Naturally, however, there should be better chances of finding the deep-living forms deep in the mud than other worms with less pronounced burrowing habits.

As mentioned before, an adverse relationship between numbers of chironomid larvae (*Chironomus anthracinus*) and tubificids (*Potamothrix hammoniensis*) was observed by JÓNASSON (1972). The same kind of relationship was assumed by BRINKHURST and KENNEDY (1965).

Pontoporeia affinis and larvae of Tanypodinae and Chironomini are probably the most mobile invertebrates recorded in these investigations.

Big filtrating chironomid larvae like *Chironomus plumosus* are most vulnerable to bottom predating fish like "suckers", but the larvae can stay quite deep in their U-shaped tubes, especially at high oxygen concentrations (*cf.* BRUNDIN, 1951), thereby reducing their chances of being eaten by fish.

LENZ (1931), BERG (1938), COLE (1953), KAJAK (1963), BRINKHURST and KENNEDY (1965), and SÄRKKÄ and PAASIVIRTA (1972) have all been aware that some chironomid larvae, *Corethra* larvae or tubificid worms rapidly withdraw into the sediments and congregate at a certain depth if they become aware of a foreign object like a sampler entering the sediments.

The question is now whether this microstratification sampler — which both takes the core and divides it into thin strata in much less than a second — is swift enough to get the big larvae of *Chironomus plumosus*, for instance, at their proper levels of residence in the mud. In any case there is now little doubt that particularly the smallest and most fragile bottom invertebrates are incapable of moving far either vertically or horizontally in the timelapse between the moments when the sampler enters the mud and when it is released.

VI. SUMMARY

The microstratification technique presented here primarily seems to have confirmed some general ideas as to where various bottom invertebrates are dwelling in relation to the mud-water interface.

Naidid oligochaetes were concentrated at the interface, i.e. rarely below a mud depth of 2—4 cm, which is in full agreement with previous works by COLE (1953), STANCZYKOWSKA (1966), SCHIEMER *et.al.* (1969), HOWMILLER and BEETON (1970), SÄRKKÄ and PAASIVIRTA (1972) and BRINKHURST and BRINKHURST *et.al.* (in a series of works) and others. By now it seems quite clear that most naidids are more or less bound to the mud surface — or to submerse vegetation (which was not studied here).

On the whole, tubificids penetrated here considerably deeper than naidids, even to depths of about 15 cm in the mud, but with maxima of concentration between two and four cm (*cf.* LENZ, 1931; BERG, 1938; PODDUBNAJA, 1961; PODDUBNAJA and SOROKIN, 1961; BRINKHURST and KENNEDY, 1965; SOROKIN, 1966; PATARIDZE, 1967; SCHIEMER *et.al.*, 1969; JÓNASSON, 1969, 1972; BRINKHURST *et.al.*, 1969; SÄRKKÄ and PAASIVIRTA, 1972). Some tubificid species like *Limnodrilus hoffmeisteri*, *Potamothrix hammoniensis*, and *Po-*

tamothrix vejdovskyi were with few exceptions, the most deep-penetrating species. *Potamothrix heuscheri* and *Tubifex tubifex* were also capable of penetrating deeply, while *Aulodrilus pluriseta*, in particular, but also *Bothrioneurum vejdovskyanum*, *Aulodrilus pigueti* and some other tubificids displayed as superficial habits as any naidids. The former tubificids are well-known deep-burrowers (*cf.* Sapkarev, 1959; Poddubnaja, 1961; Brinkhurst and Kennedy, 1965; Jónasson, 1972; Särkkä and Paasivirta, 1972) with the adult worms generally penetrating deepest. These deep migratory movements are not necessarily related to feeding (see discussion). *Aulodrilus pluriseta* often occurs in mud rich in plant fragments (Brinkhurst and Jamieson, 1971), which makes it more or less bound to the mud surface. The *A. pluriseta* specimens picked out alive from the sediment chambers of the sampler were all, on each occasion, dwelling in tubes of clay lying on the mud surface reminiscent of the tubes of some chironomid larvae.

Bigger specimens of *Chironomus plumosus* were easily distinguishable from other chironomid larvae in that they were dwelling quite deep in the mud (cf. Lenz, 1931; Berg, 1938; Brundin, 1951; Jónasson, 1969; Särkkä and Paasivirta, 1972) — often down to 15 cm. It is difficult to say if this is a consequence of repulsive movements by the larvae away from the sampler. Most other chironomid larvae were fairly well concentrated to the upper two centimetres of the mud.

Pontoporeia affinis was generally found a few centimetres below the mud surface, which is also in good agreement with the author's general experience. Ostracoda and Cladocera were located close to the interface, while Copepoda as a rule were the deepest penetrating organisms. Since the bottom material was sorted alive with no preserving additives there should be no confusion concerning dead organisms in the material. In three surveys out of four *Cyclops* spp. had their maxima of occurrence at a depth of about ten centimetres in the sediments. *Cyclops* specimens were quite often found at depths of even about 20 centimetres. Wheather they were dormant or not is difficult to say (cf. Elgmork, 1959), but they were all quite agile when sorted out.

Pisiids were generally found in the top 2 centimetres of the sediments, but they could also be encountered deeper — at about 10 centimetres (*cf.* also Berg, 1938, who found them at considerable depths).

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I. INTRODUCTION

Interaction between fish sp
the favourite topics of Sw
since the 1950s. The relati
of the North Scandinavian
one, two or three species
empty of fish, have provide
of comparing allopatric po
sympatric ones, as well as
introducing new species. A
regards the late history
mountain lakes has been:
either brown trout or ch
(2) addition of a new spec
produce a two-species sys
addition of a third species
e.g. whitefish, burbot and p
As regards the interaction
(*Salmo trutta* L.) and artic
(L.)), early Norwegian ex
existence of food competi
Studies in Swedish lakes
benthic animals, above al
SARS, for which the two
ultimate result being a decr
an "interactive segregation
(NILSSON 1965, 1967). Sin
observed in different coexi
gonus (SVÄRDSON 1954, NI
and NILSSON 1962). Whi
lakes containing arctic cha
char populations (EKMAN
(1961) listed 14 lakes whe
appeared or had markedl
introduction of whitefish
either the big whitefish we
hatched char fry or the eli
result of severe food compe
as well as the adult fish.