

THE ECOLOGY OF MARINE MICROBENTHOS I. THE QUANTITATIVE IMPORTANCE OF CILIATES AS COMPARED WITH METAZOANS IN VARIOUS TYPES OF SEDIMENTS

By TOM FENCHEL

Marine Biological Laboratory, Helsingør, Denmark.

ABSTRACT

An investigation of the quantitative importance of protozoans – especially ciliates – has been undertaken in Scandinavian waters. Ciliates were found in numbers from 10^6 to 4×10^7 individuals per m^2 representing 0.03-2.3 grammes wet weight per m^2 . Highest numbers were found in fine sand and in localities with a rich growth of sulphur-bacteria. In these sediments ciliates are 10 to 100 times more numerous than the total number of metazoans, and their biomass is of the same order or sometimes larger than the biomass of the micro-metazoans (nematodes, turbellarians, gastrotrichs etc.). In coarser sand ciliates are fewer, and micro-metazoans play a larger quantitative role. This distribution is explained by the small size and other morphological adaptations making ciliates able to inhabit the small interstia of fine sand, and also their ability to endure reducing and anaerobic conditions. In the detritus layers which cover clayey and muddy sediments ciliates are few in number and play a small role compared with metazoan groups, such as nematodes, which may sometimes be as numerous as ciliates.

A comparison with the enumeration of the benthic metazoans in Nivå Bay carried out by Muus (1967) shows that 93% of all animals in the bay are ciliates which, however, only comprise 0.4% of the total animal biomass.

Large dinoflagellates were found in numbers of 10^5 to 1.5×10^7 per m^2 . Euglenoids are less numerous, normally fewer than 5×10^5 per m^2 . Naked amoebae seem also to play a small quantitative role; more than 10^5 per m^2 were rarely found.

Ciliates show a maximum population size in summer, but this maximum may be obscured by other factors in more exposed localities. Large populations of active animals are found throughout the year.

The importance of ciliates in community respiration is discussed. It is concluded that in localities with fine sand and in sulphureta the ciliates account for a larger part than the micro-metazoa, and that the ciliates contribute significantly to the energetics of these communities.

INTRODUCTION

During the last decades there has been a wide interest in the structure and function of the ecosystem constituted by the sea-bottom and its flora and fauna, especially in the role played by smaller organisms, since their ecology was, until recently, little known. Thus several ecological studies on small invertebrates have

appeared (e. g. Jansson, 1966; Muus, 1967; Pennak, 1951; Renaud-Debyser, 1963; Renaud-Debyser & Salvat, 1963; Smidt, 1951; Wieser, 1960, and Wieser & Kanwisher, 1961).

Also, the ecology of marine bacteria and protophytes has been studied intensively during the later years (see Oppenheimer, 1963 and Wood, 1965, 1967 for references).

The ecology of protozoans, however, has drawn less attention, mainly due to technical difficulties in quantitative enumeration. Benthic protozoans cannot be counted in their substratum without a tremendous amount of work, nor can they be extracted from the sediment by narcotization or/and washing. Furthermore they must either be studied alive or treated with a time-consuming cytological technique in order to be identified. On the other hand protozoans do not lend themselves to bacteriological technique. The role played by protozoans in the ecosystem is therefore little known. Due to lack of evidence they are often considered to be unimportant. Thus Pennak (1951) considers protozoans to be "seldom abundant" in marine beaches, and Dogiel (1965 p. 591) writes: "The Flagellata and Ciliata occupy a modest place in the benthonic marine fauna".

The present paper is the first in a series describing various aspects of the ecology of marine micro-benthos with special emphasis on ciliates. Following papers will describe food-chains, physical and chemical properties of sediments, vertical zonation of factors and fauna in the sediments, relations to other organisms, growth in cultures, and ecological succession. The purpose of the present paper is to report on the quantitative importance of ciliates as compared with other animal groups in various marine sediments, while the qualitative distribution will be described in later papers.

As mentioned above, little quantitative work on marine benthic protozoans has appeared. Fjeld (1955) studied the ciliates of sand quantitatively. However, with the extraction method employed (washing the sand with sea-water) the majority of the haptic forms were lost during the process and his results are probably one to two orders of magnitude too low. Nor did he relate his findings to a standard area of the sea-bottom. Since the ciliate fauna changes quantitatively as well as qualitatively at various depths in the sediment his results can not be evaluated. Borrer (1963) in his study on the benthic ciliate fauna in Florida also made some quantitative studies. Although his method of enumeration (direct counting) is reliable he did not refer his findings to a standard area of the sea-bottom. Mare (1942) tried to enumerate protozoans of marine sediments by bacteriological methods, viz. a dilution culture method. This gives a quite false picture of the fauna, since only forms feeding on heterotrophic bacteria will thrive in such cultures. In fact, of ciliates she found only a few bacteria-feeding species. At least one of these species (*Uronema marinum*) forms cysts, so the method does not tell anything about the number of active animals at any specified moment.

Fenchel & Jansson (1966) in a paper on the vertical zonation of the micro-

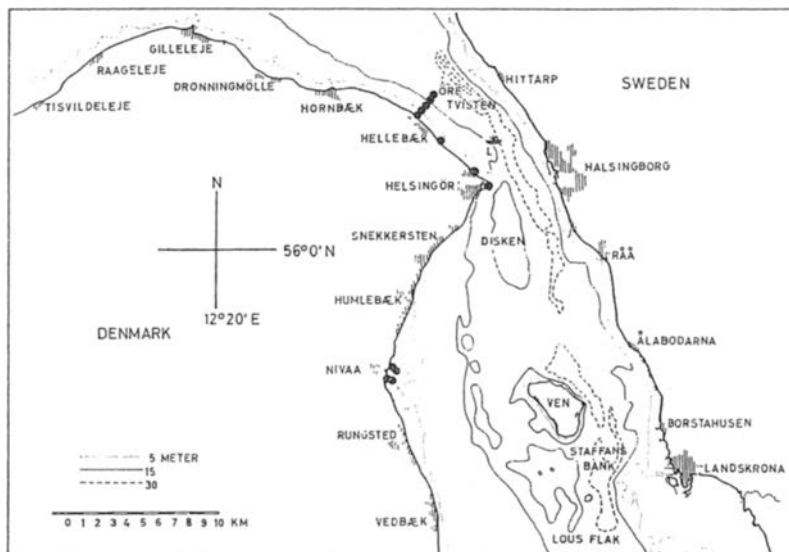


FIG. 1. Map of the northern part of the Sound showing the sampling stations.

fauna gave a quantitative estimate of the number of ciliates in a brackish water beach in the Baltic Sea. In the work mentioned the methods were similar to those used in the present paper.

Among the many persons who have in some way helped me in my work I should like here to express my gratitude to Miss Harriet Hansen for her invaluable assistance and especially for undertaking a large part of the laborious quantitative work.

MATERIAL AND METHODS

The present paper is based on 76 quantitative samples which, besides representatives from other taxonomic groups, contained in all 83,370 ciliates. The sampling localities will all be described in detail in following papers; here they will only be listed together with short characterizing notes.

I. Askö, an island in the Baltic Sea south of Stockholm. Samples were taken in a sheltered bay near the laboratory on poorly sorted, sulphide containing sand and on detritus covered clay. One sample was taken on an exposed sandy beach on the other side of the island. All samples are from August 1966 and June-July 1967.

II. Øresund (Fig. 1). – A. Several localities were sampled in a line perpendicular to the coast in the northern part of the Sound in January-April 1966 and in May-June 1967 at depths from 0.5 to 25 metres. The sediments are fine homogeneous sand with more or less detritus, clean homogeneous medium sand, and clayey

sand from the deepest localities. – B. A few samples were taken at Julebæk in a sheltered locality behind sandbars at 0.2 m depth in May 1967. The sediment is fine sand. – C. 28 samples were taken at the beach outside the Marine Biological Laboratory in the period October 1966-September 1967 at 0.2-0.5 metres depth. The sediment is fine homogenous sand. – D. A few samples were taken in gravel at 0.3 m depth off the Kronborg Castle in June 1966. – E. Several stations were sampled regularly in Nivå Bay in all seasons of the year. Nivå Bay is a shallow sheltered bay with homogenous medium sand and with growth of *Ruppia* and *Zostera*. Stations dominated by colourless or purple sulphur bacteria were also sampled.

III. The Isefjord, a fjord in the northern part of Zealand. Samples were taken in a sheltered cove close to the Isefjord Laboratory. The sediment is fine sand rich in detritus and with patchy growth of *Zostera*. The samples were taken at depths from 0.2 to 1 metre in April 1967.

All samples were taken with a pvc-tube with an internal diameter of 2.1 cm. The tube was pressed about 20 cm into the sediment, closed in the top with a cork, withdrawn and corked in the lower end. In the laboratory the upper cork was replaced by a cork with a bore fitted with a glass-tube and a piece of rubber-tubing closed by a clamp. The sampling tube was placed in a rack and the lower cork was removed. By opening and closing the clamp it is possible to make the sediment core slide downwards stepwise, and each time 1, 2, or 3 cm of the core appears below the sampling tube it is cut free and allowed to fall into a 3 cm high cylindrical container with the same internal diameter as the sampling tube (Fig. 2). This method was found superior to the conventional method of splitting sediment cores, viz. by pushing the sediment upwards with a piston. By the method employed the original zonation, and especially the sediment surface, is much better preserved and the core segments are easily secured in separate containers. The supernatant water is also preserved over the uppermost sediment segment.

If the sediment was very coarse or expected to contain only a few animals the whole core segment of 3.5, 7.0, or 11.5 cm³ (depending on the length of the segment) was extracted for microfauna. In most cases, however, a subsample was taken in each core segment with a pvc-tube with an internal diameter of 1.31 cm (area: 1.0 cm²) so that 1, 2 or 3 cm³ of sediment was extracted.

By the method employed it is possible at the same time to study the vertical zonation and to secure all animals below a known area of the sea-bottom.

In all capillary sediments, even those with strongly reducing properties, a significant number of ciliates may be expected 6-8 cm below the surface, and in cleaner sand it is necessary to extract sand down to 20 cm below the surface in order to obtain all the animals. In some localities a significant number of ciliates were found in the deepest part of the cores, but the cores were not taken longer than 21 cm, since friction along the sides of the core would then disturb the zonation. (All stations described in the present paper are permanently water covered.

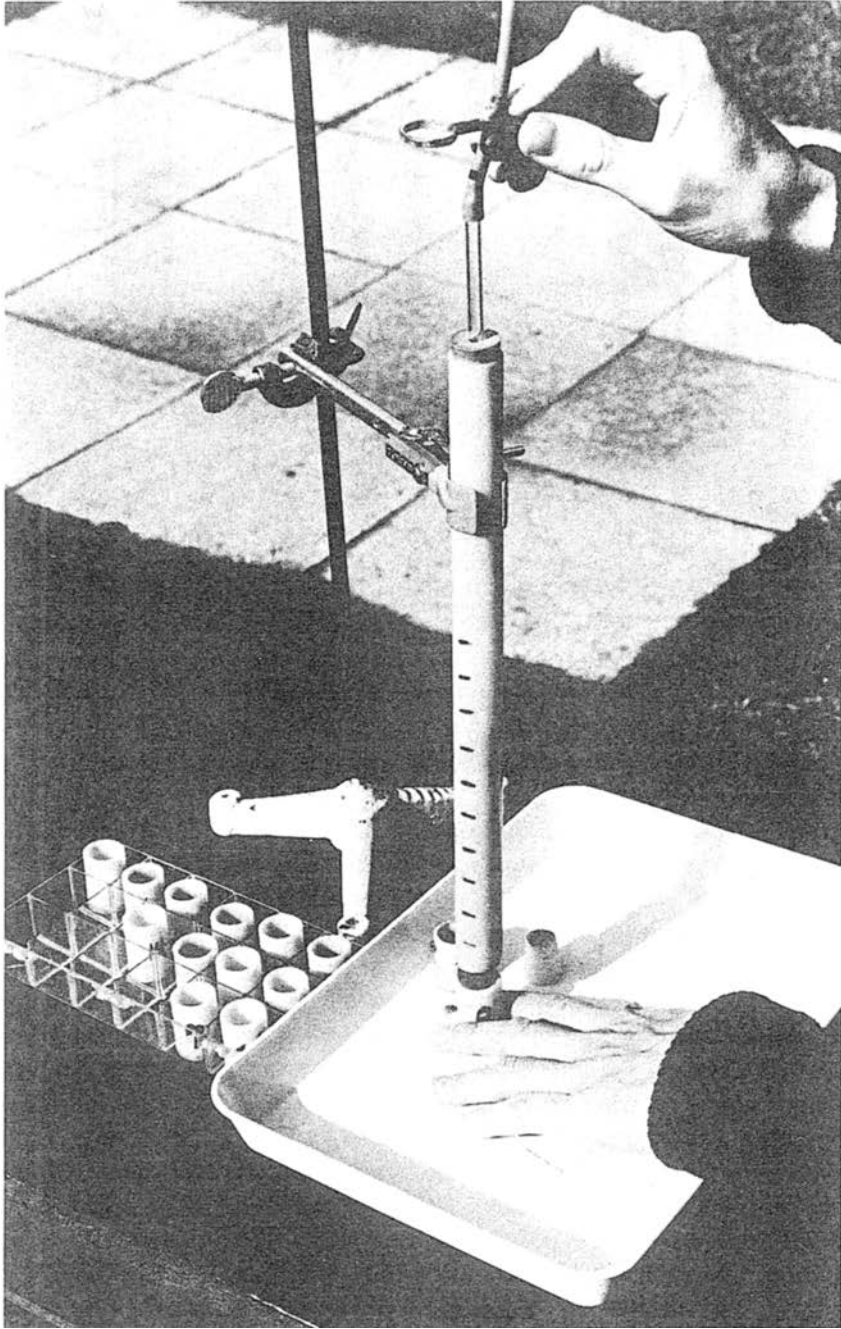


FIG. 2. Vertical splitting of a sediment core.

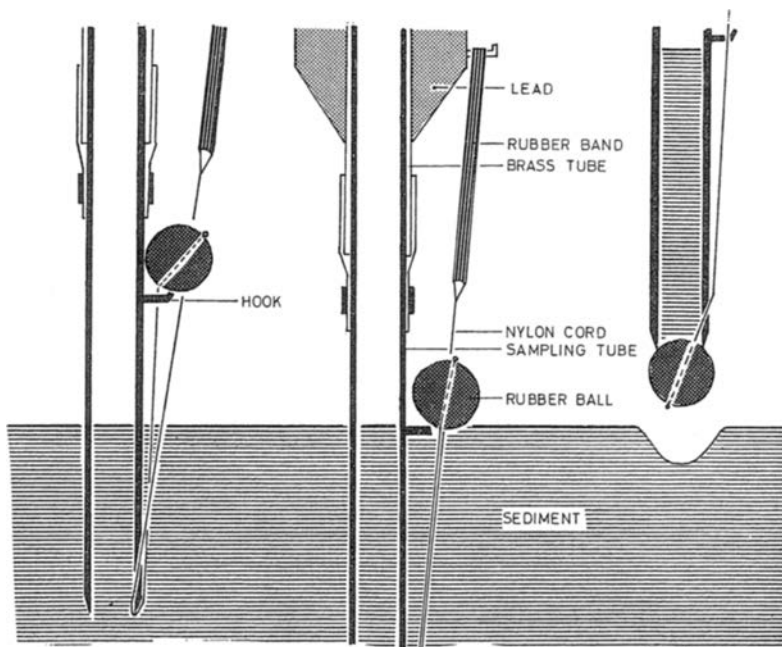


FIG. 3. Sampling tube mounted on a corer shown when descending into the sediment, when the ball is released, and when ascending.

Above the water-line and in tidal areas ciliates and other animals may be found much deeper in the sediment).

Samples from more than 5 metres depth were taken with a Moore and Neill corer (see Barnes, 1959 for description) fitted with the above mentioned pvc sampling tubes. Clean sand tends to be washed out from below when the corer is on its way up in spite of the top-valve of the corer. Dr. E. Kannevorff therefore kindly suggested the following modification to me which solves the problem satisfactorily (Fig. 3). A small hole is made 0.5 cm from the lower end of the sampling tube. A nylon cord is drawn through the hole. In one end it is attached to a hard rubber ball (diameter 2.3 cm) and in the other end to a strong rubber band which in its turn can be attached to the corer. A small hook made of pvc is welded to the sampling tube 15-20 cm from the lower end.

When a sample is to be taken the sampling tube is placed in the corer and the rubber band is attached to the corer. The rubber band should be stretched in this "released" position and the rubber ball thus closes the opening of the sampling tube firmly. The rubber ball is then fastened by the hook by further stretching of the rubber band and the corer is lowered towards the bottom. When the sampling tube has descended sufficiently into the sediment the rubber ball is released from the hook by the sediment surface, and when the corer ascends the sediment core is supported from below by the ball. In spite of the simple and costless construc-

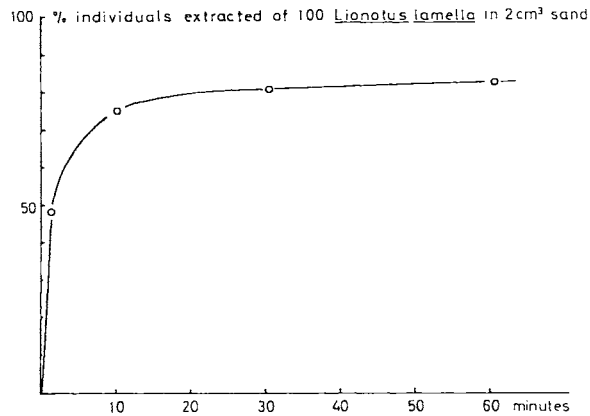


FIG. 4. Extraction of 100 *Lionotus lamella* from 2 cm³ of sand as function of time.

tion it works well giving 15-20 cm long undisturbed sediment cores. Only the lowermost cm of sediment is disturbed by the passage of the nylon cord and should be discarded. Nylon cords and rubber bands must be renewed frequently because of wear.

The "sea-water ice" method of Uhlig was used for extracting the microfauna (a detailed description and discussion of the method may be found in Uhlig, 1964, 1966). Since the volumes of sediment extracted (in most cases 2 or 3 cm³) were smaller than those recommended by Uhlig (25 cm³), extraction filters with a diameter of only 2.1 cm were used. As a standard the filters (nylon gauze) had a mesh size of 120 μ but for extractions of coarse sand a mesh size of 265 μ was used.

The sea-water used for receiving the extracted animals and for making the sea-water ice was aged sea-water of approximately the salinity of the sampling locality (6‰ in the Baltic, 20‰ elsewhere). As a standard, each subsample was extracted for 1 hour with 2 refillings of ice and 2 or 3 changes of the containers receiving the extracted animals (evaporating dishes). Extracted animals are nearly always in good condition, they may be used for initiating cultures, and will often keep alive for days in the dishes into which they were extracted.

Uhlig (1964) found an extraction efficiency of about 90% for ciliates and about 75% for turbellarians in his preliminary experiments. During the present investigation the efficiency was checked on several occasions. The ciliates used originated either from cultures or were extracted from a natural sand sample prior to the experiment. 20-100 individuals of a single species were placed in 2 cm³ clean moist sand which was then extracted and the numbers of animals that appeared after 1, 10, 30, and 60 minutes were counted. The following species were used: *Frontonia marina*, *Lionotus lamella*, *Metopus contortus*, *Sonderia schizostoma*, and *Trachelo-raphis kahli*. A typical result of an experiment is shown in Fig. 4. In all cases the

extraction was nearly completed after 30 minutes. The efficiency was found to vary between 70 and 90%. It is probable that the efficiency is somewhat higher when extracting natural samples since manipulation of the animals in the experiments may lead to some mortality. However, it must be stressed that all enumerations give minimum figures, and that the efficiency of the extracting procedure cannot be stated more accurately than above. Flagellates seem to be extracted with the same efficiency and speed as ciliates. Nematodes, as mentioned by Uhlig, seem to be less well extracted. My observations on sand samples after extraction sometimes indicated an efficiency as low as 60%. The extraction efficiency of amoebae, tardigrades, rotatorians, gastrotrichs, harpacticoids, ostracods, and annelids is unknown and may well be lower than that of ciliates.

Different species are extracted at different rates. For instance, in a sample of fine sand *Remanella* spp., *Lacrymaria* spp., *Mesodinium pupula* and dinoflagellates will be nearly completely extracted within a few minutes, while *Geleia* spp., *Kentrophorus* spp., *Aspidisca* spp. and most metazoans appear later.

Much detritus in the samples make counting of the animals more difficult since some detritus will pass through the filter.

Non-capillary sediments (clay and clayey sand) cannot be extracted, but in these sediments practically all ciliates are confined to the uppermost few mm of loose sediment. The few samples of this sort which were treated quantitatively, were counted directly. The uppermost layers were pipetted from the sampling tubes into petridishes with sea-water and the microfauna was counted under the dissecting microscope.

Mats of filamentous cyanophyceans and sulphur bacteria prolong extraction and if they are strongly developed it pays to tear them apart with needles before extraction.

The animals were counted under the dissecting microscope by picking them up one by one with a pipette from the evaporating dishes. Since a sample corresponding to 1 cm² surface may contain up to 4000 and often 1-2000 ciliates, in addition to other organisms, it is necessary to identify the most common (about 100) species under the dissecting microscope. The species of most ciliate genera can be identified in this way. For the small species of genera as *Cyclidium*, *Cristigera*, *Plagiocampa*, etc. and most oxytrichids this is not possible, however, and the species of some problematic genera such as *Tracheloraphis* were not identified to species.

It takes 4-8 hours to extract, count and identify the contents of a core sample corresponding to 1 cm² with about 2000 ciliates, making allowance for a few identifications of difficult species under the microscope. All samples were extracted and counted on the day of collection.

The biomass of ciliates was estimated volumetrically. Single ciliates were placed in a "Roto-Compressor" (for description see Heunert & Uhlig, 1966) and the length of the unpressed animal was measured. It was then pressed until it

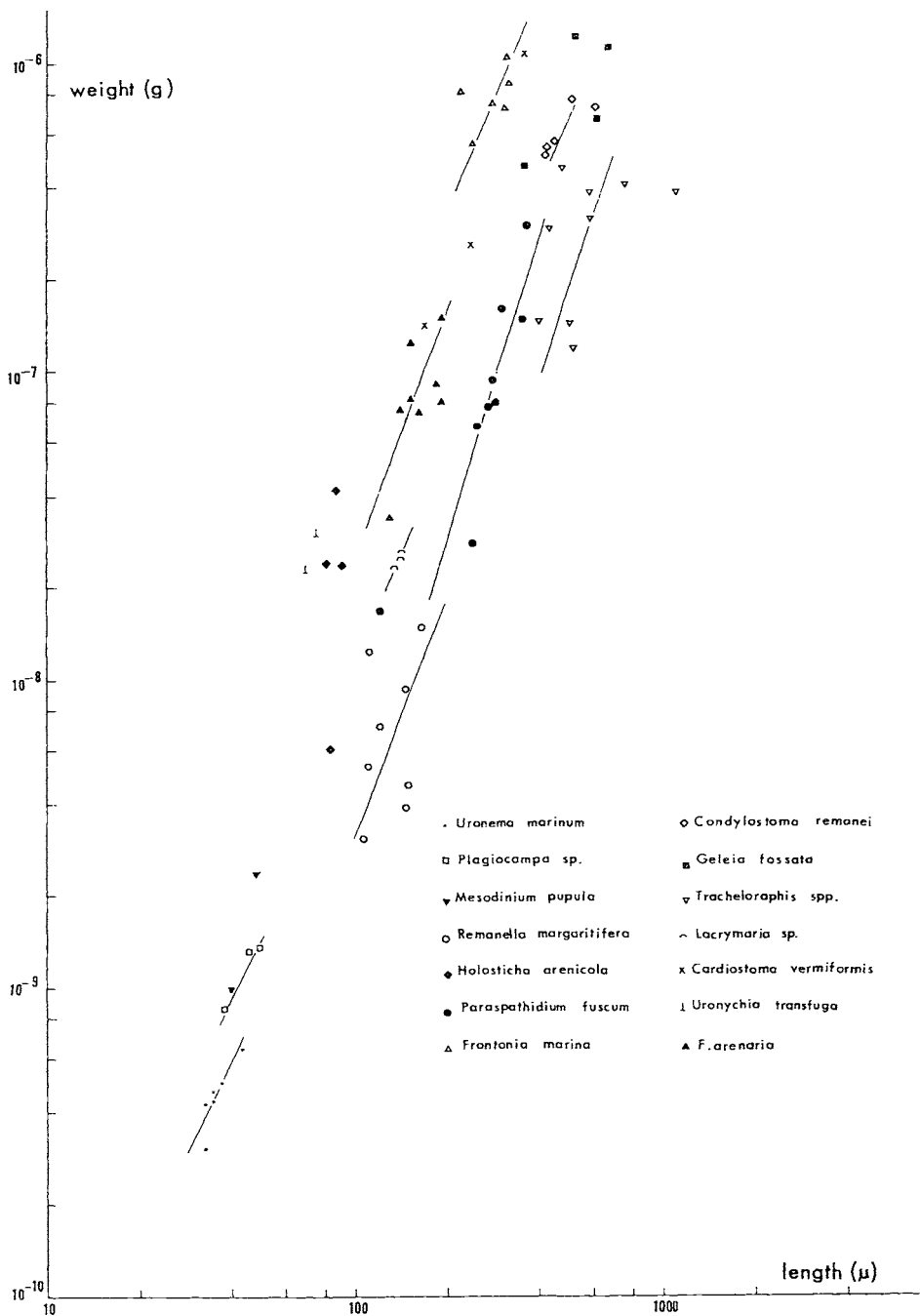


FIG. 5. Length and estimated wet weight of 71 specimens comprising 14 species of ciliates.

had plane-parallel sides. Its thickness was measured by reading the scale on the fine adjustment of the microscope. Its outline was traced with a camera lucida and the surface area calculated by weighing. The specific gravity of ciliates was put to 1. A varied number of specimens comprising 14 species were measured in this way (Fig. 5). For these species the average weight was used when calculating the biomass. The weight of other species was estimated from Fig. 5 by the length and by resemblance in shape to measured species.

The weights of gastrotrichs, nematodes, turbellarians, harpacticoids, ostracods, and archiannelids were taken from Renaud-Debyser & Salvat (1963) while the weights of rotifers, tardigrades and oligochaetes were estimated from their dimensions.

RESULTS AND DISCUSSION

The findings from 9 samples from 9 different types of sediments and depths are shown on Figs. 6 (individuals per m²) and 7 (grammes per m²). In all localities between 10⁶ and 4 × 10⁷ ciliates per m² are found. Largest numbers (> 10⁷ per m²) are found in fine sand (median grain size: 125-250 μ) and in localities with strongly reducing sediments and a rich growth of sulphur bacteria (sulphureta, represented by the Nivå localities). In all these localities the number of ciliates far exceeds the number of metazoans. In coarser sand and gravel ciliates are less numerous and micro-metazoans become more important. Here the latter are also represented by a number of groups not or rarely present in fine sand (annelids, ostracods). In the detritus layer on the surface of muddy and clayey sediments ciliates play a comparatively small role and may even be exceeded in numbers by nematodes and turbellarians.

In fine sand and in sulphureta the ciliates normally constitute 0.5 to 1.5 g per m² (more than 2 g per m² is sometimes found) which is about the same as the total weight of micro-metazoa, while in coarser sediments and in detritus the biomass of ciliates is far exceeded by that of micro-metazoans. (In and on non-capillary sediments the concept "microfauna" is not well defined, thus acarines, chironomids and oligochaetes – included in Figs. 6 and 7 – are normally not considered as microfauna. In sand the microfauna is clearly defined as the interstitial fauna in contrast to larger forms which burrow in the substrate.)

The water line of strongly exposed beaches contains a poor fauna, as demonstrated by the Askö sample.

Other protozoan groups, e.g. large dinoflagellates (genera such as *Amphidinium*, *Gymnodinium*, and *Peridinium*), euglenoids and naked amoebae were also enumerated in some of the samples. The large dinoflagellates occur in numbers between 10⁵ and 1.5 × 10⁷ per m². Euglenoids are rare but most commonly found in sulphureta (10⁵-10⁶ per m²). Amoebae seem to be of minor importance (usually fewer than 10⁵ per m²) but this may be due to inefficiency of extraction.

The above described composition of the fauna in various sediments may be explained by two factors, a mechanical and a chemical one.

As previously discussed by many authors (see Swedmark, 1964 for references) the size of interstitia is a limiting factor for the mesopsammon. Within some ciliate groups forms with a very small body size (c. 20 μ) have developed. Large forms with specialized body shapes, are also found, e. g. thread-like (*Trachelocerca* spp.) or thin, leaf-like, only a few microns thick (*Remanella* spp. and *Kentrophorus* spp.). These "microporal" forms (Fauré-Fremiet, 1950; Dragesco, 1960) are specially adapted to move in the small interstitia of fine sand. Only few metazoans have achieved such extreme morphological adaptations to life in small interstitia, and consequently the ciliates dominate this environment. In coarser sand with larger interstitia a much higher number of metazoan "life-forms" are able to exist and consequently metazoans play a much larger role in these sediments.

The relation between median grain size and the size of the interstitia, however, is not a simple one, since the grade of sorting also plays a significant role. Nevertheless, in homogenous sands it may be taken as a rule that ciliates play the largest role in the sediments with the finest grain sizes.

In clayey sediments the interstitia are clogged and no interstitial fauna occurs. A fauna dominated by nematodes is found in these sediments, and on the detritus covered surface a rich and varied microfauna may be found in which the ciliates, however, play a comparatively small role.

As shown by Fenchel & Jansson (1966) many ciliates can live deep in the sediment under anaerobic and reducing conditions where few or no metazoans are found. This is in accordance with the fact that ciliates play a dominating role in sulphureta where most metazoans can live only on the sediment surface. In contrast to fine sand, coarse sand is often oxidized far down and this also explains the larger role played by metazoans in these sediments. In clayey and muddy sediments reducing conditions are common, but being unable to burrow, ciliates are here only found on the thin oxidized surface layer.

In his memoir on Danish lagoons and estuaries Muus (1967) reports on the numbers and biomass of all benthic metazoans weighing more than 10^{-6} g, found in the summer in the Nivå Bay. In Fig. 8 his findings are combined with my enumerations of animals weighing less than 10^{-6} g. The weight category 10^{-6} to 10^{-5} g comprises nematodes, turbellarians, harpacticoids and ostracods which were also enumerated by me. These findings (average of samples taken in the period April-July: 8.3×10^5 individuals = 3.7 g per m^2) are in good accordance with those of Muus who used direct sorting of sediment samples. The weight category 10^{-9} to 10^{-6} g comprises ciliates, rotifers, chaetonotid gastrotrichs, and tardigrads, but the ciliates constitute more than 90% by weight and about 99% by numbers of this category.

Thus it can be seen that the ciliates constitute 93% of the total number of benthic animals living in the bay and about 0.4% of the biomass.

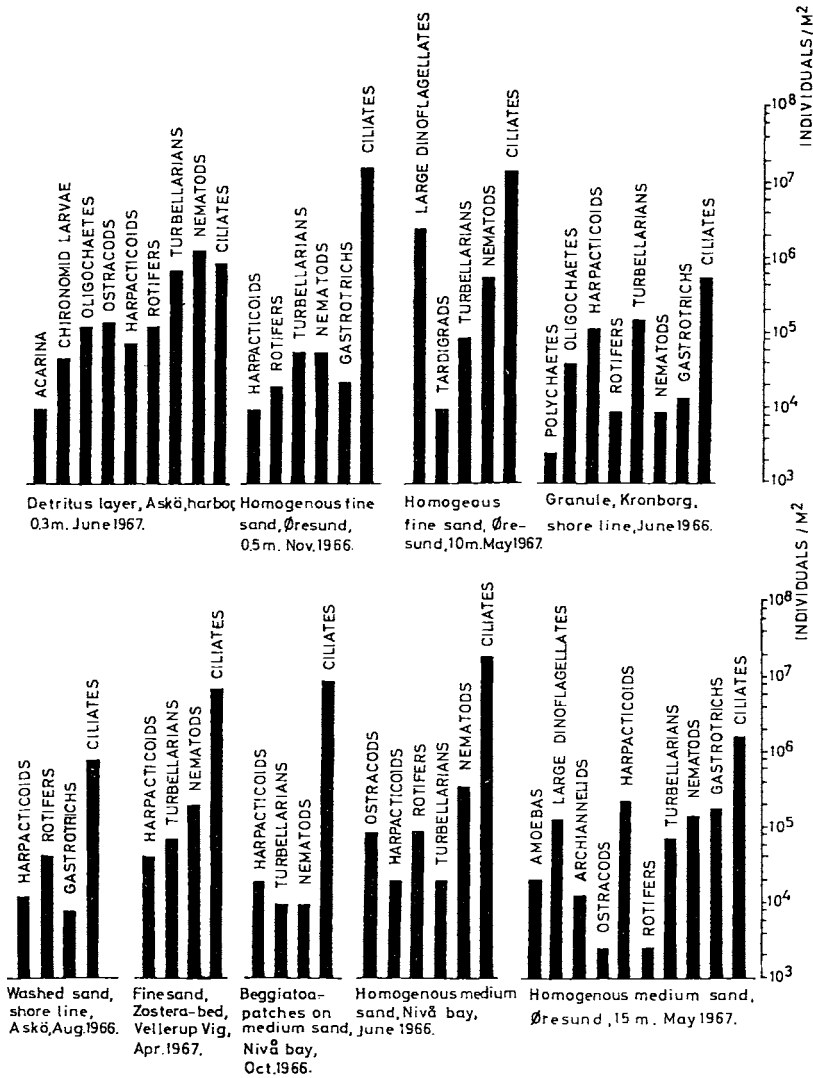


FIG. 6. The microfauna composition of 9 quantitative samples from 9 different localities shown as individuals per m².

The numbers of animals – including microfauna – is usually considered to decrease with increasing depth. Disregarding samples from the shallow and very fertile Nivå Bay such a relation was not found (compare the findings from sandy bottom at 0.5, 10 and 15 metres depth from Øresund on Figs. 6-7). However, no samples were taken from below 25 m, and the type of sediment varies at various depths in Øresund. Possibly, sampling at greater depths in an area with a more

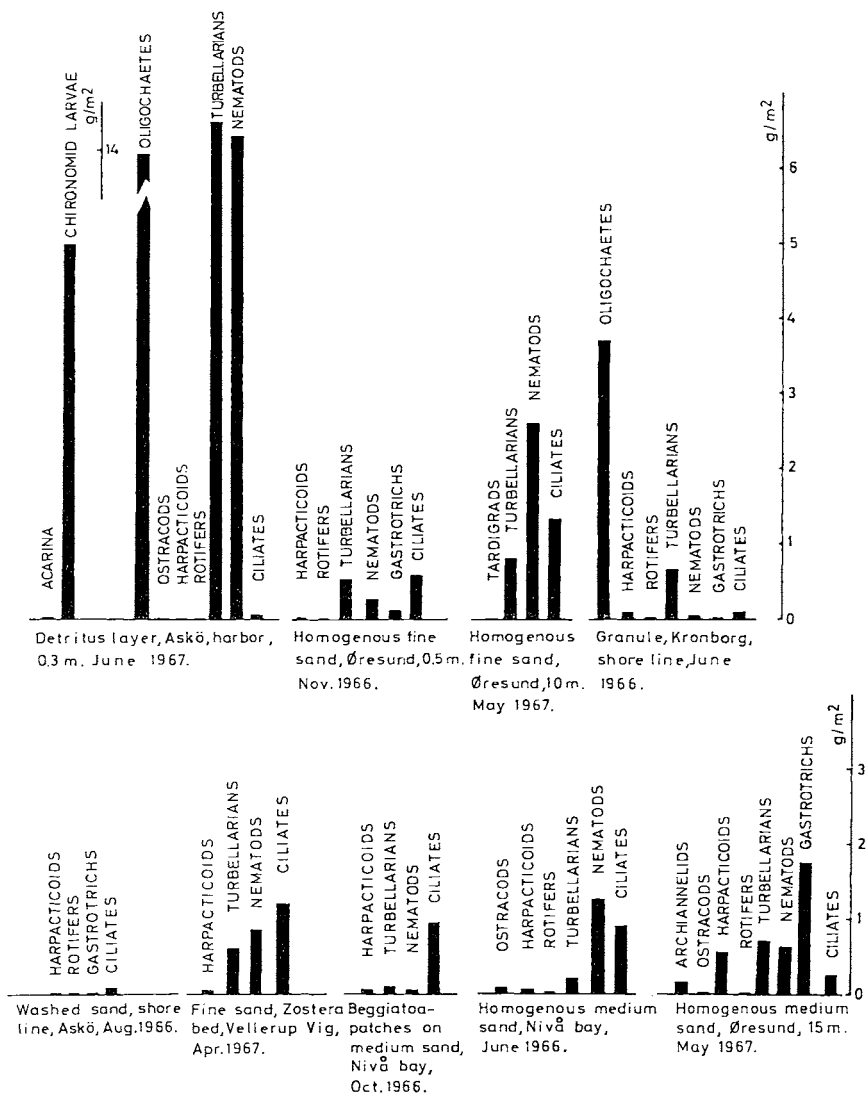


FIG. 7. The microfauna composition of the 9 samples from Fig. 6, but shown as grammes per m².

homogenous sediment distribution would demonstrate this general trend for ciliates, too.

Figs. 9 and 10 show the number of ciliates and micro-metazoans throughout a year in a sandy beach at 0.5 metres depth at Helsingør and in *Beggiatoa*-patches in a sheltered cove in Nivå Bay. The metazoans (in the Helsingør samples mainly nematodes, macrodasyoids, and turbellarians and in Nivå mainly nematodes, tur-

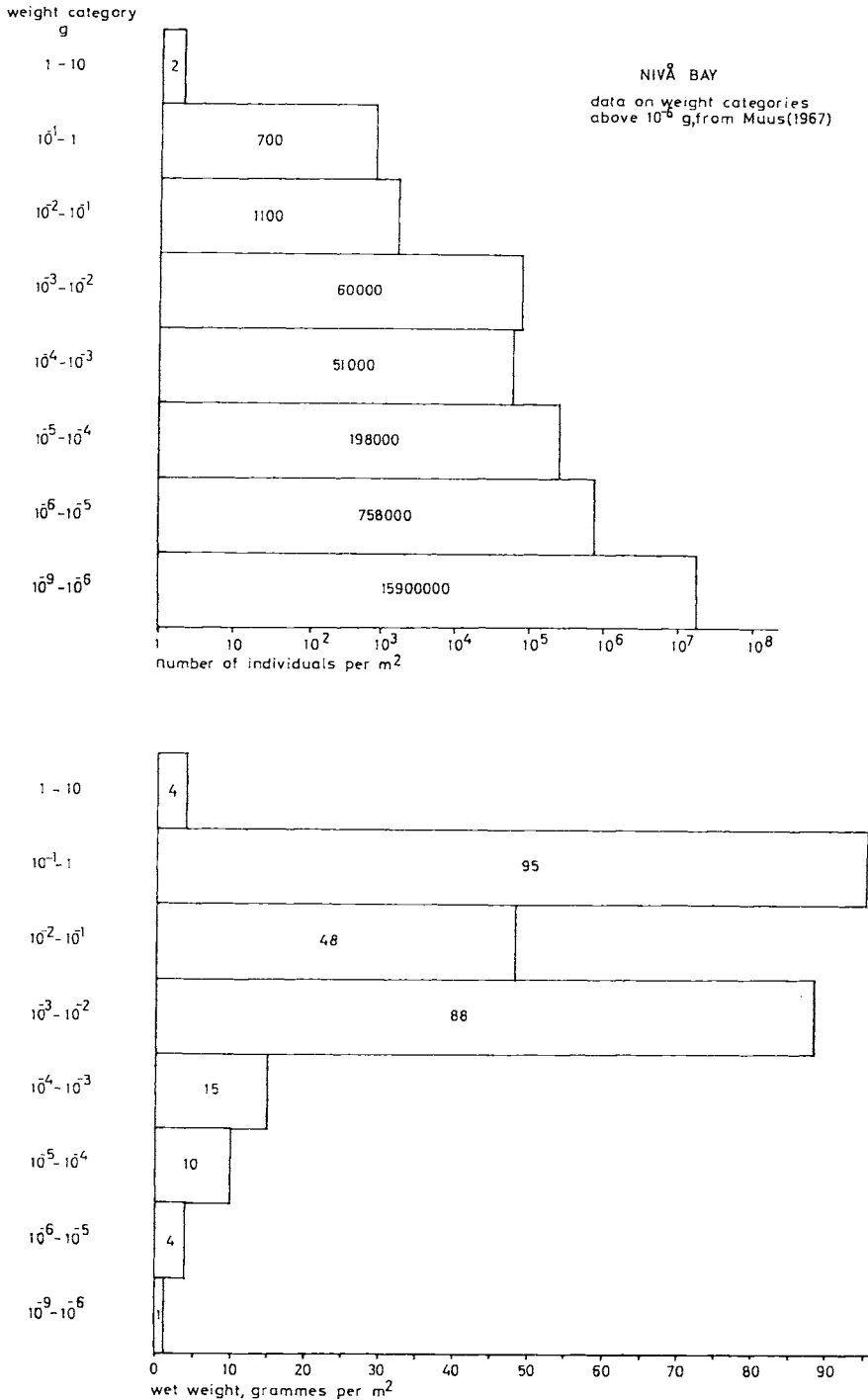


FIG. 8. The quantitative importance of different weight categories of benthic animals from Nivå Bay in summer.

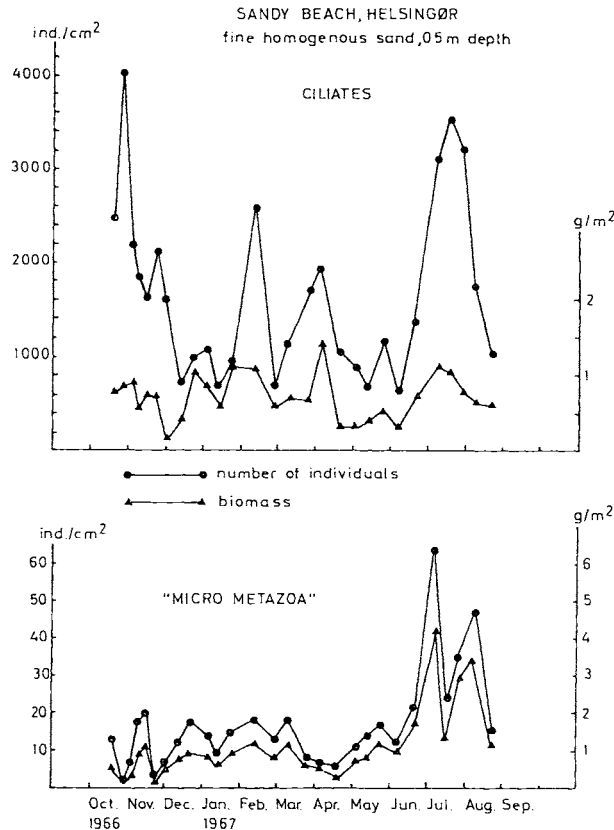


FIG. 9. Numbers and biomasses of ciliates and micro-metazoans in 28 samples in an Øresund beach from October 1966 to August 1967.

bellarians, rotifers, and harpacticoids) show an obvious summer peak, as previously demonstrated by several authors (Muus, 1967; Smidt, 1951). A maximum in the ciliate population is also seen in the sheltered Nivå locality. In the more exposed Helsingør locality this is obscured mainly by accumulations of driftweed (early fall 1966 and late winter 1967) followed by an increase in the ciliate population. The biomass curve does not show similar large peaks since the ciliate succession on decaying driftweed initiates with a dominance of small species.

These year cycles will be described later in full detail and are mentioned here only to demonstrate that ciliates are usually most numerous in summer, though this may be changed by other factors, and that there is a significant number of ciliates throughout the year (in the period January-March 1967 the water temperature of Øresund was constantly below 2°C).

It is of interest to know the relative importance of the various animal groups in the total respiration of the community. Estimates have been made on marine

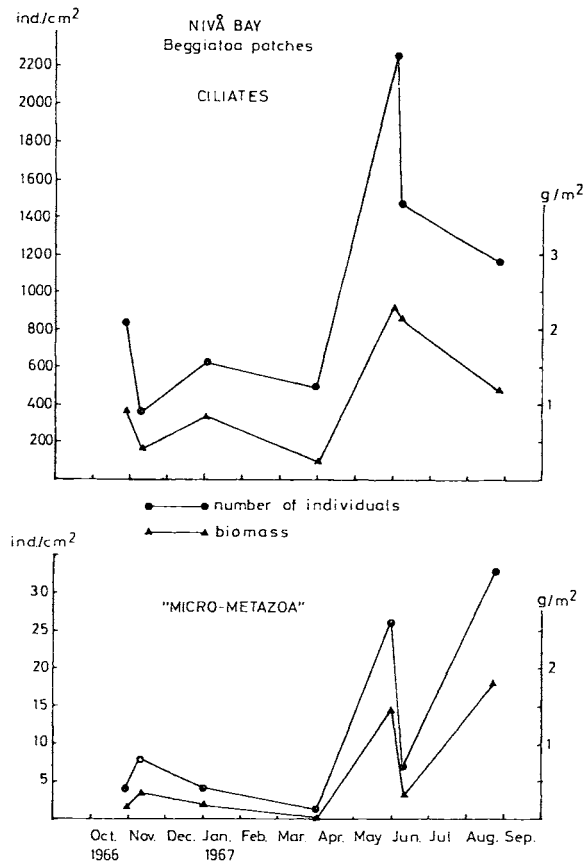


FIG. 10. Numbers and biomasses of ciliates and micro-metazoans from 6 samples taken in *Beggiatoa* patches in Nivå Bay from October 1966 to August 1967.

benthos by Wieser & Kanwisher (1961) and Carey (1967). These papers conclude that bacteria and microfauna are of far larger importance than the macrofauna. Wieser and Kanwisher who studied the ecology of a muddy *Spartina*-flat found that 10-15% of the bottom respiration was due to metazoans, 25-33% to nematodes while the rest was considered to be due to protozoans and bacteria. Unfortunately, technical difficulties still prevent obtaining values of respiration for the large number of protozoan species, of which the great majority have not yet been kept in culture. Thus, the relative importance of bacterial and protozoan respiration in the bottom cannot yet be estimated.

Comparisons of the metabolic importance of ciliates and larger metazoans are problematic. Considerations based on biomass will underestimate and consideration based on numbers will overestimate the importance of the ciliates due to the relation between metabolism and body size. In sediments where biomasses of cili-

ates and micro-metazoans are about the same (fine sand and sulphureta) the ciliates must account for a large part of community respiration; this becomes clear when Wieser & Kanwisher's results and the small size of ciliates are kept in mind.

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