

Systematics, ecology and feeding biology of estuarine nematodes

CENTRALE LANDBOUWCATALOGUS



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SYSTEMATICS, ECOLOGY AND FEEDING BIOLOGY OF ESTUARINE NEMATODES

Proefschrift

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doctor in de landbouwwetenschappen,

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Dr. C.C. Oosterlee,

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VOORWOORD

Dit proefschrift is tot stand gekomen uit de interactie tussen eigen nieuwsgierigheid en de wetenschappelijke en sociale ambiance die de Groningse collega's creëerden. De relatie met marien biologisch onderzoek werd voor mij gelegd door dokter Wolters, als uitvloeisel van zijn duidelijke opvattingen omtrent de verhouding mens/arbeid/gezondheid.

Doordat het onderwerp van studie, estuariene nematoden, onbewerkt is aan nederlandse instellingen voor wetenschappelijk onderzoek, lag een omvangrijk maar gecompliceerd werkterrein open. Gekoesterd noch geteisterd door visionaire leermeesters kon vrijmoedig een weg gebaad worden door een baaierd van wriemelend klein grut. Tijdens deze expeditie werd op beslissende momenten steeds ondersteuning in de naaste omgeving gevonden: Victor de Jonge attendeerde mij op de mogelijkheid organismen te isoleren met behulp van ludox; met Wim Admiraal werd de Oost Friesche Plaat bestudeerd; met Frank van Es werden nematoden op een dieet van bacteriën gezet; met Arjen Kop werd populair gepubliceerd; Franciscus Colijn commentarieerde het schrijfwerk; Huub Schröder vervulde de rol van veelzijdig biechtvader; tenslotte werd in Karin Romeyn een medewerkster gevonden die het gehele onderzoek op vastberaden wijze in een stroomversnelling bracht. Professor Den Hartog was deze bedrijvigheid niet ontgaan en, terwijl Professor Wieser uit Innsbruck goedkeurend over zijn schouder toekeek, stimuleerde hij mij dit proefschrift te schrijven.

Voor het uiteindelijk tot stand komen van dit boekwerkje dank ik de volgende personen en instellingen:

Geert Kamstra voor het drukklaar maken van tekst en illustraties.

Joke Poelstra voor het spontaan aangeboden razendsnelle typewerk en Hil Lochorn voor de al even flitsende voltooiing, Anneke Bol voor het drukwerk.

De afdelingen Plantensystematiek en Microbiologie van de Rijks Universiteit Groningen voor het leveren van studenten. De studenten Karel Hemmes, Erik Kremer, Chris Brouwer en vele anderen voor hun doorgaans uitstekende bijdragen aan het onderzoek.

Het PWH dat personele lasten droeg waarvoor binnen de regulaire instellingen geen gelden werden gevonden.

STELLINGEN

1. De metabolische activiteit van meiofauna in benthische ecosystemen dient in situ gemeten te worden door middel van het aanbieden van gelabeld voedsel aan deze fauna.
B. Kuipers et al. (1981). Mar. Ecol. Prog. Ser. 5: 215-221.
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W. Wieser (1953). Ark. Zool. (2) 4: 439-484.
3. De rol van benthische meiofauna-organismen als voedsel voor larvale stadia van macrofauna-organismen wordt onderschat.
4. Het door Gerlach beschreven verschijnsel van "gardening" door nematoden wordt beter gedekt door het begrip "cultivating".
S.A. Gerlach (1978). Oecologia 33: 55-69.
5. Alhoewel manlijke nematoden bij het opsporen van een partner om te copuleren zeer opportunistisch te werk gaan in agar-cultures, worden zij in natuurlijk biotoop door attractie-stimulantia gestuurd.
6. Procesmetingen in kunstmatig milieu, aan uit hun biotoop geïsoleerde nematoden, worden verricht aan stervenden.
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G. Graf et al. (1982). Mar. Biol. 67: 201-208.
7. De genegenheid van vooruitstrevende Nederlanders voor opstandelingen op 20.000 km afstand is verwant aan de gevoelens van jeugdigen voor Winnetou, E. Presley en J. Cruyff.
8. Een wetsontwerp met betrekking tot de vermogensaanwasdeling zou aan betekenis winnen wanneer de vermogensafwasdeling in dezelfde geest wettelijk geregeld zou worden.

9. Het gemak waarmee deskundigen op het gebied van krabben, slakken en garnalen uitspraken doen over meiofauna, doet denken aan de olifantentemmer die meent beroepshalve reeds kenner van vlooientheaters te zijn.
10. Indien daartoe in de gelegenheid gesteld, zou de "bijzondere leerstoel alternatieve methoden van land- en tuinbouw" de verlening van een eredoctoraat aan Pee Pastinakel in overweging behoren te nemen.
11. Onderzoek aan mariene nematoden zou op meer ondersteuning kunnen rekenen wanneer deze organismen de buitenwereld aanblikten met een even trouwhartige oogopslag als de zeehond.

Stellingen behorende bij het proefschrift van L.A. Bouwman
(1983)

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HOGESCHOOL
VLAORNINGEN

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CHAPTER I

INTRODUCTION

The Ems Estuary

The Wadden Sea, a shallow coastal sea located along the Dutch, German and Danish coast and separated from the North Sea by a series of barrier islands, harbours three extensive estuaries formed by the rivers Elbe, Weser and Ems: the latter has the most westerly estuary (Fig. 1a, b). In the Middle Ages, storms

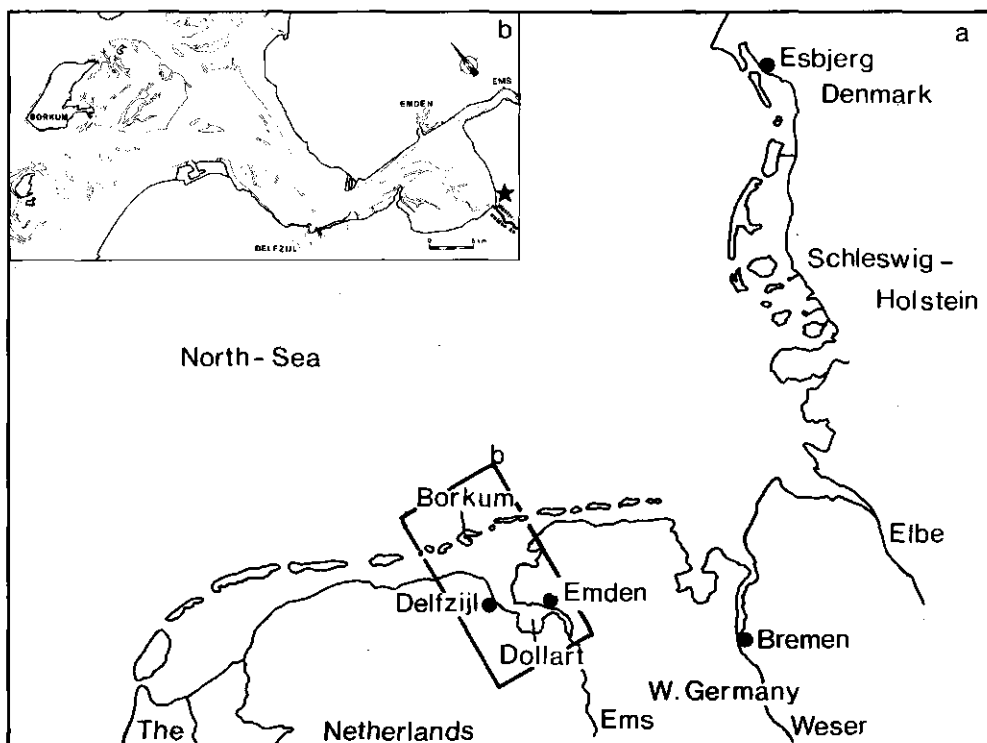


Fig. 1a. Map of the Wadden Sea.

1b. Map of the Ems estuary, * Nieuwe Statenzijl.

created an inner basin in the Ems estuary, the Dollart, nowadays a sheltered area which mainly consists of tidal mudflats; into the Dollart a tiny river, the Westerwoldsche A, dis-

charges fresh water at Nieuwe Statenzijl (Fig. 1b). The length of the estuary, from Nieuwe Statenzijl to the island of Borkum, is c. 50 km, its area is c. 500 km². In the estuary three geographical zones can be distinguished: the lower reaches (part of the Wadden Sea proper), the middle reaches and the upper reaches (the Dollart). A considerable part of the estuary (c. 50%) consists of tidal flats, which are more extensive towards the upper reaches where mud-flats cover c. 80% of the area. The flats emerge twice daily and the duration of the exposure depends on their elevation; in the Dollart e.g. the flats are exposed for c. 80% of the time.

In the southern part of the Dollart large amounts of organically polluted water are sluiced at Nieuwe Statenzijl. Annually, c. 30,000 tons carbon, mainly rapidly degradable organic waste originating from potato-flour factories, is discharged into the estuary by the river Westerwoldsche A (Van Es, 1977). Approximately 70% of this organic waste is mineralized in the Dollart (Van Es, 1982), in the water as well as in the sediment; this demands a large amount of oxygen and results in an anaerobic environment in the vicinity of the discharge-point (Fig. 2), especially in the autumn when the bulk of the waste is sluiced (Schröder and Van Es, 1980).

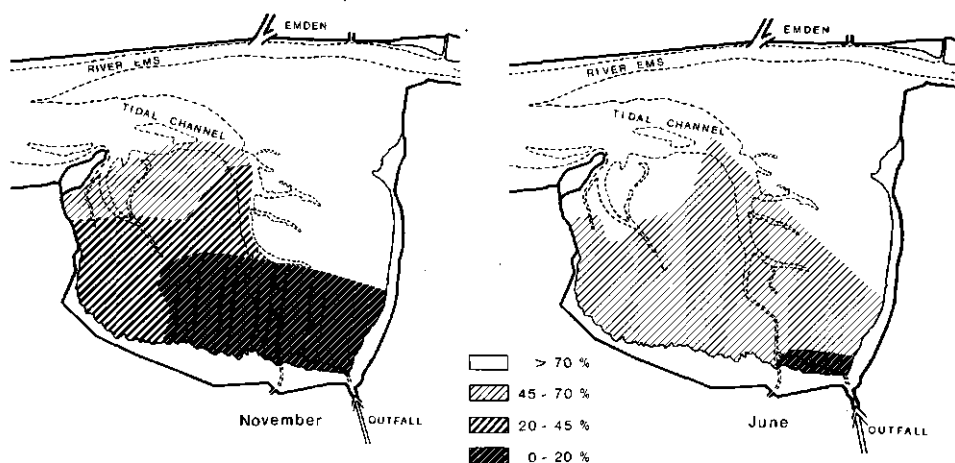


Fig. 2. Oxygen saturation (%) in the water covering the tidal flats in November 1974 during the amylum campaign and in June 1975. (Borrowed from Van Es, 1982.)

Influenced by the discharge of fresh water, salinity is low close to Nieuwe Statenzijl but increases seawards and at Borkum salinity values are nearly marine. As a result of decreasing current velocity, small organic particles (detritus) accumulate in the surface layers of the sediment of the central parts of the tidal flats. Consequently, the concentration of organic carbon in the surface layers of the sediments in the estuary is high, especially in the sheltered and in the more inland parts. Therefore, conditions for the growth of bacteria are favourable, and because the tidal flats are exposed to daylight regularly, and concentrations of nutrients such as nitrogen, phosphorus and silicon are not limiting, conditions also favour the development of diatoms.

The dense populations of diatoms and bacteria also serve as food for the benthic fauna. For practical reasons this fauna is usually divided into three categories, the micro-, meio- and macrofauna (Fig. 3).

The Meiofauna

The meiofauna comprises the benthic animals intermediate in size between the microfaunal organisms (ciliates, amoebes, flagellates, foraminifers, etc.) and the macrofaunal organisms (gastropods, bivalves, polychaetes and crustaceans). The meiofauna is defined as the benthic metazoa that can pass through a sieve with a mesh size of 1 mm.

In all estuaries, including that of the Ems, nematodes are the predominant meiofaunal taxon. They are widely distributed and occur in nearly all benthic biotopes, e.g. in coarse sands, fine sands, in muds, in the surface layers and at depths down to 30 cm and on the surface of littoral macrophytes. No other meiofauna taxon is as widely distributed as the nematodes; expressed in terms of biomass, nematodes are also the predominant group and the number of different species in estuarine habitats is not equalled or exceeded by any other taxon.

The Nematodes

Nematodes are studied in the agricultural, veterinary and medical sciences mainly because they can be harmful to crops, animals and people. Interest in marine free-living nematodes, however, is small; in the Netherlands only De Man from Leiden (+1930) and Schuurmans Stekhoven from Utrecht (+1955) have

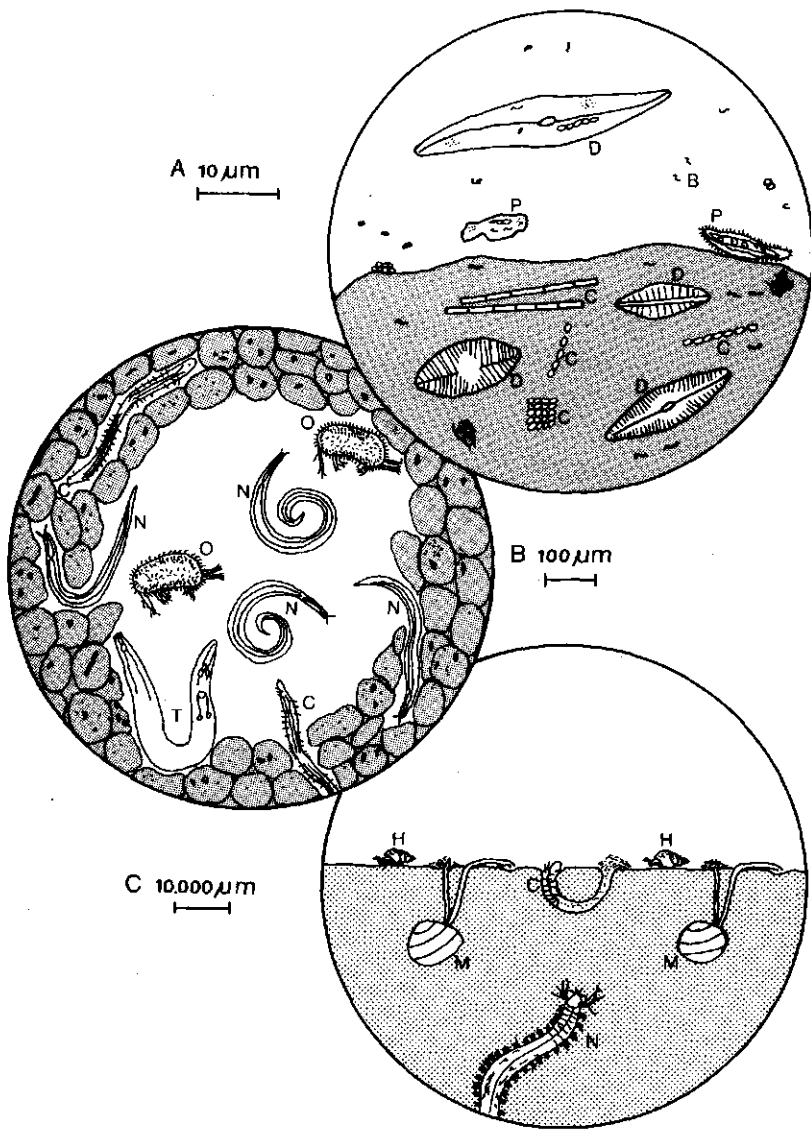


Fig. 3. The benthic flora and fauna.

- A. The microflora and fauna located on the surface of a sand-grain and in the interstitial water. D = diatoms, B = bacteria, C = cyanophytes, P = protozoa.
- B. The meiofauna, located in the interstitial spaces. N = nematodes, O = ostracods, T = turbellarians, C = oligochaetes.
- C. The macrofauna, located on and within the sediment. H = *Hydrobia ulvae*, M = *Macoma balthica*, N = *Nereis diversicolor*, C = *Corophium volutator*.

studied them. In neighbouring countries, various established institutions have been engaged in the study of nematodes for some time.

Nematodes are simply built animals, consisting of two concentric tubes, connected at the anterior end by the walls of the buccal cavity and posteriorly by the anus. The outer tube consists of three consecutive layers: a cuticle, a hypodermis and a muscular layer, interrupted by four hypodermal strings. The inner tube functions as a digestive tract, composed of a muscular oesophagus anteriorly and the intestine posteriorly. In the body cavity, between the two tubes, various glands develop (e.g. ovaria and testes) (Fig. 4). In general, nematodes reproduce sexually and after copulation females release

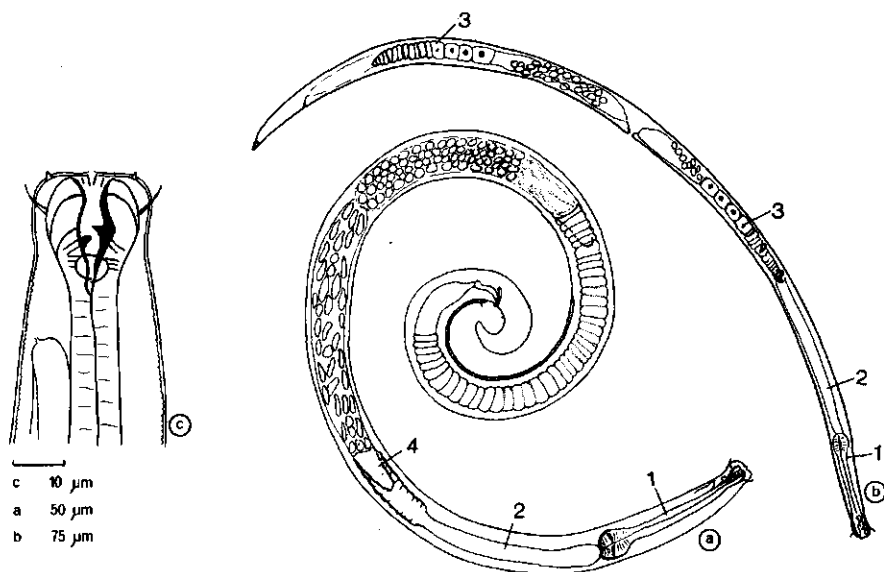


Fig. 4. The nematode species *Microlaimus robustidens* Stekhoven and de Coninck 1933. a = male, b = female, c = head, 1 = oesophagus, 2 = intestine, 3 = ovary, 4 = testis.

eggs from which the larvae hatch. After four moults the young larvae become adults with completely developed sex organs; then the next cycle can start. A cycle can last from several days to up to one year, depending on the species and on environmental factors. Most estuarine nematode species vary in length from 0.5 to 2.5 mm and feed on bacteria, diatoms, protozoa and small metazoans, including nematodes; these food items are abundant in the sediments of tidal flats.

Aims of this study

The present study aims to describe the relationship between nematodes and the estuarine environment. The specific survival strategies of nematodes living in different habitats were studied.

First it was necessary to develop a new method to separate nematodes from sediments rich in small particles, as none of the traditional methods of doing this are quantitatively reliable (Chapter II).

After the nematodes had been isolated, attention was paid to their taxonomy. The early marine nematologists such as Bastian, Bütschli and De Man carried out their research on nematodes from coastal areas in north-west Europe; their work has been continued by other scientists, and as a consequence, relatively much is known about the systematics of nematodes from this region, though the nematodes from the Ems estuary have not been studied before. It was expected that most of the nematodes isolated in the course of the present study would belong to species that are already known and have been described in the literature. However, when studying nematode ecology one has to delve deeply into taxonomy and, therefore, much attention was paid to comparing the species isolated from the Ems estuary with existing descriptions. Many additions, improvements and corrections to these descriptions resulted and some species new to science were described (Chapter III).

The distribution patterns of nematode species were investigated and several nematode associations were distinguished. In the estuary there is a great variety of biotopes, due to the existence of many physical, chemical and biological gradients such as: current velocity, duration of irradiation, salinity, oxygen levels, presence/absence of macrofauna. Each biotope is conditioned by specific environmental

parameters which in turn determine the specificity of the microflora and microfauna. The abundance, species composition and dynamics of populations of microorganisms interact with the nematode populations and determine their specific structure. The habitat selects for specific feeding strategies among the nematodes and this relationship depends to a large extent on the type, density, distribution and purity of the food organisms specific to the habitat; the buccal cavity and the structures within the cavity indicate the feeding biology of the species concerned (Fig. 5). Wieser (1953) was the first

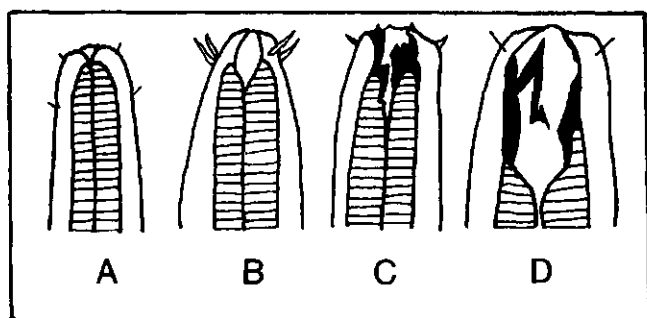


Fig. 5. Nematode heads with different types of buccal cavities and structures. a = buccal cavity almost absent, b = buccal cavity conical without structures, c = buccal cavity with cuticularized walls and teeth, d = wide buccal cavity with a strongly developed tooth.

to relate specific nematode associations to particular biotopes on the basis of assumptions about the relations between buccal structures and feeding biology and environment. In the present research these relationships were investigated for various biotopes in the Ems estuary (Chapter IV).

To study the role of nematodes as grazers on microorganisms, the feeding behaviour of several nematode species was studied in the laboratory, in agar cultures with various types of food. Feeding strategies and consumption techniques were investigated and morphology, feeding biology and ecology were related to each other by means of laboratory observations and experiments (Chapter V).

As this study was part of extensive biological and chemical investigations into the effects of organic pollution on the estuary, special attention was focused on the area in the vicinity of the discharge-point of waste-water at Nieuwe Stantenzijl. The complete meiofauna, including oligochaetes and harpacticoids, was studied, and its structure and dynamics were related to the prevailing environmental conditions of which the waste-discharge is an integral part (Chapter VI).

In the general discussion (Chapter VII) the relationship between nematodes and the organisms they consume, are discussed; the feed-back of the grazing process on the microbenthos populations is elucidated in that chapter and finally suggestions for future research are proposed.

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CHAPTER II

A Simple Density Separation Technique for Quantitative Isolation of Meiobenthos Using the Colloidal Silica Ludox-TM*

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Abstract

A simple, quantitative density separation method is described. The method is based on differences in specific weight between meiobenthos and sediment. Nematodes and copepods could be separated from sediment and detritus when samples were suspended in Ludox-TM, a colloidal silica. Organisms float at the surface, while sediment particles sink. Results obtained with this new method were compared with the well-known decantation method. For a quantitative isolation of nematodes from sediments, rich in coarse detritus, a maximum volume of 7 cm³ sample could be used. For copepods this maximum was 13 cm³. For such sediments the density method is more reliable than the decantation method. The time needed for sorting the meiobenthic organisms is reduced to about 30% compared with the former method. The new method can be used for preserved as well as for fresh sediment samples and can also be applied for the isolation of small polychaetes, small oligochaetes, larvae of some macrofaunal groups and net-zooplankton.

Introduction

In estuaries with sheltered areas, which are usually rich in detritus and fine-grained sediments, the most abundant component of the meiobenthos is generally formed by the nematodes while copepods often rank second. Quantitative isolation and subsequent analysis of such populations are rather difficult, because detritus particles hamper detection of organisms under the dissecting microscope. For the extraction of meiobenthic organisms from sandy sediments several methods are applied. Uhlig *et al.* (1973) described the specific efficiency of methods such as decantation, elutriation and sea water ice treatment. The same methods can be used for quantitative isolation of meiobenthic organisms from muddy sediments, but this is very time-consuming due to the presence of detritus particles which make hand-sorting necessary. Heip *et al.* (1974) modified the method described by Jenkins (1964) to isolate nematodes and copepods from muddy sediments by centrifugation in a saccharose solution. However, they

had to repeat the centrifugation procedure several times to harvest the population of nematodes quantitatively. Bowen *et al.* (1972) introduced density gradients built up from the colloidal silica Ludox-AM to separate different groups of marine zooplankton from each other. The method described in this paper is based on the use of Ludox-TM for quantitative separation of meiobenthic organisms from detritus as well as from the fine-grained sediment fraction. The use of Ludox-TM (specific weight 1.39 g cm⁻³) instead of Ludox-AM (specific weight 1.19 g cm⁻³) is not essential for the method described in this paper. Ludox-TM was chosen because separation of other, heavier sediment components is under investigation. These results will be published in the near future. Attention was focused on nematodes and copepods, as being the most abundant groups in the localities investigated.

Materials and Methods

Surface sediment from the upper 0.5 cm was collected from tidal mud flats at five different localities in the Ems estuary (Fig. 1). The collected samples were brought to the laboratory, put into

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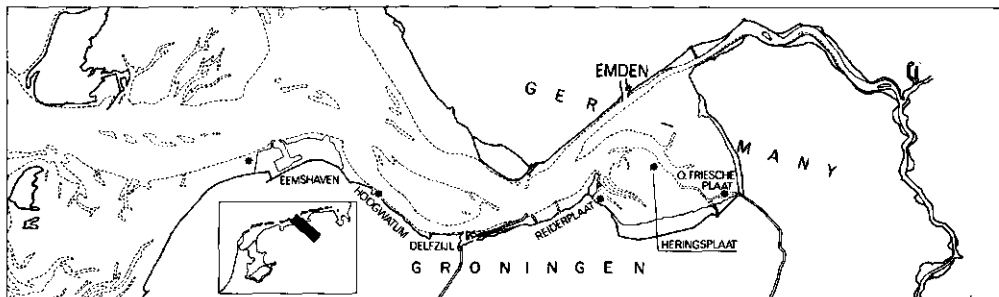


Fig. 1. Map of the sampling stations Eemshaven, Hoogwatum, Reiderplaat, Heringsplaat and Oost Friesche Plaat

a plastic beaker and the sediment diluted by 15 to 20% (v/v) with sea water until a slurry was obtained. The slurry was homogenized by a variable speed IKA-Werk stirring machine (Janke & Kunkel K.G., Staufen, Breisgau, FRG) with a propeller. The number of revs/min of the stirrer was dependent on the kind of sediment. The stirrer was adjusted to between 800 and 1200 revs/min to achieve thorough mixing. A propeller size of 65% of the beaker diameter proved to be effective. To prevent settling of sand grains, a T-piece was attached to the lower side of the propeller. This T-piece rotated just above the bottom of the beaker. After 10 min stirring, subsamples were taken while stirring was continued by a plastic syringe (2.5 cm³) from which the conical top had been cut off. Other series of subsamples were taken by a plastic syringe (20 cm³) with a pore of 4 mm at the conical top. The subsamples were divided at random into two series. One series was processed by decantation and sieving, the second series by the method described in this paper.

Decantation Method

Nematodes

Subsamples of 1.5 or 2.0 cm³ of fresh sediment were distributed between two glass tubes of 16 x 1.5 cm. These were half-filled with sea water and whirled at full speed for 20 sec on a Vortex Genie mixer, type EP 900 (Scientific Industries, Inc., USA). The larger sediment particles were allowed to settle

for 8 sec, then the supernatant was poured out through a 35 µm mesh-sieve of nylon gauze. This procedure was repeated at least 5 times. Residues were checked for the presence of nematodes. The meio-benthic organisms were washed out of the sieve with sea water, collected in a Petri dish and counted under a dissecting microscope.

Copepods

Subsamples of 17.5 cm³ were put in about 100 ml of sea water in 250 ml flasks. The flasks were placed on a magnetic stirrer and the suspensions were stirred vigorously for about 20 sec. The subsequent procedure was the same as described for nematodes.

Density Separation Method

In this procedure, differences in specific weight between meiofauna and other sediment components were used to separate these fractions. For our purpose Ludox-TM was used. Ludox is the trade name of a colloidal silica polymer (Du Pont, 1973). The specific weight of the undiluted product is 1.39 g cm⁻³ and will be considered here as 100%. The product is toxic to all living organisms and may contain insoluble floccules of Ludox in the gel-form, which can be removed by filtering the Ludox over a thick layer of gauze bandages and paper filter (Schleicher & Schüll, nr. 520 b II). Beakers (14 x 9 cm diameter) were filled with 300 ml 25% (v/v) Ludox-TM. Subsamples of 1.5 or 2.0 cm³ of fresh sediment

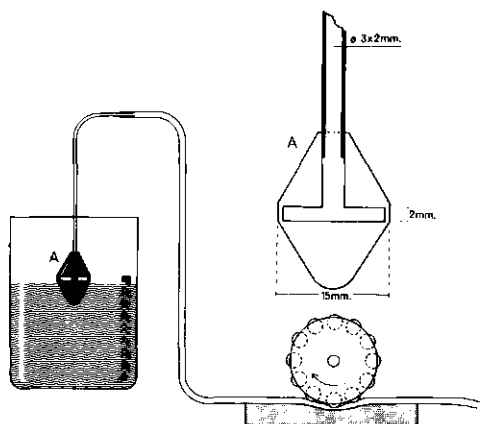


Fig. 2. Arrangement for pumping a water layer upon the Ludox surface. The peristaltic pump is adjusted to a capacity of 15 ml min^{-1} . A: Detail of conical part through which the water is pumped in a horizontal direction upon the Ludox surface. Conical part is made of PVC and tube of stainless steel

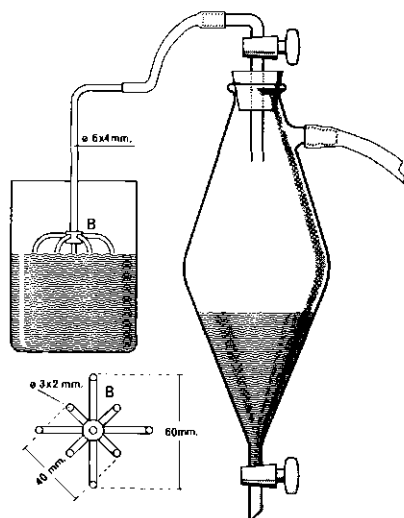


Fig. 3. Arrangement for collecting the floating meiobenthic organisms from the Ludox surface. Organisms are caught in the vacuum flask (volume about 1.8 l) and drawn off through the lower valve. Then the flask is rinsed with distilled water to remove the Ludox as well as the meiobenthic organisms retained. B: Detail of the sucking-apparatus through which water layer and subsequent Ludox top layer are transported to the vacuum flask. Tubes are made of stainless steel and central part of PVC

were put in 25 ml glass tubes and half-filled with 25% (v/v) Ludox-TM. Then 1 ml formaldehyde (37%) was added, the tubes stoppered and vigorously shaken by hand for some seconds. Next, one of the beakers with Ludox was placed on a magnetic stirrer and the sediment was added while stirring vigorously with a teflon-coated bar ($5.5 \times 1.1 \text{ cm}$). The 25 ml tubes were washed out with Ludox. The stirring was continued for some minutes and then the beaker was removed from the stirrer and used as a flotation chamber. With the apparatus shown in Fig. 2, a 0.5 cm thick layer of distilled water was pumped onto the surface of the Ludox to prevent desiccation, which would have caused transformation of the Ludox into the gel-form, possibly disturbing the procedure at a later stage. After about 16 h, the heavy sediment particles and the bulk of the detritus had sunk to the bottom, while meiobenthic organisms floated near the Ludox surface. The upper 2.5 cm of the liquid containing the organisms were removed by the suction arrangement shown in Fig. 3, using a vacuum pump with a capacity of $5 \text{ N m}^3 \text{ h}^{-1}$ air. The removed suspension was caught in a vacuum flask. Thereafter, the meiobenthic organisms in suspension were poured on a $35 \mu\text{m}$ mesh-sieve of nylon gauze on which the organisms were rinsed with distilled water to remove the Ludox. The meiobenthic organisms were washed out of the sieve with distilled water, collected in a Petri dish and counted under a dissecting microscope. To check the sediment residues on retained meiobenthic organisms, some series of flotation chambers were filled again with Ludox, stirred and treated according to the procedure described above.

As the sediment of Station Hoogwatum was rich in coarse detritus, it was investigated which sample volume could be separated quantitatively within one run. Subsamples with increasing volume were taken in the usual way.

Results

Tables 1 and 2 present the numbers of counted nematodes and copepods, respectively, isolated according to the two different methods. The statistical evaluation, two residue check series, and sediment qualification are given as well. As the data of each of the series pointed to a normal distribution, Student's *t*-test was applied to investigate differences between the decantation method and the density method. It appeared that no statistically significant differences existed between both series of counts of

Table 1. Data and analysis of counted nematodes obtained with decantation method and density method without preservation and shaking. RC: Residue check

	Station											
	Eemshaven			Hoogwatum			Reiderplaat			Heringsplaat		
	Decan- tation	Density		Decan- tation	Density		Decan- tation	Density		Decan- tation	Density	
cm ³ sedi- ment sample	1.5	1.5	RC	2.0	2.0		2.0	2.0		1.5	1.5	RC
No. of nematodes	84	93	0	244	314		32	13		95	141	0
	88	97	0	246	288		36	8		127	110	0
	100	77	0	217	294		26	16		128	142	0
	91	77	1	241	249		27	19		129	136	0
	83	102	0	212	309		18	24		124	138	0
	76	95	0	198	238		29	21		104	133	0
	97	85	0	245	313		28	17		175	144	0
	90	83	1	290	298		26	18		139	133	0
	92	84	0	244	248		21	16		133	144	0
	87	97	0		297		32	21		129	139	0
Mean	88.80	89.00		237.44	284.80		27.50	17.30		128.30	136.0	
Standard deviation	6.94	8.91		26.49	28.82		5.30	4.52		21.18	9.98	
Student's t-test												
Student's t		0.056			3.715			4.631			1.040	
Degrees of freedom		18			17			18			18	
Significance level		>0.1			<0.01			<0.001			>0.1	
Sediment qualifica- tion	Coarse-grained, not much detritus			Coarse-grained, many coarse par- ticles of organ- ic detritus			Fine-grained, many fine par- ticles of organ- ic detritus			Coarse-grained, not much detritus		
										Practically no sand grains, many very fine particles of organic detritus		

Table 2. Data and analysis of counted copepods obtained with decantation method and density method

	Station Eemshaven		
	Decan- tation	Density	Residue check
cm ³ sediment sample	17.5	17.5	
No. of copepods	71	79	0
	92	62	0
	103	94	0
	80	86	0
	73	89	0
	84	95	0
	78	89	0
	70	91	0
	74	96	0
	67		
Mean	79.20	86.78	
Standard deviation	11.16	10.65	
Student's t-test			
Student's t		1.510	
Degrees of freedom		17	
Significance level		>0.1	
Sediment qualifica- tion	Coarse-grained, not much detritus		

Table 3. Data and analysis of counted nematodes obtained with decantation method, density method without preservation and shaking, density method without shaking and density method as described in this paper

	Station Reiderplaat			
	Decan- tation	Density, no shaking, no preservation	Density, no shaking	Density
cm ³ sediment sample	2.0	2.0		2.0
No. of nematodes	32	13		26
	36	8		22
	26	16		14
	27	19		23
	18	24		17
	29	21		14
	28	17		21
	26	18		25
	21	16		23
	32	21		25
Mean	27.50	17.30		20.10
Standard deviation	5.30	4.52		3.81
Student's t-test				
Student's t		4.631		3.585
Degrees of freedom		18		18
Significance level		<0.001		<0.01
				>0.1

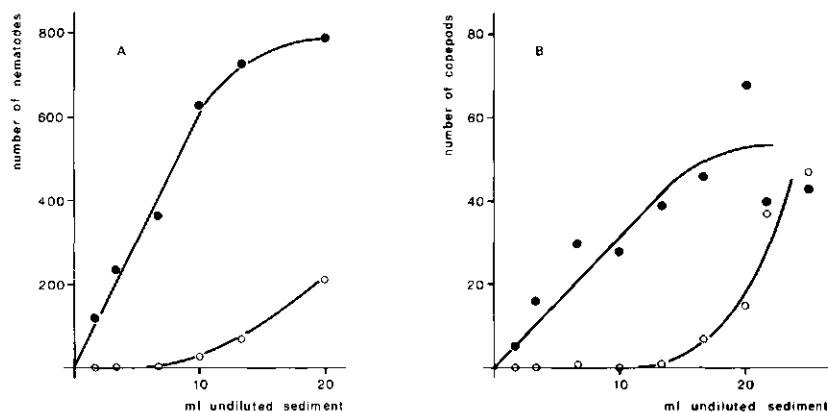


Fig. 4. Relation between increasing sample volume and number of isolated nematodes and copepods obtained with the density separation method. Samples were obtained from Station Hoogwatum, where the sediment was rich in coarse detritus. Filled circles: counted numbers of organisms after the density separation procedure; open circles: counted numbers of organisms after repeated treatment of the residue

nematodes for Stations Eemshaven, Heringsplaat and Oost Friesche Plaat (Table 1) and of counts of copepods for Station Eemshaven (Table 2). For Stations Hoogwatum and Reiderplaat on the other hand, a statistically significant difference was calculated between nematode counts according to the two methods. With the density method, on an average, significantly more specimens ($P < 0.01$) were counted for the station Hoogwatum but significantly fewer specimens ($P < 0.001$) for the station Reiderplaat. It should be mentioned that in density-processed residues no specimens normally were found (Tables 1 and 2). Two additional experiments were made to investigate the deviating results of the Reiderplaat series. One experiment was carried out according to the density method with unpreserved samples and without shaking by hand, another was carried out according to the density method with 4% formaldehyde-preserved samples but without shaking by hand and the third series was handled according to the density method procedure as described in this paper. The results are given in Table 3. From Table 3 it is obvious that preservation and shaking by hand before the Ludox treatment improve the recovery. Using the improved procedure, no statistical differences between the two isolation methods could be indicated for the Reiderplaat series.

Fig. 4 presents the relationship between sediment volume and the recovery of nematodes and copepods in the first and in the second Ludox treatment. For the nematode fraction it appeared that sediment samples up to 7 cm³ could be processed within one density separation run, for copepods the size of this volume was 13 cm³. If more sediment has to be processed a second Ludox run may be necessary.

Discussion

For Station Hoogwatum, differences in counts between the decantation method and the density method can be explained by many small specimens escaping detection as they were hidden by coarse particles of detritus. The nematode fraction obtained by the density method contained a small amount of detritus, whereas the decantation method failed to separate the bulk of this material from the nematodes. It is suggested here that, especially for small-sized specimens and larvae, the decantation method may lead to inaccurate results. Moreover, repeated hand-sorting after each resuspension of the decanted fraction is very time-consuming.

An investigation of the species composition of the four Reiderplaat series showed that the difference between the

two methods for that station was caused by the presence of great numbers of Chromadoridae which were attached to very small sand grains by their tail gland. These organisms could be separated quantitatively by the decantation method. In the density method, however, those organisms attached to the sand grains were prevented from floating to the surface of the Ludox. Shaking by hand detached the nematodes from the sand grains, while either preservation with 4% formaldehyde or anaesthetization with chloroform prevented renewed adherence. Moreover, preservation with 4% formaldehyde did not affect floating of the organisms and consequently did not lower recovery (Table 3). This is due to the relatively large particle size (21 to 24 μ m, Dupon brochure) of the polymer silica which prevents Ludox particles from penetrating dead organisms. Although the organic detritus content is very different at the stations Eemshaven, Heringsplaat and Oost Friesche Plaat (Tables 1 and 2), counting results by the decantation method and the density method did not differ significantly. Usually, however, the average yield for the density method is somewhat higher. Moreover, the Chromadoridae could have been missed since at first the density method was carried out without preservation and shaking by hand.

A certain relation was observed between the diameter of the flotation chamber and the maximum sample volume required to obtain quantitative separation. For sediments which are rich in coarse detritus, relatively large samples can be separated at one run. When the sample concentration is too high (Fig. 4), organisms can be caught by coarse-grained detritus particles and in this way be retained in the residue. This might be one reason why Heip et al. (1974) could not separate all nematodes at a single centrifugation.

It was not possible to check the suitability of the density method for small oligochaetes, small polychaetes or larvae of some macrofaunal groups in the way described for nematodes and copepods. This was either due to too small numbers of organisms or to their small size. The long, thin specimens of the oligochaetes and polychaetes were damaged during the mixing procedure. However, we are sure that for these organisms the density method as described here may also be used, if mixing is omitted. In the second run specimens of these groups were never found. The method is not applicable to molluscs and ostracods. The density method was also tested for zooplankton by J.W. Baretta

(Netherlands Institute for Sea Research). The method gave a very satisfactory separation between detritus and net-plankton.

Preserved as well as unpreserved nematodes did not show any damage or change of structure and taxonomically important details were in excellent condition for species identification after a Ludox treatment.

To prepare meiobenthic fractions for biomass estimation by a carbon analyzer only some cleaning by hand-sorting of organic detritus particles is necessary after the separation procedure with Ludox.

From current investigations in our laboratory it seems possible to isolate nematodes alive from sediments with dialyzed Ludox-TM. This means that Ludox-TM itself does not influence the viability of these organisms.

A disadvantage of the use of Ludox-TM is its property to dry rapidly and consequently to change into the insoluble gel-form. The main advantages of the method are its simplicity and the possibility to work with large series of chambers, often necessary for ecological purposes. The time necessary for hand-sorting in the density method is reduced to about one third of the time needed in the decantation method.

Acknowledgement. We are indebted to Miss E. Engelsman who performed most of the laboratory analyses.

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CHAPTER III

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A Survey of Nematodes from the Ems Estuary¹⁾

Part I: Systematics

By L. A. BOUWMAN

With 27 Figures

Abstract

As part of extensive biological and chemical investigations in the Ems estuary a survey of the nematode fauna has been carried out. Altogether 121 different species were isolated from the tidal flats, the bottoms of the rivers Ems and Westerwoldsche A and as epifauna from some higher plants. The following species are new to science: *Aegialoalaimus setosa*, *Eleutherolaimus amasi*, *Paracanthocheilus sabulicolus* and *Trefusia multipapillatum*. A new name, *Paralinhomoeus flevensis*, is proposed for *Paralinhomoeus tenuicaudatus* STEKHOVEN 1935. 3 species could not be identified and 1 of these, *Paralinhomoeus* sp., is probably a new one, though lack of sufficient specimens prevented presentation as a new species.

Introduction

The Ems estuary, located in the north-east of The Netherlands, constitutes the border area with the Federal Republic of Germany (Fig. 1). It is shaped by the interaction between the Wadden Sea and the main source of fresh water, the river Ems. A potato-flour industry, founded in the region that borders the south-west part of the estuary, discharges its effluent mainly through a small river, the Westerwoldsche A, into the estuary. For direct discharge of effluent into the estuary a pipe-line was constructed from the industrial area to the estuary. Lack of knowledge about the biological effects of an increased discharge of organic waste-materials directly into the estuary led to the formation of the research group "Biological Research Ems-Dollart Estuary (BOEDE)", which team has the task to describe the present status of the estuary.

Meiofauna is one of the subjects investigated. As a part of meiofaunal research a survey of nematodes, the principal component of this fauna, was carried out. A tradition of marine nematological research in The Netherlands was founded by DE MAN († 1930), continued by SCHUURMANS STEKHOVEN († 1955) and stopped with the latter's death. About nematodes from the Ems estuary practically no knowledge exists, though neighbouring estuaries have been taken stock of extensively.

The Ems estuary

The length of the estuary is 60 km, from the freshwater inlet point at Nieuwe Statenzijl, to the island of Borkum. Its width varies from 4 km (Reider peninsula) to 20 km

¹⁾ Publication no. 37 of the project "Biological Research in the Ems-Dollart estuary".

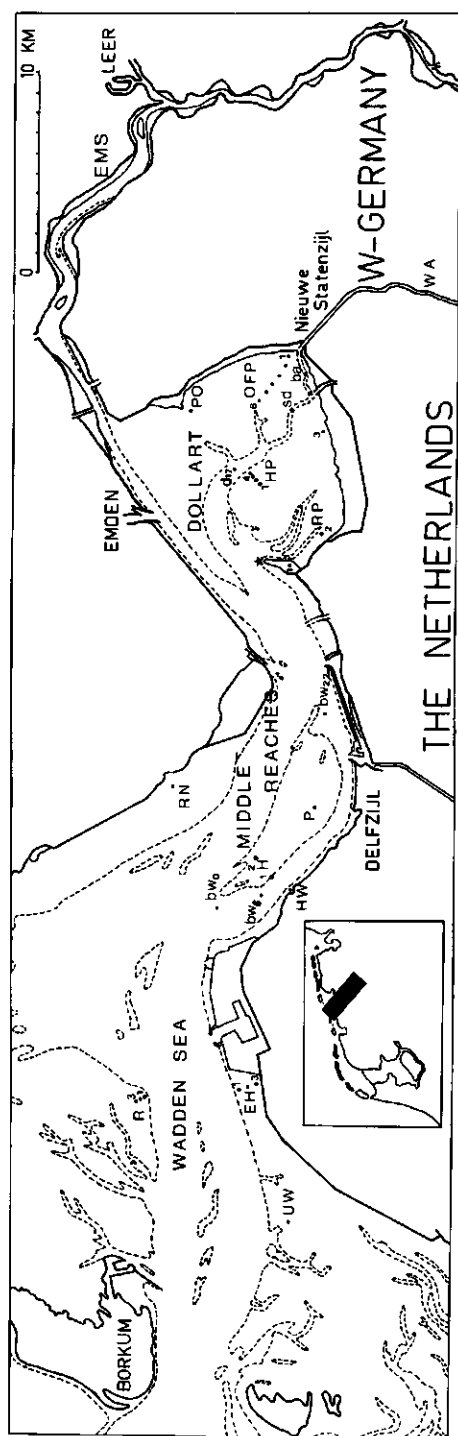


Fig. 1. Map of the Ems estuary with sampling stations and transects:

- UW = Uithuizerwad permanent quadrat (100 m/100 m)
- R = Ransel transect, 3 stations
- EH = Eemshaven transect, 3 zones
- H = Hond transect, 2 stations
- HW = Hoogwatum permanent quadrat (10 m/10 m)
- RN = Rysumer Nacken permanent quadrat (10 m/10 m)
- P = Paap permanent quadrat (10 m/10 m)
- RP = Reiderplaat, 3 stations
- HP = Heringsplaat transect, 4 stations
- OFF = Oost Friesche Plaat transect, 6 stations
- PO = Pogum permanent quadrat (10 m/10 m)

Other abbreviations:

bw₀, bw₂₂ and d₁₇ are numbers of buoys on subtidal sampling stations

WA = Westerwoldsche A

(mouth). Total surface covers about 800 km², of which 50% consists of tidal flats. Geographically 3 subregions can be distinguished: the Wadden, from the island of Borkum to the northern part of the tidal flat Hond, the middle reaches of the estuary from the northern Hond to the Reider peninsula and the Dollart. In the estuary many gradients exist parallel with the direction of the tidal movements and at right angles to the shores and low tide marks of the tidal flats. In the direction of Nieuwe Statenzijl the mean salinity decreases, as well as the median particle diameter of the sediments and the thickness of the oxidized sediment zone. In the same direction the silt- and clay contents of the sediment increase, as well as densities of benthic algae and bacteria. The same gradients, except for salinity, occur at right angles to the shores and low tide marks of tidal flats. Besides these natural gradients, the estuary is influenced by a man-made pollution containing organic waste-materials mainly discharged at Nieuwe Statenzijl, partly at Hoogwatum. This discharge is concentrated in autumn and causes periodically anaerobic circumstances in water and sediment of the Dollart. During the potato-flour campaign about 25% of the Dollart is regularly exposed to anaerobic circumstances in part II (Ecology) of this article physical-chemical characteristics of the estuary will be discussed more extensively.

Sampling method

Sediment samples were taken at low tide with 2.4 cm \varnothing tubes. The cores were divided (in vertical direction) into 1 cm slices except the upper zone which was most times cut into two slices of 0.5 cm thickness. From the slices a subsample of 1 cm³ was taken from which all nematodes were isolated. Nematodes were isolated by means of decantation from sandy sediments and by means of flotation on a ludox-surface from muddy sediments. The nematodes were processed to glycerin and mounted in permanent slides if necessary.

Sampling

The following aims were pursued:

Identification of species and their distribution all over the estuary. Vertical distribution of species. Analyses of species-associations and their distribution on different scales in the estuary. Check on the biological relevancy of a geographical subdivision of the estuary. For these purposes samplings have been carried out in 11 permanent quadrats and transects on tidal flats and in 6 subtidal stations on the bottom of the main channel (Fig. 1, Annex).

Taxonomical research

121 different species have been identified, of which four are new to science. On the following pages these species are discussed and if necessary described. The sequence and nomenclature of these species is mainly according to the Bremerhaven Checklist of GÉRLACH and RIEMANN (1973, 1974), though some alterations occur. A species is considered to be widely distributed if it has been recorded from at least two different conti-

nents. In this connection, identifications of ALLGEN have been neglected if no clear illustration was presented. For characterization of the local distribution of species, isolated single specimens outside their usual distribution area have been neglected as well. The nematode fauna could be differentiated into several vertically arranged, well-distinguished subfaunas. The upper fauna generally extended to depths down to about 2 cm, with a maximum of 5 cm. Often a particular fauna just below the upper fauna could be distinguished in a layer of about 1 cm thickness. In the layers below the latter, one or more different faunas of the lower sediment layers extended to depths down to 30 cm.

Enumeration of species, descriptions and remarks

Signification of the abbreviations used in the taxonomical descriptions:

- a = total length/maximum width
- amd = distance amphid from anterior end, as distance/head diameter
- aml = amphid length, as amphid length/head length
- amw = amphid width, as amphid diameter/corresponding body diameter
- b = total length/esophagus length
- bcl = buccal cavity, as buccal cavity length/head diameter
- c = total length/tail length
- cc = cephalic capsule, as capsule length/capsule width
- cs₁ = cephalic setae (type 1, 2, 3 . . .), as setae length/head diameter
- ep = excretory pore, as distance from anterior end/esophagus length
- g = gubernaculum, as gubernaculum length/spicula length
- ga = gubernaculum apophysis, as apophysis length/spicula length
- hd = head, as head diameter/body diameter at end of esophagus
- l = total length in mm
- nr = nerve ring, as distance from anterior end/esophagus length
- pap = number of preanal elements
- sp = spicula, as spicula length/anal diameter
- t = tail, as tail length/anal diameter
- tt = width of the tail tip, as width/anal diameter
- v = vulva, as distance from anterior end $\times 100$ /total length

In the following enumeration all species isolated from the Ems estuary are recorded. The abbreviations used have the following signification:

- epif. = epifauna on higher plants
- just bel.up.l. = just below upper sediment layers
- low.sed.l. = lower sediment layers
- up., low.sed.l. = upper and lower sediment layers
- up.sed.l. = upper sediment layers
- w.d. = widely distributed (over different continents)

Nematode species isolated from 11 sampling stations and -transects, located on tidal flats in the Ems estuary and from 6 subtidal stations, as well as their global and vertical distribution

Species	Distribution Global Local	Vertical
Order Araeolaimida de CONINCK and STEKHOVEN 1933		
Family Rhabdolaimidae CHITWOOD 1951		
<i>Synglaimus striatocaudatus</i> DE MAN 1888	w.d. RP1,3	up.sed.l.
Family Leptolaimidae OERLEY 1880		
<i>Anomacron elegans</i> DE MAN 1922	Europe HP1,2 OFF5,6 Po	up.sed.l.
<i>Leptolaimus luridus</i> TIMM 1963	w.d. EH2	low.sed.l.
<i>Leptolaimus papilliger</i> DE MAN 1876	w.d. H2 RP1,3 HP1,2,4 OFF1,2,3,4,5,6, Po	up.sed.l.
<i>Stephanolaimus elegans</i> DITLEVSEN 1918	Europe R3	low.sed.l.
<i>Stephanolaimus flevensis</i> STEKHOVEN 1935	Europe UW	low.sed.l.
Family Camacolaimidae MICOLETZKY 1924		
<i>Camacolaimus tardus</i> DE MAN 1889	w.d. R2	up.sed.l.
Family Axonolaimidae FILIPJEV 1918		
<i>Aegialolaimus elegans</i> DE MAN 1907	Europe EH2,3 HW Pa	up.sed.l.
<i>Aegialolaimus selosa</i> sp. n.	UW	up.,low.sed.l.
<i>Ascolaimus elongatus</i> BÜTSCHLI 1874	w.d. R1,2,3 EH2 UW H1 H2 HW Pa HP1,2	up.,low.sed.l.
<i>Axonolaimus paraspinosus</i> STEKHOVEN and ADAM 1931	Europe EH2 H2 HW Pa RN RP1,2 HP1,2,3,4 OFF6	up.,low.sed.l.
<i>Axonolaimus</i> cf <i>spinosus</i> BÜTSCHLI 1874	w.d. OFF6	up.sed.l.
<i>Odontophora rectangularis</i> LORENZEN 1971	Europe R1,2,3 EH1,2 UW H1 Pa	low.sed.l.
<i>Odontophora selosa</i> ALLGEN 1929	w.d. EH2 UW H2 HW	just bel.up.l.
Order Monhysterida FILIPJEV 1929		
Family Siphonolaimidae FILIPJEV 1918		
<i>Cyartoneuma germanicum</i> JUARIO 1973	Europe EH2 UW	just bel.up.l.
<i>Cyartoneuma zosterae</i> ALLGEN 1929	Europe R1 EH1,2,3 UW H1 Pa RN	up.sed.l.
Family Linhomoeidae FILIPJEV 1922		
<i>Desmolaimus zeelandicus</i> DE MAN 1880	w.d. H2 HW RP3 OFF2,3,4,5,6	up.,low.sed.l.
<i>Metalinhomoeus bifurmis</i> JUARIO 1974	Europe EH2 H1 H2 HW	low.sed.l.

<i>Metalinhomoeus typicus</i> DE MAN 1907					low.sed.l.
<i>Terschellingia longicaudata</i> DE MAN 1907					just bel.up.l.
<i>Eleutherolaimus amasi</i> sp. n.					up.sed.l.
<i>Eleutherolaimus stenosoma</i> DE MAN 1907					up.sed.l.
<i>Paralinhomoeus flevensis</i> sp. n.					up.sed.l.
<i>Paralinhomoeus itenensis</i> ALLGEN 1933					up., low.sed.l.
<i>Paralinhomoeus cf lepturus</i> DE MAN 1907					up.sed.l.
<i>Paralinhomoeus</i> sp.					not observed
Family Monhysteridae DE MAN 1876					
<i>Monhystera</i> cf <i>anophthalma</i> LORENZEN 1969	Europe RP1				up.sed.l.
<i>Monhystera disjuncta</i> BASTIAN 1864	w.d. EH3 RP3 HP1 OFP1				up.sed.l.
<i>Diplotelmoloides islandicus</i> DE CONINCK 1943	Europe EH3				epif. <i>Fucus</i> sp.
Family Xyalidae CHITWOOD 1951					epif. <i>Spartina</i> sp.
<i>Cobbia traefusiaformis</i> DE MAN 1907	w.d. UW				up.sed.l.
<i>Daptonema biggi</i> GERLACH 1965	Europe EH3 HP1				up.sed.l.
<i>Daptonema fallax</i> LORENZEN 1971	Europe EH2				up.sed.l.
<i>Daptonema invagiteroum</i> PLATT 1973	Europe R1,2,3 UW H1				up., low.sed.l.
<i>Daptonema cf kornoense</i> ALLGEN 1929	w.d. UW				up.sed.l.
<i>Daptonema cf normadicum</i> I and II DE MAN 1890	w.d. I: HW Pa II: R1,2,3 EH1,2,3 H1				up.sed.l.
<i>Daptonema ozygera</i> DE MAN 1888	w.d. H2 HW Pa RN RP1,2,3 HP3 OFP4,5,6				up.sed.l.
<i>Daptonema procerum</i> GERLACH 1951	w.d. H2 HW Pa RP2,3 HP2,4 OFP1,2,3,4,5,6, Po				up.sed.l.
<i>Daptonema setosum</i> BÜTSCHLI 1874	w.d. R1,3 EH1,2,3 UW H1 H2 HW Pa RN				up.sed.l.
	RP2,3 HP1,3,4 OFP1,2,3,4,5 Po				
<i>Daptonema trabeculosum</i> G. SCHNEIDER 1906	Europe RP3				up.sed.l.
<i>Daptonema xygliforme</i> WIESER and HOPPER 1967	w.d. HP1,4 OFP4,5,6 Po				up.sed.l.
<i>Daptonema</i> sp.	EH2 UW				low.sed.l.
<i>Metadesmolaimus pandus</i> LORENZEN 1971	Europe H1 HP1,2,3,4				up.sed.l.
<i>Paramonohystera riemannii</i> PLATT 1973	Europe R1,2,3 EH1,2,3 UW H1 H2 HW Pa RN				low.sed.l.
<i>Theristus acer</i> BASTIAN 1865	w.d. UW HW Pa RP3				up.sed.l.
<i>Theristus longus</i> PLATT 1973	Europe EH2				low.sed.l.
<i>Theristus pertensis</i> BRESSLAU and STEKHOVEN 1935	w.d. R3 EH2 Pa HP1				up., low.sed.l.
<i>Theristus cf subcurvatus</i> LORENZEN 1977	Europe R1,2				low.sed.l.
<i>Trichotheristus mirabilis</i> STEKHOVEN and DECONINCK 1933	Europe R1,2				low.sed.l.

(Continued)

Species	Distribution Global Local	Vertical
Family Sphaerolaimidae FILIPJEV 1906		
<i>Sphaerolaimus balticus</i> G. SCHNEIDER 1906	w.d. EH1 UW H1 H2 HW Pa RP2 HP1,4 OPF5,6 Po	up.sed.l.
<i>Sphaerolaimus gracilis</i> DE MAN 1876	w.d. RP2 HP4 OFFP1,2,5 Po	up.sed.l.
<i>Sphaerolaimus hirsutus</i> BASTIAN 1865	w.d. UW H2 HW RN RP3 HP1 Po	up.sed.l.
Order Desmodorida DE CONINCK 1965		
Family Desmodoridae FILIPJEV 1922		
<i>Microloaimus conothelis</i> LORENZEN 1973	Europe R3 EH2 UW	low.sed.l.
<i>Microloaimus globiceps</i> DE MAN 1880	w.d. RP1,3 HP1,4 OFFP1,2,3,4,5,6 Po	up.sed.l.
<i>Microloaimus robustidens</i> STEKHOVEN and DECONINCK 1933	Europe EH3 H1 H2 HW Pa	up.sed.l.
<i>Calomicrolaimus honestus</i> DE MAN 1922	w.d. UW Pa	up., low.sed.l.
<i>Calomicrolaimus marinus</i> SCHULZ 1932	Europe R2,3 UW H1 Pa	up.sed.l.
<i>Molgolaimus allgeni</i> GERLACH 1950	Europe EH2 UW	low.sed.l.
<i>Metachromadora remanei</i> GERLACH 1951	w.d. RN RP1,2,3	just bel.up.l.
<i>Metachromadora suecica</i> ALLGEN 1929	Europe R1,2,3 EH1,2,3 UW H1 HW	up.sed.l.
<i>Metachromadora vivipara</i> DE MAN 1907	Europe EH1,2,3 UW H1 HW HP1,4	up.sed.l.
<i>Spirinia parasitifera</i> BASTIAN 1865	w.d. R2,3 HW	low.sed.l.
<i>Leptonemella aphanothecae</i> GERLACH 1950	w.d. R2,3 UW	low.sed.l.
<i>Dasytemella cf. albatensis</i> WARWICK 1973	Europe R2 EH1,2	low.sed.l.
Family Monoposthiidae FILIPJEV 1934		
<i>Monoposthia costata</i> BASTIAN 1865	w.d. EH3	up.sed.l.
<i>Monoposthia mirabilis</i> SCHULZ 1932	w.d. R1,2,3 EH1,2 UW H1	up., low.sed.l.
Family Richtersiidae KRETS 1929		
<i>Richtersia inaequalis</i> RIEMANN 1966	Europe UW	up.sed.l.
Order Chromadorida FILIPJEV 1929		
Family Comesomatidae FILIPJEV 1929		
<i>Sabatieria celtica</i> SOUTHERN 1914	w.d. HW RN	up.sed.l.
<i>Sabatieria longispinosa</i> ALLGEN 1935	Europe R1,2,3 EH1,2,3 UW H1	low.sed.l.

<i>Sabatieria pulchra</i> G. SCHNEIDER 1906	w.d.	R1,3 EH3 H2 HW Pa RN RP1,2,3 HP1,2,3	just bel.up.l.
<i>Sabatieria cf strigosa</i> LORENZEN 1971	Europe UW	OFFP1,2,3,4,5,6 Po	not observed
Family Chromodoridae FILIPJEV 1917			
<i>Chromadora nudicapitata</i> BASTIAN 1865	w.d.	HW (1.5 km north of pq)	epif. <i>Zostera</i> sp.
<i>Astrochromadora microlaima</i> DE MAN 1889	Europe R1,2,3 EH1,2,3 UW H1 H2 HW Pa RN	RP1 HP3,4	up.sed.l.
<i>Prochromadorella attenuata</i> GERLACH 1952	w.d.	HW (subtidal BWO)	not observed
<i>Prochromadorella longicaudata</i> KREIS 1929	Europe EH2 UW		up.,low.sed.l.
<i>Euchromadora vulgaris</i> BASTIAN 1865	w.d.	HP1	up.sed.l.
<i>Dichromadora cephalata</i> STEINER 1916	w.d.	EH1,2,3 H2 HW RN RP1,3 HP1,2	up.,low.sed.l.
		OFFP2,3,4,5,6 Po	
<i>Dichromadora geophila</i> DE MAN 1876	w.d.	Pa RP1,2 HP1,2,3,4 OFFP1,2,3,4,5,6, Po	up.sed.l.
<i>Hypodoniolaimus balticus</i> G. SCHNEIDER 1906	w.d.	EH2,3 H2 HW RP3 HP4 OFFP2,3,4,5,6 Po	up.sed.l.
<i>Hypodoniolaimus setosus</i> BÜTSCHLI 1874	w.d.	R1,3 EH1 UW H1	up.sed.l.
<i>Innocuonema tentaculundum</i> DE MAN 1890	w.d.	H1 H2 HW Pa RN RP2 HP1,2,3,4	up.sed.l.
		OFFP1,4,5,6 Po	
<i>Neochromadora poecilosoma</i> DE MAN 1893	w.d.	EH2 UW H1 H2 HW RP2	up.sed.l.
<i>Neochromadora trichophora</i> STEINER 1921	Europe R1,2,3 EH1,2,3 UW H1 Pa		up.,low.sed.l.
<i>Ptycholaimellus ponticus</i> FILIPJEV 1922	w.d.	H2 HW Pa RN RP1,2,3 HP1,4	up.sed.l.
		OFFP1,2,3,4,5,6 Po	
<i>Spilophorella paradoxa</i> DE MAN 1888	w.d.	RP1,3 OFFP3,4,5,6 Po	up.sed.l.
Family Cyatholaimidae FILIPJEV 1918			
<i>Neotonchus cf coreundus</i> GERLACH 1956	w.d.	EH2 UW H1	low.sed.l.
<i>Pomponema selectima</i> PLATT 1973	Europe R1,2,3 EH1,2 UW H1 Pa		up.,low.sed.l.
<i>Paracanthonchus caecus</i> BASTIAN 1865	w.d.	R1,2,3 EH1,2,3 H1 H2 HW Pa HP1	up.sed.l.
<i>Paracanthonchus sabulicolus</i> sp. n.		R1,2 UW	low.sed.l.
<i>Paracyatholaimus pentodon</i> RIEMANN 1966	Europe R2,3 UW		up.sed.l.
<i>Paracyatholaimus proximus</i> BÜTSCHLI 1874	Europe OFFP6 Po		up.sed.l.
<i>Pracacanthonchus punctatus</i> BASTIAN 1865	Europe EH2 UW H2 HW Pa RN RP1,2 HP1,3,4		up.sed.l.
Family Choanolaimidae STEKHOVEN and ADAM 1951			
<i>Halichoanolaimus robustus</i> BASTIAN 1865	w.d.	HP (subtidal D17)	not observed

Species	Distribution Global Local	Vertical
Order Enoplida FILIPJEV 1929		
Family Tripyloidae FILIPJEV 1918		
<i>Bathylaimus cf. capacosus</i> HOPPER 1962	w.d. R1,3	up.sed.l.
<i>Tripyloides marinus</i> BÜTSCHLI 1874	w.d. R1 EH2,3 HW RN RP1 HP1,2,3,4 OFP1,3,4,5,6 Po	up.sed.l.
<i>Rhabdocoma</i> sp.	R2	just bel.up.l. low.sed.l.
<i>Trefusia multipapillatum</i> sp. n.	R1,2,3 EH1,2,3 UW	
Family Oxystominae CHITWOOD 1935		
<i>Nemanema cylindratICAUDATUM</i> DE MAN 1922	w.d. EH3 OFP4,5,6 Po	up.sed.l.
<i>Oxystomina elongata</i> BÜTSCHLI 1874	w.d. H2 HW RN	up.sed.l.
<i>Oxystomina unguiculata</i> STEKHOVEN 1935	w.d. RP2	just bel.up.l.
<i>Thalassolaimus tardus</i> DE MAN 1893	Europe EH2 UW H2	just bel.up.l.
<i>Halalaimus gracilis</i> DE MAN 1893	w.d. H2 HW Pa RN RP2 HP1,2,3,4 OFP3,4,5,6 Po	up.sed.l.
Family Enoplidae DUJARDIN 1845		
<i>Chaetonema riemannii</i> PLATT 1973	Europe R3 EH1,2,3 UW H1	up.sed.l.
<i>Enoploilaimus propinquus</i> DE MAN 1922	Europe R1,2,3 EH1,2 UW H1	up.sed.l.
<i>Enoploilaimus cf. vulgaris</i> DE MAN 1893	Europe HW (subtidal BWO)	not observed
<i>Mesacanthion audax</i> DITLEYSEN 1918	Europe H1	up.sed.l.
<i>Mesacanthion diplochma</i> SOUTHERN 1914	Europe R2,3 EH2 UW	up.sed.l.
<i>Enoploides cf. labiatus</i> BÜTSCHLI 1874	w.d. EH1,2 UW H1 HW HP1,2,3	up.sed.l.
<i>Enoplus brevis</i> BASTIAN 1865	w.d. HP2	up.sed.l.
Family Anoplostomatidae GERLACH and RIEMANN 1974		
<i>Anoplostoma viviparum</i> BASTIAN 1865	w.d. EH2,3 UW HW RP1,2 HP1,2,3,4 OFP1,2,3,4,5,6	up.sed.l.
Family Oncholaimidae FILIPJEV 1916		
<i>Mononcholaimus separabilis</i> WIESER 1953	w.d. R1,2,3 EH1 UW	up.sed.l.
<i>Oncholaimellus calvadocius</i> DE MAN 1890	Europe R1,2,3 EH1 UW H1 H2 HW RN	up.sed.l.
<i>Viscacia glabra</i> BASTIAN 1865	w.d. EH3 H2 HW	up.sed.l.

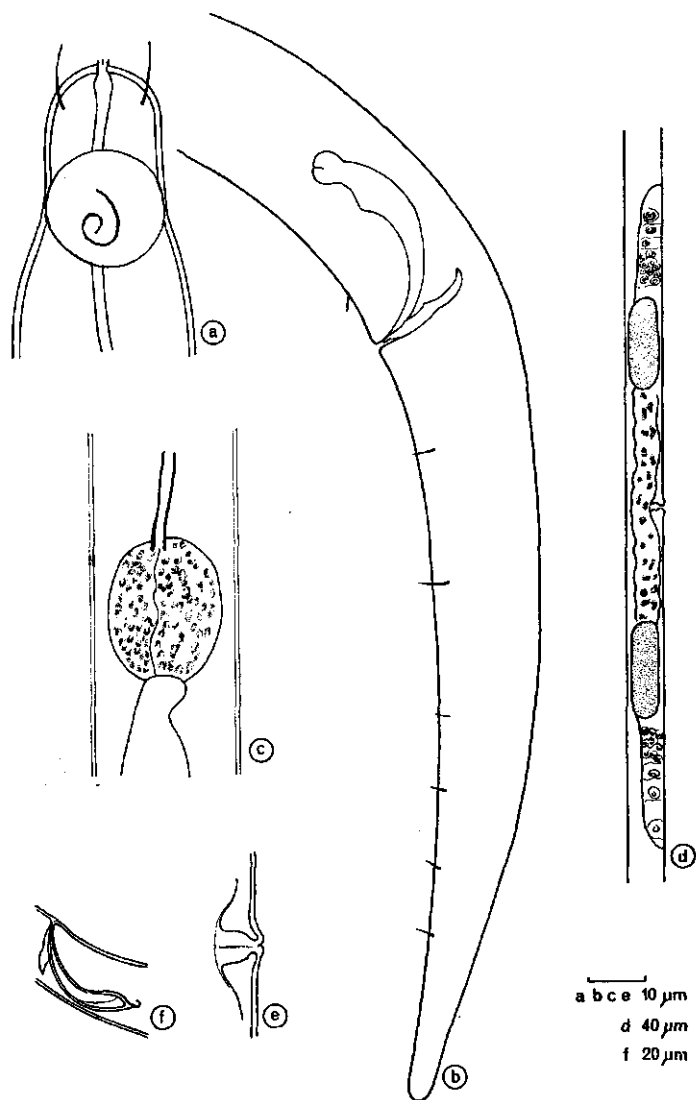
<i>Viscosia rustica</i> KREIS 1929	Europe R1,2,3 EH1,2,3 UW HW OFP1,5	up.sed.l.
<i>Viscosia viscosa</i> BASTIAN 1865	Europe R1,2,3 EH1,2,3 UW H1 H2 HW Pa RN RP2 HP1,2,3,4 OFP1,2,3,4,5,6 Po	up.sed.l.
<i>Adoncholaimus fuscus</i> BASTIAN 1865	w.d. HP1,2,3,4	up.sed.l.
<i>Adoncholaimus thalassophygas</i> DE MAN 1876	Europe Pa HP1 OFP1,2	up.sed.l.
<i>Oncholaimus brachycercus</i> DE MAN 1889	w.d. R3 EH2 RP3 HP1	up.sed.l.
Family Enchelididae FILIPJEV 1918		
<i>Calyptronema marzeberi</i> DE MAN 1922	w.d. UW HW Pa RN RP1,3 HP1,3 OFP4,5,6 Po	up.sed.l.
Order Rhabditida CHITWOOD 1933		
Family Rhabditidae OERLEY 1880		
<i>Rhabditis marina</i> BASTIAN 1865	w.d. OFP1	up.sed.l.
Family Diplogasteridae STEINER 1919		
<i>Eudiplogaster paramatus</i> W. SCHNEIDER 1937	Europe RP2 HP2 OFP1,2,3,4,5,6 Po	up.sed.l.
Order Tylenchida THORNE 1949		
Family Tylenchidae OERLEY 1880		
<i>Tylenchus fucicola</i> DE MAN 1892	Europe RP2 OFP6	up.sed.l.

Aegialoalaimus setosa sp. n. (Fig. 2)

Number of specimens isolated: 2 males, 4 females, 1 larva

Description:

	l	a	b	c	v	sp	t
♂	1.6	53	10.6	13.3		1.6	5.0
♂	1.5	64	10.2	11.6		1.6	5.5
♀	1.4	48	9.6	13.3	52		6.0
♀	1.6	53	11.0	11.5	52		5.8
♀	1.8	56	12.1	14.4	49		5.3

Fig. 2. *Aegialoalaimus setosa* sp. n.

a) male head, b) male tail, c) terminal bulb, d) ovaries, e) vulva, f) spicula

Body shape: cylindrical, tapering towards both ends, neckregion slightly constricted
 Cuticle: very finely annulated, no setae except in cephalic and male tail region
 Head: diameter $0.75 \times$ diameter at end of esophagus
 Buccal cavity: a slight moderation of the anterior part of the esophagus lumen, which can hardly be distinguished from the latter
 Labial setae: 6 very minute setae around the aperture of the buccal cavity
 Cephalic setae: 4, length $0.5 \times$ head diameter
 Amphids: the body is constricted on a level with the amphids; amphids are circular to slightly ovoid, spiral-shaped, diameter $1 \times$ corresponding body diameter in both sexes
 Esophagus: the walls of the esophagus lumen are sclerotized; the outer wall is indistinct; a clear ovoid terminal bulb is present, measuring $0.15 \times$ total esophagus length
 Nerve ring: located at $0.5 \times$ esophagus length from anterior end
 Excretory pore: not observed
 Ovaries: amphidelphic, reflexed
 Vulva: with prominent lips
 Vagina: sclerotized
 Preanal seta: present, short
 Spicula: curved, with a ventral expansion at $0.35 \times$ total length from proximal end; length $40-45 \mu\text{m}$
 Gubernaculum: $0.4 \times$ spicula length
 Tail: at two thirds of its length more abruptly decreasing in width; male tail with short ventral setae, female tail without; tip bluntly rounded, width $0.2 \times$ anal diameter

Cyartoneura germanicum JUARIO 1973

Number of specimens isolated: 2 males, 2 females

Discussion: the species has been isolated and described once and sufficiently by JUARIO; the specimens from the Ems estuary do not add any new information, so only morphometrical data are presented; JUARIO mentions that the cephalic setae measure $0.5 \times$ head diameter, however in his drawing the setae are $0.25 \times$ corresponding head diameter; in the Ems specimens the cephalic setae are $4 \mu\text{m}$ long, which is about half the corresponding head diameter; the cephalic setae of JUARIO's specimens are also $4 \mu\text{m}$ long, so his drawing seems to be incorrect in this respect.

Metalinhomoeus biformis JUARIO 1974 (Fig. 3)

Number of specimens isolated: 3 males, 2 females, 4 larvae

Description:

	l	a	b	c	v	sp	t
♂	3.5	155	22.7	21.8		1.0	8.3
♂	2.8	123	18.7	15.9		0.8	9.0
♂	3.6	138	21.6	21.2		0.9	8.0
♀	4.0	168	27.0	20.7	51		10.0
♀	3.1	120	24.0	20.9	55		8.2

Body shape: cylindrical; about equal width from terminal bulb to anus
 Cuticle: very finely annulated; no setae except in cephalic and male tail region
 Head: not set off; diameter $0.65 \times$ diameter at end of esophagus
 Buccal cavity: cupshaped, moderately sclerotized

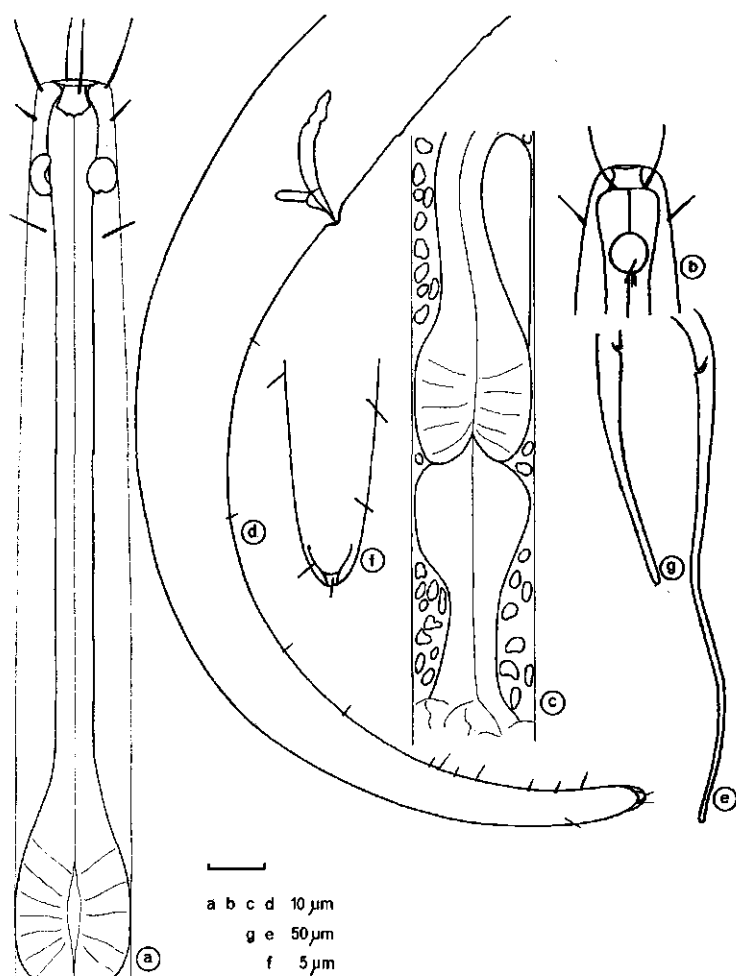


Fig. 3. *Metalinhomoeus biformis*

a) anterior part of male, b) male head, c) terminal bulb, d) male tail, e) long female tail, f) tip of male tail, g) normal female tail

Labial papillae: not observed

Cephalic setae: 4, length $0.9 \times$ corresponding head diameter

Cervical setae: 2, $0.4 \times$ length of cephalic setae; inserted between buccal cavity and amphids

Amphids: $1 \times$ head diameter behind anterior end, circular, spiral-shaped, diameter $0.4 \times$ corresponding body diameter

Post-amphidial setae: 2, $0.4 \times$ length of cephalic setae

Excretory pore: often indistinct; located at $0.6 \times$ esophagus length from anterior end

Nerve ring: not observed

Esophagus: dilated anteriorly, with more or less pear-shaped terminal bulb

Cardia: elongate

Intestine: indistinct, body lumen filled with net-like structures

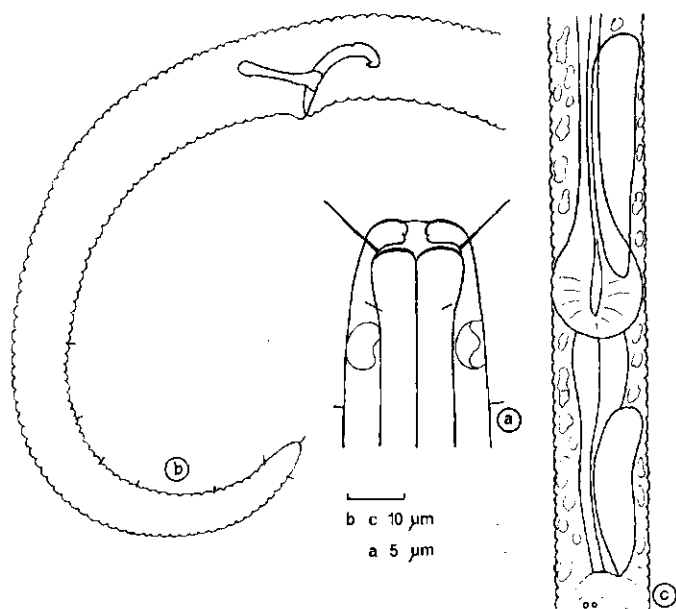


Fig. 4. *Metalinhomoeus typicus*

a) male head, b) male tail, c) terminal bulb

Ovaries: amphidelphic, outstretched

Spicula: curved, 25 μm

Gubernaculum: with dorsal apophysis, 0.25 \times length of spicula

Tail: male tail with short ventral setae, particularly dense in posterior part; 2 terminal setae present; tail tip characteristic; female tail without setae

Discussion: From the same samples from which females with tails of about 10 anal diameters lengths were isolated, 1 female and 3 larvae with much longer tails have been isolated. These long-tailed paratypes were identical with the holotype in all other respects: ♀ 1 (2.6), a (99), b (19.8), c (6.6), v (49), t (26). The species has been described in detail because of slight differences with JUARIO's description. JUARIO mentions that males have short and females have long tails. However, among the females from the Ems estuary long — as well as short tail specimens occur.

Metalinhomoeus typicus DE MAN 1907 (Fig. 4)

Number of specimens isolated: 4 males, 1 female

Description:

	l	a	b	c	v	sp	t
♂	2.5	156	17.7	17.7		1.3	7.3
♂	2.3	142	14.7	17.7		1.2	8.0
♀	2.4	129	15.5	15.5	54		10.0

Body shape: cylindrical, about equal width from terminal bulb to anus

Cuticle: anterior part finely annulated, posterior part coarsely annulated; no setae except in cephalic and male tail region

Head: not set off, diameter $0.7 \times$ diameter at end of esophagus

Buccal cavity: typical, moderately sclerotized

Labial papillae: not observed

Cephalic setae: 4, length $0.65 \times$ corresponding head diameter

Cervical setae: 2, $0.25 \times$ length of cephalic setae, inserted between buccal cavity and amphids

Amphids: $1 \times$ head diameter from anterior end; circular, spiral-shaped, diameter $0.4 \times$ corresponding body diameter

Post amphidial setae: 2, minute, at right angles to the cervical setae

Excretory pore: at $0.6 \times$ esophagus length from anterior end

Nerve ring: not observed

Esophagus: dilated anteriorly, terminal bulb oval

Cardia: elongate

Ovaries: amphidelphic, outstretched

Spicula: curved, with a characteristic proximal hook, $20 \mu\text{m}$

Gubernaculum: with a dorsal apophysis which is proximally cephalate; length of the apophysis $0.7 \times$ spicula

Tail: male tail with few short ventral setae

Discussion: the species described resembles *Metalinhomoeus biformis* JUARIO 1974 in many respects and in fact of a number of other specimens it could not be decided whether they belong to the one or the other species; however, cephalic, cervical and post-amphidial setae of *M. typicus* are shorter, the posterior part of the body is more coarsely annulated, the apophysis of the gubernaculum is longer and distinctly cephalate, the specimens are more slender and the esophagus is longer.

Eleutherolaimus amasi sp. n. (Fig. 5)

Number of specimens isolated: dozens of males, females and larvae

Description:

	l	a	b	c	v	sp	t
♂	2.3	89	11.5	15.8		1.1	6.4
♂	2.2	95	10.6	14.2		1.3	7.3
♂	2.3	88	12.5	14.0		1.4	7.1
♀	2.5	95	11.6	18.0	56		8.4
♀	2.5	97	12.9	19.4	58		7.4
♀	2.4	92	13.2	17.6	56		7.5

Body shape: cylindrical, gradually tapering towards the ends

Cuticle: smooth, no body setae except in cephalic, esophageal and tail region

Head: not set off; diameter $0.45 \times$ diameter at end of esophagus

Buccal cavity: cylindrical, $1.5-2.0 \times$ as long as wide; slender buccal ring present

Cephalic setae: 4 short setae $0.3 \times$ head diameter, 4 long setae $1.0 \times$ head diameter

Subcephalic setae: 2, dorsal/ventral, length $1.0 \times$ head diameter

Post-amphidial setae: 2, length $0.7 \times$ head diameter

Amphids: at $1 \times$ head diameter from anterior end, just posterior to the bottom of the buccal cavity; circular with posterior aperture, diameter $0.45 \times$ corresponding body diameter

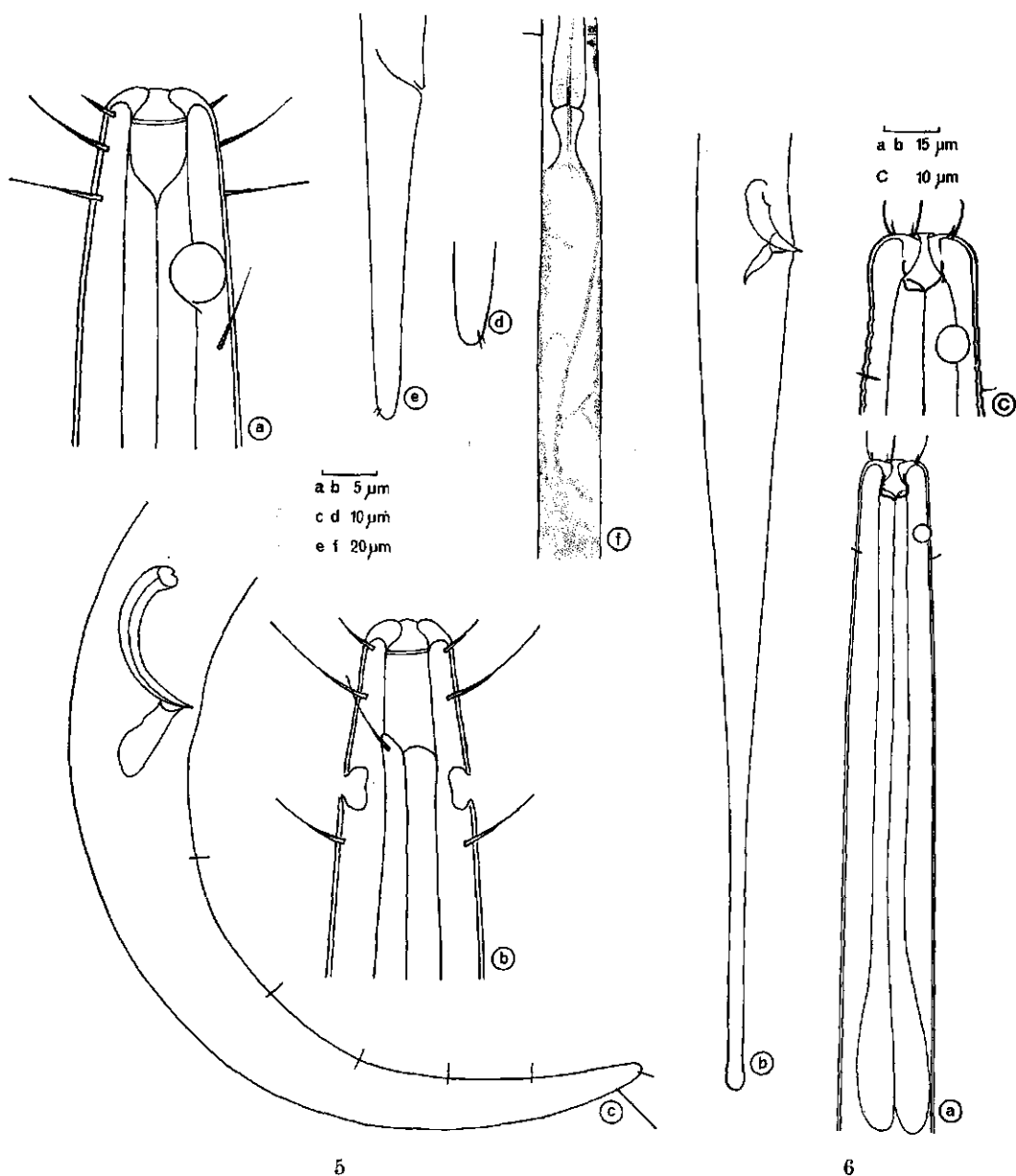


Fig. 5. *Eleutherolaimus amasi* sp. n.

a) female head, b) male head, c) male tail, d) tip of male tail, e) female tail, f) posterior part of esophagus

Fig. 6. *Paralinhomoeus ilenensis*

a) anterior part of male, b) male tail, c) male head

- Esophagus: few scattered body setae present, lengths $0.3 \times$ corresponding body diameter; cylindrical, posteriorly slightly dilated
 Excretory pore: at $0.6 \times$ esophagus length from the anterior end
 Nerve ring: just anterior to the excretory pore
 Cardia: elongate
 Ovaries: amphidelphic, outstretched
 Vulva: with protruding lips
 Vagina: sclerotized
 Spicula: curved, longer than the anal diameter, proximal end cephalate, median septum present, length $30-35 \mu\text{m}$
 Gubernaculum: with a broad dorsal apophysis which is weakly sclerotized; apophysis length $0.5 \times$ spicula length
 Tail: female tail with 2 short subterminal setae; male tail with 5 pairs of subventral setae and 2 pairs of subterminal dorsally located setae, one pair short, the other quite long

Discussion: The species described has some affinity to *E. doliolum* WIESER 1959, which species is however poorly described. The latter species is shorter, the tail is less slender and the buccal cavity is provided with 4 transverse rings; affinity to *Eumorpholaimus norvegicus* ALLGEN 1947 exists as well, but ALLGEN does not mention post-amphidial setae and tail setae, though his presentation of the arrangement of the cephalic setae, the buccal cavity, the amphids, the spicula and the male tail is very similar to the species from the Ems estuary; probably *E. amasi* is identical with *E. cf. stenosoma* RIEMANN 1966, of which, unfortunately, only a female has been described. *E. stenosoma* DE MAN 1907 and *E. amasi* are distributed over the same estuarine zone; within this zone *E. stenosoma* is most numerous in silty sediments while highest densities of *E. amasi* have been found in sandy sediments; however, co-occurrence has been observed also.

Paralinhomoeus ilenensis ALLGEN 1933 (Fig. 6)

Number of specimens isolated: 2 males, 1 female

Description:

	l	a	b	c	v	sp	t
♂	2.6	100	14.3	11.4		1.1	9.5
♂	2.7	98	16.6	13.4		1.1	8.2
♀	2.2	88	14.8	11.8	54		10.0

- Body shape: cylindrical, slightly tapering towards anterior end, heavily tapering towards posterior end; head diameter $0.75 \times$ diameter at end of esophagus; width of terminal part of the tail $0.15 \times$ anal diameter
 Cuticle: annulated; no body setae except in head region
 Head: slightly set off, cuticle not annulated
 Buccal cavity: with sclerotized walls and irregular, sclerotized structures on the bottom
 Cephalic setae: 4 setae $0.45 \times$ head diameter, paired with 4 setae $0.15 \times$ head diameter and 2 single setae $0.15 \times$ head diameter
 Amphids: at $1 \times$ head diameter from anterior end; circular, width $0.3 \times$ corresponding body diameter
 Post-amphidial setae: 2, slightly longer than the short cephalic setae
 Esophagus: cylindrical, with protracted terminal bulb

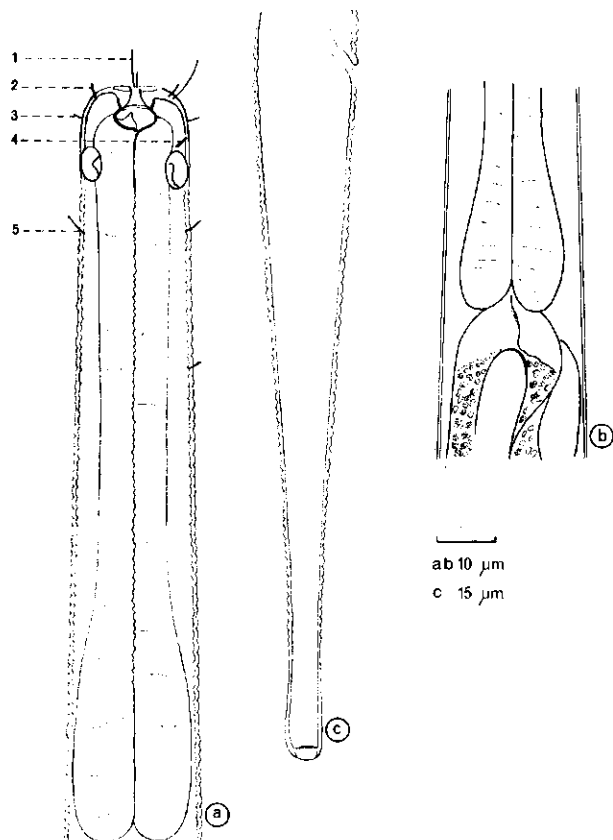


Fig. 7. *Paralinhomocus cf lepturus*

a) anterior part of female, b) terminal bulb, c) female tail

Nerve ring and excretory pore: not observed

Cardia: elongate

Spicula: curved, with a pointed elevation at the ventral side near the proximal end, length $25\text{ }\mu\text{m}$

Gubernaculum: with dorsal apophysis $0.5\times$ spicula length

Tail: without setae; the terminal part is cylindrical

Discussion: Identification as *P. ilenensis* ALLGEN 1933 seems to be reasonable, though the longer cephalic setae are slightly shorter; the shape of the buccal cavity, the presence of sclerotized structures on the basis, the position and width of the amphids, the spicula, gubernaculum and the tail are identical with ALLGEN's description, though he did not notice the post-amphidial setae; GERLACH 1963 puts the emphasis on the presence of a double proximally knobbed spiculum; however, this has not been observed in the Ems specimens.

Paralinhomoeus cf lepturus DE MAN 1907 (Fig. 7)

Number of specimens isolated: 1 female, 2 larvae

Description:

	l	a	b	c	v	t
♀	3.3	80	17.2	18.7	52	6.9

Body shape: cylindrical, slightly tapering towards anterior end; head diameter $0.75 \times$ diameter at end of esophagus; diameter tail tip $0.35 \times$ anal diameter

Head: slightly set off, cuticle smooth

Buccal cavity: cupshaped with a vestibulum, heavily sclerotized walls, a buccal ring and a sclerotized tooth-like structure

Cephalic setae: the exact number could not be determined (Fig. 7a)

setae type	length*)	number
1	0.45	?
2	0.11	?
3	0.11	2

*) length in head diameters

type 1 and 2 comprise the most anterior circle; just posterior to this circle setae type 3 are inserted

Cervical setae: 1 short seta (type 4) has been observed, just anterior to an amphid

Post-amphidial setae: 2 (type 5) with the same length as type 2, 3 and 4

Amphids: circular, located at $0.65 \times$ head diameter from anterior end, well behind the basis of the buccal cavity; width $0.3 \times$ corresponding body diameter, cryptospiral with posterior aperture; just posterior to the amphids the body is slightly constricted and from that end the cuticle is annulated

Esophagus: terminal bulb present

Nerve ring: at middle of the esophagus

Excretory pore: not observed

Cardia: elongate

Ovaries: amphidelphic, outstretched

Tail: gradually tapering towards the end; tip slightly clavate; the width at the tip is one third of the anal diameter in the female as well as in the larvae

Paralinhomoeus flevensis sp. n. (Fig. 8)

Number of specimens isolated: 3 males, 3 females, dozens of larvae

Description:

	l	a	b	c	v	sp	t
♂	4.1	77	19.3	21.8		1.0	4.0
♂	3.5	71	15.7	16.1		1.1	4.4
♂	4.1	73	18.9	17.8		1.0	4.1
♀	4.1	78	19.7	18.9	49		5.0
♀	3.9	74	19.1	15.8	49		6.7
♀	2.6	62	15.4	11.1	?		6.9

Body shape: cylindrical, tapering towards the ends; head diameter $0.65 \times$ diameter at end of the esophagus; width of the tail-tip $0.10-0.15 \times$ anal diameter

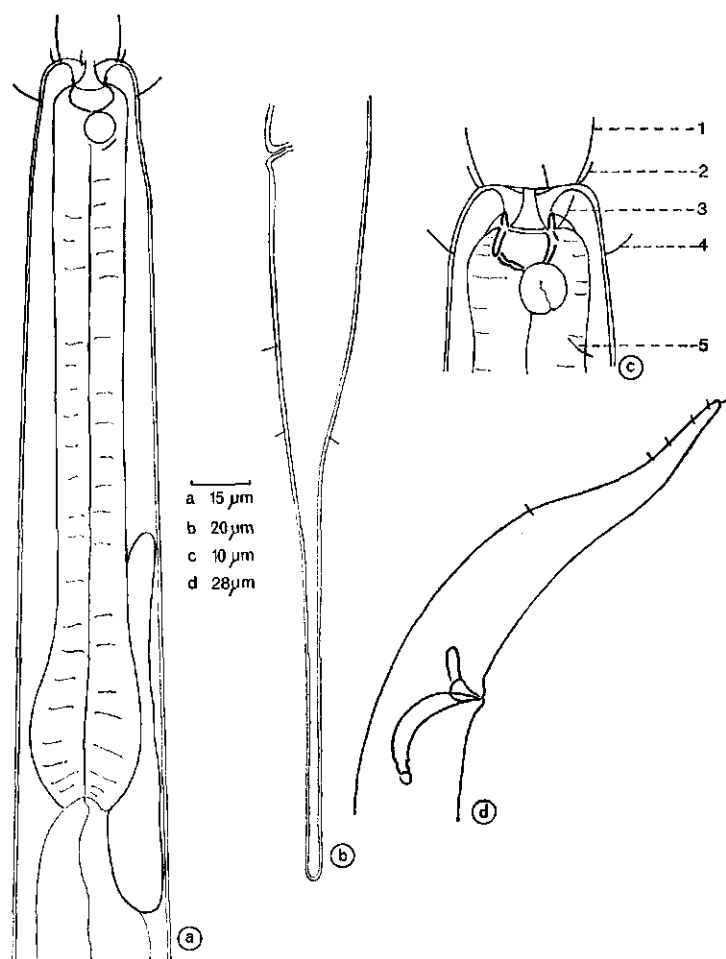


Fig. 8. *Paralinhomoeus flevensis* sp. n.

a) anterior part of female, b) female tail, c) female head, d) male tail

Cuticle: very finely annulated; no body setae except in cephalic and esophageal region and on the tail

Head: set off

Buccal cavity: typical, with sclerotized walls and buccal ring

Cephalic setae: 3 circles of setae could be observed, type 1 and 2, type 3, type 4 (Fig. 8c)

setae type	number	length*)
1	4	0.50
2	6	0.15
3	2 (?)	0.25
4	4	0.20

*) length in head diameters

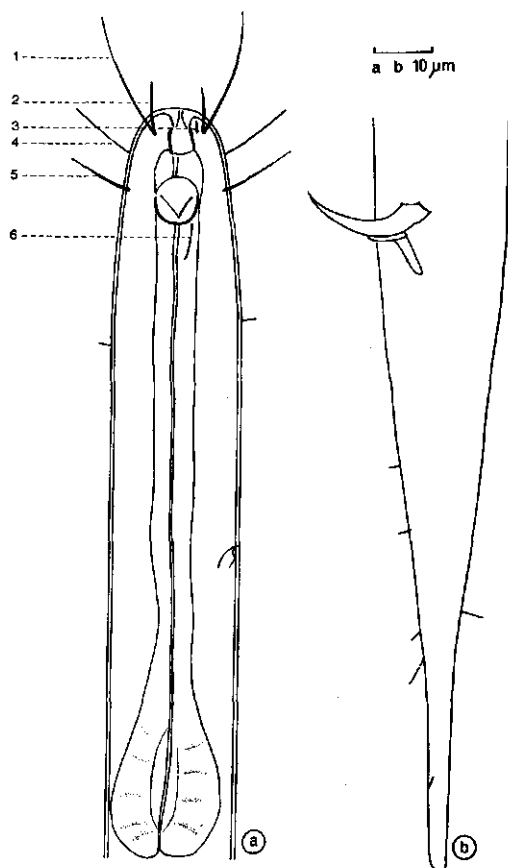


Fig. 9. *Paralinhomoeus* sp.
a) anterior part of male, b) male tail

Amphids: circular, cryptospiral, located $0.5 \times$ head diameter from anterior end; width $0.3 \times$ corresponding body diameter; just posterior to the buccal cavity

Post-amphidial setae: 2, length $0.20 \times$ head diameter

Esophagus: terminal bulb present

Nerve ring: not observed

Excretory pore: located $0.6 \times$ esophagus length from anterior end

Cardia: elongate

Ovaries: amphidelphic, outstretched

Spicula: curved, length $55-65 \mu\text{m}$

Gubernaculum: with dorsal apophysis, $0.4 \times$ spicula length

Tail: anterior half tapering, posterior half cylindrical; few short setae present

Discussion: The species described is related to *P. lepturus* DE MAN 1907 and *P. tenuicaudatus* BÜTSCHLI 1874; the specimens differ from *P. lepturus* in the following details: tooth-like buccal structure absent, the terminal part of the tail is at least twice as slender. The width of the posterior part of the tail suggests a relationship with

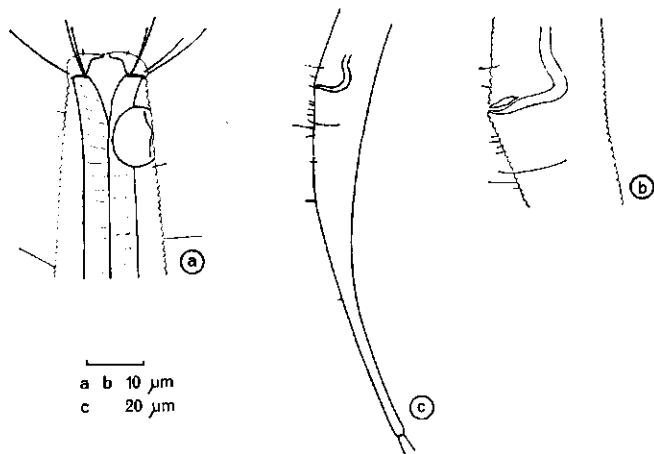


Fig. 10. *Daptonema fallax*
a) male head, b) spicula, c) male tail

P. tenuicaudatus, however for synonymization with this species the cephalic setae are much too long. The combination of cephalic setae type 1 with a length of $0.5 \times$ head diameter and a tail with a terminal part $0.10 \times$ anal diameter wide, has been observed only in STEKHOVEN's description of a male specimen from the Zuiderzee (1935). He presented this specimen incorrectly as *P. tenuicaudatus* BÜTSCHLI and GERLACH (1963) points out that the tail of the specimen presented by STEKHOVEN is probably broken off and in the Bremerhaven Checklist the specimen is listed as *P. lepturus*. However, from the previous it is evident that the species described, as well as STEKHOVEN's male specimen, are not identical with the two mentioned species, but belong to a separate species.

Paralinhomoeus sp. (Fig. 9)

Number of specimens isolated: 1 male

Description:

	l	a	b	c	sp	t
♂	2.5	111	19.5	22.3	1.1	5.0

Body shape: cylindrical, slightly tapering towards the anterior end, heavily tapering towards the posterior end; head diameter $0.7 \times$ diameter at end of esophagus, posterior part of tail $0.15 \times$ anal diameter wide

Cuticle: very finely annulated, no body setae except in cephalic, esophageal and tail region

Head: not set off

Buccal cavity: moderately sclerotized walls, relatively small, cupshaped with vestibulum

Cephalic setae: 2 circles of setae could be observed, the anterior circle comprising type 1, 2 and 3, the second circle comprising setae type 4 (Fig. 9a)

Subcephalic setae: present, on a level with the amphids

Post-amphidial setae: present, just posterior to the amphids

Anterior setae (Fig. 9a):

	type	number	length
cephalic	1	4	1.4
	2	4	0.5
	3	2	0.2
	4	2	0.8
subcephalic	5	4	0.8
postamphidial	6	2	0.4

Amphids: circular, anterior half less distinct than posterior half; located at $0.75 \times$ head diameter from anterior end, width $0.4 \times$ corresponding body diameter

Esophagus: cylindrical with terminal bulb

Excretory pore: at $0.6 \times$ esophagus length from anterior end

Nerve ring: not observed

Spicula: curved, length $25 \mu\text{m}$

Gubernaculum: with dorsal apophysis, length apophysis $0.35 \times$ spicula length

Tail: heavily tapering towards the end; setae present mainly along the ventral side; possibly the tail is longer in reality but broken off in this specimen

Discussion: The specimen described is related to *P. conspicuus* GERLACH 1957 from Brazil, however, the amphids width and the length of the subcephalic setae are different. Because only 1 specimen has been isolated yet, the organism has not been presented as a new species.

Daptonema fallax LORENZEN 1971 (Fig. 10)

Number of specimens isolated: dozens of males; females and larvae not distinguished from other species

Description:

	l	a	b	c	sp	t
♂	1.0	53	4.9	8.0	1.2	6.7
♂	1.0	48	4.8	7.8	1.1	6.7

Body shape: cylindrical, tapering towards the ends; head diameter $0.65 \times$ diameter at end of esophagus; pronounced tapering in anterior half of the tail, posterior half cylindrical

Cuticle: annulated, no setae except in tail and esophagus region

Head: slightly set off

Buccal cavity: typical

Labial papillae: 6, minute

Cephalic setae: 10, of which 6 measure $1.0 \times$ head diameter; 4 of these setae are paired with subequal setae

Cervical setae: 2, minute

Amphids: circular with an indistinct outline, $0.7 \times$ head diameter from anterior end, width $0.6 \times$ corresponding body diameter

Post amphidial setae: short, just posterior to the amphids

Nerve ring and excretory pore: not observed

Esophagus: cylindrical

Spicula: with a typical belly-like curve in the proximal part, slightly longer than the anal diameter, length $20-25 \mu\text{m}$

Gubernaculum: present, without apophysis

Pre- and postanal setae: conspicuous

Tail: with terminal setae

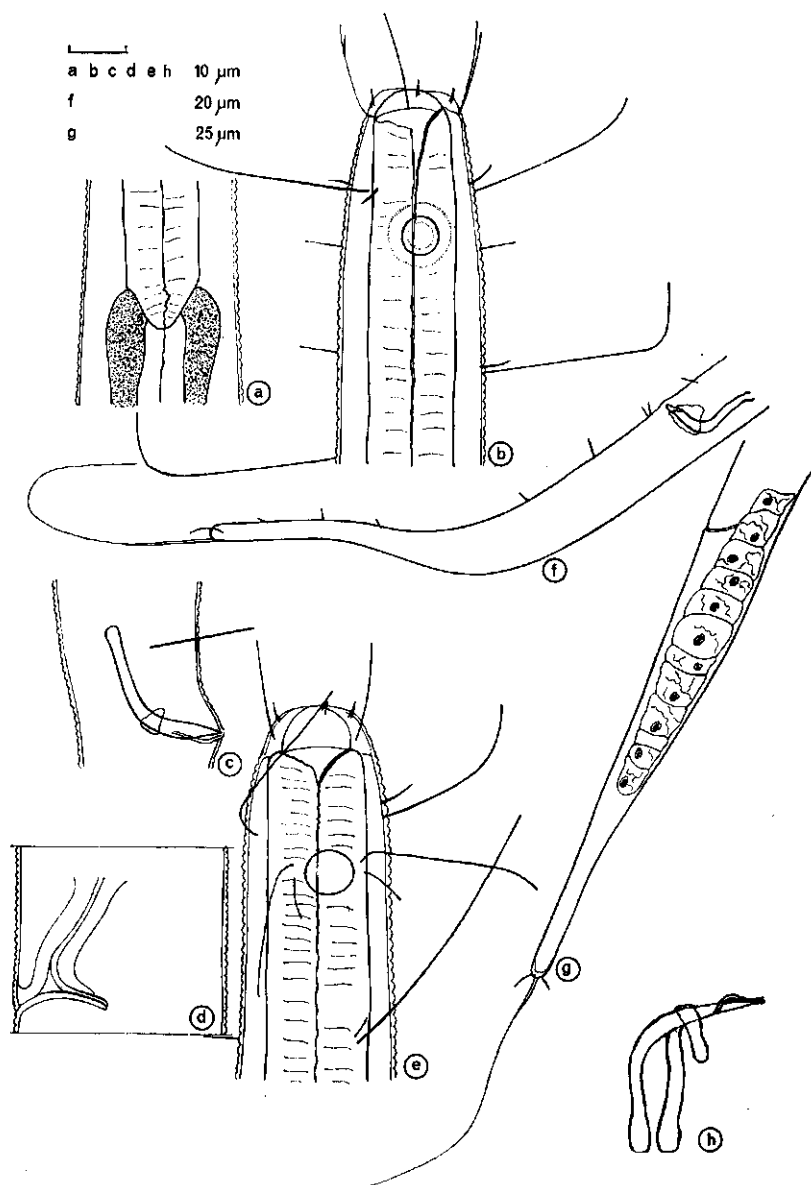


Fig. 11. *Daptonema invagiferum*

a) cardia, b) male head, c) spicula, d) vulva, e) female head, f) male tail, g) female tail, h) spicula.

Discussion: LORENZEN (1971, 1977) described *Daptonema fallax* and considers the species to be quite variable; in 1971 he presented specimens with few body setae, in 1977 he presented specimens with many setae, regularly distributed all over the body; the Ems specimens almost lack body setae and agree well with LORENZEN's first description; particularly the arrangement of setae in the anal region is totally identical.

Daptonema invagiferum PLATT 1973 (Fig. 11)

Number of specimens isolated: dozens of males, females and larvae

Description:

	l	a	b	c	v	sp	t
♂	1.3	34	5.3	8.2		1.3	6.0
♂	1.3	43	4.8	8.9		1.4	5.4
♂	1.3	42	5.2	7.9		1.4	6.9
♀	1.5	40	4.7	7.4	71		6.8
♀	1.3	34	4.5	7.1	69		6.2
♀	1.4	44	4.4	7.4	70		6.7

Body shape: cylindrical, tapering towards the ends; cephalic, cervical and tail setae present; long preanal setae observed in males

Cuticle: annulated

Head: often invaginated, width $0.55 \times$ diameter at end of esophagus

Buccal cavity: asymmetric, the walls on the dorsal side are more heavily sclerotized, buccal ring present

Labial papillae: 6, short, setaeform

Cephalic setae: 10, of which 2 are singles and 8 are combined into 4 subequal couples; setae length $1 \times$ head diameter

Cervical setae: 4 pairs of a long and a short seta; length of the long setae up to $2 \times$ head diameter, short setae $0.2 \times$ head diameter

Setae on amphids level: in the males 4 setae, length $0.4 \times$ head diameter; in the females pairs of a long and a short seta are inserted at both sides of the 2 amphids; the lengths of these setae are equal to the lengths of the cervical setae

Post-amphidial setae: up to 4 groups of pairs of long and short setae have been observed; length of the long setae up to $3.5 \times$ head diameter; these setae are located in the esophageal region

Amphids: circular, located at $1.2 \times$ head diameter from anterior end; in the males several concentric circles can be observed; width amphids in males $0.45 \times$ corresponding body diameter, in females $0.30 \times$ corresponding body diameter

Esophagus: cylindrical

Nerve ring and excretory pore: not observed

Cardia: sunk into the intestine

Preanal setae: in males only; up to 10 single setae have been observed, lengths up to $3.5 \times$ head diameter

Ovary: prodelphic, outstretched

Vulva: typical, sclerotized

Spicula: proximally knobbed, bend almost rectangularly, length $30-35 \mu\text{m}$

Gubernaculum: less sclerotized than the spicula and therefore often hard to detect; short indistinct apophysis present; bow-shaped tubes terminating at both sides of the anus

Tail: the female tail is characteristically filled with up to a dozen cells with clear nuclei; on the male tail short scattered ventral setae are present; male and female tail carry 1 long subterminal seta with a length of up to $4.2 \times$ anal diameter and 2 short terminal setae; the tail of a number of specimens was broken off and therefore bluntly rounded without terminal setae

Discussion: PLATT's description (1973) is the first and only one; the specimens described from the Ems estuary agree with this description though the long cephalic setae, the spicula and the terminal setae are longer; particularly the terminal setae may be

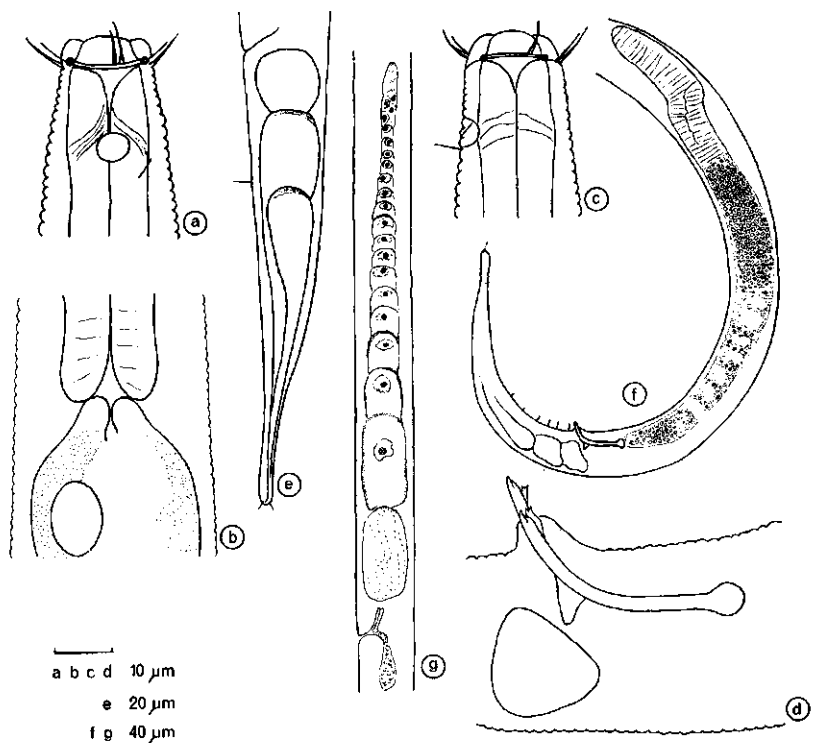


Fig. 12. *Daptonema cf. normadicum* I

a) female head, b) cardia, c) male head, d) spicula, e) female tail, f) testis, g) ovary

very long though shorter ones have been observed as well; most spicula were located normally, however, location in the body centre as described by PLATT has been observed as well.

Daptonema cf. normadicum I and II DE MAN 1890 (Fig. 12 and 13)

Number of specimens isolated: dozens of males, females and larvae

Description type I (Fig. 12):

	l	a	b	c	v	sp	t
♂	1.2	28	5.9	6.8		1.4	5.4
♂	1.2	31	5.9	6.6		1.4	5.4
♂	1.1	28	5.5	7.2		1.4	4.6
♀	1.1	34	5.0	6.5	65		6.5
♀	1.1	25	5.0	7.0	67		5.6
♀	1.3	26	5.9	7.1	68		5.3

Body shape: from the middle gradually tapering towards the ends; head diameter $0.45 \times$ diameter at end of esophagus

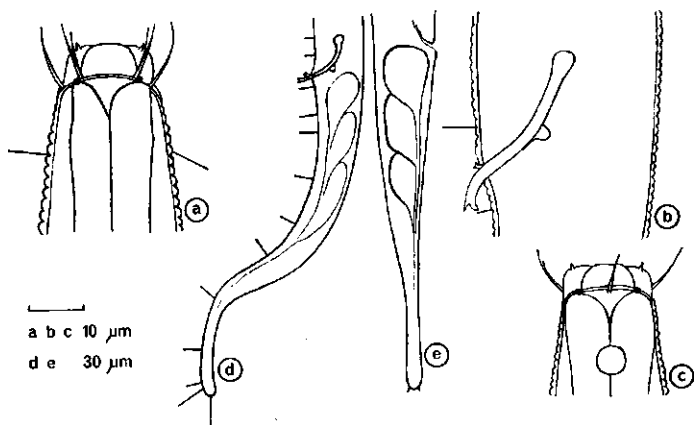


Fig. 13. *Daptonema cf. normandicum* II

a) male head, b) spicula, c) female head, d) male tail, e) female tail

Cuticle: very coarsely annulated in the anterior half of the esophageal zone; the rest of the body annulated moderately; few, short, scattered setae occur over the total body length

Head: not set off

Buccal cavity: typical, buccal ring with conspicuous knobs present

Labial papillae: inconspicuous

Cephalic setae: 10, of which 6 measure $0.5 \times$ head diameter; 4 of these setae are paired with subequal setae

Amphids: slightly oval, located $1.0 \times$ head diameter from anterior end; width in males $0.30-0.35 \times$ head diameter, in females $0.20-0.25$

Cervical setae: absent

Post-amphidial setae: present, short

Esophagus: cylindrical, characteristic striation present on a level with the amphids and slightly dilated on that level as well

Excretory pore and nerve ring: not observed

Male gonad: the anterior part of the vas deferens, which is located dorsally, is connected by means of a very characteristic bend with the ventrally located posterior part

Spicula: complicated, almost rectangularly curved; each spicula with 2 parallel, forked but different tips; proximally knobbed; length $40-45 \mu\text{m}$

Gubernaculum: with small dorsal apophysis

Female gonad: prodelphic, located median, outstretched; post vulval-sack present

Tail: with 3 conspicuous gland cells; male tail with ventral setae; terminal setae present in both sexes, but in males twice as long as in females

Discussion: in literature there is much confusion about the species *Daptonema normandicum*; all descriptions are different in details; the Ems specimens type I are characterized by the lack of cervical setae; the spicula are identical with the description by RIEMANN 1966 of *Theristus cf. normandicus*, however, in many other respects the specimens are different: the Ems specimens have no cervical setae and less wide amphids which are not inconspicuous in the males.

Description type II (Fig. 13):

	l	a	b	c	v	sp	t
♂	1.1	32	5.2	6.8		1.2	5.8
♂	1.2	32	5.2	7.1		1.0	5.7
♂	1.2	29	5.7	6.7		1.0	5.7
♀	1.2	29	4.3	6.6	63		5.8
♀	1.4	25	5.1	7.0	59		5.8
♀	1.4	33	5.4	6.7	65		6.4

Body shape: gradually tapering from the middle towards the ends

Cuticle: very coarsely annulated over the total body length, particularly the anterior esophageal zone; no body setae except in head, esophageal and tail region

Head: not set off, width $0.55 \times$ diameter at end of esophagus

Buccal cavity: typical with buccal ring and knobs

Labial papillae: 6, short but clear

Cephalic setae: 10, of which 6 measure $0.6 \times$ head diameter; 4 of these setae are paired with subequal setae

Amphids: in most specimens, males, females and larvae, the amphids are invisible or indistinct; located at $0.75 \times$ head diameter from anterior end, circular, in males width $0.35 \times$ corresponding body diameter, in females $0.25 \times$

Cervical setae: absent

Post-amphidial setae: present

Nerve ring and excretory pore: not observed

Esophagus: cylindrical

Cardia: elongate

Spicula: bend, proximally knobbed, bifurcate tip, and with a secondary element that is bifurcate as well; length $30-35 \mu\text{m}$

Gubernaculum: with a small dorsal apophysis

Male gonad: vas deferens with a less characteristically bend if compared with type I

Female gonad: prodelphic, outstretched

Tail: with conspicuous gland cells, long ventral and terminal setae in the males and in the females short terminal setae only; the male tail is very characteristically bent in fixed state, female tails, however, are outstretched

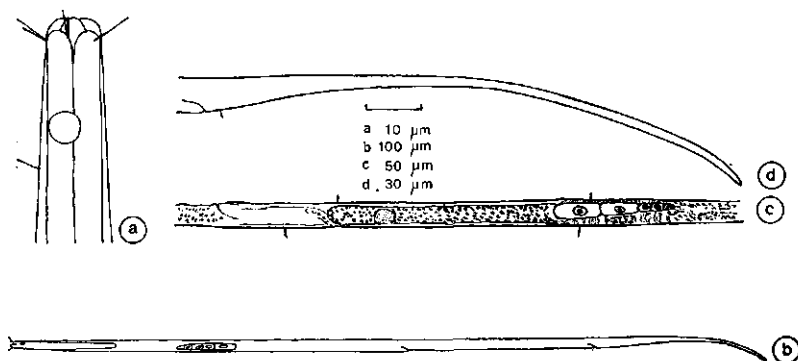


Fig. 14. *Daptonema* sp.

a) female head, b) entire female, c) ovary, d) female tail

Discussion: the specimens belonging to *D. cf. normandicum* type II differ from type I in the following respects: cephalic setae are slightly longer, labial papillae are distinct, amphids are inconspicuous, esophagus less striated and dilated on a level with the amphids, male tail characteristically bent, ventral and terminal setae on male tail longer; however, for many qualities with discriminatory value, gradual transitions have been observed; type I is mainly distributed in the brackwater zone, type II in the more marine part of the estuary, though cooccurrence may happen incidentally; it is concluded that a revision of the *normandicum*-conglomerate is necessary.

Daptonema sp. (Fig. 14)

Number of specimens isolated: dozens of females and larvae

Description:

	l	a	b	c	v	t
♀	1.3	62	7.3	4.7	53	17
♀	1.3	64	7.6	4.4	50	20
♀	1.3	50	7.5	4.8	52	16

Body shape: slender, cylindrical, with a very long slender tail; females abruptly narrowed posterior to the vulva

Cuticle: very slightly annulated with few, short setae, scattered over the total body length

Head: not set off, width $0.45 \times$ diameter at end of esophagus

Buccal cavity: typical

Labial papillae: minute

Cephalic setae: 10, of which 6 measure $0.75 \times$ head diameter; 4 of these setae paired with subequal setae

Amphids: circular to slightly oval; located $2 \times$ head diameter from anterior end; width $0.4 \times$ corresponding body diameter

Post-amphidial setae: 2, length $0.3 \times$ corresponding body diameter

Nerve ring and excretory pore: not observed

Esophagus: cylindrical

Cardia: sunk into the intestine

Ovary: prodelphic, outstretched

Tail: anterior one third tapering, posterior two thirds cylindrical; width of posterior part $0.2 \times$ anal diameter; tail tip rounded, no terminal setae; tail length $0.20\text{--}0.25 \times$ total body length

Discussion: no males were isolated, possibly no males exist; affinity exists to *Daptonema proprium* LORENZEN 1972, of which species the amphids are located more anteriorly and the tail carries short terminal setae; affinity to *Daptonema spirum* GERLACH 1959 exists as well, however the Ems specimens are twice as long.

Theristus cf. subcurvatus LORENZEN 1977

Number of specimens isolated: 3 males

Discussion: the specimens isolated are identical with LORENZEN's description; to this description no new information can be added, but morphometric measurements of the Ems specimens are different from LORENZEN's specimens; the Ems specimens

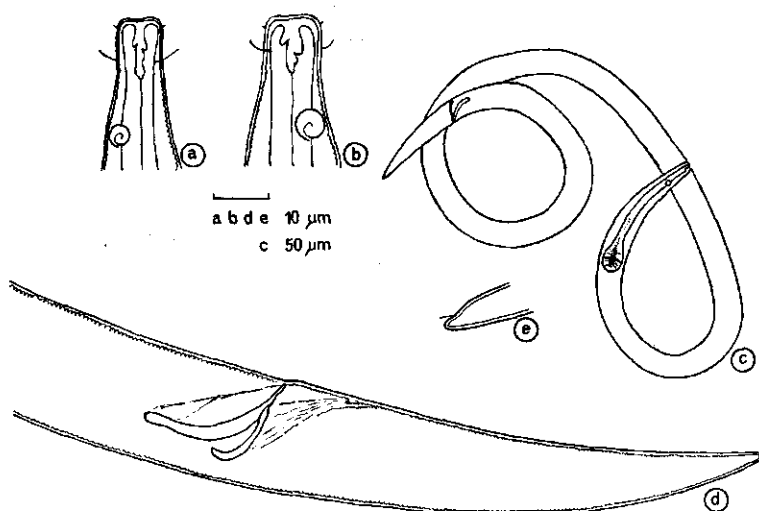


Fig. 15. *Calomicrolaimus honestus*

a) male head, b) female head, c) entire male, d) male tail, e) tip of male tail

are at least $1.5\times$ as long as LORENZEN's specimens while the lengths of tail and esophagus and the body width do not differ; therefore the ratios a, b and c are almost twice the sizes of LORENZEN's ratios.

	l	a	b	c	sp	cs ₁	cs ₂	amw	amd	hd	t	ga
♂	1.5	59	8.3	13.8	0.9 (19 μm)	?	0.5	0.8	0.6	0.7	5.7	0.15
♂	1.5	63	?	12.0	1.0 (19 μm)	1.0	0.45	0.8	0.9	?	6.9	0.20
♂	1.6	59	8.8	14.8	0.9 (18 μm)	1.0	?	?	0.8	0.7	5.1	0.15

Calomicrolaimus honestus DE MAN 1922 (Fig. 15)

Number of specimens isolated: 4 males, 6 females, dozens of larvae

Description:

	l	a	b	c	v	sp	t
♂	0.8	41	7.3	10.3		1.5	4.0
♂	1.0	53	8.0	12.8		1.3	4.2
♂	1.0	51	9.2	13.7		1.5	4.1
♀	0.9	31	7.8	9.3	54		5.8
♀	0.9	37	7.7	9.3	47		5.0
♀	0.9	30	7.7	8.8	47		4.7

Body shape: heavily tapering towards the anterior end; head diameter $0.40-0.45\times$ diameter at end of esophagus; tail gradually tapering towards the end; in fixed state, males always curled, females occasionally outstretched

Colour of fixed specimens: gold yellow-pink

Cuticle: slightly annulated, no setae except cephalic setae

Head: not set off, no constriction just before the anterior end, cuticle not annulated

Buccal cavity: depth $1 \times$ head diameter, moderately sclerotized, 1 dorsal and 2 subventral teeth

Labial papillae: minute

Cephalic papillae: 6 short often indistinct setae

Cephalic setae: 4, length $0.25-0.50 \times$ head diameter, very slender

Amphids: circular, cryptospiral with posterior aperture, inner spiralization slightly visible; width $0.25-0.45 \times$ corresponding body diameter, located $1.5-2.2 \times$ head diameter from anterior end

Esophagus: cylindrical, terminal bulb present, almost no pharyngeal dilation

Nerve ring and excretory pore: not observed

Female gonads: amphidelphic, outstretched

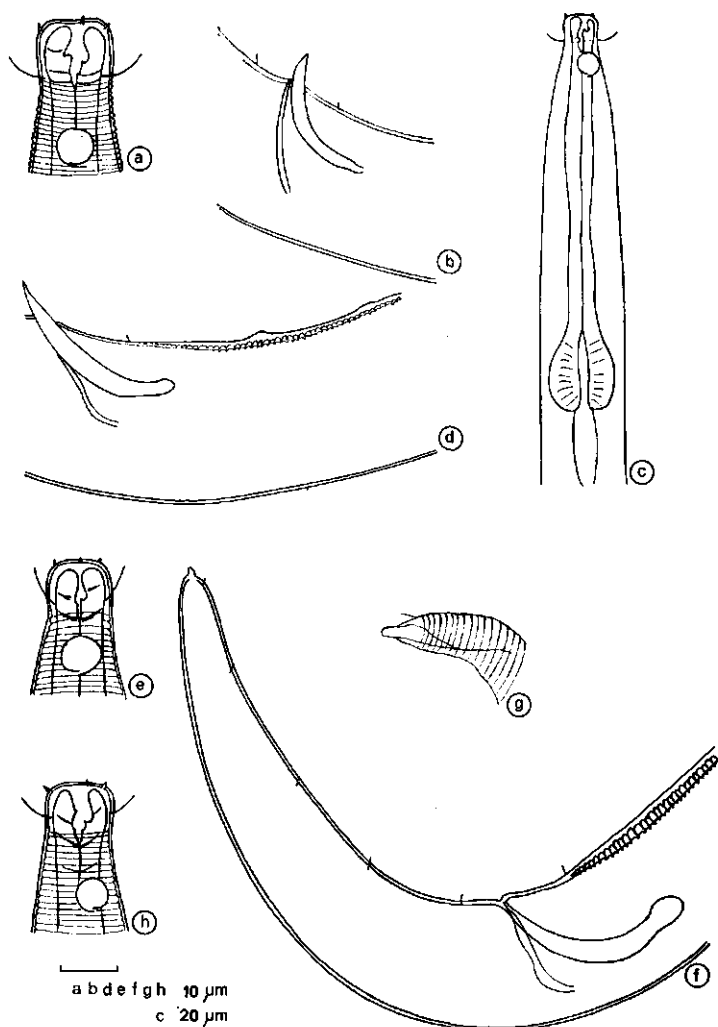


Fig. 16. *Calomicrolaimus marinus*

a) male head, b) spicula male 1, c) anterior end male 2, d) Spicula male 2, e) head male 3, f) tail male 3, g) tail tip male 3, h) female head

Spicula: curved, length $25\mu\text{m}$, do not contrast much with their surroundings

Gubernaculum: spoonlike, parallel to the spicula, length $0.5 \times$ spicula length

Male preanal zone: ventrally more coarsely annulated; 2 preanal papillae present but not always distinct

Tail: conical, in males terminal seta present

Discussion: GERLACH 1950 states that the species *C. honestus* is very variable and probably a conglomerate of different closely related species; indeed, most descriptions differ slightly from each other, however the Ems specimens agree with DE MAN 1922 and with JENSEN's recent description (1979).

Calomicrolaimus marinus SCHULZ 1932 (Fig. 16)

Number of specimens isolated: 7 males, 1 female, 1 larva

Description:

	l	a	b	c	v	sp	t
♂	1.6	70	10.8	17.4		1.3	4.2
♂	1.3	48	10.2	19.5		1.3	3.9
♂	1.4	47	10.0	15.0		1.2	3.7
♀	1.3	33	8.7	12.5	50		4.6

Body shape: cylindrical, tapering towards the ends; head diameter $0.45-0.55 \times$ diameter at end of esophagus; in fixed state, males as well as females, outstretched or bent but never curled.

Colour of fixed specimens: gold-yellow

Cuticle: moderately annulated, anterior esophageal region coarsely annulated; no body setae except cephalic setae and preanal seta and terminal seta in the males

Head: distinctly set off, cuticle not annulated

Buccal cavity: depth $1 \times$ head diameter, moderately sclerotized, 1 dorsal and 2 subventral teeth

Labial papillae: minute

Cephalic papillae: distinct

Cephalic setae: 4, very distinct, length $0.5 \times$ head diameter

Amphids: circular to slightly oval, cryptospiral with posterior aperture; spiralization not visible, located at $1.1-1.4 \times$ head diameter from anterior end; width in males $0.5 \times$ corresponding body diameter, in females 0.35

Nerve ring and excretory pore: not observed

Esophagus: dilated anteriorly, typically striated in buccal and cervical region; terminal bulb present

Spicula: curved, proximally slightly knobbed, length $25-35\mu\text{m}$

Gubernaculum: spoonlike, parallel to the spicula, length $0.50-0.75 \times$ spicula length

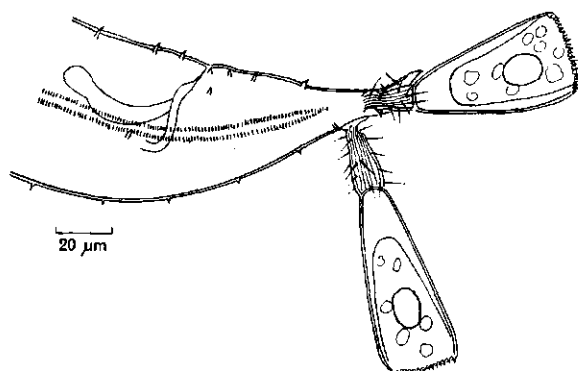
Male preanal zone: 3 types of preanal cuticular zones have been distinguished in specimens from the same sample

1. preanal cuticle unchanged, short seta present
2. at a distance of $0.3 \times$ anal diameter anterior to the anus, the cuticle is thickened and very coarsely annulated; short preanal seta present at the starting point of the cuticular thickening
3. as for 2 but with papillae-like cuticular elevations

Female gonads: amphidelphic, outstretched

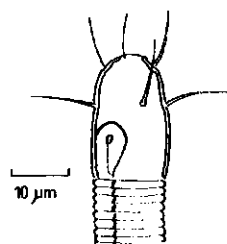
Tail: conical with subventral short setae in the males

Discussion: the species *C. marinus* SCHULZ 1932 has been described insufficiently up till now; descriptions of SCHULZ 1932, DE CONINCK and STEKHOVEN 1933 and GERLACH



17

Fig. 17. *Metachromadora remanei*
Male tail with epifauna



18

Fig. 18. *Dasynemella cf. albaensis*
male head

1950 differ among each other; SCHULZ is the only author who points to the presence of preanal papillae and a seta in the male and ventrally located setae on the male tail; moreover he presents an amphid without inner spiralization; all these features have been observed in the Ems specimens as well; however, the spicular apparatus, as drawn by SCHULZ, is quite different from the spicula of the Ems specimens; probably SCHULZ did not observe a representative spiculum because he had only 1 male specimen at his disposal; the spicula, as described by DE CONINCK c.s. and GERLACH are identical with the spicula of the Ems specimens; these authors, however, present amphids with a conspicuous inner spiralization and did not notice the preanal seta and papillae nor the ventral tail setae in males; anyway it is quite probable that all described specimens mentioned are identical.

Close affinity to *C. honestus* exists; buccal cavity, male genital apparatus and morphometric ratios do not differ; the difference between the two species, isolated in the Ems estuary, is based on the following characteristics.

	<i>C. honestus</i>	<i>C. marinus</i>
length	0.80—1.0 mm	1.30—1.60 mm
colour in fixed state	gold/yellow-pink	gold/yellow
cuticle	moderately annulated	coarsely annulated in cervical region
head	not set off	set off
cephalic papillae	setiform	papilliform
amphids distance from anterior end	1.5—2.2 × head diameter	1.1—1.4 × head diameter
preanal seta in male	absent	present
subventral setae in male tail	absent	present
pharyngeal striation	inconspicuous	conspicuous

Metachromadora remanei GERLACH 1951 (Fig. 17)

Number of specimens isolated: 3 males, 4 females and dozens of larvae

Discussion: the species has been described sufficiently by GERLACH 1951 and HOPPER 1969; a male tail, however, has been drawn because of the presence of epifaunal suctoria; the phenomenon of parasitism or commensalism of suctoria on nematodes has been mentioned first by BASTIAN 1865 for *Spirinia parasitifera*; the suctoria have been observed on the tails of this species in the Ems estuary as well; the suctoria are restricted to the tails, of males, females as well as larvae, in *M. remanei* and in *S. parasitifera*.

Dasynemella cf albaënsis WARWICK 1973 (Fig. 18)

Number of specimens isolated: 2 males, 2 larvae

Discussion: the species has been described sufficiently by RIEMAN 1966 and WARWICK 1973; the specimens from the Ems estuary differ slightly from these descriptions; the Ems specimens are more slender and the amphids in the males are twice the size of the amphids drawn by WARWICK; in all other respects the specimens are identical.

	l	8 a	b c	hd	cs ₁	cs ₂	amw	amd	aml	cc	t	sp	g
♂	1.9	116	? 15.7	0.75	0.8	0.95	0.50	1.1	0.4	1.8	7.1	1.7 (29 μm)	0.6
♂	1.6	116	? 17.2	0.80	0.7	0.95	0.50	1.2	0.4	1.7	7.2	1.5 (25 μm)	0.6

Sabatieria pulchra G. SCHNEIDER 1906 (Table 1)

Number of specimens isolated: dozens of males, females and larvae

Discussion: The species is distributed all over the estuary but only numerous just below the upper sediment layers in the muddy parts of the Dollart and of the middle reaches of the estuary. Small differences between specimens from different localities occur and it is doubtful if they all belong to the same species. Recently the species has been redescribed by RIEMANN 1966 and by JENSEN 1979 and all Ems specimens were in agreement with these descriptions and fell within the described variability. Table 1 presents morphometrical data of specimens from 8 different localities. Data of females are only presented if they were isolated from samples in which the closely related species *S. celtica* SOUTHERN 1914 did not occur because females of both species cannot be distinguished easily. The main difference between specimens from different localities was the number of preanal appillae. Generally this number is fairly constant and amounts to 6 all over the estuary except in specimens from sampling station Oost Friesche Plaat 2, situated near the fresh water inlet point at Nieuwe Statenzijl. At this station the average number of papillae is 8. For the stations Hoogwatum pq and Oost Friesche Plaat 2 the number of papillae was checked for 10 more specimens, isolated from different samplings. For Hoogwatum males the average number was again 6 (5, 6, 6, 6, 6, 6, 6, 6, 6, 7) and for the Oost Friesche Plaat again 8 (7, 7, 7, 8, 8, 8, 8, 8, 9, 9). JENSEN 1979 observed

Table 1. Morphometrical data of specimens *Sabatieria pulchra* from 8 different sampling stations

Station		l	a	b	c	v	t	cs	hd	sp	ga	amw	amd	ep	pap
OFP1,2	♂	1.9	28	10.2	12.7		3.0	0.35	0.30	1.3	0.30	0.60	0.30	0.58	7
		1.8	26	9.1	12.4		2.9	0.40	0.35	1.1	0.35	0.60	0.40	0.63	9
	♀	1.6	29	8.8	13.3		2.9	0.30	0.35	1.3	0.35	0.60	0.30	0.67	8
		1.9	28	9.1	14.8	52	3.0	0.35	0.25			0.50	0.40	?	
OFP6		1.8	32	9.2	15.0	49	3.2	0.30	0.35			0.60	0.35	?	
	♂	2.0	26	9.4	14.1	50	3.5	0.40	0.30			0.60	0.35	0.62	
	♀	1.9	30	8.7	14.1		2.9	0.30	0.30	1.2	0.40	0.60	0.45	?	6
		1.8	34	9.8	14.7	48	3.3	0.45	0.30			0.60	0.45	0.63	
Po	♂	1.5	27	9.4	12.0		3.3	0.35	0.35	1.2	0.45	0.60	0.25	0.65	6
RP	♀	1.7	25	9.2	13.8	50	3.3	?	0.30			0.60	0.20	0.63	
		1.7	34	9.0	13.5		4.6	0.20	0.35	1.3	0.35	0.65	0.30	0.57	6
	♂	1.7	32	8.6	12.0		3.5	0.25	0.30	1.2	0.30	0.70	0.35	0.66	6
		1.6	30	8.0	11.9		3.9	0.25	0.40	1.5	0.35	0.60	0.30	0.63	6
bw _{2a}	♀	1.8	30	8.9	12.0	54	3.8	0.40	0.30			0.60	0.30	0.62	
		1.6	33	7.6	11.6	51	3.8	0.30	0.30			0.60	0.30	0.61	
		1.6	32	8.0	10.6	51	4.4	0.30	0.30			?	0.20	0.63	
	♂	1.7	33	8.6	13.3		3.2	0.30	0.35	1.2	0.40	0.60	0.40	0.62	6
P		1.8	32	9.2	13.0		3.4	0.30	0.35	1.3	0.35	0.60	0.40	0.61	6
	♀	1.7	36	8.9	12.7		3.5	0.30	0.35	1.2	0.45	0.60	0.35	0.65	6
		1.7	39	9.8	13.8	48	3.6	0.40	0.40			0.60	0.25	0.61	
		1.9	34	9.4	12.2	50	3.6	0.30	0.35			0.60	0.35	0.59	
H		1.8	36	9.4	12.1	50	4.4	0.40	0.30			0.60	0.50	0.65	
	♂	1.5	26	7.8	12.4		3.3	0.20	0.35	1.4	0.45	0.80	0.45	0.68	5
	♀	1.9	31	8.8	12.6	49	3.3	0.30	0.30			0.60	0.35	0.58	
	♂	1.5	27	8.0	11.7		2.9	0.25	0.30	1.1	0.40	0.70	0.30	0.63	6
HW		1.8	308	9.4	12.8		3.1	0.30	0.25	1.2	0.40	0.70	0.35	?	6
		1.6	29	9.3	12.3		3.3	0.30	0.30	1.4	0.40	0.70	0.40	0.61	6
	♀	1.8	27	9.5	11.8	50	3.6	0.45	0.25			0.60	0.35	?	
		1.6	34	8.2	13.4	53	3.8	0.35	0.30			0.50	0.40	?	
R		1.4	29	7.5	10.5	50	3.8	0.50	0.30			0.50	0.50	0.66	
	♂	1.8	38	8.6	12.4		3.3	0.30	0.40	1.3	0.40	0.70	0.40	0.64	6
	♀	2.3	34	10.4	14.2	48	3.8	0.35	0.30			?	0.40	0.65	

mainly 7 or 8 preanal papillae in specimens from Finland and DE MAN 1922 mentioned the same numbers for specimens from the Zuiderzee. From these observations it is evident that in oligohaline areas a *S. pulchra* type is present with about 2 papillae more on an average than in mesohaline and polyhaline estuarine zones. Splitting the species for this reason is irrelevant because overlaps occur.

Amphids diameters amount $\pm 60\%$ of the corresponding body diameter. However from the sample — station Paap a male was isolated on a depth of 8 cm with amphids 80% and only 5 papillae. The specimen corresponds fairly well with RIEMANN'S (1966 page 178) description of a male from the Elbe estuary and probably it belongs to a species on its own although it does not deviate from *S. pulchra* in all other respects and overlaps with intermediate amphids diameters (70%) occur as well.

Summary: within the species *S. pulchra* 3 types can be distinguished

1. with 7—8 papillae, amphids 60%, in oligohaline areas, just below the sediment surface
2. with 6 papillae, amphids 60%, in poly- and mesohaline areas, just below the sediment surface
3. with 5 papillae, amphids 80%, probably in lower sediment layers from poly- and mesohaline areas

Neotonchus cf corcundus GERLACH 1956 (Fig. 19)

Number of specimens isolated: 3 males, 2 females

Description:

	l	a	b	e	v	sp	t
♂	1.1	56	8.5	12.1		1.3	5.2
♂	0.9	47	7.9	10.9		1.3	4.6
♂	1.1	55	8.7	11.9		1.2	4.7
♀	0.9	38	7.0	?	62		?
♀	1.0	35	8.0	12.3	56		4.6

Body shape: cylindrical, slightly tapering towards the ends; head diameter $0.7 \times$ diameter at end of esophagus, tail tip diameter $0.3-0.4 \times$ anal diameter

Cuticle: very finely annulated and punctated; scattered setae of up to $0.35 \times$ corresponding body diameter length, occur over the total body length

Head: not set off

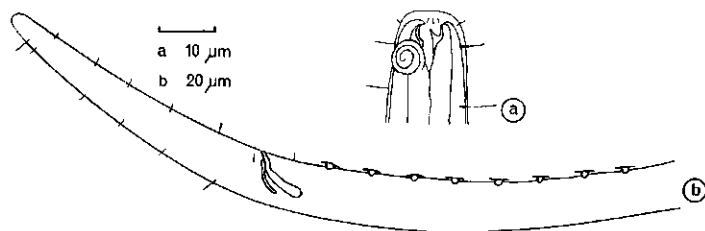


Fig. 19. *Neotonchus cf corcundus*
a) male head, b) male tail

Buccal cavity: typical *Microtalamus*-like, distinctly sclerotized, with 1 big dorsal and 2 small sub-ventral teeth

Labial papillae: minute

Cephalic setae: 4, length $0.25 \times$ head diameter

Amphids: at $0.25-0.35 \times$ head diameter from anterior end, width $0.5 \times$ head diameter, spiral-shaped with 3.5 turns

Post-amphidial setae: length $0.3 \times$ corresponding body diameter

Esophagus: without anterior dilation, with terminal bulb

Nerve ring and excretory pore: not observed

Ovaries: amphidelphic, probably reflexed

Spicula: very characteristically bent, length $20 \mu\text{m}$

Gubernaculum: $0.6 \times$ spicula length

Preanal papillae: numbers 8, 8 and 10, elevated; preanal seta present

Tail: with bluntly rounded tip, width $0.40 \times$ anal diameter, without terminal setae; male tail with short subdorsal and subventral setae, female tail without

Discussion: the Ems specimens differ slightly from GERLACH's description; the specimens are more slender, the tails are longer and the presence of a preanal seta in the males and the tail setae has not been mentioned by GERLACH; VITIELLO 1970,

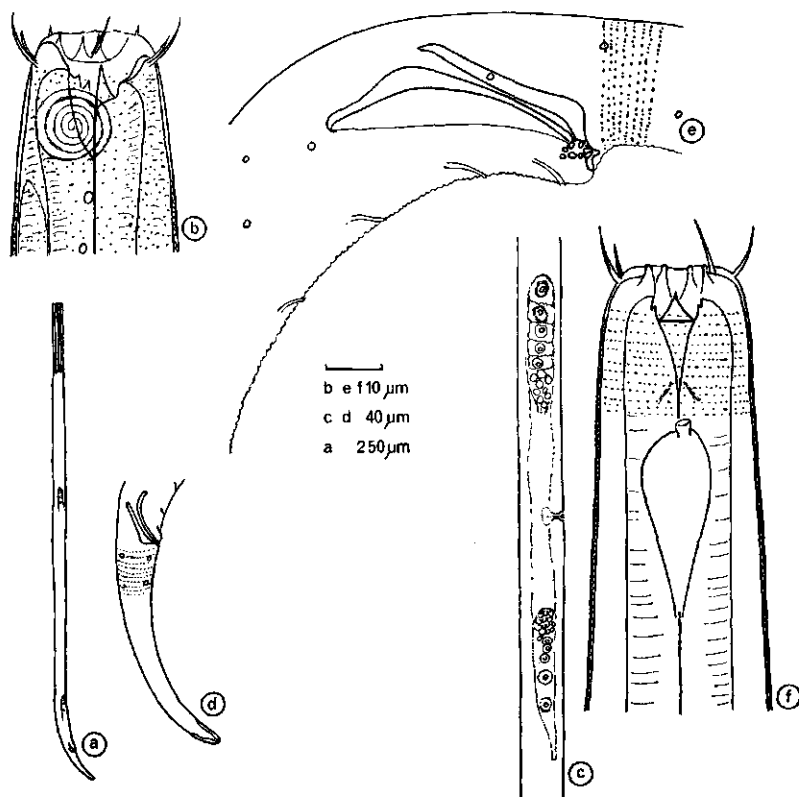


Fig. 20. *Paracanthonchus sabulicolus* sp. n.

a) entire male, b) male head, c) ovaries, d) male tail, e) spicula, f) anterior part of female

however, described a male specimen as *N. cf. corcundus* in which the morphometrical ratios agree with the Ems specimens and which specimen carries a preanal seta and tail setae as well, close affinity to *N. meeki* WARWICK 1971 exists as well; this species bears setae according to the arrangement in the Ems specimens, but this species is shorter and has fewer preanal papillae.

Parueanthonechus sabulicolus sp. n. (Fig. 20)

Number of specimens isolated: dozens of males, females and larvae

Description:

	l	a	b	c	v	sp	t
♂	1.7	53	6.8	12.1		1.9	4.4
♂	1.6	49	6.5	11.1		1.9	4.4
♂	1.5	42	6.4	11.1		1.9	4.2
♀	1.8	56	6.5	12.2	54		5.8
♀	1.8	35	6.5	12.2	54		4.6
♀	1.7	43	6.3	9.9	54		5.2

Body shape: cylindrical, tapering towards the ends; head diameter $0.7 \times$ diameter at end of esophagus
Cuticle: annulated and punctated without lateral differentiation; large dots present all over the body;

4 anterior dots arranged laterally in one row, on the rest of the body two sublateral rows are present while the arrangement in the tail is irregular; few scattered setae occur all over the body

Buccal cavity: cyathiform, large dominating dorsal tooth, 2 pointed subventral teeth

Labial papillae: often indistinct because of retracted buccal cavity

Cephalic setae: 10, of which the 6 longer setae measure $0.45 \times$ head diameter; 4 of these setae are paired with subequal setae, length $0.30 \times$ head diameter

Amphids: located $0.5 \times$ head diameter from anterior end; circular, width $0.45 \times$ corresponding body diameter, spirialized, 5 turns

Esophagus: cylindrical slightly dilated posteriorly

Excretory pore: often very conspicuous, located $1.2 \times$ head diameter from anterior end

Nerve ring: not observed

Ovaries: amphidelphic, reflexed

Spicula: curved, with a very irregular width and a proximal hook, length $40-45 \mu\text{m}$

Gubernaculum: distally truncate, subdistal accessory piece present with laterally located assembly of up to 12 small teeth; $0.7 \times$ spicula length

Preanal tubuli: 4, with increasing distance from each other in anterior direction; the most anterior tubulus located at $60 \mu\text{m}$ from the cloaca

Tail: conical, without setae

Discussion: this species did not agree with any already described species; it is closely related to *P. caecus* BASTIAN 1865, however the males have only 4 preanal tubuli, the excretory pore is located more anteriorly and ovoviviparous females have not been observed.

Bathylaimus cf. capacosus HOPPER 1962

Number of specimens isolated: 3 males

Discussion: this species has been described by HOPPER 1962, 1968; RIEMANN 1966 described specimens from the Elbe estuary which were closely related to this species

but of which the females deviated in details from the original description; unfortunately no female individuals were isolated from the Ems estuary, but the 3 males were identical with RIEMANN's description and if compared with HOPPER's description 2 slight differences were noticed: no setae on a level with the amphids were observed and segmentation of cephalic setae is inconspicuous; lengths and morphometrical ratios are more according with HOPPER's specimens than with RIEMANN's specimens.

	l	a	b	c	t	sp	cs ₁	cs ₂	hd	amw	amd
♂	1.6	50	5.2	16.5	3.3	1.3	0.7	1.5	0.6	0.25	2.3
						(34 μ m)					
♂	1.5	50	5.0	16.7	3.3	1.3	0.8	1.6	0.6	0.25	1.6
						(31 μ m)					
♂	1.6	50	5.1	16.5	3.3	?	0.7	1.3	0.7	?	1.5

Rhabdocoma sp. (Fig. 21)

Number of specimens isolated: 1 larva

Description:

	l	a	b	c	t
lv	1.3	68	7.1	2.7	38

Body shape: cylindrical, slender, tapering towards the ends, with a very long tail which measures about one third of the total length

Cuticle: smooth, no setae except in the anterior region

Head: not set off, width $0.6 \times$ diameter at esophagus end

Buccal cavity: conical

Labial papillae: minute

Cephalic setae: 6, articulation indistinct, length $0.75 \times$ head diameter

Amphids: typical, 2 concentric circles, width $0.35 \times$ corresponding body diameter, $1.7 \times$ head diameter from anterior end

Cervical setae: 4, located just anterior to the amphids, length $0.45 \times$ corresponding body diameter

Esophagus: cylindrical, without terminal bulb or dilation

Tail: width of the posterior cylindrical part $0.5 \times$ anal diameter, without setae

Discussion: only RIEMANN 1966 mentions representatives from the genus *Rhabdocoma* isolated in north-west Europe; the Ems specimen is closely related to *Rhabdocoma* species

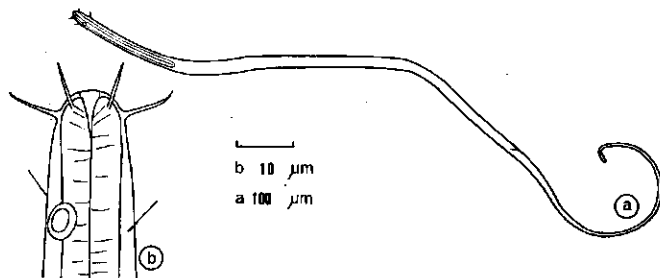


Fig. 21. *Rhabdocoma* sp.

a) entire larva, b) larva head

Nr. 1 RIEMANN 1966; position and width of the amphids, position and length of cervical setae, total length and width and length of the tail agree with RIEMANN's specimen; however the cephalic setae of the Ems specimen are shorter, indistinctly articulated and post-amphidial setae have not been observed; Ems as well as Elbe specimens are closely related to *Rhabdocoma americana* COBB 1920; the length of the cephalic setae of the Ems specimen corresponds with COBB's species; however, since only a larval stage has been isolated a species identification could not be made though synonymity with *R. americana* seems probable.

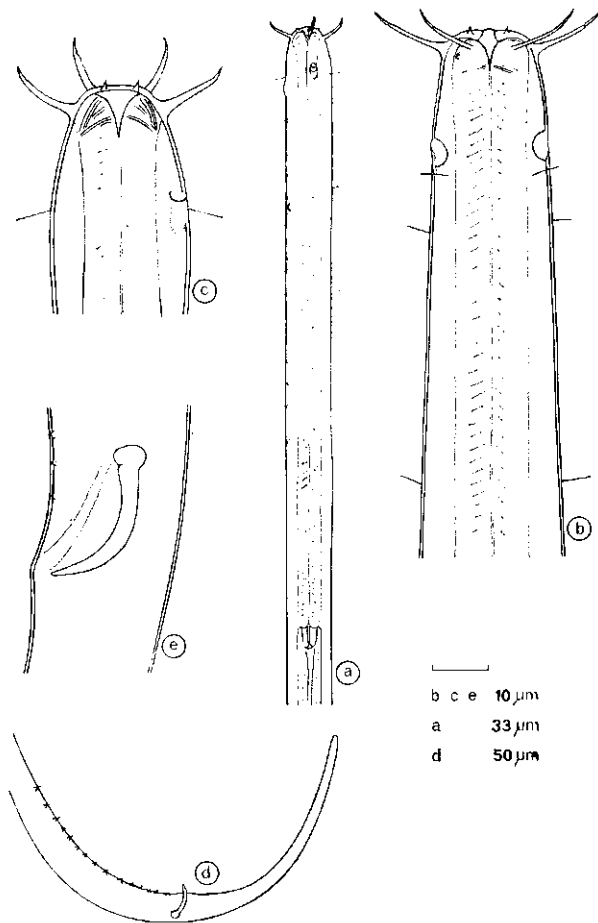


Fig. 22. *Trefusia multipapillatum* sp. n.

a) anterior part of male, b) male head, c) female head, d) male tail, e) spicula

Trefusia multipapillatum sp. n. (Fig. 22)

Number of specimens isolated: dozens of males and larvae, 4 females

Description:

	l	a	b	c	v	sp	t
♂	2.9	129	10.0	17.3		1.3 (30 μ m)	7.4
♂	3.3	112	10.1	15.8		1.1 (31 μ m)	8.0
♂	3.1	112	8.9	15.7		1.3 (30 μ m)	8.6
♀	3.0	126	10.1	15.2	58		11.1
♀	3.1	126	9.6	16.0	60		12.0
♀	2.8	120	9.2	12.8	57		11.3

Body shape: cylindrical, tapering towards the ends, slender, irregularly widened just posterior to the amphids, anterior attenuation starts on a level with the amphids

Cuticle: smooth, no setae except cephalic setae and setae in the esophageal zone

Head: set off, width $0.7 \times$ diameter at end of esophagus

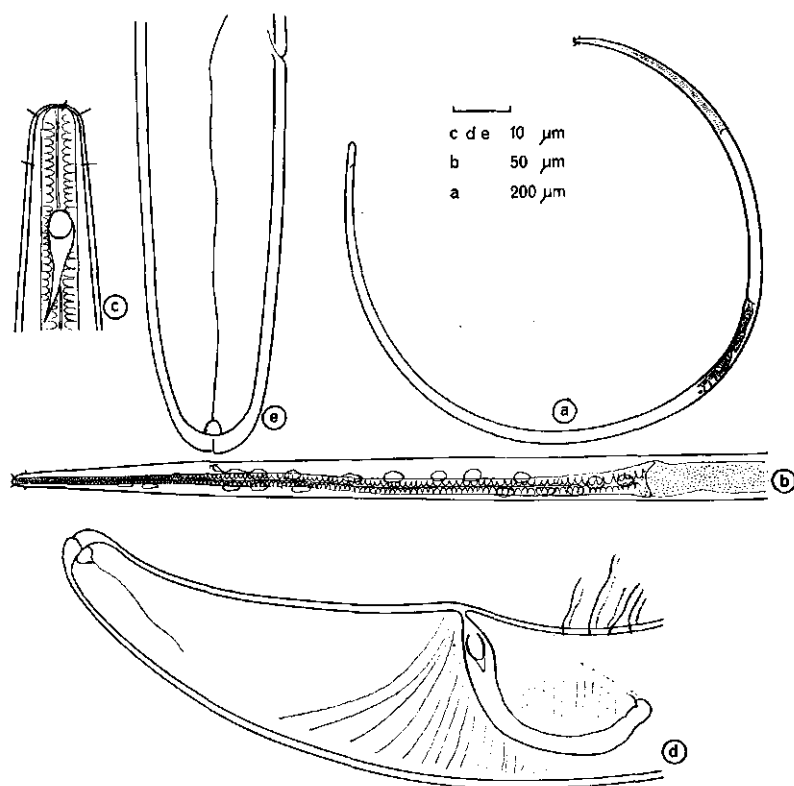


Fig. 23. *Nemanema cylindratICAUDATUM*

a) entire female, b) anterior part of female, c) male head, d) male tail, e) female tail

Buccal cavity: very small, conical

Labial papillae: distinct, short

Cephalic setae: 6, articulated, length $0.8 \times$ head diameter

Amphids: $1.0 - 1.5 \times$ head diameter from anterior end; variable pouchlike shape

Subcephalic setae: 4, on a level with or just behind the amphids

Cervical papillae: 11 - 16 minute papillae have been observed at the ventral side of the esophageal zone of males; most anteriorly located papilla just posterior to the amphids, posterior papilla well before the esophagus end

Esophagus: cylindrical with anterior dilation, without terminal bulb; besides subcephalic setae, up to 2 pairs of opposite setae present in esophageal zone

Excretory pore: distinct, at $0.2 \times$ esophagus length from anterior end

Nerve ring: not observed

Cardiac: elongate

Ovaries: amphidelphic, reflexed

Spicula: slender and curved, proximally enlarged

Preanal papillae in males: 12 - 18

Gubernaculum: absent

Tail: gradually attenuating, tip rounded, width of the tip $0.3 \times$ anal diameter, no setae

Discussion: the species described is closely related to *T. litoralis* ALLGEN 1932, which species has been redescribed by RIEMANN 1966: Ems specimens are of about equal length as ALLGEN's species and head, amphids, setae and spicula do not differ; however the Ems specimens are more slender, have shorter tails and possess more than twice as many preanal papillae; close affinity to *T. schiomeri* ORT 1977 exists as well: numbers

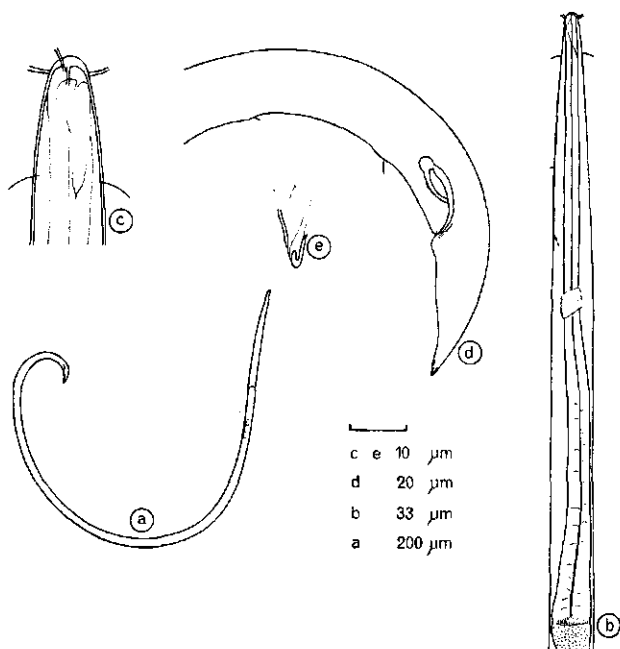


Fig. 24. *Thalassolaimus tardus*

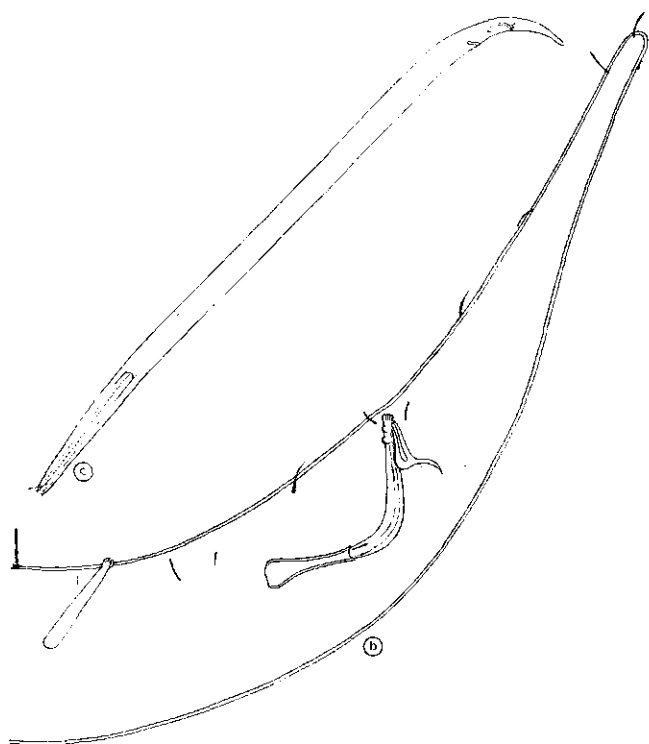
a) entire male, b) anterior part of male, c) male head, d) male tail, e) tip of male tail



Fig. 25. *Mesacanthion audax*
a) male head, b) male tail, c) entire male

of cervical as well as preanal papillae are about the same in both species, the tails have equal lengths, but Ott's species is shorter, less slender and has a different, more compact spiculum.

<i>T. species</i>	<i>multipapillatum</i>	<i>schiemeri</i>	<i>litoralis</i> (ALLGEN)	(RIEMANN)
length	2.8—3.3	1.8—2.6	2.5	2.9
a	112—129	45—57	70	87
t	7.4—12.0	5.5—6.2	15—20	14
spicula	slender	thick	slender	slender
sp. length	30 μm	53—55 μm	30 μm	34 μm
cervical papillae	11—16	15		11
preanal papillae	12—18	14		5—7



Nemanema cylindratICAUDATUM DE MAN 1922 (Fig. 23)

Number of specimens isolated: 3 males, 2 females, 5 larvae

Description:

	l	a	b	c	v	sp	t
♂	2.6	74	5.5	41		1.6 (37 μm)	2.5
♂	3.1	73	5.9	48		1.6 (40 μm)	2.5
♂	3.0	90	6.1	47		1.5 (37 μm)	2.5
♀	3.4	69	5.6	45	34		2.9
♀	3.0	71	5.4	46	35		2.5

Body shape: cylindrical; with a very short, less attenuated, bluntly rounded tail and a conspicuously attenuating anterior part; neck diameter 0.3 × diameter at end of esophagus

Cuticle: smooth, no body setae except cervical setae and preanal setae in males; subcuticular large cells present, mainly in esophageal and preanal region

Head: not set off, buccal cavity minute

Anterior setae: 6, length 0.25 × corresponding body diameter

Subanterior setae: 4, length 0.15 × corresponding body diameter

Amphids: pouchlike, 1.6 × corresponding body diameter from anterior end

Esophagus: widening in posterior direction

Excretory pore: distinct, located 0.3 × esophagus length from anterior end, in males and in females

Nerve ring: not observed

Ovary: postdelphic, reflexed

Spicula: curved

Gubernaculum: oval ring

Preanal setae: in males a cluster of 4 pairs of setae with different lengths is present

Male anal zone: cuticle conspicuously striated

Tail: with a distinct terminal aperture, tail tip width $0.35 \times$ anal diameter

Discussion: the specimens described correspond in all respects with STEKHOVEN's description 1935; however, the distinct preanal setae in the males have not been described before; these setae have been observed in all male specimens, which were isolated from different sample stations on different dates, so the suspicion that these setae are artefacts such as fungal hyphae is rejected.

Oxystomina unguiculata STEKHOVEN 1935

Number of specimens isolated: 1 female

Discussion: the specimen isolated is identical with STEKHOVEN's description; on a level with the amphid-apertures 2 pairs of very small setae are present which can be overlooked easily; STEKHOVEN does not mention these setae, however TIMM 1967 has also observed them in estuarine specimens from the Sunderbans, East Pakistan, the present Bangla Desh.

Thalassolaimus tardus DE MAN 1893 (Fig. 24)

Number of specimens isolated: 1 male, 2 females

Description:

	l	a	b	c	v	sp	t
♂	2.1	83	6.1	35		1.2 (29 μ m)	2.6
♀	2.3	88	6.8	33	22		3.5
♀	1.6	63	5.7	28	30		3.6

Body shape: cylindrical, gradually tapering towards anterior end, more abruptly towards posterior end; tail very short

Cuticle: smooth, no setae except cephalic, cervical and male preanal setae

Head: not set off, diameter $0.25 \times$ diameter at end of esophagus

Buccal cavity: practically absent, walls of the anterior part of the esophagus lumen sclerotized, forming a slitlike cavity

Cephalic setae: 6 pairs of setae of equal length, $0.65 \times$ corresponding head diameter

Amphids: typical shape, length $3 \times$ head diameter, aperture located slightly posterior to the insertions of the cephalic setae

Cervical setae: inserted on a level with the posterior end of the amphids; 4, length $0.5 \times$ corresponding body diameter

Excretory pore: located $0.35-0.40 \times$ esophagus length from anterior end

Nerve ring: at $0.45-0.50 \times$ esophagus length from anterior end, just posterior to the excretory pore

Esophagus: gradually dilating in posterior direction

Ovary: postdelphic, reflexed

Spicula: consisting of 2 plates, connected by the proximal knob

Gubernaculum: small, parallel to the distal end of the spicula

Preal anal papillae: 2 slight elevations, provided with very thin setae which can easily be overlooked
 Tail: short, conical, tip provided with caudal capsule, glands with ventrally located subterminal aperture

Discussion: the specimens described correspond in all respects with the description by DE MAN 1907; dimensions, morphometrical ratios, position and size of different structures are identical; however, in DE MAN's description from 1893 and in STEKHOVEN 1935, the authors do not mention the presence of the caudal capsule nor the preanal setae in the male; WIESER 1953 considers *T. tardus* to be characterized by the absence of a caudal capsule, based on the insufficient information by DE MAN and by STEKHOVEN; probably *T. mediterraneus* VITIELLO 1970 is synonymous with *T. tardus*; VITIELLO's specimens agree in many respects with DE MAN's description, the tails, however, are a little bit shorter, the amphids less elongated and the excretory pore is located more anteriorly.

Mesacanthion audax DITLEVSEN 1918 (Fig. 25)

Number of specimens isolated: 1 male

Description:

	l	a	b	c	sp	t
♂	4.0	33	5.1	16.2	1.9	3.6

Body shape: gradually tapering towards the ends

Cuticle: smooth, no body setae except in cephalic, cervical, preanal and tail region

Head: set off, cuticle thickened, width $0.30 \times$ diameter at end of esophagus

Buccal cavity: conical, three mandibles with median teeth

Labial setae: 6, length $0.4 \times$ head diameter

Cephalic setae: inserted on a level with the middle of the buccal cavity; the exact number of setae could not be determined because of very close parallelism of these setae; however pairs of 1 long ($1.45 \times$ head diameter) and 1 short ($1.0 \times$ head diameter) seta could be observed

Subcephalic setae: most anterior group inserted on a level with the bottom of the buccal cavity, comprising pairs of a long and a short seta; posterior group located $4 \times$ head diameter from anterior end

Esophagus: cylindrical, few, short, scattered setae occur in the esophageal zone

Amphids, nerve ring, excretory pore: not observed

Spicula: curved, a cuff is present at $0.35 \times$ total length from proximal end; lateral, at both sides 2 blunt teeth were visible and the tip of the spicula was provided with notches as well; length $142 \mu\text{m}$

Preal anal element: sticklike, at $2.5 \times$ anal diameter from anus; length $0.5 \times$ corresponding body diameter

Gubernaculum: triangular with a curved dorsal apophysis

Pre- and post anal setae: few, scattered, located ventrally and subventrally

Tail: gradually tapering, tip bluntly rounded

Discussion: the only description up to now is by DITLEVSEN 1918; the Ems specimen is identical with this description in all respects; however, DITLEVSEN did not notice that cephalic and subcephalic setae are paired as is clear from the present description.

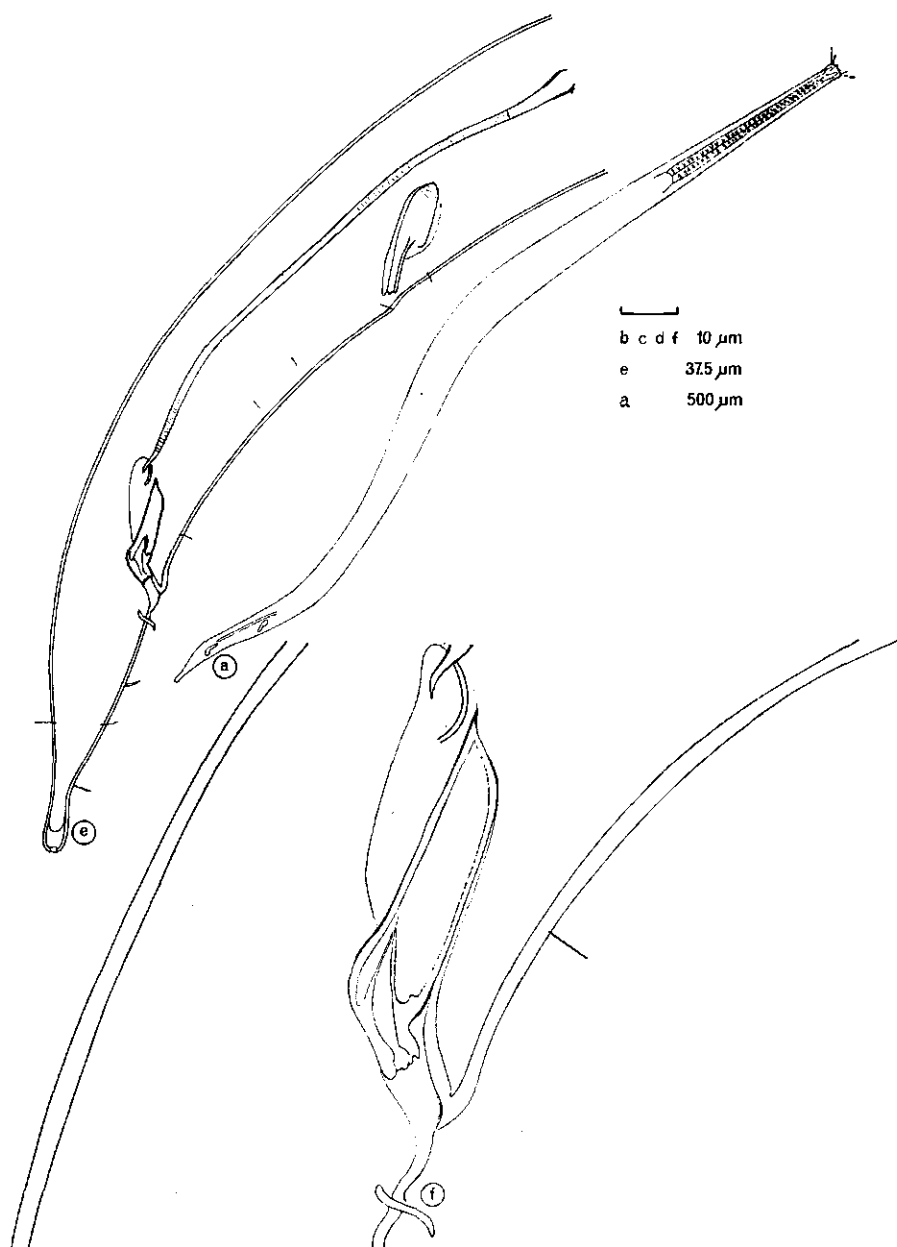
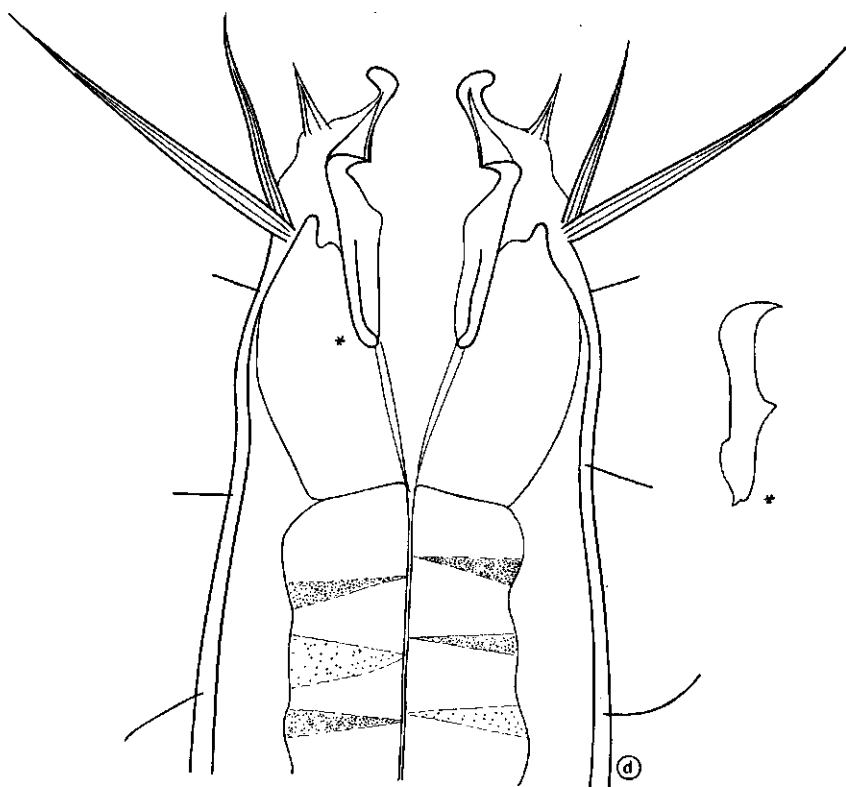
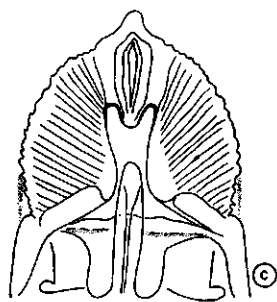
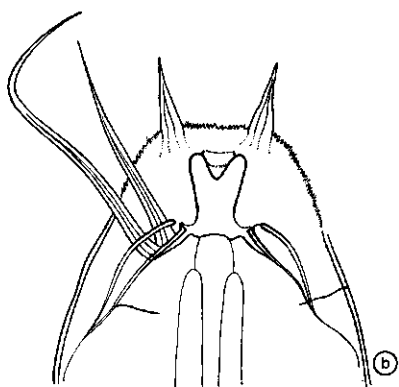


Fig. 26. *Enoploides cf. labiatus*

a) entire male, b, c, d) female head (different focus depths), e) male tail, f) spicula



Enoploides cf labiatus BÜTSCHLI 1874 (Fig. 26)

Number of specimens isolated: 6 males, 10 females, dozens of larvae

Description:

	l	a	b	c	v	sp	t
♂	3.7	22	4.7	20.5		5.0 (330 μ m)	2.7
♂	2.8	26	4.3	18.6		5.9 (300 μ m)	2.9
♂	2.8	29	4.1	17.0		5.5 (300 μ m)	2.9
♀	2.9	25	4.1	16.4	58		3.5
♀	2.5	27	4.0	15.1	57		3.3
♀	2.3	25	4.6	15.1	57		3.1

Body shape: gradually tapering towards both ends from the middle of the body; head width $0.6-0.7 \times$ diameter at end of esophagus, width of the tail tip $0.25 \times$ anal diameter

Cuticle: smooth, few short setae scattered all over the body

Head: set off

Lips: conspicuously striated, anterior ends curled outwards, shell-shaped

Labial setae: 6, length $0.25 \times$ head diameter

Cephalic setae: 6 with a length of $1 \times$ head diameter, of which 4 are paired with shorter setae, length $0.5-0.6 \times$ head diameter; posterior to these setae short, slender setae are present on a level with the middle of the buccal cavity and also on a level with the base of this cavity

Buccal cavity: conical, 3 mandibles are present, each with 2 anterior tips and a toothlike structure in the middle

Pharynx: roundish, very distinct

Nerve ring: located $0.3 \times$ esophagus length from anterior end

Amphids: not observed

Excretory pore: indistinct, aperture probably on a level with the base of the buccal cavity

Esophagus: sinuate, gradually attenuating parallel with the body width

Ovaries: amphidelphic, reflexed

Spicula: very long and slender, both spicula of equal length, retracted in fixed state; distally a sub-terminal ventrally located barbed hook is present; the spicula are striated except the terminal ends

Gubernaculum: length, $1 \times$ anal diameter; complicated, anterior to the spicula when these are protruded

Preanal element: distance to the anus $3 \times$ anal diameter, length $0.85 \times$ corresponding body diameter

Post-anal cuticular element: characteristically s-curved

Tail: claviform with mainly ventral setae

Discussion: probably because of insufficient descriptions by BÜTSCHLI and by STEKHOVEN 1935, there is much confusion about this species; STEKHOVEN 1935 and WIESER 1953 consider the species to be synonymous with *E. spiculohamatus* SCHULZ 1932, GERLACH and RIEMANN 1974, however, present both species as being different in their checklist; BÜTSCHLI described a female only and STEKHOVEN's description is a very rough one and fundamental details are not presented; SCHULZ, however, gives a description of details such as the mandibles, the male genital apparatus and the post-anal element; these structures are identical with the corresponding elements in the Ems specimens; it is concluded that it is highly probable that *E. labiatus* is synonymous with *E. spiculohamatus* and that the confusion is mainly caused by the insufficient description by STEKHOVEN.

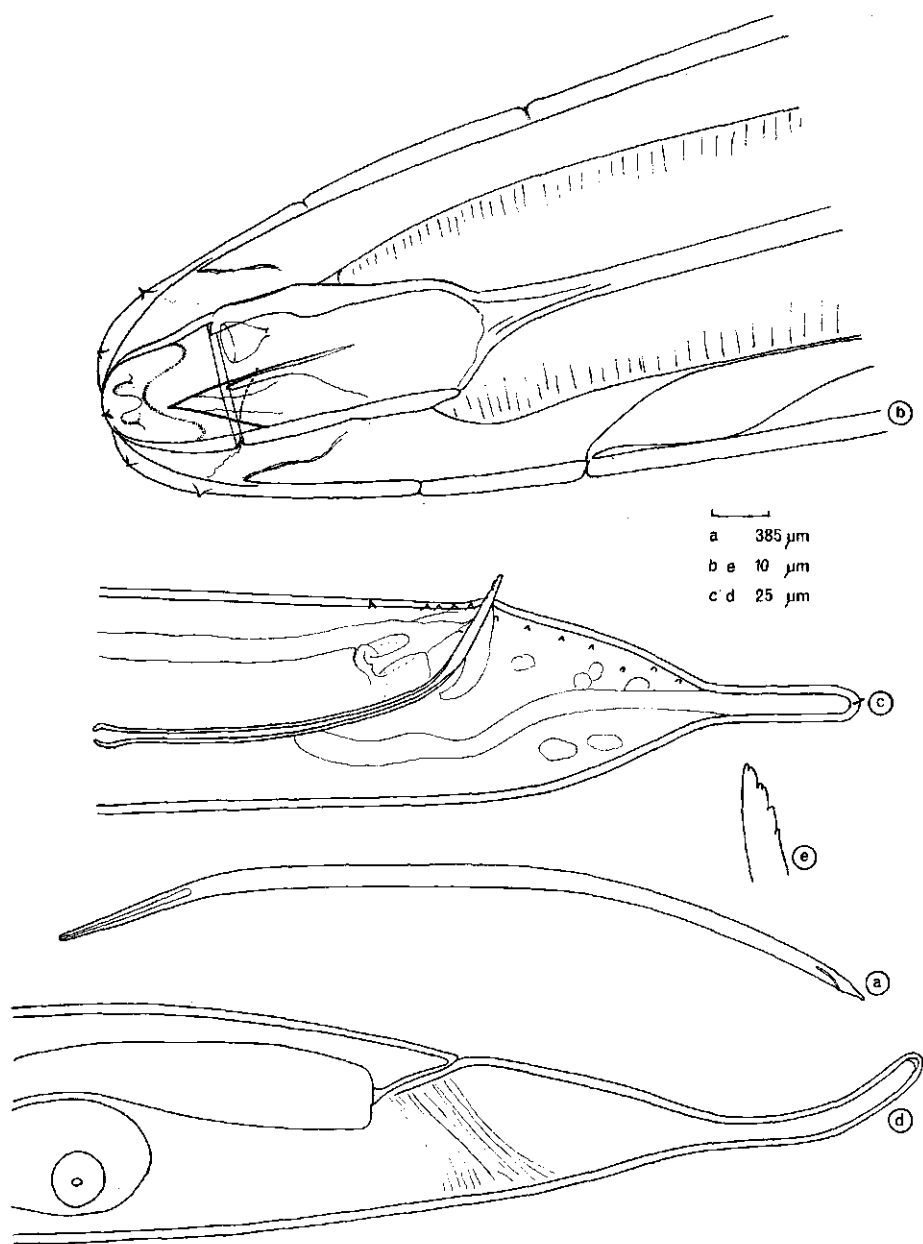


Fig. 27. *Adoncholaimus fuscus*

a) entire male, b) male head, c) male tail, d) female tail, e) spicula tip

Adoncholaimus fuscus BASTIAN 1865 (Fig. 27)

Number of specimens isolated: dozens of males, females and larvae

Description:

	l	a	b	c	v	sp	t
♂	5.1	34	6.2	28		2.4 (200 μ m)	1.9
♂	4.2	36	5.5	23		2.5 (185 μ m)	2.2
♂	6.2	42	8.3	35		2.1 (210 μ m)	1.8
♀	3.6	29	?	21	42		2.5
♀	4.2	32	6.4	26	48		2.4
♀	4.8	29	6.4	25	54		3.0

Body shape: gradually tapering towards the ends from the middle of the body

Cuticle: smooth, no setae

Head: not set off, width $0.3 \times$ diameter at end of esophagus

Labial and cephalic papillae: present

Buccal cavity: almost rectangular, length/width = 2.5, this ratio is very constant; large subventral tooth, small more posteriorly located second subventral tooth and small dorsal tooth present; buccal ring on a level with the tips of the small subventral and dorsal tooth; walls heavily sclerotized

Amphids: aperture on a level with the buccal ring

Excretory pore: located $2 \times$ head diameter from anterior end

Nerve ring: at $0.45 \times$ esophagus length from anterior end

Esophagus: dilated posteriorly

Cardia: elongate, triangular, sunk into the intestine

Ovaries: amphidelphic, reflexed

Exit pore demanian system: very conspicuous, $1.5-2.5 \times$ anal diameter anterior to the anus

Spicula: curved, proximally knobbed, very long and slender; dorsal side of the tip provided with tooth like irregularities

Gubernaculum: parallel to the spicula, solid, $0.25 \times$ spicula length

Preanal papillae: 5, the posterior 4 close together, the most anterior 1 apart

Tail: ratio conical part/slender part = 1; row of subventral papillae and short terminal seta present in male

Discussion: originally *A. fuscus* was discriminated from *A. lepidus* DE MAN 1889, among other respects, by the lack of papillae on the male tail and in the cloacal region; HOPPER 1969, however, presents a *A. fuscus* male specimen with tail papillae; the Ems specimens are characterized by the presence of tail and preanal papillae; in many male specimens these papillae, particularly the preanal papillae, were indistinct, in a few they were quite clear; probably these papillae have been overlooked up to now.

Zusammenfassung

Eine Übersicht über die Nematoden des Ems-Dollart-Ästuars

Im Rahmen eines umfangreichen Umweltforschungs-Auftrags wurde die Nematodenfauna des Ems-Ästuars untersucht. Dabei sind aus Sedimentproben der Wattflächen und der Fahrrinnen der Ems und der Westerwoldschen A 121 Arten isoliert worden. Auch die Epifauna einiger höherer Pflanzen wurde untersucht. Die folgenden Arten sind neu für die Wissenschaft: *Aegialolaimus setosa*, *Eleutherolaimus amasi*, *Paracanthonchus sabulicolus* und *Trefusia multipapillatum*. Für *Paralinho-*

moeus tenuicaudatus STEKHOVEN 1935 wird der Name *Paralinhomoeus flevensis* vorgeschlagen. Drei Arten sind nicht identifiziert worden; eine dieser Arten, *Paralinhomoeus* sp., ist wahrscheinlich neu für die Wissenschaft, wurde jedoch nicht als neue Art beschrieben, weil nur ein Exemplar vorliegt.

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CHAPTER IV

A Survey of Nematodes from the Ems Estuary
Part II: Species Assemblages and Associations

By L.A. Bouwman

ABSTRACT

The occurrence of nematode species, orders, feeding-types and species assemblages and associations and their distribution at different scales over the Ems estuary, are investigated and compared with other northwest European estuaries. The formation of species assemblages and associations is discussed in relation to feeding habits and biotope characteristics. Two main faunas were distinguished: one in the Wadden Sea, the other in the Dollart, both extending into the middle reaches of the estuary. In the lower sediment layers a characteristic fauna was found that consisted of species that were absent from, or only occasionally present in the upper sediment layers. It is concluded that faunal associations from the lower sediment layers originate from marine subtidal locations, whereas the associations from the upper sediment layers of tidal flats are specific to estuarine tidal conditions. A characteristic fauna, dominated by diatom-puncturing species was found as part of a complete ecosystem in the organically polluted tidal flats in the vicinity of the freshwater discharge-point in the Dollart. Bacteria and diatoms are both important as food sources for intertidal nematodes, though the stable part of the nematode fauna mainly feeds on bacteria while the part that fluctuates seasonally mainly feeds on diatoms.

I. INTRODUCTION

Studies have already been made of the nematode faunas of various northwest European estuaries, e.g. of the rivers Blyth (Capstick, 1959), Elbe (Riemann, 1966), Exe (Warwick, 1971) and the former Zuiderzee (De Man, 1922; Stekhoven, 1931, 1936, 1954). Gerlach (1953) has also paid much attention to coastal nematode faunas. With the exception of the Blyth estuary,

which was less thoroughly investigated, about 120 different nematode species were identified per estuary by the authors cited above, and Gerlach mentioned 190 species along salinity gradients ($0.5 \text{ ‰} \rightarrow 35 \text{ ‰ S}$) on the North Sea and Baltic coasts. Because most nematode species only occur in scattered locations and are not abundant, it is probable that the authors mentioned must have overlooked some species. The number of different nematode species per estuary is probably nearer 200. Towards the freshwater, nematode faunas become impoverished, thus the highest numbers of different species are found in the marine parts of estuaries. Warwick isolated 10 species from the upper reaches of the Exe estuary (c. 6 ‰ S), 30 from the middle reaches (c. 21 ‰ S) and 72 from the lower reaches (c. 30 ‰ S). Gerlach roughly distinguished 9 habitats characterized by different species assemblages (exposed versus sheltered; sand versus mud; Cyanophyceae, Enteromorpha spp. and Vaucheria spp. present versus absent; $0.5 \rightarrow 35 \text{ ‰ S}$). Riemann also distinguished 9 groupings of species along the longitudinal axis of the Elbe estuary. In the Blyth estuary, Capstick found that nematode associations differed less markedly along the sampled axis because the salinity gradient was less steep (c. $27 \text{ ‰} \rightarrow$ c. 31 ‰ S). Of the authors mentioned, only Capstick recorded nematode densities: in the Blyth estuary he found that density decreased up the channel from c. 180 to 50 specimens cm^{-2} , and the highest density he observed was 300 specimens cm^{-2} . These figures are still far below the highest densities recorded by Rees (1940) in a tidal mud-flat, by Teal and Wieser (1966) in a salt marsh and by Warwick and Price (1979) in an estuarine mud-flat, which were respectively, 1,000, 1,600 and 2,300 specimens cm^{-2} .

Nematode species feed selectively on bacteria, diatoms, protozoa or on larger prey (including other nematodes) or less selectively on mixtures of these food items. Direct absorption and assimilation of dissolved organic molecules has also been shown to occur among nematodes (Chia and Warwick, 1969; Lopez, Riemann and Schrage, 1979). The organism or mixture of organisms on which a species actually feeds depends on the size and armature of the buccal cavity (Wieser, 1953). Small cavities without armature probably only permit feeding on bacteria, whereas larger cavities also permit larger particles such as diatoms and protozoa to be ingested. Buccal armature brings the possibility of puncturing prey and ingesting the contents of diatoms or, when heavy armature is present, the contents of other nematodes. However, only a few nematode

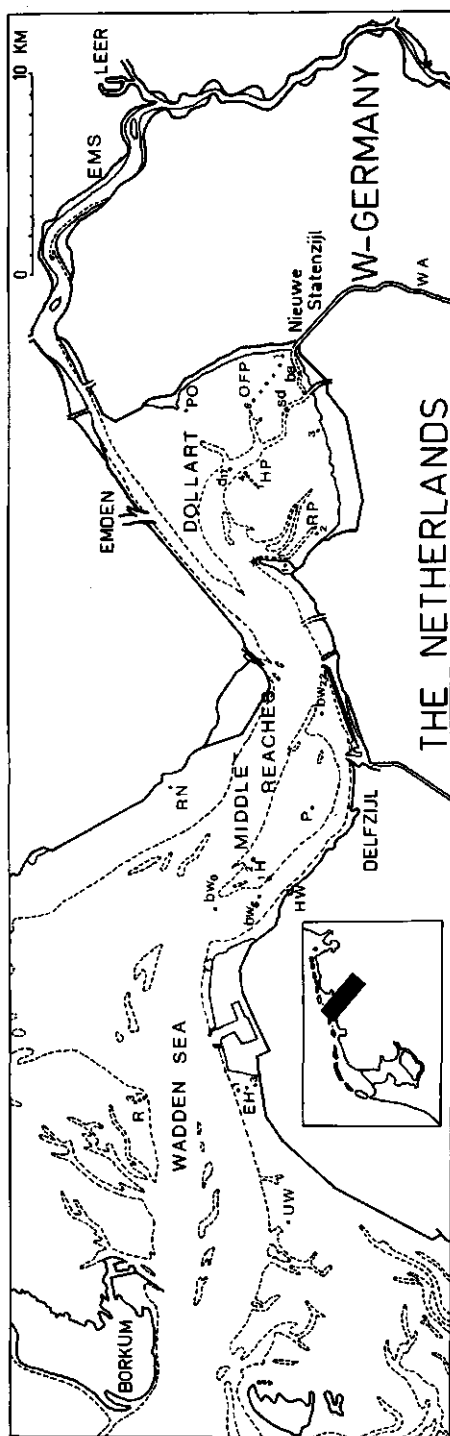


Fig. 1. Map of the Ems estuary showing sampling stations and transects.

UW = Uithuizerwad permanent quadrat (100m/100m)

R = Ransel transect, 3 stations (L = 300 m)

EH = Eemshaven transect, 3 sampling zones (L = 700 m); OFF = Oost Friesche Plaat transect, 6

EH₂ permanent quadrat (10 m/10 m)

H = Hond transect, 2 stations (L = 1,500 m)

HW = Hoogwatum permanent quadrat (10 m/10 m)

RN = Rysumer Nacken permanent quadrat (10 m/10 m)

P = Paap permanent quadrat (10 m/10 m)

RP = Reiderplaat, 3 stations; RP₂ permanent quadrat

(10 m/10 m)

HP = Heringsplaat transect, 4 stations (L = 450 m)

OFF = Oost Friesche Plaat transect, 6

stations (L = 2,500 m); OFF₂

permanent quadrat (10 m/10 m)

Po = Pogum permanent quadrat (10m/10 m)

* = Reider peninsula

species have been observed when actually feeding (von Thun, 1968; Tietjen et al., 1970; Romeyn et al., 1983). These observations agree with Wieser's classification into 4 feeding-types: selective deposit feeders (bacteria), non-selective deposit feeders (bacteria, protozoa, diatoms), epigrowth feeders (bacteria, diatoms, diatom contents) and omnivores (all food items plus larger prey e.g. other nematodes). The epigrowth feeders graze upon the epiflora or epifauna on the surface of solid substrata whereas deposit feeders ingest prey out of the suspension in the interstices of the sediment. Generally, nematode associations are comprised of representatives of the 4 feeding-types, though the relative proportions depend on the type of habitat. Sheltered tidal flats, which constitute the main part of estuaries, allow bacteria and diatoms to grow abundantly in their surface layers. Therefore in such areas, non-selective and epigrowth feeders predominate whereas omnivores predominate in the more wave-exposed habitats (Wieser, 1953, 1959).

Little is known about the vertical distribution of species within the sediment. Ott (1972) studied the vertical distribution of nematodes in the sediment of an intertidal sand-flat and observed that the lower sediment layers were inhabited by a characteristic nematode fauna and not by an impoverished surface fauna. Also the surface of macrophytes that live in tidal areas is colonized by particular species that are not present in the nearby sediments (Otto, 1936; Gerlach, 1953; Ohm, 1964; Glowacka et al., 1976).

Knowledge about seasonal fluctuations in the community structure of estuarine nematode associations is also sparse, probably because numerous faunal analyses are necessary to follow shifts within the associations. Authors (Warwick, 1970; Juario, 1975) generally agree that in sublittoral nematode faunas, species compositions do not change systematically over the year and that the species belonging to these associations probably breed throughout the year as well. Abiotic conditions in sublittoral sediments do not vary so much because they are buffered by the overlying water column. In tidal areas, however, seasonal influences are not mitigated by the water column and thus the flora and fauna of the sediment are influenced directly. Under the climatic conditions prevailing in northwest Europe, macrozoobenthos and microphytobenthos show definite seasonal cycles. Generally, microphytobenthos shows a production peak in early spring which extends into the summer (Cadée and Hegeman, 1974; Colijn and

De Jonge, in press). Therefore it is not surprising that Tietjen (1964) observed a seasonal succession within the nematode fauna from an estuarine habitat in New England, where epigrowth feeders predominate in spring and summer and deposit feeders and omnivores predominate in autumn and winter. Skoollum and Gerlach (1971) analysed seasonal fluctuations in the abundance of a number of intertidal species and distinguished also specific peaks in different seasons.

The research on the nematode fauna from the Ems estuary reported in this paper was carried out from 1975 to 1980. The distribution of the species over the estuary, and their taxonomy, were discussed in a previous paper (Bouwman, 1981). In this paper attention is mainly focused on the distribution of assemblages and associations of nematode species at different scales: a) distribution over the estuary (Dollart, middle reaches, Wadden Sea); b) distribution within these 3 zones; c) distribution along transects up to several kms long; d) vertical distribution within the sediment. These distributions are also described in terms of different orders and in terms of groups of species classified according to feeding-type. Special attention is paid to: e) the nematode fauna of the bottom of the channel; f) the epifauna on the surface of the most common macrophytes in the area. Seasonal fluctuations in the composition of the nematode associations are analysed and correlated with fluctuations in the proportion of certain feeding-types. The size of sample needed to ensure that the sample is representative of the real population is discussed in connection with the identification of species associations and their diversity. Finally, special attention is focused on the nematode fauna in the vicinity of the waste-water discharge-point at Nieuwe Statenzijl (Fig. 1).

2. ENVIRONMENTAL CONDITIONS IN THE EMS ESTUARY

Basic information on the Ems estuary was given by the author in an earlier paper (Bouwman, 1981) and by Van Es et al. (1980). The following environmental conditions determine whether or not a nematode fauna will develop in a certain habitat and what the community structure will be: the presence of interstitial water and its salinity and oxygen content; median grain size and grain size distribution of the sediment; current velocity of the overlying water; duration of tidal emersion, correlated with the irradiance; frequency of stress situations e.g. anaerobic conditions, presence of free hydrogen sulfide and fluctuations in salinity and in temperature.

Basically, nematodes need a solid substratum, water, oxygen and food, whereas conditions such as salinity, sediment characteristics, current velocity of the overlying water, frequency and nature of stress situations, composition, quality and amount of food determine which species will constitute the nematode fauna in a particular habitat.

Table 1. Sediment characteristics from 6 sampling stations as determined by the Bedrijfslaboratorium voor grond- en gewasonderzoek, Oosterbeek, The Netherlands

Station	Sediment composition (weight percentages)				Median grain size (μm)	Sorting coefficient Φ	Phi quartile of skewness SKQ Φ	Degree of Sorting
	Organic carbon	CaO_3	Particles < 16 μm	Particles > 16 μm				
Eemshaven 2 (EH)	0.1	4.0	1.7	94.2	125	0.08	+0.03	good
Hoogwatum (HW)	1.9	11.9	15.8	70.4	95	0.75	+0.35	good
Paap (P)	0.8	6.0	5.3	87.9	117	0.38	+0.23	good
Reiderplaat 2 (RP)	1.6	8.3	20.4	69.7	65	0.73	+0.23	good
Heringsplaat 1 (HP)	0.4	3.9	4.0	91.7	129	0.13	+0.08	good
Oost Friesche Plaat 2 (OFF)	2.7	7.7	28.7	60.9	58	1.55	+0.90	moderate

Table 1 shows sediment characteristics from six sampling stations (Fig. 1). At all stations the sediment mainly consists of very fine sand (grain size 59-129 μm). The sediments are wellsorted, except at station OFF₂, where the sediment must be described as moderately sorted because of the presence of a considerable amount of badly-sorted small particles. The amounts of small particles (< 16 μm) in the sediment from different sampling stations differ greatly. The sediment from stations HW, RP₂ and OFF₂ contains a large amount of small particles, and is therefore very soft and muddy, whereas the sediment from the other stations contains fewer small particles and is more cohesive and sandy.

Table 2 presents mean, minimum and maximum salinities as measured by means of conductive measurements (Plessey, model 623 ON, Laboratory Salinometer) in the water retained in tidal flat-pools sampled during low tide. At each of the 6 stations salinity was measured at least 20 times over a period of 3 years. The table indicates that the sampled habitats range from almost marine to nearly freshwater conditions. It is evident that salinities below 10 ‰ S can occur from the mouth of the estuary to the vicinity of the point of fresh-

water discharge at Nieuwe Statenzijl. Obviously, the tidal

Table 2. Mean, minimum and maximum salinities as measured by means of conductivity measurements in the water retained in tidal flat pools and sampled during low tide

Station	Mean salinity (‰)	Min. S	Max. S
Eemshaven 2	28.55 ± 2.65	23.97	32.15
Hoogwatum	25.31 ± 5.08	8.60	31.13
Paap	22.88 ± 5.07	9.90	29.56
Reiderplaat 2	17.89 ± 6.04	8.04	29.72
Heringsplaat 1	18.58 ± 5.13	10.30	25.64
Oost Friesche Plaat 2	13.60 ± 4.96	3.49	20.78

flats in the middle reaches and in the Dollart, particularly at station OFP₂, experience greater fluctuations in salinity than the tidal flats in the Wadden Sea. It should be noticed that chlorometric measurements according to Mohr give much lower values for station OFP₂: 0.5 → 4.5 ‰ Cl⁻.

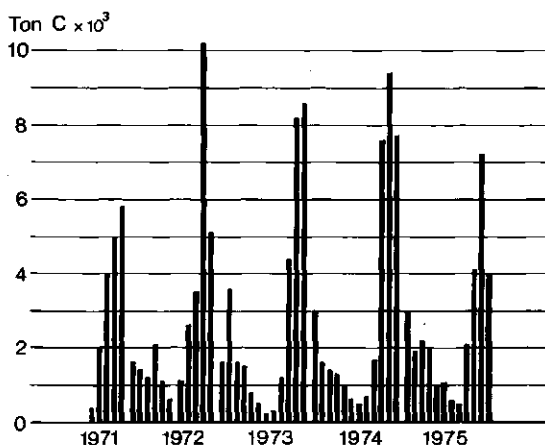
Vast amounts of approximately 30.10⁶ kg carbon (Van Es, 1977) are discharged into the estuary annually, mainly in autumn. These waste materials originate from a potato-flour industry that discharges its effluent into a small river, the Westerwoldse A, which enters the estuary at Nieuwe Statenzijl (Bouwman, 1981). The processing of the potatoes begins in September and therefore the discharge is mainly concentrated in autumn (Table 3). This waste-water regularly causes anaerobic conditions in a considerable part of the Dollart, but the tidal movements that allow the flats to emerge twice daily enable the surface layers of the tidal flats to reoxidize (Van Es et al., 1980). Thus all tidal flats in the estuary have oxidized surface layers, though at stations OFP₁ and OFP₂ the oxidized zone is only about 2 mm thick.

MATERIALS AND METHODS

Sampling methods are described in Bouwman (1981).

In this paper the term "assemblage" is used to describe species compositions that were not actually found in the field but have been assembled from various real associations (for example: the assemblage of species from the Wadden Sea). The term "association" is used for real species compositions, ac-

Table 3. Monthly discharge at Nieuwe Statenzijl of organic materials as tons of carbon (data provided by the Rijksinstituut voor Zuivering van Afvalwater)



tually present in samples from the field (for example: the association of species at station EH₀₋₁ cm. 8.1., 1978).

Faunal affinity (similarity) between assemblages/associations of nematodes was calculated on the basis of percentage of similarity. The similarity between 2 assemblages/associations can be found by comparing the percentage dominance of their constituent species and calculating the element common to both populations, i.e.,

$$\% \text{ similarity} = \frac{\sum \text{common}}{\sum \text{species}} \times 100$$

Distribution of nematodes in the sediment is aggregated for total numbers as well as for numbers per species. Therefore faunal associations from replicate sediment samples from the same habitat differ. However, along estuarine gradients, the species composition of nematode associations changes systematically. Thus the associations change qualitatively towards seawalls and low tide levels, parallel with the salinity gradient, vertically within the sediment, and in certain cases, over time (Capstick, 1959; Gerlach, 1953; Wieser, 1959a; Tietjen, 1969; Warwick, 1971; Ott, 1972; Platt, 1977). To ensure that the nematode species compositions isolated from sediment samples from this discontinuous estuarine system are representative of actual nematode associations, the following sample analyses were done. Ten random sediment samples per

quadrat were taken from stations UW (100x100 m), HW (10x10 m) and OFP₂ (10x10 m). The stations are located in the middle of tidal flats and the sediment surface within a quadrat had apparently similar sedimentological and biological characteristics. First, samples were cut vertically into slices, as usual, and the faunal similarity between various layers was checked. If the fauna located in the upper sediment layers differed considerably (> 60%) from the faunas located more deeply, two or three nematode associations were distinguished in the vertical plane. The degree of faunal affinity between single samples from one sediment-zone was calculated, as well as the affinity between all possible independent combinations of samples. From the results of these manipulations the deviation from the real nematode community structure was calculated for single samples with a fixed number of nematodes and for different sample combinations.

For the characterization of nematode assemblages from the three distinguished estuarine zones, results of faunal analyses from different stations were combined, irrespective of the affinity between the combined associations, the sampling dates and the vertical location of the associations.

However, for the characterization of nematode associations along transects, replicate samples from the same station or samples from different stations were combined only when the faunal affinity between the nematode samples was $\geq 60\%$. For the sake of convenience the following criteria were used in this research: nematode associations were considered not to differ if their affinity was at least 60%, to be related if the overlap ranged from 40 to 60% and to differ if the overlap was less than 40%.

Diversity indices can be used to characterize nematode associations and to describe faunal gradients. Such indices reflect certain aspects of the community structure, such as number of different species and distribution of specimens over the species. Diversity increases when the number of different species increases and when specimens are more equally distributed over the species. For practical reasons the following index was used:

$$D = C \cdot (100 - \sqrt{f_1^2 + f_2^2 + \dots + f_n^2})$$

$C \leq D \leq 100$ = diversity index

f_1 = relative frequency (%) of a particular species in an association

n = number of different species in an association

C = correction factor for sample size

for maximum diversity, i.e. all specimens belong to different species, C has such a value that $D = 100$

for 50 specimens (minimum sample size used) $C = 1.165$, for 200 specimens (maximum sample size used) $C = 1.076$

for a monoculture, comprising specimens belonging to 1 species, $D = 0$.

Remarks on the actual ingestion of food items are not always supported by data in the text but are mainly based on the author's microscopic observations on the feeding behaviour of species in agar cultures.

Key to the abbreviations used:

A = Araeolaimida, M = Monhysterida, D = Desmodorida, C = Chromadorida, E = Enoplida, R = Rhabditida, T = Tylenchida; 1A = selective deposit feeder, 1B = non-selective deposit feeder, 2A = epigrowth feeder, 2B = omnivore (predator).
E=Europe, w.d. = widely distributed.

4. RESULTS

4.1. Sample size, similarity (affinity) and diversity

Species analyses and affinity between replicate samples from quadrats UW, HW and OFP₂ (see Fig. 1) are presented in Table 4. From this table it is evident that the fauna from the upper sediment layers differs considerably from the fauna located more deeply. The similarity between nematode associations from the surface layers and from the zones below the surface was less than 40% at stations UW and HW. According to the criteria described earlier, it is justifiable to distinguish between the faunas from different layers. The majority of species from the surface layers did not occur in the sediment zones below the surface layers, and vice versa. However, predominant species were occasionally isolated outside their favoured layer. Similarity between single samples and sample combinations was calculated for the quadrats investigated (Table 4, Fig. 2). It is clear that enlarging the sample size increases similarity between samples; however, similarity increases only slightly when more than 3 samples are combined. For stations UW₀₋₂ and 3-8cm and HW_{0.0-0.5} cm, combinations of 3 samples with altogether about 120 specimens differed by about 30%, on average, between each other and differed by 20%, on average, from the species composition of the combination of 10 samples. The indices of diversity of the nematode fauna

Table 4. Vertical distribution of nematode specimens over species, orders and feeding-types in sediment-layers from different depths. Faunal analysis from the quadrats located in the middle of tidal flats in the Wadden Sea (UW), the middle reaches (HW) and the Dollart (OFF₂). Combined results from ten samples, taken 9.12.1975 (UW), 20.5.1975 (HW), 17.5.1979 (OFF₂).

Uithuizerwad (UW)	sediment layer (cm)			Hoogwatum (HW)		sed. l. (cm)		Oost Friesche Plaatz, (OFF ₂)		sed. l. (cm)	
	0-2	3-8	> 8			0.0-0.5				0.0-0.3	
Number of specimens identified	420	320	130	Number of specimens identified		450		240		500	
Species	Species			Species		Species		Species		Species	
<i>Viscosia rustica</i>	37%	1%	4%	<i>Paracanthonechus caseus</i>	22%	0%	0%	<i>Eudiplogaster paramatus</i>	85%		
<i>Pomponema sedecima</i>	7	2	1	<i>Necochromadora poeatlosoma</i>	14	+	+	<i>Dichromadora geophila</i>	8		
<i>Necochromadora trichophora</i>	7	23	3	<i>Atrochomadora micro-</i>	11	+	+	<i>Adoncholaimus thalasso-</i>	3		
				<i>latma</i>				<i>phygas</i>			
<i>Hypondontolaimus setosus</i>	6	+	+	<i>Eleutherochlamys stenosoma</i>	7	0	0	<i>Leptolaimus papilliger</i>	2		
<i>Sphaerolaimus balticus</i>	5	0	0	<i>Viscosia viscosa</i>	6	0	0	<i>Anoplostoma viviparum</i>	1		
<i>Monoposthia mirabilis</i>	2	24	2	<i>Daptonema setosum</i>	5	0	0	<i>Microchlamys globiceps</i>	+		
<i>Sabatieria longispinosa</i>	1	10	15	<i>Sabatieria pulchra</i>	2	91	91	<i>Aconolaimus spinosus</i>	+		
<i>Paracanthonechus sabulicolus</i>	1	9	10	<i>Odontophora setosa</i>	3	6	6				
				Other species	30	3	3				
<i>Odontophora rectangularis</i>	+	1	20								
<i>Prochironomella longicauda</i>	+	+	18								
Other species	34	29	27	(number of other species)	18	100%	100%	No organisms > 0.3 cm			
(number of other species)	25	24	20								

Orders		Orders		Orders		Orders	
Araeolaimida	2%	3%	23%	Araeolaimida	6%	Araeolaimida	3%
Monhysterida	14	10	11	Monhysterida	29	Rhabditida	85
Desmodorida	7	33	8	Desmodorida	1	Desmodorida	+
Chromadorida	27	44	54	Chromadorida	54	Chromadorida	8
Enoplida	50	10	8	Enoplida	10	Enoplida	4
	100%	100%	100%		100%		100%
Feeding-types		Feeding-types		Feeding-types		Feeding-types	
1A	1%	6%	5%	1A	2%	1A	2%
1B	12	24	49	1B	36	1B	1
2A	33	66	41	2A	52	2A	94
2B	54	4	5	2B	10	2B	3
	100%	100%	100%		100%		100%

Affinity between faunas from different depths Affinity between faunas from different depths

1)	2)	3)	1)	2)	3)
0-2/3-8	26%	20/49	0.0-0.5 = 1.0	8%	6/22
0-2/ > 8	21%	19/45			
3-8/ > 8	46%	20/40			

- 1) depths of the sediment layers compared
- 2) affinity between the nematode associations compared
- 3) number of species in common/total number of species

of 3 combined samples from the two stations were 65 to 75. From these observations it was decided that to characterize nematode faunas that had indices of diversity of about 70, three samples with each about 40 specimens had to be combined. However, at stations $HW_{>0.5cm}$ and OFF_2 similarity between single samples was more than 80% because of the very low values (less than 20) for the diversity indices of the nematode associations at these stations. To ascertain small-scale

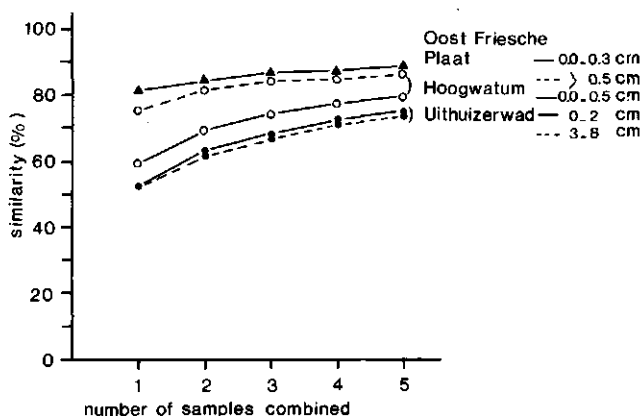


Fig. 2. Faunal similarity between replicate samples and sample combinations (see table 4).

Table 5. Number of nematode species per estuarine zone, per order, per feeding-type, and their global division (key to the abbreviations in materials and methods)

estuarine zone	number of species/order							/feeding-type				global		Σ
	A	M	D	C	E	R	T	1A	1B	2A	2B	E	w.d.	
Wadden Sea (R, UW, EH, H ₁)	5	12	9	8	9	0	0	8	15	15	5	31	12	43
Wadden Sea + middle reaches	3	8	3	3	2	0	0	3	9	6	1	9	10	19
Middle reaches (H ₁ , HW, RN, P)	0	2	0	8	2	0	0	2	2	2	1	2	5	7
Middle reaches + Dollart	0	3	1	2	1	0	0	1	3	3	0	0	7	7
Dollart (RP, HP, OFF, Po)	4	5	1	5	4	2	1	3	6	6	7	8	14	22
Entire estuary	2	7	1	5	8	0	0	1	10	5	7	7	16	23+
Σ	14	37	15	25	26	2	1	18	45	37	21	57	64	121 species

faunal differences along transects, samples were taken and analysed according to the criteria as described here: to characterize nematode associations with low diversity indices, two samples each with about 40 specimens were analysed; for associations with diversity indices of about 70, 3 samples with altogether 120 specimens were analysed.

4.2. Distribution of nematode species, orders and feeding-types over the three estuarine zones

In a previous paper (Bouwman, 1981) nematode species isolated in the Ems estuary and the sample stations from which they were isolated were recorded. In Table 5, numbers of different nematode species are recorded according to their presence in the Wadden Sea, the Wadden Sea plus the middle reaches of the estuary, the middle reaches, the middle reaches plus the Dollart, the Dollart, the whole estuary. The numbers of species from a particular estuarine zone that are restricted to Europe or have been recorded also on other continents is mentioned and the distribution of species over the 4 feeding-types and 7 orders are also presented.

Two faunas can be distinguished at a large scale: a Wadden Sea fauna and a Dollart fauna. Both faunas penetrate into the middle reaches of the estuary, but this area does not really have its own typical fauna. The Wadden Sea fauna comprises at least twice as many species as the Dollart fauna. More research will undoubtedly result in the discovery of even more Wadden Sea species than Dollart species. Only a few species proved to be present in all three estuarine zones. However, these species were not evenly distributed and most of them preferred a particular part of the estuary.

The species from the Ems estuary belong to 7 orders: Monhysterida 37, Chromadorida 26, Enoplida 26, Desmodorida 15, Araeolaimida 14, Rhabditida 2 and Tylenchida 1. Normally, species belonging to the Rhabditida and the Tylenchida are widespread in terrestrial habitats, and the 3 species belonging to these orders that were isolated in the Dollart (*Rhabditis marina*, *Eudiplogaster pararmatus*, *Tylenchus fucicola*) are thought to have invaded the brackishwater habitat. The species belonging to the other orders are originally true marine species. Monhysterida is the order with the most species in all the estuarine zones whereas Chromadorida and Enoplida rank equal second. Desmodorida are almost entirely confined to the Wadden Sea and only 2 species are present in the Dollart (*Metachromadora remanei*, *Microlaimus globiceps*). Araeolaimida

is the order with the fewest species; species belonging to this order occur in all parts of the estuary and in the Wadden Sea area; they mainly prefer the lower sediment layers. As compared to the surveys from the estuaries of the rivers Blyth, Exe and Elbe, the number of Enoplida species, isolated from the Ems estuary, is relatively small, whereas the number of Monhysterida species is relatively high. The sharp decline in Desmodorida species towards the freshwater source in estuaries has also been observed by other authors (Gerlach, 1953; Riemann, 1966).

The Wadden Sea species peter out towards the Dollart. Whereas at any sample station in the Wadden Sea area 60% of the total number of identified Wadden Sea species can be isolated, this percentage decreases to about 40% at station H₁ and to about 20% at stations from the middle reaches, while in the Dollart these species are absent. The Dollart species peter out towards the Wadden Sea. Whereas at any station in the Dollart, except stations OFP_{1,2,3}, about 65% of the total number of identified Dollart species can be isolated, this percentage decreases to about 25% at the stations from the middle reaches and in the Wadden Sea area these species are very scarce. Station H₁, located at low tide level on a tidal flat in the mouth of the estuary, is still a true Wadden Sea site, colonized by species such as *Daptonema invagiferum*, *Daptonema cf. normandicum* type II, *Metachromadora suecica*, *Monoposthia mirabilis*, *Sabatieria longispinosa*, *Hypodontolaimus setosus*, *Neochromadora trichophora*, *Chaetonema riemannii*, and *Enoplo-laimus propinquus*. This station and the species mentioned mark the boundary between the largely marine Wadden Sea area and the transitional middle reaches. The species mentioned do not occur at Station H₂, which is very muddy in contrast to station H₁. Station H₂ is 1,500 m away from station H₁ and actually marks the seaward boundary of the distribution of Dollart species such as *Axonolaimus paraspinosus*, *Desmolaimus zeelandicus*, *Daptonema oxyerca*, *Daptonema procerum*, *Ptycholaimeilus ponticus* and *Halalaimus gracilis*. Station RP₁ on the Reider peninsula is still a true Dollart station, where no Wadden Sea species occur. On the neighbouring station P in the middle reaches of the estuary, however, the number of Dollart species is dramatically less and a few Wadden Sea species are already present. Thus the Reider peninsula is not only a geographical boundary between the Dollart and the Ems basin, but it also marks the boundary between a brackish habitat and a transitional brackish/marine habitat.

When the species isolated were classified according to feeding-types the result was: selective deposit feeders (1A) 18 spp., non-selective deposit feeders (1B) 45 spp., epigrowth feeders (2A) 37 spp., omnivores (2B) 21 spp. The 4 feeding-types were represented in each of the different estuarine zones. Type 1B outnumbers the other types in all zones of the estuary. Type 2A ranks second in the Wadden Sea and in the middle reaches, but type 2B ranks second in the Dollart. Most of the species distributed all over the estuary belong to types 1B and 2B.

Of the 121 species isolated, 63 are widely distributed over various continents and 58 have so far only been isolated in Europe. Most species only occurring in the Dollart and the middle reaches, and the species distributed all over the estuary, have also been isolated in other continents. However, the majority of species occurring only in the Wadden Sea, have not been isolated outside Europe. Probably the physical, chemical and biological conditions in brackish-water habitats are very similar in different parts of the world, and therefore nematode faunas from these biotopes are similar as well.

To enable the faunas from different estuarine zones to be compared, the results of faunal analyses in different seasons from all the stations belonging to a particular estuarine zone were combined (Table 6). From this table it is evident that Desmodorida species such as *Metachromadora vivipara*, *Metachromadora suecica*, *Monoposthia mirabilis* and *Calomicrolaimus honestus* peter out towards the Dollart and are not replaced in the same abundance by other Desmodorida species. The same decrease was observed for Enoplida species such as *Viscosia rustica*, *Oncholaimellus calvadosicus*, *Enoplolaimus propinquus*, *Trefusia multipapillatum* and *Chaetonema riemannii*, which were not replaced by other Enoplida species in the same abundance either. However, parallel to the decrease in the proportion of specimens belonging to the orders mentioned, the proportion of specimens belonging to the Monhysterida and Chromadorida increases towards the Dollart, though different species dominate in different zones: *Paramonohystera riemannii* (M), *Neochromadora trichophora* and *Sabatieria longispinosa* (C) in the Wadden Sea area; *Daptonema setosum* and *Daptonema oxycera* (M), *Atròchromadora microlaima* and *Sabatieria pulchra* (C) in the middle reaches; *Daptonema setosum* (M), *Sabatieria pulchra*, *Dichromadora geophila* and *Ptycholaimeilus ponticus* (C) in the Dollart. The importance of specimens belonging to the Araeolaimida is relatively small in all estuarine zones. In the

Table 6. Relative species composition (%) of the nematode assemblages of the three estuarine zones, obtained by combining faunal analyses from the various sampling stations in the areas concerned. Samples taken from 1975 to 1980.

Species dominance %/ estuarine zone		Number of species/order				D.			
Species		W.S.	m.r.	D.		W.S.	m.r.	D.	
<i>Metastrongyloides vivipara</i>		9.0%	0.5%	+		8	7	6	
<i>Paramonohystera rtemanni</i>		8.7	4.0	-		22	21	17	
<i>Viscoxia rustica</i>		7.2	-	-		12	6	5	
<i>Neochromadora trichophora</i>		5.8	+	-		17	13	12	
<i>Sabatieria longispinosa</i>		5.0	-	-		17	10	11	
<i>Oncholaimellus calvadosicus</i>		4.9	0.4	+		1	1	1	
<i>Monoposthia mirabilis</i>		4.7	-	-		0	0	1	
<i>Metastrongyloides suecica</i>		4.6	+	-					
<i>Ascolaimus elongatus</i>		4.1	1.5	+					
<i>Atrichromadora microlaima</i>		4.0	18.2	0.3		7.8%	16.1%	6.1%	
<i>Daptonema normandicum</i> II		3.6	-	-		23.2	33.8	29.0	
<i>Enoplolaimus propinquus</i>		3.2	-	-		20.7	2.1	3.0	
<i>Viscoxia viscosa</i>		3.0	5.8	1.9		38.7	38.7	46.7	
<i>Odontophora rectangula</i>		3.0	0.4	-		24.0	9.3	9.8	
<i>Trefusia multipapillatum</i>		2.5	-	-		24.3	+	5.4	
<i>Parastrongylus caecus</i>		2.4	4.3	-				+	
<i>Daptonema invagiferum</i>		1.9	-	-					
<i>Daptonema setosum</i>		1.9	6.7	11.1		100%	100%	100%	
<i>Pomponema sedecima</i>		1.7	0.2	-					
<i>Chaetonema rtemanni</i>		1.6	-	-					
<i>Hypodontolaimus setosus</i>		1.5	-	-		12	7	6	
<i>Daptonema</i> sp.		1.2	-	-		26	24	19	
<i>Parastrongylus sabulicolus</i>		1.1	-	-		28	19	16	
<i>Theristus longus</i>		1.1	+	+		11	8	12	
<i>Calomicrolaimus honestus</i>		1.0	0.3	+					

Number of species/feeding-type

1A
1B
2A
2B

Wadden Sea area *Ascolaimus elongatus* is the dominating representative of this order, in the middle reaches *Odontophora setosa* and in the Dollart *Leptolaimus papilliger*.

The proportion of specimens belonging to feeding-type 1B increases considerably towards the Dollart, mainly at the expense of the specimens type 2B, whereas the proportions of specimens type 2A remains fairly stable throughout the estuary. The proportion of specimens type 1A was low in all parts of the estuary. Similarity between the nematode assemblages from the different zones was low: 8% (Wadden Sea/Dollart), 28% (Wadden Sea/middle reaches) and 31% (middle reaches/Dollart). The number of species common to two different zones was less than half the total number of species from the two zones.

4.3. Distribution of nematode species within the three estuarine zones

The distribution of species within the estuarine zones varies from species to species. Some species were found at all sampling stations/transects within a particular zone (Table 7): in the Wadden Sea out of a total of 85 spp., 16 spp. were found at the 4 sampling sites investigated; in the middle reaches 11 spp. out of 56 spp.; in the Dollart 17 spp. out of 52 spp. The species present at all sampling sites in a particular estuarine zone constitute the basis of the assemblages from these areas and form the major part of the associations at the various sampling stations/transects: i.e. 50-60% of the associations at the various sampling sites in the Wadden Sea, 60-70% in the middle reaches and 70-80% in the Dollart. However, most of the species that occurred in a particular estuarine zone were not found at all sampling sites in that zone. Often they were very scarce which resulted in few isolations only (less than 10 specimens per species).

4.4. Distribution of nematode species, orders and feeding-types along transects

To ascertain small-scale faunal differences, samples taken along the following transects (Fig. 1) were analysed: R, EH, H, HP, OFP (Table 8). Transects R, EH, H and HP were situated on tidal flats, perpendicular to the low tide levels. One station was always located at the low tide level and another in the centre of the flat (R, H, HP) or at the sea-wall (EH). The stations at low tide level were sandy, whereas along the transects the amount of small particles in the sediment increased

Table 7. Nematode species found at all sampling sites in the appropriate area of distribution.

Wadden Sea (UW, R, EH, H₁), 16 species out of a total of 85 species present in the area:

Ascolaimus elongatus, *Odontophora rectangula*, *Cyartonema zosterae*, *Daptonema setosum*, *Paramonohystera riemannii*, *Metachromadora suecica*, *Monoposthia mirabilis*, *Sabatieria longispinosa*, *Atrochromadora microlaima*, *Hypodontolaimus setosus*, *Neochromadora trichophora*, *Pomponema sedecima*, *Chaetonema riemannii*, *Enoplolaimus propinquus*, *Oncholaimellus calvadosicus*, *Viscosia viscosa*

Mean proportion of specimens belonging to these species in samples from the various sampling sites in the Wadden Sea area: 57% ± 11%.

Middle reaches (H₂, HW, RN, P), 11 species out of a total of 56 species present in the area:

Euletherolaimus stenosoma, *Daptonema oxycerca*, *Daptonema setosum*, *Paramonohystera riemannii*, *Sabatieria pulchra*, *Atrochromadora microlaima*, *Innocuonema tentabundum*, *Ptycholaimellus ponticus*, *Praeacanthocheilus punctatus*, *Halalaimus gracilis*, *Viscosia viscosa*

Mean proportion of specimens belonging to these species in samples from the various sampling sites in the middle reaches: 66% ± 10%

Dollart (RP, HP, OFP, Po), 17 species out of a total of 52 species present in the area:

Leptolaimus papilliger, *Daptonema procerum*, *Daptonema setosum*, *Sphaerolaimus balticus*, *Sphaerolaimus gracilis*, *Microlaimus globiceps*, *Sabatieria pulchra*, *Dichromadora cephalata*, *Dichromadora geophila*, *Hypodontolaimus balticus*, *Innocuonema tentabundum*, *Ptycholaimellus ponticus*, *Tripyloides marinus*, *Halalaimus gracilis*, *Viscosia viscosa*, *Calyptronema maxweberi*, *Eudiplogaster pararmatus*

Mean proportion of specimens belonging to these species in samples from the various sampling sites in the Dollart: 72% ± 25%.

except at the HP transect where the sediment was sandy with a considerable amount of small particles along the whole transect. The OFP transect was silty at all sample stations and did not reflect a sediment gradient but a salinity gradient (c. 50/00 \rightarrow c. 150/00 Cl⁻¹).

From table 8 it is evident that the 3 sampled transects in the Wadden Sea (R, EH, H) show a common phenomenon: towards sea-walls and centres of tidal flats, the proportion of Desmodorida and Chromadorida increased at the expense of the proportion of Enoplida (notice: Desmodorida nearly absent along the transect H). In general, Enoplida are interstitial predators and omnivores, whereas Desmodorida and Chromadorida feed on the epigrowth of sediment particles; the increasing proportion of the latter orders towards the seawalls and centres of tidal flats reflects the increasing frequency of algae, bacteria and protozoa on the surface of sediment particles. In the Dollart the transition in the nematode fauna along transects was less clear, probably because along the transects investigated the sediments do not vary as much in composition as in the Wadden Sea. Along the OFP transect, however, faunal differences probably reflect gradients other than differences in epigrowth on sediment particles. Stations 1 and 2 are regularly exposed to large fluctuations in physical and chemical conditions, caused by low oxygen saturation values in the water discharged at Nieuwe Statenzijl, by sudden temperature changes during the long emersion and by changes in salinity and the presence of hydrogen sulphide. It seems reasonable to expect that species such as *Eudiplogaster pararmatus* and *Dichromadora geophila* would be more resistant to environmental stress than *Ptycholaimellus ponticus*, which is morphologically and behaviourally similar and is a predominant species in the Dollart except at stations OFP_{1,2}. Along transect HP the nematode fauna did not change; similarity between the various stations was more than 60%, except for station HP₃, which was dominated by the species *Metadesmolaimus pandus*.

4.5. Vertical distribution of nematode species, orders and feeding-types in various parts of the estuary (Table 4)

In the Wadden Sea area, the nematode fauna of the lower sediment layers was found to be dominated by species such as *Sabatieria longispinosa* ($a > 90$), *Odontophora rectangula* ($a > 100$), *Trefusia multipapillatum* ($a > 110$), *Paramonohystera riemannii* ($a > 50$) and *Daptonema* sp. ($a > 50$) (a = length/width ratio). These species do not normally occur in the upper sediment layers and are characterized by their similar body shape: all are very long and slender and consequently

Table 8. Relative proportion (%) of nematode species, orders and feeding-types in the upper sediment layers of samples taken along transects perpendicular to dikes and low tide levels

Ransel transect (samples taken 6.7.1976)				
specimens identified per station: 215				
depth of the samples analysed: 5 cm (st.1), 2 cm (st. 2,3)				
Species	st. 1	st. 2	st. 3	Orders
<i>Enoplaimus propinquus</i>	36%	18%	11%	Araeolaimida
<i>Oncholaimellus calvadostus</i>	23	16	8	Monhysterida
<i>Monoposthia mirabilis</i>	10	18	14	Desmodorida
<i>Metachromadora suecia</i>	6	9	21	Chromadorida
<i>Neochromadora trichophora</i>	6	5	8	Enoplida
<i>Daptonema cf. normandicum</i> II	1	1	10	
<i>Ascolaimus elongatus</i>	1	5	5	
<i>Paracanthonehus caecus</i>	1	7	4	
Other species	16(10)	21(11)	19(12)*	
	100%	100%	100%	
*) number of different species in parentheses				
Feeding-types				
1A	1%	0%	0%	
1B	7	11	23	
2A	24	44	52	
2B	68	45	25	
	100%	100%	100%	
Eemshaven transect (samples taken 27.6.1977)				
specimens identified per zone: 325				
depth of the samples analysed: 2 cm				
Species	zone 1	zone 2	zone 3	Orders
<i>Oncholaimellus calvadostus</i>	18%	5%	5%	Araeolaimida
<i>Metachromadora vivipara</i>	17	17	35	Monhysterida
<i>Neochromadora trichophora</i>	15	11	4	Desmodorida
<i>Viscosia viscosa</i>	13	6	4	Chromadorida
<i>Daptonema cf. normandicum</i> II	10	5	2	Enoplida
<i>Chaetonema riemanni</i>	8	10	1	
<i>Paracanthonehus caecus</i>	1	8	11	
<i>Atrachromadora microlaima</i>	1	11	15	
Other species	17(15)	26(16)	23(19)	
	100%	100%	100%	
feeding types				
1A	0%	1%	1%	
1B	22	25	12	
2A	45	61	75	
2B	33	13	12	
	100%	100%	100%	

Table 8 (continued)

Hond transect (samples taken 17.11.1977)

specimens identified per station: 275

depth of the samples analysed: 2 cm (st.1), 1 cm (st.2)

Species	st. 1	st. 2	Orders	st. 1	st. 2
<i>Enoplosia propinquus</i>	24%	0%	Araeolaimida	11%	11%
<i>Daptonema cf. normandicum</i> II	12	1	Monhysterida	24	29
<i>Oncholaimellus calvadosticus</i>	11	1	Desmodorida	2	0
<i>Ascolaimus elongatus</i>	10	2	Chromadorida	16	53
<i>Viscosia viscosa</i>	7	3	Enoplida	47	7
<i>Atrochromadora microstoma</i>	1	37		100%	100%
<i>Eleutheroelaimus stenosoma</i>	2	14			
<i>Innocuonema tentabundum</i>	4	8			
<i>Daptonema setosum</i>	1	7	Feeding-types		
<i>Odontophora setosa</i>	1	6	1A	1%	2%
Other species	27(18)	21(18)	1B	37	41
	100%	100%	2A	17	51
			2B	45	6
				100%	100%

Heringsplaat transect (samples taken 27.7-1977)

specimens identified per station: 200

depth of samples analysed: 5 cm

Species	st.1	st.2	st.3	st.4	Orders	st.1	st.2	st.3	st.4
<i>Metadesmolaemus pandus</i>	15%	15%	47%	24%	Araeolaimida	12%	6%	8%	9%
<i>Diochromadora geophila</i>	14	22	8	18	Monhysterida	30	24	60	32
<i>Anoplostoma viviparum</i>	13	18	5	0	Desmodorida	3	0	0	4
<i>Ascolaimus paraspinosus</i>	10	6	6	6	Chromadorida	26	31	12	32
<i>Adoncholaimus fuscus</i>	2	10	7	8	Enoplida	29	39	20	23
<i>Viscosia viscosa</i>	5	4	4	9	Rhabditida	0	0	+	0
<i>Innocuonema tentabundum</i>	3	5	3	9		100%	100%	100%	100%
Other species	38(16)	20(15)	20(14)	26(15)					
	100%	100%	100%	100%	Feeding-types				
					1A	9%	2%	3%	4%
					1B	50	51	73	39
					2A	29	30	12	36
					2B	12	17	12	21
						100%	100%	100%	100%

Table 8 (continued)

Oost Friesche Plaat transect (samples taken 14.3.1977)

specimens identified per station: 120

depth of the samples analysed: 0.5 cm (st. 1, 2), 1.0 cm (st. 3+4+5+6)

Species	st. 1.	st. 2	st. 3 +...	Orders	st. 1.	st. 2.	st. 3 +...
<i>Dichromadona geophila</i>	67%	12%	4%	Araeolaimida	0%	0%	3%
<i>Eudiplogaster paramatus</i>	15	31	3	Monhysterida	7	55	38
<i>Daptonema procerum</i>	7	38	30	Desmodorida	1	0	4
<i>Ptycholaimellus ponticus</i>	0	2	38	Chromadorida	68	14	51
Other species	11(3)	17(4)	25(15)	Enoplida	9	1	1
				Rhabditida	15	31	3
	100%	100%	100%		100%	100%	100%
				Feeding-types			
				1A	0%	0%	4%
				1B	16	54	44
				2A	84	44	52
				2B	0	2	+
					100%	100%	100%

have higher length/width ratios than the species from the upper sediment layers where length/width ratios are generally from 30 to 40. Thin species have a high surface/volume ratio and this is probably advantageous in surroundings with low oxygen pressure. The range of these species extends to depths of 30 cm. The predominance of *Paramonohystera riemannii* and *Daptonema* sp. and the occurrence, though less abundantly, of species such as *Metalinhomoeus biformis*, *Metalinhomoeus typicus*, *Daptonema invagiferum*, *Theristus longus*, *Theristus pertenuis*, *Theristus* cf. *subcurvatus* and *Trichotheristus mirabilis* (Bouwman, 1981) results in about 50% of the fauna from the lower sediment layers being Monhysterida species; about 25% of the nematodes from the lower sediment layers in the Wadden Sea area belong to the Chromadorida and almost 20% to the Araeolaimida and finally few specimens belong to the Desmodorida and Enoplida. Rare species such as *Leptolaimus luridus*, *Stephanolaimus elegans*, *Stephanolaimus flevensis*, *Microilaimus conothelis*, *Molgolaimus allgeni*, *Leptonemella aphanothecae* and *Dasynemella* cf. *albaënsis* were also isolated only from the lower sediment layers in the Wadden Sea area. About 75% of the specimens were non-selective deposit feeders (1B) and about 15% were epigrowth feeders (2A), whereas selective deposit feeders (1A) and omnivores (2B) were very scarce.

In the middle reaches of the estuary and in the Dollart, the nematode fauna of the transition zone between aerobic upper layers and anaerobic lower layers in muddy sediments was dominated by the species *Sabatieria pulchra*. In the upper layers this species was only found in small numbers, but in the semi-aerobic transition zone it was often quite numerous. This species probably prefers low oxygen pressure and is tolerant of hydrogen sulphide and feeds on the bacteria that are associated with this sediment zone (Bouwman, 1978). Generally, the nematode fauna in muddy sediments, whether tidal or subtidal, is dominated by Comesomatidae, to which family the genus *Sabatieria* belongs. In brackishwater habitats, *Sabatieria pulchra* is the most numerous member of this family (De Man, 1922; Wieser, 1960; Riemann, 1966; Warwick, 1971; Jensen, 1979, 1981; Gourbault, 1981). In the middle reaches of the estuary *Sabatieria pulchra* was accompanied by *Odontophora setosa* and sometimes the latter species was even more numerous. In sandy sediments in the middle reaches, without a high content of small particles, the two latter species were absent. However, *Paramonohystera riemannii*, a predominant species from the lower sediment layers in the Wadden Sea

area, was also the most abundant species in the lower layers in the sandy parts of the middle reaches. Because of the predominance of the mentioned species, non-selective deposit feeders (1B) dominated the fauna from the lower sediment layers in the middle reaches, accounting for 75 to 100% of the nematode fauna.

In the muddy tidal flats in the Dollart, the fauna from the sediment layers below the surface did not differ much from the corresponding fauna in the middle reaches. In this part of the estuary *Sabatieria pulchra* was again the predominant species from the lower sediment layers but *Odontophora setosa* was absent in the Dollart. *Sabatieria pulchra* was very scarce near the freshwater discharge-point at Nieuwe Statenzijl (stations OFP_{1,2}) and also along the HP transect. A fauna specific to the lower sediment layers was observed at station OFP₆. This fauna was dominated by the species *Desmolaimus zeelandicus*, which was found to a depth of 6 cm. At other stations in the Dollart and in the middle reaches this species was also specific to lower sediment layers but it was sparsely distributed. Non-selective deposit feeders (1B) were the predominant feeding-type in the lower sediment layers in the Dollart too.

4.6. Fauna from the bottom of the main channel

Table 9 presents the results of a survey of nematodes from the channel bottom at various buoys. At the most seaward channel stations BW₀ and 6, the current velocity seems to be too high for nematodes to settle as abundantly as in the neighbouring tidal flats. However, the specimens isolated

Table 9. Fauna from the channel bottom at 6 sampling sites (samples taken 27.9.1979).

Sample station	Sediment	Nematode density	Community structure
bw ₀	coarse sand	< 1 specimen.cm ⁻³	normal diversity
bw ₆	coarse sand	< 1 specimen.cm ⁻³	(8 ind. from 60 cm ³ only)
bw ₂₂	silt	± 100 specimen.cm ⁻³	monoculture <i>S. pulchra</i>
d ₁₇	silt + coarse detritus	± 20 specimen.cm ⁻³	normal diversity
sd	silt + coarse detritus	0 specimen.cm ⁻³	
ba	silt + coarse detritus	± 10 specimen.cm ⁻³	normal diversity

belonged to species that also occur in the tidal flats; thus no characteristic bottom fauna existed in this part of the estuary but only a fauna that was impoverished by comparison with that of the tidal flats. At station BW₂₂, located in the middle reaches of the estuary, the sediment was very silty and contained much coarse detritus, and the fauna consisted of one species only, *Sabatieria pulchra*, at a very high density. Sample stations D₁₇, SD and BA in the Dollart contained no (SD) or few nematodes. Species found at these stations were also found in the neighbouring flats. Anaerobic conditions near the freshwater discharge-point and the current velocity are probably responsible for the very low densities of nematodes in the sediment of the river bottom in the Dollart and in the northern part of the estuary, whereas conditions in the middle part of the estuary are obviously favourable for the development of *Sabatieria pulchra*.

4.7. Epifauna of nematodes on macrophytes present in the Ems estuary

Table 10 shows macrophytes, the stations where they were found and indicates whether a particular epifauna was present. The epifauna is considered to be specific if the species present on the macrophyte are not common in the surrounding sediment. The species of macrophyte without specific epifauna were all those that were lying prostrate on the sediment (*Ulva* sp., *Chaetomorpha* sp.) or, if growing erect, attained heights of less than 15 cm (*Salicornia* sp.). However, the surface of the leaves of erect-growing *Spartina* sp. was colonized by specimens *Diplolaimelloides brucei*, a species that

Table 10. Epifauna specific to several common macrophytes (samples taken 23.10.1979).

Macrophyte	Sampling station	Specific epifauna	Nematode species
<i>Fucus</i> sp.	EH	+	<i>Monhystera disjuncta</i> and <i>Rhabditis marina</i>
<i>Salicornia</i> sp.	EH	-	-
<i>Spartina</i> sp.	EH	+	<i>Diplolaimelloides brucei</i>
<i>Ulva</i> sp.	EH	-	-
<i>Chaetomorpha</i> sp.	HW	-	-
<i>Zostera</i> sp.	HW	+	<i>Chromadora nudicapitata</i>

was not isolated from any sediment in the estuary. The surface of *Fucus* sp., found about 60 cm above the sediment attached to piles, was colonized by specimens of *Monhystera*

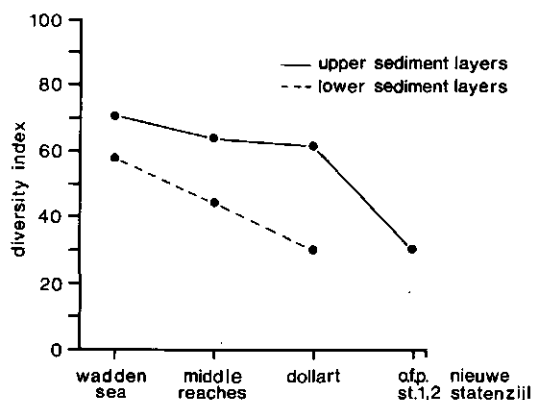


Fig. 3. Mean values of the diversity index along the longitudinal axis of the estuary as calculated for the fauna from the upper and the lower sediment layers.

disjuncta and, in smaller numbers, *Rhabditis marina*. The latter two species were infrequently isolated from sediments from different parts of the estuary, but were not permanent residents at any of the stations investigated. These species probably only arrived in the sediment after *Fucus* sp. had been deposited on the surface of the sediment. Finally the species *Chromadora nudicapitata* proved to be present on the surface of the leaves of *Zostera* sp., but was not isolated from any sediment sample taken from the estuary.

4.8. Values of the diversity index of nematode associations from different parts of the estuary

From Fig. 3 it is evident that in most parts of the estuary the index of diversity of the nematode associations from the upper sediment layers ranges from 60 to 70, while the diversity indices of the faunas from the lower sediment layers are generally below 60. Values for the diversity index in different parts of the estuary are mean values from dozens of sample analyses from the various sampling stations. Faunas with higher or lower diversity indices occur all over the estuary; the mean diversity index of the nematode fauna from

the upper sediment layers at station Po in the southeast Dollart was as high as at EH in the Wadden Sea (69.5 to 69.7 respectively). However, from Fig. 3 it is evident that the average value for the diversity index tends to decrease towards the freshwater discharge-point at Nieuwe Statenzijl. Lower values result when one species is predominant, a situation that often arose because of the presence of many larvae of one species during a reproduction peak of that species. In the vicinity of the outfall, diversity decreased very sharply. This was not only caused by a fall in the numbers of different species but also due to uneven distribution over the species. Values for the nematode fauna from the lower sediment layers were considerably lower than corresponding values from the upper layers. The diversity of the fauna from these sediment layers also decreased towards the freshwater discharge-point.

Table 11 presents the seasonal composition of the nematode associations as analysed on the level of orders at station EH_{pq} in 1979. The Desmodorida from the upper sediment layers were dominated by *Metachromadora vivipara* and *Metachromadora suecica*, the Monhysterida by several *Daptonema* species, the Chromadorida by species such as *Paracanthonus caecus*, *Neochromadora poecilosoma*, *Neochromadora trichophora* and *Atrochromadora microlaima*, while the Enoplida were dominated by *Oncholaimellus calvadosicus* and *Viscosia rustica* (see also Table 8). The Monhysterida from the lower sediment layers were dominated by the species *Paramonohystera riemannii*. From these data it is evident that in winter the fauna from the upper layers was dominated by Enoplida, in spring by Monhysterida and in summer and autumn by Desmodorida and Chromadorida. This sequence of dominance is confirmed by incidental observations in other years. The observed succession parallels the increase in Chromadorida and Desmodorida along transects on tidal flats in the Wadden Sea and probably reflects the surplus of food in summer for the epigrowth feeders which mainly belong to the Chromadorida and Desmodorida. In the lower sediment layers no clear seasonal changes were observed and *Paramonohystera riemannii* dominated this nematode association throughout the year.

Table 11 also shows that in 1979 the species composition at station OFP₂ changed gradually throughout the year, though for periods of several months the structure was relatively stable. Fluctuations were caused by the alternation of dominance between the species *Dichromadora geophila* and *Eudiplo-*

Table 11. Seasonal changes in orders at station EH₂ and in species at station OFP₂ (samples taken in 1979).

Eemshaven ₂	Upper sediment layers [%]				Lower sediment layers [%]			
	Feb.	April	June	Dec.	Feb.	April	June	Dec.
Araeolaimida	12	7	10	10	11	4	7	7
Monhysterida	9	64	4	19	52	79	89	83
Desmodorida	26	13	44	35	6	4	2	5
Chromadorida	5	9	29	28	23	9	29	28
Enoplida	48	7	13	8	4	4	1	2
Rhabditida	-	-	-	-	4	-	-	-
	100	100	100	100	100	100	100	100

Oost Friesche Plaat ₂				
Species	March	July	Sept.	Nov.
<i>Diachromadora geophila</i>	80	54	36	1
<i>Euliplogaster pararmatus</i>	9	10	54	83
<i>Anoplostoma viviparum</i>	1	0	1	3
<i>Leptolaimus papilliger</i>	10	0	5	6
<i>Adoncholaimus thalassophygas</i>	0	0	1	4
<i>Daptonema setosum</i>	0	36	1	0
<i>Axonolaimus spinosus</i>	0	0	1	1
<i>Microlaimus globiceps</i>	0	0	1	1
<i>Tripylodes marinus</i>	0	0	0	1
	100	100	100	100 +

gaster pararmatus which together accounted for an average of 80% of the nematode fauna at that station; on one sampling date (July), the species *Daptonema setosum* accounted for a considerable proportion of the nematode association (36%). The remaining species belonged to species such as *Leptolaimus papilliger*, *Anoplostoma viviparum* and *Adoncholaimus thalassophygas*. The 2 dominant species and also *Daptonema setosum* feed primarily on diatoms, so there are probably reasons other than fluctuating food densities that influence the changes in relative dominance between the 2 species mentioned.

4.10. Densities and biomass of nematodes

The average density of nematodes in the tidal flats of the Ems estuary was found to be 200 specimens.cm⁻² (2 x 10⁶.m⁻²). On average the specimens were distributed over a column about

10cm deep and 75% of them were concentrated in the upper 2cm of the sediment. However, in wave-exposed biotopes the densities of nematodes were much lower and did not exceed 40 specimens.cm⁻², while in more sheltered areas the number of specimens attained 400.cm⁻² and in the vicinity of the outfall at Nieuwe Statenzijl more than 1,000 specimens.cm⁻² were counted. In sandy sediments the nematode fauna extended to depths of about 25 cm, and in muddy sediments hardly any nematodes were found below a depth of 5 cm. In the vicinity of the outfall almost all the specimens were concentrated in the upper 0.3 cm of the sediment.

Mean meiofauna biomass was found to be 350 ± 100 mg carbon.m⁻²; usually 50-100% of this biomass consisted of nematodes.

5. DISCUSSION

The data presented in the previous section reveal the structure and distribution of species assemblages and associations at different scales over the Ems estuary. Generally, these results agree with observations made by other researchers in the estuaries of the rivers Elbe, Exe and Blyth and in the former Zuiderzee. The principles that determine the genesis of associations in various biotopes have already been explained by Wieser (1953, 1969). His explanation, however, is largely hypothetical, and is based on an estimation of the ability of various species to seize various types of prey. Biotopes that favour the development of epigrowth on the surface of particles of the sediment favour the development of epigrowth feeders; biotopes where particles and organisms settle favour the development of deposit feeders; and in coarser sediments with only small amounts of deposits and less dense epigrowth, omnivores (predators) are most numerous.

Knowledge about feeding, reproduction, life cycles, tolerances, in a word, basic physiology, is necessary to understand the formation of associations in relation to the conditions offered by specific biotopes. Understanding of the genesis of nematode associations has only slightly improved since Wieser's speculations because of the lack of knowledge about the basic physiology of the numerous nematode genera and species. Nematode species from the marine environment need a solid substratum, water and food. Most species obviously prefer interstitial life, only a few species prefer the surface of rocks or macrophytes and some are probably indifferent in this respect. Because most nematode species in marine and brackish environments are of marine origin, they need

more or less saline water, though tolerance of lower salinity obviously characterizes typical estuarine species. Actual observations on what food item or items species feed on are scarce. Consequently it is largely unknown how to cultivate most species in the laboratory and little experimental work has been done on marine nematode species. Most species, however, will flourish, at least for a couple of days or weeks, in agar of the appropriate salinity and with various food items mixed through it (diatoms, protozoa, bacteria). This enables ingestion or the puncturing of diatoms and larger prey, such as other nematodes, to be observed easily under the microscope (Maertens, 1975).

The habitat of the Ems estuary mainly consists of tidal sand-flats and mud-flats that emerge twice daily. This biotope offers adverse physical and chemical conditions for originally sublittoral marine nematode species. Nematode assemblages in sublittoral marine muds are dominated by species belonging to genera such as *Sabatieria*, *Spirinia*, *Terschellingia*, *Odontophora* and *Desmolaimus* (Warwick and Buchanan, 1970; Ward, 1973; Jensen, 1974; Lorenzen, 1974; Decraemer, 1975; Vitiello, 1976; Tietjen, 1977, 1980). Submerged estuarine mud sediments are predominantly colonized by members of the same genera (Vitiello, 1974; Goubault, 1981). In the Ems estuary *Sabatieria pulchra*, *Terschellingia longicaudata*, *Odontophora setosa*, *Spirinia parasitifera* and *Desmolaimus zeelandicus* predominate, e.g., the nematode fauna from the sediment just below the surface layer at station HW, located in the middle reaches of the estuary. This indicates that a predominant part of the subtidal marine nematode fauna from muddy sediments extends into subtidal and tidal estuarine habitats. In the Dollart, only the species *Sabatieria pulchra* and *Desmolaimus zeelandicus* were isolated from the sediments just below the surface, whereas the other species were probably absent because of their intolerance of lower salinities.

The nematode fauna from the lower sediment layers of the tidal flats in the outer parts of the Ems estuary consists partly of rarer species that have also been isolated from subtidal sediments (*Leptolaimus luridus*, *Stephanolaimus elegans*, *Stephanolaimus flevensis*, *Odontophora rectangula*, *Metalinhomoeus typicus*, *Trichotheristus mirabilis*, *Spirinia parasitifera*, *Neotonchus* cf. *corcundus*) and partly of species that have only recently been described, probably because they are absent from or seldom occur in the upper sediment layers (*Metalinhomoeus biformis* Juario 1974; *Daptonema* sp. Bouwman

1981; *Paramonohystera riemannii* Platt 1973; *Theristus* cf. *subcurvatus* Lorenzen 1977; *Theristus longus* Platt 1973; *Microlaimus conothelis* Lorenzen 1973; *Dasynemella* cf. *albaensis* Warwick 1973; *Paracyatholaimus pentodon* Riemann 1966; *Trefusia multipapillatum* Bouwman 1981). Few specimens constituting the associations in the lower sediment layers belonged to species which favour the upper sediment layers. As in the middle reaches and the Dollart, most species and specimens from the lower sediment layers in the Wadden Sea also belong to the non-selective deposit feeders. However, almost nothing is known about what the species mentioned feed on and how they feed. Diatoms probably do not play an important role in the food web from the deeper sediment layers; this seems to be confirmed by observations on the contents of the alimentary tract of various nematode species. Bacteria probably constitute the main source of food for species from these layers. Colonies of particular bacterial groups, such as sulphide-oxidizing and sulphate-reducing bacteria occur in micro-niches that are patchily distributed in the oxidized sediment zone below the surface layers of the sediment (Schröder and Van Es, 1980); some nematode species probably feed selectively on these types of prey. The predominance of non-selective deposit feeders suggests that food is mainly ingested from the interstitial water and not as epigrowth from the sediment particles.

One of the ways that the surface of tidal flats differs from the surface of subtidal sediments is the presence of a dense standing crop of microphytobenthos. A considerable number of species and specimens that belong to the Chromadoridae (*Atrochromadora microlaima*, *Dichromadora geophila*, *Hypodontolaimus balticus*, *Ptycholaimellus ponticus*, *Chromadorita guidoschneideri*, *Chromadora nudicapitata*), and a species such as *Eudiplogaster pararmatus*, feed selectively by sucking out the contents of diatoms (Romeyn et al., 1983; Bouwman et al., in prep.). Species that belong to the Xyalidae (*Daptonema* cf. *normandicum* I and II, *D. procerum*, *D. oxycerca*, *D. setosum*, *D. trabeculosum*, *D. xyaliforme* and others) and to the Cyatholaimidae (*Paracyatholaimus proximus*, *Praeacanthocheilus punctatus*) also feed on diatoms, though these species ingest entire cells (observations made by the author). These diatom feeding species represent a considerable proportion of the nematode fauna from the upper sediment layers in the middle reaches and in the Dollart, the southeastern part included. With the exception of *Daptonema setosum* and *D. oxycerca*, these species have not been recorded in marine sublittoral sediments. Thus

these diatom feeding species characterize the nematode fauna from the upper sediment layers of tidal flats in estuarine habitats. The preference of these species for diatoms as food and their tolerance of reduced salinities reflect two of the main differences between faunas from sublittoral sediments and those from tidal estuarine sediments. The distribution of these nematode species over the estuary probably mainly results from differences in tolerance in salinity: *Eudiplogaster pararmatus* is almost restricted to the southeastern part of the Dollart; *Dichromadora geophila* is numerous in all parts of the Dollart; *Chromadorita guidoscheideri*, *Paracyatholaimus proximus* and *Daptonema xyaliforme* were isolated at various sampling stations in the Dollart but not in the southeastern part; *Ptycholaimellus ponticus* and *Daptonema procerrum* were numerous in the Dollart except the southeastern part and were also isolated at all sampling stations in the middle reaches, however, in smaller numbers; distribution of *Atrochromadora microlaima*, *Daptonema normandicum* I and II and *Praeacanthochus punctatus* was almost restricted to the middle reaches and the Wadden Sea proper; *Daptonema setosum*, *Daptonema oxycerca* and *Hypodontolaimus balticus* were distributed all over the estuary, however, *Daptonema oxycerca* was not isolated from the southeastern part of the Dollart.

Unfortunately almost nothing is known about the feeding habits of the predominant species from the upper sediment layers of tidal flats in the Wadden Sea area. These species, *Metachromadora vivipara*, *Metachromadora suecica*, *Monoposthia mirabilis* (Desmodorida) and *Neochromadora trichophora* (Chromadorida) belong to genera that are assumed to feed on epigrowth; no actual observations have been made on the way of feeding or food ingestion, but the contents of the alimentary tract suggest that diatoms are not part of the diet. Thus, these species probably feed on bacteria and/or protozoa or other small organisms, which they scrape off from the surface of sediment particles. In the future, attention needs to be focused on the feeding habits of species belonging to these genera. Some of these predominant species from the surface layers of tidal flats (sandy margins excluded) in the Wadden Sea have been recorded occasionally in nearshore subtidal sediments (Ward, 1973; Tietjen, 1977, 1980) but not in offshore subtidal sediments (Lorenzen, 1974; Juario, 1975). Other members of the genera *Metachromadora* and *Neochromadora*, e.g., *M. remanei* and *N. poecilosoma* were found to be more abundant in the middle reaches and/or the Dollart. Another *Monoposthia* species, *M. costata*, was found to be present at the EH transect

near the sea-wall in a pool with *Spartina* sp. Along the EH transect *M.vivipara* was most numerous in the silty part near the sea-wall whereas *M.suecica* predominated in the sandy part near the low tide level. The observations on the distribution of these species over the Ems estuary agree with findings in other estuaries (see also Platt, 1977). It is concluded that members of the genera *Metachromadora*, *Neochromadora* and *Monoposthia* also characterize the nematode fauna from the upper sediment layers of tidal estuarine habitats. The species *M.suecica*, *N.trichophora* and *M.mirabilis* predominate in sandy sediments with almost marine salinity, whereas *M.vivipara*, *N.poecilosoma* and *M.costata* are most numerous in silty sediments with reduced salinity. However, the success of these species in the estuarine environment is not well understood, mainly because of lack of knowledge on feeding habits.

The predominance of Enoplidae and Oncholaimidae in the sediment along the low tide level in the outer parts of the Ems estuary agrees with Wieser (1953). This predominance probably results from the following factors: interstitial space (grain size), food availability and inherent properties of the species concerned. The species belonging to these families (*Enoplolaimus propinquus*, *Mesacanthion diplochma*, *Enoplodes* cf. *labiatus*, *Mononcholaimus separabilis*, *Oncholaimellus calvadosicus*, *Viscosia rustica*) are among the largest from the estuary and thus it is clear that the relatively large interstitial spaces in the sediment along the margins of the tidal flats offer a favourable habitat for them. These species are considered to be omnivores with the ability to catch prey up to their own size. In the interstitial biotope along the margins of the flats, these predatory species probably feed on other, epigrowth-feeding nematodes. The life cycles of Enoplidae and Oncholaimidae species investigated in the laboratory (Von Thun, 1968; Wieser and Kanwisher, 1960; Hopper and Meyers, 1966a) and in the field (Skoolmun and Gerlach, 1970; Lorenzen, 1974; Smol et al., 1980) proved to take from several months up to one year. Thus these types of nematodes produce 1 or 2 generations annually. Because reproductive potential is probably inversely proportional to the length of the life cycle these species are expected to produce relatively few offspring. This has been confirmed by laboratory experiments (Wieser and Kanwisher, 1960; Von Thun, 1968; Smol et al., 1980) with species such as *Enoplus communis*, *Adoncholaimus thalassophygas* and *Oncholaimus oxyuris* which produced up to 25 eggs per female, whereas opportunistic species such as *Rhabditis marina* and *Monhystera microphthalmia*, which belong to the

epifauna on *Fucus* sp. etc., can produce at least 100 eggs per female (Tietjen, 1970; Van Brussel, 1979). The life cycles of the latter species take from several days up to a few weeks under optimum conditions. The life cycles of the diatom-feeding Chromadoridae (c. 1 month), Cyatholaimidae (c. 1.5 month) and Xyalidae (1 → 2 months) are shorter whereas their reproductive potential is greater than that of the Enoplidae and Oncholaimidae (Hopper and Meyers, 1966a; Tietjen, 1967; Tietjen et al., 1970; Gerlach and Schrage, 1971; Tietjen and Lee, 1972; 1973, 1977; Vranken et al., 1981; Romeyn et al., 1983). It is therefore justifiable to conclude that the nematode fauna from the margins of the tidal flats in the Wadden Sea is less productive than the nematode fauna from the centre of the flats. Because of the relatively low growth rates and reproductive potential of the Oncholaimidae/Enoplidae assemblages the densities (numbers and biomass) of this particular fauna may be relatively high.

Compared with the structure of species assemblages/associations in various parts of the Ems estuary, the structure of the nematode fauna at the stations OFF₁ and 2 is different. Most species present at these stations have also been recorded from the upper reaches of the estuaries of the Exe, Elbe and Weser (Riemann, 1979). At stations OFF₁ and 2 high densities of nematodes were concentrated in the upper 0.3 cm of the sediment. No vertical zonation could be observed, probably because the sulphide zone extends almost to the surface of the sediment (> 0.3 cm depth). Therefore the species *Sabatieria pulchra*, which is abundant in the sediment just below the surface in all parts of the Dollart (except transect HP), lacks its preferred environment at stations OFF₁ and 2 and was absent at that site. The structure of the nematode fauna was simple. At many samplings 18 different species were isolated in total whereas only the species *Eudiplogaster pararmatus* and *Dichromadora geophila* occurred in significant numbers. Because the two latter species feed selectively on diatoms (puncturing) the associations are dominated by epigrowth feeders. This contrasts with the associations at other sampling stations in the Dollart and the middle reaches, where non-selective deposit feeding proved to be the predominant way of ingesting food. The mechanism of selection for these nematode species is the subject of more comprehensive studies and is dealt with in other papers (Admiraal et al., 1983; Romeyn et al., 1983; Bouwman et al., in prep.).

To sum up: it is clear that in estuarine conditions the nematode fauna is impoverished compared with faunas under

sublittoral marine conditions. However, in the lower sediment layers communities do exist that do not differ essentially from subtidal marine nematode communities. In the surface layers of the tidal flats, relatively rapid-growing nematode assemblages/associations occur which reflect the presence of dense, but seasonally fluctuating microphytobenthos. Along the margins of tidal flats in the outer part of the estuary the relatively slow-growing nematode assemblages/associations reflect the larger size of the interstitial spaces there as compared with the centres of the flats, and also reflect the smaller amount of prey. In the surroundings of the freshwater discharge-point in the Dollart there is a dense nematode fauna, concentrated in a very thin surface layer. This fauna mainly consists of two diatom-puncturing species. On the surface of some marine macrophytes specific fast growing nematode associations occur, which probably reflect the abundance of food.

The influx of vast amounts of anaerobic, organically polluted wastewater in autumn decreases the already low diversity of the nematode fauna around the discharge-point. However, a relatively dense population of diatom-puncturers remains throughout the year.

6. ZUSAMMENFASSUNG

Die Nematodenfauna des Ems-Ästuars wird nach der Verteilung der Arten, Ordnungen sowie der verschiedenen Ernährungstypen gegliedert und mit den aus anderen nordwesteuropäischen Ästuaren vorliegenden Befunden verglichen. Danach werden bestimmte Artengemeinschaften (Biozönosen) von Nematoden beschrieben und ihre möglichen Bindungen an bestimmte Habitateigenschaften diskutiert. In den oberen Sedimentschichten lassen sich zwei Faunentypen unterscheiden, eine im Wattenmeer, die andere im Dollart. Vertreter beider Faunentypen kommen auch im Mittelgebiet des Ems-Ästuars vor. In den tieferen Sedimentschichten findet sich eine spezielle Nematodenfauna, deren Arten zum grössten Teil in den oberen Sedimentschichten nicht vertreten sind. Während die Nematodenbiozönosen der oberen Sedimentschichten für Ästulare charakterisch zu sein scheinen, gilt dies nicht für die Faunen der tieferen Sedimentschichten. Letztere weisen viel Übereinstimmung mit der Nematodenfauna des Sublittorals auf. Die mit organischen Abwässern verschmutzte Wattfläche in der Nähe der Flussmündung weist als Teil eines eigenen Ökosystems eine besondere Nematodenfauna auf, in der Arten dominieren, die als Nahrung

Diatomeen aussaugen. Für die im Aufwuchs lebenden Nematoden stellen die Diatomeen im Frühling und im Sommer wahrscheinlich die wichtigste Nahrungsquelle dar.

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CHAPTER V

Occurrence and feeding biology of some nematode species in
Aufwuchscommunities

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ABSTRACT

Nematode associations occurring on the surface of littoral macrophytes, cyanophytes, and decaying materials drifted ashore, are dominated by few species which do not occur, or are very rare, in the sediment. As part of the survival strategy, the feeding strategy of several nematode species from these biotopes was studied. Feeding behaviour of specific "Aufwuchs" species differs markedly from that of sediment inhabiting species. The latter have to select food particles out of a majority of similarly sized inedible particles whereas "Aufwuchs" species can afford to feed non-selectively because suitable food is abundant and relatively pure in their biotope.

INTRODUCTION

In estuarine environments, nematodes occupy almost all available niches (Bouwman, 1983). Some species only occur in very specific biotopes, others are more widely distributed. Several authors, listed in table A, noticed the predominance of members of the families of the Monhysteridae, Rhabditidae and Chromadoridae in nematode associations found on the surface of littoral macrophytes, mats of cyanophytes and decaying materials drifted ashore (debris). From henceforth species found in these biotopes will be referred to as "Aufwuchs" species. Some of these species are restricted to Aufwuchs communities and do not occur in the adjacent sediment (Bouwman, 1981, 1983; Warwick, 1979). To survive in a specific biotope, a species has to be adequately adapted to this biotope. About this relationship between species and biotope, knowledge is scarce.

Aim of this study was to survey the nematode associations in Aufwuchs communities and in the adjacent sediment, and to analyse the different survival strategies of nematode species found. Therefore, the feeding biology of specific Aufwuchs

species was compared to that of specific sediment inhabiting species. As feeding is an important aspect of the survival strategy of nematodes (Warwick, 1981) it may play a major role in the characteristic distribution of the nematode species.

Table A. Literature reporting on the occurrence of typical Aufwuchs species.

Family	Species	Found on	Literature (authors)
Monhysteridae	<i>M. disjuncta</i>	<i>Fucus</i> macroalgae	Ohm 1964
	<i>M. parva</i>	breakwaters	De Coninck and Stekhoven 1933 Schütz and Kinne 1955 Hopper and Meyers 1967
		<i>Thalassia</i>	Ohm 1964
		<i>Fucus</i> salt marshes	Bilio 1966; Lorenzen 1969
	<i>D. brucei</i>	<i>Spartina</i>	Hopper 1970; Warwick 1981
	<i>D. oschei</i>	<i>Enteromorpha</i> <i>Spartina</i>	Meyl 1954; von Thun 1968 Lorenzen 1969
Rhabditidae	<i>R. marina</i>	rotting seaweeds	Inglis and Coles 1961
		breakwaters	De Coninck and Stekhoven 1933 Schütz and Kinne 1955
		<i>Enteromorpha</i>	Otto 1936
		<i>Zostera</i>	Tietjen et al. 1970
Chromadoridae	<i>C. nudica- pitata</i>	<i>Enteromorpha</i>	Otto 1936
		<i>Cladophora</i>	Wieser 1959, 1960
		<i>Fucus</i>	Ohm 1964
		<i>Thalassia</i>	Hopper and Meyers 1967
		<i>Sargassum</i>	Ott 1957; Kito 1982
		salt marshes	Bilio 1966
		various bio- topes	Wieser 1952; De Man 1922; Warwick 1971; Platt 1977; Gerlach 1953

MATERIALS AND METHODS

Sampling

Samples were taken from the sampling stations Eemshaven, Hoogwatum, Reide (Fig. 1), located in the Ems estuary, and from the German Wadden Island of Mellum. The following material was sampled at these stations:

	Eemshaven	Hoogwatum	Reide	Mellum
macrophytes	<i>Spartina</i> sp. <i>Fucus</i> sp. <i>Ulva</i> sp.	<i>Zostera</i> sp.	<i>Salicornia</i> sp. <i>Enteromorpha</i> sp.	
cyanophytes			<i>Oscillatoria</i> sp.	<i>Oscill.</i> sp.
debris	+			
sediment	+	+	+	+

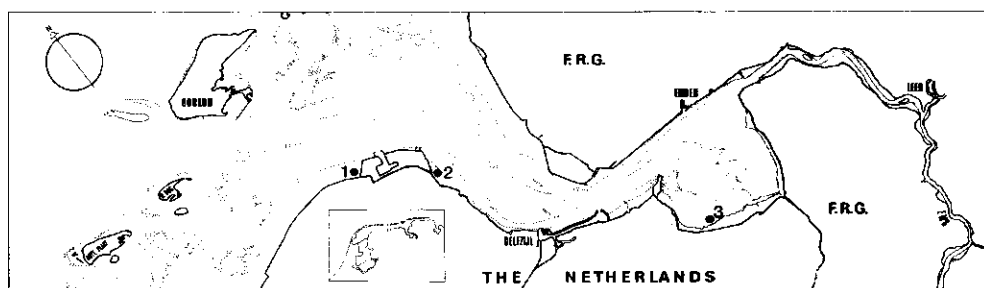


Fig. 1. Map of the Ems estuary with the sample stations. 1 = station Eemshaven, 2 = station Hoogwatum, 3 = station Reide.

At low tide samples of *Ulva*, *Zostera* and *Enteromorpha* were collected from the sediment on which they were lying; consequently, these samples contained a considerable amount of sediment. *Salicornia* and *Oscillatoria* were collected from a tidal creek. *Fucus* was sampled from breakwaters on which they were attached c. 60 cm above the sediment. The samples from Mellum originated from the so called "Farbstreifensandwatt" (FSSW), a laminated biotope, composed of a thin surface layer of sediment (c. 3 mm thick), covering a compact mat of cyanophytes (c. 2 mm); below this mat a reddish zone, consisting of bacteria from the genus *Chromatium*, is found; underneath this zone the sediment is black due to the presence of iron sulphide. Samples from the FSSW and from the sediment at the other sampling stations were taken in triplicate with plastic tubes (\varnothing 2.4 cm).

In the laboratory the nematodes were separated from their hosts by means of stirring with seawater. Sediment inhabiting nematodes were collected by means of a density separation technique using the colloid silica gel Ludox T.M. (De Jonge and Bouwman, 1977). To characterize nematode associations, 120 specimens per sample were identified (Bouwman, 1983). The vertical distribution of nematode species in the FSSW was studied by determination of specimens found in one cm thick slices of sediment down to a depth of 8 cm. The compact mat of *Oscillatoria* in the FSSW was separated from the sediment and analysed for nematodes separately.

Observations in the laboratory

From the survey it became evident that a number of nematode species appeared to be restricted to the Aufwuchs communities and did not occur in the adjacent sediment. These Aufwuchs species were intensively studied in the laboratory. Observations were made on the contents of the digestive tract of species sampled from the field and of species originating from laboratory cultures with various types of food (e.g. bacteria and algae). The feeding behaviour of some specific Aufwuchs species and that of specific sediment inhabitants was studied with an inverted microscope; for this, observation chambers type B (Maertens, 1975) were filled with a thin layer of agar containing food organisms such as diatoms and other unicellular algae. To ingest food, the nematodes make pumping movements with their muscled oesophagus; the frequency and the

degree of continuity of the pulsations were recorded.

Cultivation and feeding experiments

Cultivation

To compare the feeding biology of nematode species from different biotopes, attempts were made to culture characteristic Aufwuchs species and also some sediment inhabiting species, in agar cultures containing several types of food. The agar cultures (Difco bacto agar, 5 g/l, salinity 25‰) were prepared as follows: Molten agar was mixed with a suspension of food organisms on a vortex mixer at 35 °C; droplets of this mixture were pipetted into small Petri-dishes; 20 to 40 nematodes were inoculated into the solidified agar; the Petri-dishes were sealed with parafilm and put in a perspex box, partly filled with water to prevent the cultures from dehydrating. The cultures were stored at 17 °C at a 16 h light period. The food organisms used were the diatom species *Navicula salinarum* and *Nitzschia cf. closterium* (Bacillariophyceae), the green alga *Tetraselmis* sp. (Prasinophyceae) and the red alga *Rhodomonas* sp. (Cryptophyceae). The diatom species mentioned are abundant in the mud-flats of the Ems estuary (Admiraal, 1976; Admiraal et al., 1983), the other algae are planktonic but certain stages also occur in the benthic system. The final concentration of algae in the agar cultures was c. $2 \cdot 10^6$ cells/cm³. To establish agar cultures with bacteria as food organisms, the amino acid glycine was added: final concentration in the cultures was 0.125 g/l, on which a rich bacterial flora developed. As small organic molecules are absorbed actively and assimilated by nematodes (Chia and Warwick, 1969; Lopez et al., 1979), in the agar cultures glycine is also a direct source of food for the nematodes; this was confirmed in other experiments of the present authors. However, glycine mainly acts indirectly as a growth stimulus for bacteria which in fact are the essential food item for many nematode species.

The nematode species *Rhabditis marina* Bastian 1865, *Monhystera parva* Bastian 1865, *Monhystera microphthalma* De Man 1880, *Diplolaimelloides brucei* Hopper 1970, *Diplolaimelloides oschei* Meyl 1954, *Chromadora nudicapitata* Bastian 1865 and *Chromadorita guidoschneideri* Filipjev 1929, could be cultured for many generations in the laboratory; the species *Monhystera disjuncta* Bastian 1865 and *Daptonema setosum* Bütschli 1874,

could not be cultivated for more than two generations. To check the importance of different food organisms for the various nematode species, decreases and increases in the number of specimens were recorded at intervals, in a series of culture experiments.

Feeding experiments

The amount of food organisms consumed was measured in feeding experiments with ^{14}C -labelled diatoms and bacteria as food for various nematode species. For ingestion experiments with ^{14}C -labelled diatoms as food, the following procedure was used. Exponentially growing cultures of *Navicula salinarum* (Grunow) were labelled by adding H^{14}CO_3 . After 24 h incubation in light ($100 \mu\text{E}/\text{m}^2/\text{sec}$) nearly all the label had been incorporated by the diatoms. After washing with fresh medium, the degree of labelling of the cells was 7.3 - 11.1 dpm/cell; homogeneous labelling was not ensured. Agar droplets of 0.5 cm^3 containing c. $5 \cdot 10^6$ diatom cells/ cm^3 , were inoculated with 15-20 nematodes. After various incubation periods of 2, 4 and 20 h, the nematodes were transferred twice to sterile agar for approximately 10 minutes to remove adhering labelled diatoms. The nematodes were put in scintillation vials, containing 0.5 ml demineralized water and 7 ml scintillation liquid (Insta-gel 11 Packard). After 2 days (maximum yield dpm), radioactivity was measured with a liquid scintillation counter. Blanks were treated the same way but the incubation time in agar with labelled diatoms was much shorter (c. 1.5 minutes).

Ingestion experiments with bacteria were carried out with an aerobic, heterotrophic, gram-negative bacterium; it was a curved rod, c. $1.3 \mu\text{m}$ long, motile and it was isolated from the Ems estuary. Several samples of 1 ml from a batch culture in exponential phase, were frozen in liquid nitrogen and stored. For the ingestion experiments, ^{14}C -labelled glucose (50 mCi) was added to the samples in a 30 ml serum bottle, containing 9 ml nutrients medium. After 22 h of incubation at room temperature, the cultures reached the stationary phase as assessed by spectrophotometric OD^{430} measurements. The degree of labelling of the cells was 0.015-0.018 dpm/cell at a cell density of $0.3\text{-}0.4 \cdot 10^9$ cells/ml, OD^{430} : 0.25-0.28. Densities of $0.9\text{-}1.2 \cdot 10^9$ cells/ml proved to be sufficient for the ingestion experiments. The bacteria were mixed through the agar in the same way as the diatoms. Microscopic checks of the cultures showed a homogeneous distribution of bacteria in

the agar. Incubation, and measurements of radioactivity were carried out in the same way as described for the diatom ingestion experiments.

For a preliminary determination of the incorporation of ingested food, nematodes were incubated as described for the ingestion experiments and subsequently kept for 24 h in agar with unlabelled diatoms or bacteria, whereafter radioactivity was measured. It was assumed that the ingested labelled food had been assimilated as much as possible and that the remaining label had either been excreted or respired.

All experiments were carried out at room temperature 20-23 °C. During incubation of nematodes on labelled food, grazing activity was checked visually under the microscope to ensure that experiments were only carried out with vital nematodes.

RESULTS

Survey of nematodes

Several nematode species that had not been isolated from the Ems estuary previously, were found (Table 1)

Table 1. Nematode species not isolated previously from the Ems estuary.

<i>Haliplectus dorsalis</i> Cobb 1930 (Reide)
<i>Leptolaimus puccinelliae</i> Gerlach 1959 (Reide)
<i>Monhystera microphthalma</i> De Man 1880 (Eemshaven)
<i>Sabatieria longicaudata</i> Filipjev 1922 (Hoogwatum)
<i>Chromadora macrolaima</i> De Man 1889 (Eemshaven)
<i>Chromadorina supralitoralis</i> (nec. Wieser 1951) Gerlach 1965 (Reide)
<i>Prochromadorella ditlevseni</i> De Man 1922 (Eemshaven, Hoogwatum)
<i>Halalaimus similis</i> Allgén 1930 (Eemshaven)
<i>Eurystomina terricola</i> De Man 1907 (Reide)
<i>Monhystera parva</i> Bastian 1865 (Eemshaven, Hoogwatum)
<i>Theristus flevensis</i> Stekhoven 1935 (Reide)

A limited number of species was found that dominated the Aufwuchs communities (Table 2). Specific Aufwuchs species that do not occur in the sediment were mostly members of the family of the Monhysteridae: *Monhystera disjuncta* (on *Fucus*), *Monhystera parva* (on debris), *Diplolaimelloides brucei* (on *Spartina*), *Diplolaimelloides oschei* (in *Oscillatoria* mats from the FSSW); the chromadorid species *Chromadora nudicapi-*

Sample station Hoogwatum

neumatode species	<i>Zostera</i> -sediment
<i>Monhystra parva</i>	13
<i>Chromadora nudicapitata</i>	16
<i>Daptonema normandicum</i>	2
<i>Daptonema oxyerca</i>	6
<i>Atrochromadora microlaima</i>	12
<i>Dichromadora geophila</i>	6
<i>Innacuonema tentabundum</i>	16
<i>Paracanthonus caecus</i>	7
<i>Axonolaimus parapsinosus</i>	5
<i>Halalaimus gracilis</i>	8
<i>Viscosa viscosa</i>	42
other species	7
	26(13)
	20(12)
	120
	120
	+

Sample station Reide

neumatode species	<i>Salicornia</i> -sediment	<i>Oscillatoria</i> -sediment	<i>Enteromorpha</i>
<i>Rhabditis marina</i>	6		
<i>Monhystra disjuncta</i>	8		
<i>Diploimeloides brucei</i>	26		
<i>Monhystra</i> sp.		8	1
<i>Eleutherolaimus stenosoma</i>	20		17
<i>Daptonema normandicum</i>	7	27	1
<i>Daptonema setosum</i>	1	48	25
<i>Theristus flevensis</i>	66	12	73
<i>Chromadora supracitatoralis</i>	2	8	5
<i>Ptycholaimellus ponticus</i>		1	1
<i>Paracanthonus</i> sp.	12		14
<i>Microaimus globiceps</i>	8		10
<i>Tripyloides marinus</i>	11	7	3
<i>Anoplostoma viviparum</i>	12	4	7
<i>Syringolaimus striatocaudatus</i>	12		35
other species	11(6)	12(3)	1
	120	120	6(5)
	120	120	31(11)
			+
			120

tata was abundant on *Zostera* but also in the thin top layer of the sediment of the FSSW; the rhabditid species *Rhabditis marina* was particularly numerous in the debris. Some other species, numerous in the Aufwuchs communities, were: *Atrochromadora microlaima* (on *Ulva*), *Anoplostoma viviparum* (on *Enteromorpha*), *Theristus flevensis* (on *Salicornia*) and several *Daptonema* species (in particular on debris and on *Oscillatoria*). These species, however, are also found in varying densities in the sediment (Bouwman, 1981, 1983) and therefore not considered to be characteristic representatives of a specific Aufwuchs fauna.

Observations on food intake and gut contents

Several nematode species were cultured in the laboratory on different food organisms. Food intake of these species was studied by means of direct observations through the microscope; the results were compared with the observations of gut contents of the same species, present in field samples (Table 3).

Table 3. Food intake observations on Aufwuchs- and on interstitial nematode species in laboratory cultures, and gut contents of species sampled from the field. A = Aufwuchs, S = Sediment, ? = no data. N = *Navicula salinarum*, Ni = *Nitzschia cf. closterium*, T = *Tetraselmis*, R = *Rhodomonas*.

nematode species	biotope	cultures				field gut contents
		N	Ni	T	R	
<i>D. oschei</i>	A	-	-	-	-	red coloured cells
<i>D. brucei</i>	A	-	-	-	+	green/brown coloured granules
<i>R. marina</i>	A	-	-	+	+	granules of various colours
<i>M. parva</i>	A/S	+	+	+	?	various diatom species
<i>M. disjuncta</i>	A	+	+	+	+	granules of various colours
<i>C. nudicapitata</i>	A/S	+	+	+	-	green coloured granules
<i>D. setosum</i>	S	+	+	?	?	various diatom species and cyanophytes
<i>T. flevensis</i>	S/A	-	-	?	?	brown coloured granules
<i>C. guidoschneideri</i>	S	+	-	-	-	green coloured granules

The gut of *Diplolaimelloides oschei* from field samples contained red cells, probably bacteria of the genus *Chromatium*. Diatoms were observed in the intestine of *Monhystera parva*, *Daptonema setosum* and the other *Daptonema* species isolated from the field. In laboratory cultures *Diplolaimelloides brucei* ingested the alga *Rhodomonas*; *Monhystera disjuncta* and

Monhystera parva ingested all types of algae offered. Algae were not visible in the gut of *Chromadora nudicapitata* which contained green granules; in cultures it appeared that this species consumed diatoms and other algae by puncturing the cell wall and sucking out the contents of the cell. Although the species *Daptonema setosum* ingested entire diatoms, the closely related species *Theristus flevensis* did not. The sediment inhabiting species *Chromadorita guidoschneideri* also sucked out diatoms but no other algae.

Pumping activity

The pumping activity of the oesophagus was analysed for several Aufwuchs species and for some sediment inhabiting species in agar cultures containing food organisms (Table 4).

Table 4.

Pumping activity (pulsations/minute) of Aufwuchs species and of interstitial species as observed in agar cultures with different food organisms.

A = Aufwuchs, S = Sediment, ? No data. N = *Navicula salinarum*, Ni = *Nitzschia cf. closterium*, T = *Tetraselmis*, B = Bacteria, sa = sterile agar.

nematode species	biotope	sa	N	Ni	T	B
<i>R. marina</i>	A	82	75	?	90	105
<i>D. brucei</i>	A	42	44	37	36	?
<i>M. disjuncta</i>	A	4	5	3	9	9
<i>M. parva</i>	A/S	2	4	2	1	?
<i>C. nudicapitata</i>	A/S	<1	5	?	?	?
<i>D. setosum</i>	S	<1	?	?	?	?
<i>C. guidoschneideri</i>	S	<1	<1	?	?	?

Rhabditis marina pulsed continuously with a high frequency in the presence of different food items offered (c. 90 pulses/minute). *Diplolaimelloides brucei* also pulsed with a high frequency but not continuously and therefore on average less frequent (c. 40 p/m). *Monhystera disjuncta* pulsed very irregularly, sometimes with a high frequency (c. 60 p/m) and sometimes not at all; the species always pulsed when colliding with an algal cell but also when not colliding (average frequency 6 p/m). *Chromadora nudicapitata* and *Monhystera parva* pulsed after collision with an algal cell and occasionally at other times. The sediment inhabiting species *Daptonema se-*

tosum and *Chromadorita guidoschneideri* only pulsated after colliding with a particle, which in the agar cultures usually means a food item.

Culture experiments

From the results of culture experiments with 5 nematode species on different types of food (Fig. 2) it is clear that

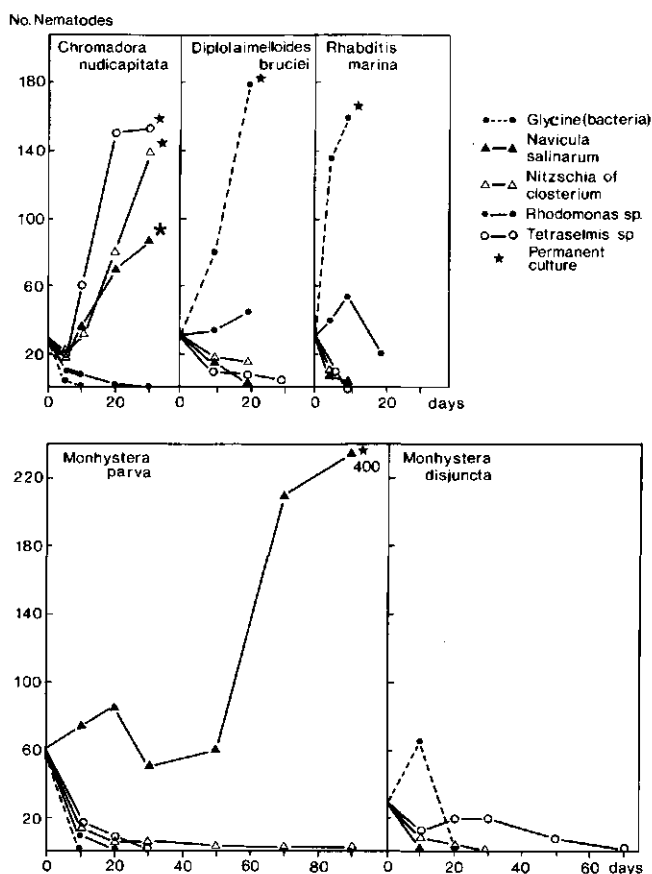


Fig. 2. Development of populations of some nematode species in agar cultures with different food organisms.

Rhabditis marina and *Diplolaimeloides brucei* are only able to increase their numbers in glycine enriched (bacteria) agar; in all other cultures *Rhabditis marina* petered out rapidly. The same results were obtained when culturing *Diplo-*

laimelloides brucei, which, however, survived longer in the agar cultures but finally also petered out in all algal cultures, *Rhodomonas* excepted; cultures of this nematode species on *Rhodomonas* were successful but the algae disintegrated after c. 20 days. *Monhystera parva* could be easily raised on the diatom *Navicula salinarum*; cultures on other algae, including the diatom *Nitzschia cf. closterium*, were not successful. *Monhystera disjuncta* reproduced in glycine enriched agar, the new generation, however, suddenly collapsed; in the algal cultures, population development varied but finally all populations petered out. *Chromadora nudicapitata* could be raised on the various types of algae offered, with the exception of *Rhodomonas*.

Feeding experiments with labelled food

The results of feeding experiments with 7 nematode species supplied with labelled diatoms and labelled bacteria, support the information already gained from observations on food intake and culture experiments. *Rhabditis marina*, *Diplo-laimeloides brucei* and *Monhystera disjuncta* ingested significant numbers of bacteria, 1700, 500 and 300 cells/h respectively (Table 5). *Monhystera disjuncta* ingested diatoms too, c. 18/h.

Table 5. Ingestion and incorporation of ^{14}C -labelled bacteria and diatoms by some Aufwuchs and some interstitial nematode species.

nematode species	biotope	average number of bacteria ingested		average number of diatoms ingested	
		/nem/h	incorp.%	/nem/h	incorp.%
<i>R. marina</i>	A	1630	21	0	
<i>D. brucei</i>	A	470	38	0	
<i>M. disjuncta</i>	A	330	53	18	22
<i>M. parva</i>	A/S	19		6	
<i>C. nudicapitata</i>	A/S	20		37	
<i>D. setosum</i>	S	6		?	
<i>C. guidoschneideri</i>	S	13		?	

Daptonema setosum did not ingest bacteria but ingested a considerable amount of diatoms (up to 13 cells/h, as measured in other experiments which are not presented in this paper).

Chromadora nudicapitata did not ingest entire diatoms but ingested a considerable amount of label by sucking out the contents of c. 37 cells/h. In agar cultures with a mixture of labelled bacteria and diatoms, *Chromadorita guidoschneideri*, *Chromadora nudicapitata*, *Monhystera parva* and *Daptonema setosum* ingested hardly any bacteria while microscopic observations during the incubation showed that numerous diatoms were ingested or sucked out. Under the prevailing experimental conditions, the incorporation of labelled carbon amounted 20-50% of the total amount of labelled carbon ingested in the experiments with bacteria and c. 20% in the experiments with diatoms.

All the information gained from observations and experiments was used to establish Fig. 3, in which the menu of five nematode species is shown.

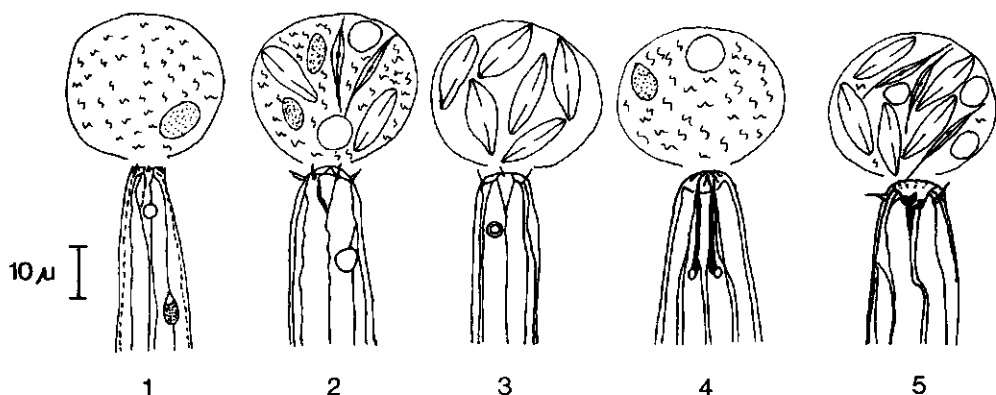


Fig. 3. Menu of five nematode species,

- | | |
|-------------------------------------|------------------------------------|
| 1 = <i>Diplolaimelloides brucei</i> | • = bacteria |
| 2 = <i>Monhystera disjuncta</i> | ● = <i>Rhodomonas</i> |
| 3 = <i>Monhystera parva</i> | ○ = <i>Tetrasselmis</i> |
| 4 = <i>Rhabditis marina</i> | ◐ = <i>Navicula salinarum</i> |
| 5 = <i>Chromadora nudicapitata</i> | ◑ = <i>Nitzschia cf closterium</i> |

DISCUSSION

The feeding behaviour of characteristic Aufwuchs species such as *Rhabditis marina* and *Diplolaimelloides brucei*, differs markedly from that of typical sediment inhabitants, e.g. *Daptonema setosum* and *Chromadorita guidoschneideri*. The behaviour of the Aufwuchs species points to a non-selective way of

feeding, characterized by the continuous pumping activity of the oesophagus. In the Aufwuchs biotope, a non-selective feeding-strategy seems to be appropriate to survive because suitable food is abundant in this biotope. The Aufwuchs nematodes do not need to select their food because food organisms are hardly mixed with similarly sized inedible particles. Sensory organs such as setae and lips which may play a role in the detection of food, are not necessary in this biotope; most Aufwuchs species do not have well developed sensory organs. No clear selection is made by the Aufwuchs species towards different food organisms; in the ingestion experiments, however, *Rhabditis marina* and *Diplolaimelloides brucei* did not consume all food organisms offered. Probably the dimensions of some of the food items are too large to be consumed by nematodes with relatively small buccal cavities. The species *Monhystera disjuncta* possesses a slightly wider buccal cavity and was able to ingest all food organisms offered in the experiments, algae as well as bacteria; although pumping of this species was often interrupted, its feeding-strategy still seems to be non-selective because pumping was not restricted to moments of collisions with a particle. The non-selective way of feeding of the specific Aufwuchs species contrasts with the selective feeding behaviour of specific sediment inhabitants such as *Daptonema setosum* and *Chromadorita guidoschneideri*. These species possess well developed sensory organs, probably used to select suitable food particles out of a majority of similarly sized inedible particles (Romeyn and Bouwman, 1983). Their feeding behaviour is adapted to the interstitial biotope as they only start oesophageal pulsations after collisions with food particles.

An intermediate position is taken by *Monhystera parva* and *Chromadora nudicapitata*, both possessing normally developed sensory organs, necessary to detect the favoured diatoms; their pumping activity, however, is not continuous, but neither is it restricted to moments of collision.

In the relation between biotope and the feeding behaviour of its inhabitants, the nematode species studied show a gradient from specific Aufwuchs species, feeding with a non-selective strategy (*Rhabditis marina*, *Diplolaimelloides brucei*) via species characteristic to Aufwuchs communities but occasionally also present in the sediment, feeding more selectively (*Monhystera parva*, *Chromadora nudicapitata*) to species found almost exclusively in the sediment and that

feed in a very selective way (*Daptonema setosum*, *Chromadora guidoschneideri*). *Monhystera disjuncta* fits in between the non-selective Aufwuchs strategists and the other groups mentioned.

The actual occurrence of a species in a specific biotope is not only determined by its feeding behaviour (Warwick, 1981). Also factors such as reproductive capacity, and tolerance to prevailing environmental conditions, e.g. salinity, free sulphide, competition and predation, will play a role in the survival strategy of nematode species. Reproductive capacity, as determined by the reproductive potential, the time needed to reach maturity and length of the reproductive period under optimum conditions varies for the different species. The reproductive capacity of *Rhabditis marina* is extremely high (Tietjen et al., 1970) as larvae mature in a few days under optimal conditions and one female produces c. 100 eggs; the reproductive capacity of *Dipholaimelloides brucei* is also high (Warwick, 1981) and assumed to be as high as that of the closely related species *Monhystera microphthalma* which females can produce hundreds of eggs per specimen (Van Brussel, 1980). *Monhystera disjuncta* is an ovoviviparous species and gravid females isolated from *Fucus* in August, contained 10-20 eggs and larvae and one specimen even contained 60 larvae. In the favoured biotope on the surface of macrophytes, the above mentioned species have the opportunity to convert the abundance of food into offspring very rapidly. With their specific method of food intake, their short life cycle and numerous offspring, these opportunists outstrip potential competitors from the interstitial biotope, thus forming almost monospecific populations on *Fucus* and *Spartina*. *Monhystera parva* and *Chromadora nudicapitata* obviously operate in a way in between the previously described opportunistic Aufwuchs species and the sediment inhabitants. The reproductive capacity of these species was not determined exactly; from agar cultures it became clear that *Monhystera parva* tended to perform a slightly lower reproductive effort than the monhysterid opportunists and that *Chromadora nudicapitata* at least performed about the same reproductive effort as its interstitial relatives.

Culture experiments underline the positioning of the different species. The characteristic Aufwuchs species *Rhabditis marina* and *Dipholaimelloides brucei* could be raised only on bacteria which probably form the bulk of food in va-

rious Aufwuchs biotopes. The more selectively feeding *Monhystera parva* could only be raised on the diatom *Navicula salinarum* though it ingested the other algae presented as well; it is possible that the nutritional value of the other algae was sufficient for individual survival but insufficient for reproduction. *Chromadora nudicapitata* increased its population on all algae offered, with the exception of *Rhodomonas*. This species and *Monhystera parva* were both found on the surface of *Zostera* which was also covered by a large amount of sediment; both species were also isolated occasionally from the interstitial biotope, though in smaller numbers. Probably these species can survive in the sediment but their ability to track down diatoms is probably not as good as that of specialized sediment inhabitants. *Monhystera disjuncta* did not consume all food items offered but was difficult to culture in the laboratory; several other researchers (Chitwood and Murphy, 1964; Von Thun, 1968) reared the species in agar supplied with various types of food, bacteria, diatoms, protozoa, etc. Protozoa, which are also numerous on the surface of *Fucus* from which *Monhystera disjuncta* was isolated, are perhaps essential for long-term cultivation of this species.

The specificity of Aufwuchs species to particular macrophytes or cyanophytes is probably caused by the specific conditions on the surface of the various hosts. For example *Fucus* produces exudates, resulting in a mucous layer rich in bacteria and protozoa; on the *Fucus* sampled from the breakwaters, however, diatoms were missing which explains the absence of diatoms in the intestines of the predominant species on *Fucus*, *Monhystera disjuncta*. *Diplolaimelloides brucei* is reported to be numerous particularly on decaying *Spartina* (Hopper, 1970; Warwick, 1981) which already indicates the importance of bacteria as food for this species; the relationship between *Spartina* and *Diplolaimelloides brucei* seems to be very specific as the nematode has not yet been isolated from other substrata. The debris offers a more diverse environment with abundant bacteria, diatoms, probably protozoa and also inedible particles; it is assumed that higher temperatures occur in the decaying materials, favouring the development of a species such as *Rhabditis marina* which belongs to the saprobic terrestrial Rhabditidae.

Because of the close contact between sediment and *Zostera* leaves, the nematode species on this substratum were less specific; selection was in favour of the diatom consuming

species *Monhystera parva* and *Chromadora nudicapitata*, which both are not considered characteristic Aufwuchs species. The predominance of *Theristus flevensis* on *Salicornia*, *Atrochromadora microlaima* on *Ulva*, *Daptonema* species on *Oscillatoria* and *Anoplostoma viviparum* on *Enteromorpha* is not well understood because these species are also numerous in various interstitial biotopes (Bouwman, 1983). The laminated biotope found in the FSSW is also considered to be an Aufwuchs biotope in which *Diplolaimelloides oschei* feeds on bacteria, including *Chromatium* and consequently it is most numerous in the *Oscillatoria* and *Chromatium* layers. This species was found to be ovoviviparous. Gravid females were observed containing about 15 larvae. This ovoviviparity was not observed by Meyl (1954, 1955) and Von Thun (1968). Von Thun cultured the species in the laboratory and would certainly have noticed this phenomenon when occurring in his cultures. Probably the ovoviviparity is a reaction on the presence of hydrogen sulphide, particularly in the *Chromatium* zone and in the deeper sediment layers. *Chromadora nudicapitata*, which feeds on algae is most numerous in the thin sediment layer covering the mat of cyanophytes.

Generally it can be concluded that several nematode species are adequately adapted to the Aufwuchs respectively interstitial biotope; not only their morphology (Wieser, 1953) but also their behaviour (Romeyn and Bouwman, 1983) is well adapted to the specific conditions prevailing in these biotopes. The feeding methods of specific Aufwuchs species are quite different from those of specific interstitial species.

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CHAPTER VI

On the ecology of meiofauna in an organically polluted estuarine mudflat

L.A.Bouwman, K.Romeyn and W.Admiraal

ABSTRACT

Biotopes located in the upper reaches of estuaries are exposed to greater physical and chemical fluctuations than biotopes located in other estuarine zones or in the marine or limnetic environment. Organisms living in the upper reaches have to cope with many different and sudden environmental changes which often reach extreme values. In order to survive, organisms from such dynamic environments need special inherent properties. The structure, distribution and seasonal changes of the benthic fauna in an organically polluted, tidal, brackish-water mudflat, lying in the upper reaches of the Ems estuary in the vicinity of an outfall, were analysed. Along a gradient towards the outfall macrofauna disappeared and the diversity of meiofauna decreased but their density increased. In the area surrounding the outfall the numbers and biomass of nematodes and oligochaetes increased rapidly in spring and remained high until autumn (c. 13×10^6 ind. \cdot m $^{-2}$; c. 2 g C.m $^{-2}$).

Recurrent stress situations around the outfall favour organisms that are able to recover rapidly from sudden environmental stress: only species having short life cycles. In the area studied the benthic fauna comprised small numbers of species, dominated by a few fast-growing diatom-feeding nematodes (*Eudiplogaster pararmatus* and *Dichromadora geophila*), and oligochaetes (*Amphichaeta sannio* and *Paranais litoralis*). The success of the non-marine nematode *Eudiplogaster pararmatus* in this biotope is determined by its brood-care for the first stage larvae which remain protected within the body of the ovoviviparous females; because this species originates from freshwater, it is not affected by lower salinities, and it also tolerates higher salinities. Although unrelated taxonomically to the latter nematode species, *Dichromadora geophila* behaves similarly with regard to tolerances, life cycle and food selection and consumption; probably because of its o-

viparity, it is less successful than *Eudiplogaster pararmatus* in the tidal flats surrounding the outfall. The success of the two naiddid oligochaete species results from their method of reproduction by means of binary fission.

All these organisms feed on benthic diatoms that are abundant in the biotope throughout the year. In spite of intensive mineralization in the mudflat, only one bacteria-feeding organism was found in abundance: the very small ($L = c. 0.5 \text{ mm}$) nematode *Leptolaimus papilliger*; as most nematodes in the interstitial biotope probably feed selectively, only species with very small buccal cavities are assumed to feed on individual bacteria; such species are scarce in general and nearly absent in the studied area. The absence of macrofauna organisms, e.g. *Nereis diversicolor*, is probably also responsible for the development of high densities of meiofauna in the upper sediment layers of the mudflats surrounding the outfall. The heavy load of organic waste entering the Dollart reduced the diversity of the benthic ecosystem, but nevertheless a simple system with various components survived in a thin 3 mm thick layer covering the sediment. This ecosystem survives because of the recurrent reoxidation of the sediment surface during emersion and comprises primary producers and primary consumers, dominated by diatoms and diatom-feeders, and also a considerable aerobic mineralization is maintained although the anaerobic processes are markedly enhanced.

INTRODUCTION

The upper reaches of the Ems estuary consist of a geographically distinct part, the Dollart. The Dollart has a freshwater input of its own, supplied by a small river, the Westerwoldsche A, which enters the area through a sluice at Nieuwe Stantenzijl (Fig. 1). As a result of the accumulation of small particles, the sediments of the tidal flats in the Dollart, which cover 80% of the area, are very muddy (median grain size = $58 \mu\text{m}$; c. 30% particles $< 16 \mu\text{m}$). Average salinity is lower than marine conditions, and strong fluctuations in salinity (c. 0.5–30 ‰) frequently occur. The duration of emersion of the tidal flats is long, and consequently the surface of these sediments is also exposed to large temperature fluctuations and to dehydration.

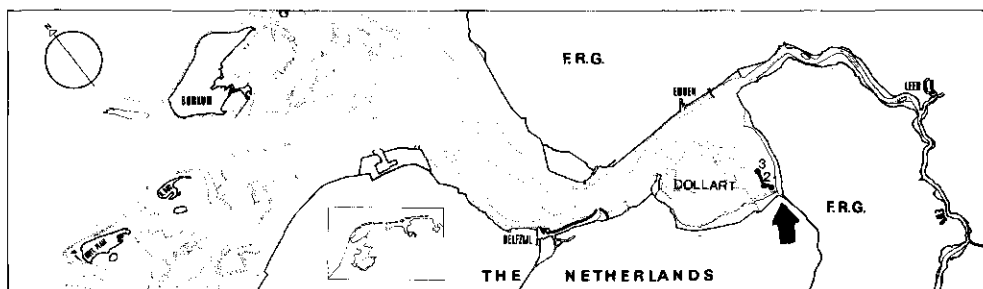


Fig. 1. Map of the Ems estuary, showing the location of the transect (●—●) on the mudflat in the southeast Dollart and the location of the outfall (➔).

Close to the Dollart, in The Netherlands, there is a large potato flour industry that discharges enormous amounts of organic waste into the Dollart at Nieuwe Statenzijl, mainly in autumn: 33×10^6 kg carbon per year (Van Es, 1977), which corresponds in autumn to c. 10×10^6 i.e. per day (inhabitant equivalents of 35 g BOD₅²⁰) (Van Es et al., 1980). These discharges cause a strong local decrease in the oxygen saturation of the water (Fig. 2), which influences the benthic flora and

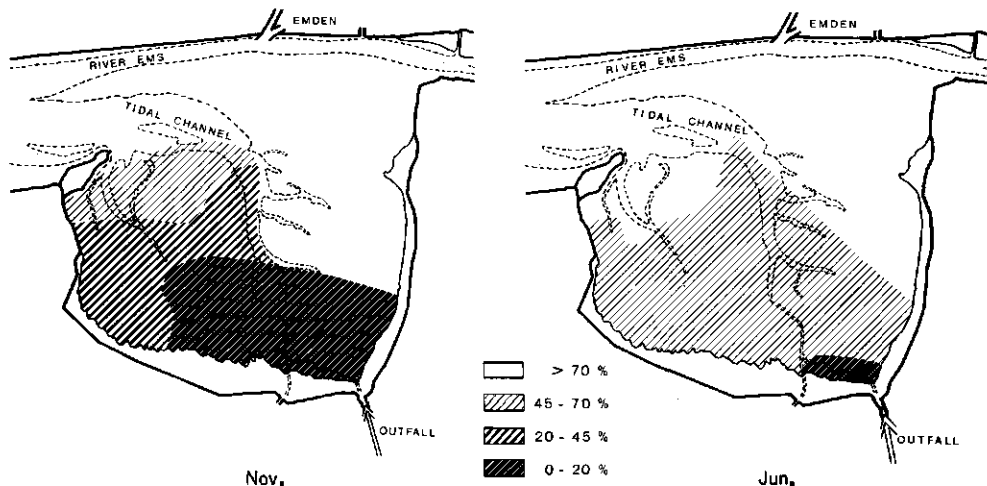


Fig. 2. Oxygen saturation (%) in the water covering the tidal flats in the Dollart in November 1974 and June 1975 (borrowed from Van Es, 1980).

fauna. Towards the outfall densities of bacteria increase,

the strongest increase being observed for the sulphate-reducing group, which indicates an increase in the proportion of the anaerobic mineralization (Schröder and Van Es, 1980). The diatom flora impoverishes in the same direction and as a result there are only a few species close to the outfall (Admiraal et al., 1983); however, biomass in terms of chlorophyll-a is high and consequently primary productivity is high too; also community respiration is higher than in the lower and middle reaches of the estuary (Van Es, 1982; Colijn and De Jonge, 1983). It is evident that the area surrounding the outfall differs considerably from the rest of the Dollart in its oxygen regime, microflora, and microfauna; its macrofauna is influenced too. Tidal flats in the Dollart are colonized by macrofaunal species such as the polychaetes *Nereis diversicolor* and *Heteromastus filiformis*, the bivalves *Macoma baltica* and *Mya arenaria*, the decapod *Corophium volutator* and the gastropod *Hydrobia ulvae*. In the area surrounding the outfall, macrofauna organisms are nearly absent; occasionally specimens of *Nereis diversicolor* occur, but these disappear in autumn (Essink, 1979; Van Es et al., 1980).

In this study attention is focused on the meiofauna in the vicinity of the outfall, where the organisms are confined to the oxidized upper 3 mm of the sediment. The structure (species composition) and distribution in time and space of the nematode, copepod (harpacticoids) and oligochaete fauna are analysed and related to environmental stress, including the organic pollution. The feeding behaviour of the meiofauna close to the outfall was investigated and related to the microflora and -fauna on which the organisms feed. In this context survival strategies of dominant species were also analysed. Finally, attention is focused on the relationship between meio- and macrofauna.

MATERIALS AND METHODS

Sampling

Three stations located on the tidal mudflat OFP (Fig. 1) were sampled monthly, except in January, October and December, throughout 1980. Station 1 was located 0.8 km from the discharge point at Nieuwe Statenzijl, station 2 at 1.2 km and station 3 at 3.2 km. Four sediment cores were taken per sta-

tion at low tide, using 2.4 cm Ø tubes. The cores were divided into slices one cm thick (4.5 cm³) for the upper 3 cm of the sediment; all the metazoans, with the exception of the ostracods, were isolated from these slices by means of flotation on a ludox surface and decantation over a 30 µm sieve (De Jonge and Bouwman, 1977): because of their specific gravity, which is too high for flotation on a ludox surface, ostracods cannot be isolated in this way. Isolated organisms were counted and the species of nematodes, oligochaetes and harpacticoids in the subsamples were identified. The turbellarians were merely counted, as were the specimens of *Nereis diversicolor* and *Corophium volutator* (the two macrofauna species present). Species compositions of the mudflat stations were obtained by combining the data of the 4 replicates.

Diversity and similarity

The following index for diversity of the nematode associations was used (Bouwman, 1983):

$$D = C \cdot (100 - \sqrt{f_1^2 + f_2^2 \dots + f_n^2})$$

($0 \leq D \leq 100$ = diversity index; f_i = relative frequency of a species in an association; n = number of different species in an association; C = correction factor for sample size).

To calculate the similarity between two nematode samples the faunal percentage of commonness was used (Sanders, 1960; Bouwman, 1983).

As it appeared that the similarity between the nematode associations from two subsamples always exceeded 60% (at station 1, 75%; at station 2, 86%; at station 3, 61%) data from the various subsamples of a sample station were always combined (Bouwman, 1983). The diversity of the other taxa was so low that data from replicate samples were simply combined.

Carbon contents of the meiofaunal taxa

The biovolumes of the nematode, oligochaete, and harpacticoid populations were converted into carbon; therefore the average carbon content of the nematode *Eudiplogaster pararmatus* and of the oligochaetes *Amphichaeta sannio* and *Paranais litoralis* was measured by means of wet oxidation with K₂S₂O₃ in an oceanographic total carbon analyser. The average carbon contents of specimens of other species were calculated by means of the ratios of the biovolumes; the carbon contents of harpacticoid

species were borrowed from Vaeremans (1977).

Observations on feeding behaviour

Food ingestion of the dominant nematode species was studied in the laboratory in several ways. Firstly, the contents of the intestines were observed while the specimens were being identified under the microscope. Only ingested diatoms could be distinguished this way; the identification of other food items within the intestines is scarcely possible. Secondly, many nematode species were cultured in agar (Romeyn et al., 1983; Admiraal et al., 1983; Romeyn and Bouwman, 1983; Bouwman et al., 1983), mixed with bacteria, protozoa, diatoms and other algae and prey-nematodes (nematodes serving as prey for other nematodes); grazing nematodes were directly observed under the microscope in special observation slides (Type B, Maertens, 1975). In this way the actual ingestion and the technique for ingesting the larger food organisms (diatoms and other algae, protozoa and prey-nematodes) could be observed. The ingestion of bacteria cannot be observed in this way, although the behaviour of grazing nematodes as observed in the observation slide may indicate whether or not a species feeds on bacteria (Bouwman et al., 1983); also the success of cultivation on different types of food indicates the food item or items needed. To obtain incontrovertible evidence that a species consumes bacteria, labelled bacteria have to be offered and the ingestion measured; this, however, was not done in this study.

The contents of the intestines of oligochaetes were also checked during the identification of species; for these too, only ingested diatoms could be distinguished. The preference of harpacticoids for particular food items was not studied.

RESULTS

Seasonal development in density and in biomass of meiofauna along the transect

The meiofauna at the 3 sampling stations consisted mainly of nematodes, oligochaetes, harpacticoids and turbellarians. Regarding total numbers, numbers of species, and biomass, the nematodes formed the largest group, oligochaetes ranked se-

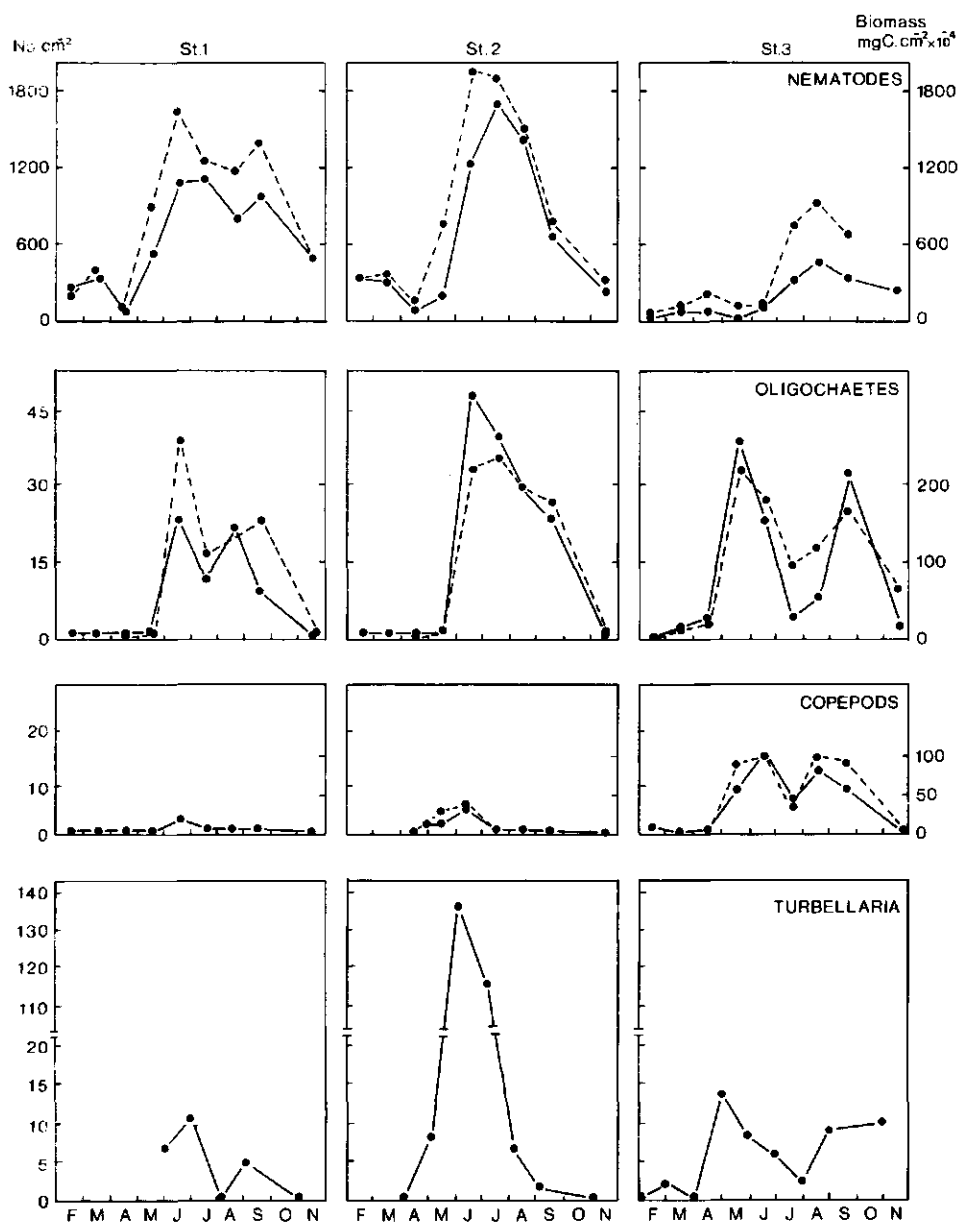


Fig. 3. Density and biomass of 4 meiofaunal taxa along the OFP-transect, throughout 1980; ●—● numbers; ●---● biomass.

cond and harpacticoids took third place, while turbellarians were only numerous in early summer at station 2 (Figs. 3 and 4). The numbers of nematodes increased towards the outfall,

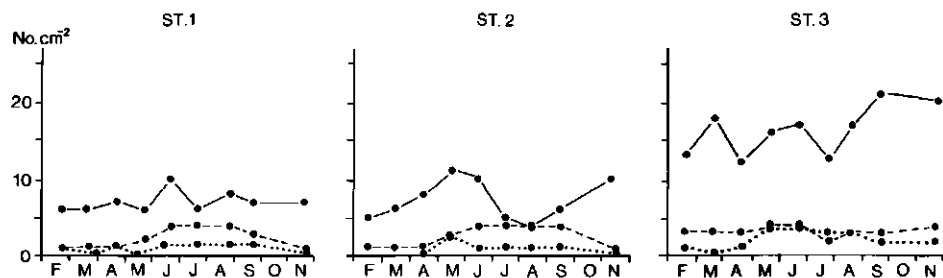


Fig. 4. Numbers of different meiofauna species along the OFP-transect; ●—● nematode species, ●---● oligochaete species, ●...● harpacticoid species.

whereas densities of oligochaetes did not differ very much along the transect and densities of harpacticoids decreased; because of the predominating nematodes, the density of meiofauna near the freshwater discharge-point throughout the year was 3 to 4 times higher than at station 3. Seasonal fluctuations close to the outfall were also more pronounced than those some distance away, and seasonal development of the various meiofaunal groups also differed between the stations. Close to the outfall all taxa started reproducing in spring, reached maxima (up to 2000 meiofauna ind..cm⁻²) in summer, and thereafter decreased abruptly or gradually to winter minima (down to 200 ind..cm⁻²). The increase in nematode density started earlier close to the outfall than further away, whereas the reverse held for the increase of oligochaetes and harpacticoids.

In winter scarcely any harpacticoids and oligochaetes were found close to the outfall, whereas the densities of nematodes remained relatively high.

At stations 1 and 2 the highest biomass, measured in summer, was c. 2000 mg carbon.m⁻²; at station 3 it was c. 1000 mg C.m⁻²; in winter these values were below 250 mg. Throughout the year, the nematodes comprised the largest number of different species: 5 to 10 at stations 1 and 2 and 12 to 21 at station 3 (Fig. 4). The number of different oligochaete and harpacticoid species was less than 5 in all 3 stations.

Probably the estuarine species minimum for nematodes is located at stations 1 and 2, whereas for oligochaetes and harpacticoids this minimum extends all along the sampled transect. The macrofauna species *Nereis diversicolor* and *Corophium volutator* were nearly absent close to the outfall but were present some distance away throughout the year.

Table 1. Nematode species isolated along the OFP-transect (stations 1, 2, 3).

	Station 1	2	3
<i>Eudiplogaster pararmatus</i>	+	+	+
<i>Dichromadora geophila</i>	+	+	+
<i>Leptolaimus papilliger</i>	+	+	+
<i>Ptycholaimellus ponticus</i>	+	+	+
<i>Microilaimus globiceps</i>	+	+	+
<i>Daptonema setosum</i>	+	+	+
<i>Daptonema xyaliforme</i>	+	+	+
<i>Paracyatholaimus proximus</i>	+	+	+
<i>Anoplostoma viviparum</i>	+	+	+
<i>Axonolaimus spinosus</i>	+	+	+
<i>Tobrilus gracilis</i>	+	+	
<i>Adoncholaimus thalassophygas</i>	+	+	
<i>Sabatieria pulchra</i>		+	+
<i>Desmolaimus zeelandicus</i>		+	+
<i>Daptonema procerum</i>		+	+
<i>Daptonema trabeculosum</i>			+
<i>Tripyloides marinus</i>			+
<i>Innocuonema tentabundum</i>			+
<i>Daptonema oxycerca</i>			+
<i>Halalaimus gracilis</i>			+
<i>Tylenchus fucicola</i>			+
<i>Viscosia viscosa</i>			+
<i>Dichromadora cephalata</i>			+
<i>Hypodontolaimus balticus</i>			+
<i>Antomicron elegans</i>			+
<i>Nemanema cylindratICAUDATUM</i>			+
<i>Sphaerolaimus</i> sp.			+

Species associations, distribution, seasonal changes and feeding of the nematodes

Along the investigated transect, 27 nematode species were isolated in all (table 1); 25 occurred at station 3, 15 at station 2 and 12 at station 1. The nematode fauna at station 1 resembled that of station 2 and thus the similarity between the associations was high, c. 70%. Almost all the species found close to the outfall also occurred at station 3, though in smaller numbers, and other species dominated at that station.

Close to the outfall the nematode associations were dominated throughout the year by only 2 species: *Eudiplogaster pararmatus* and *Dichromadora geophila* (table 2). At stations 1 and 2 on average more than 80% of the nematodes isolated were located in the upper one cm sediment layer; *Dichromadora geophila* tended to penetrate more deeply into the sediment than *Eudiplogaster pararmatus*. The remaining specimens mainly belonged to the species *Leptolaimus papilliger* and *Adoncholaimus thalassophygas*. As the distribution of the specimens over the species was very uneven, the values for diversity at these stations were very low: $D_{\text{station 1}} = 32$, $D_{\text{station 2}} = 18$ (average values). At some distance from the outfall at station 3 the nematode associations were dominated by *Sabatieria pulchra*, *Ptycholaimellus ponticus* and *Leptolaimus papilliger*. As *Sabatieria pulchra* also tended to penetrate more deeply into the sediment, the predominance of this species increased in the vertical plane (table 2). The associations at this station differed considerably from the fauna close to the outfall, consequently the average similarity was low, c. 12%. The specimens were more evenly distributed over the species and thus the values for the diversity index were higher; for the upper sediment layer D was 59, for the lower sediment layers values for D were below 50.

Similarity between samples from various months was almost as high (70%) as between replicates taken at one date. However, the similarity between samples from April and, to a lesser extent, from May, differed markedly from the samples that were taken in the other months. Thus, the only significant changes in the nematode community structure took place in spring and occurred simultaneously at the 3 stations investigated. This shift in the community structure coincided with a fall in density, and was probably caused by storms

Table 2. Average relative species composition of the nematode, oligochaete, and harpacticoid faunas at different depths along the OFP-transect.

Nematode species	Station 1			Station 2			Station 3		
	0-1 %	1-2 %	2-3 cm %	0-1 %	1-2 %	2-3 cm %	0-1 %	1-2 %	2-3 cm %
<i>E. pararmatus</i>	57	34	29	79	52	51	2	2	+
<i>D. geophila</i>	25	42	45	9	34	37	1	2	1
<i>P. ponticus</i>		+		+	1	+	18	7	11
<i>P. proximus</i>	+	+	1	+	+		4	3	+
<i>S. pulchra</i>					+		22	43	52
<i>M. globiceps</i>	1	1		+	+		9	3	7
<i>L. papilliger</i>	12	18	13	4	5	4	17	13	14
<i>D. setosum</i>	1	+	1	6	3	3	3	4	+
<i>D. xyaliforme</i>	+			+			6	3	1
<i>D. trabeculosum</i>							6	5	3
<i>D. procerum</i>							2	2	2
<i>D. zeelandicus</i>					+		2	5	5
<i>A. viviparum</i>		+	+	+	1	1	4	7	2
<i>A. thalassophygas</i>	3	4	10	1	2	4			
other species *)	+(2)	+(2)	1(2)	+(2)	+(2)		4(10)	1(9)	4(4)
number of specimens identified	1700	800	150	1800	800	300	1800	1100	500
average number of specimens per cm ²	565	70	25	560	105	35	140	65	70
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Oligochaete species									
<i>A. sannio</i>	35	7	11	66	16	+	78	72	69
<i>P. litoralis</i>	53	58	61	26	45	+	15	16	14
<i>N. elinguis</i>	6		6	7	1		1		
<i>T. costatus</i>	6	35	22	1	38		6	11	17
number of specimens identified	1200	40	20	2250	140	5	1450	450	40
average number of specimens per cm ²	7.7	0.6	0.3	15	1.7	+	11	3.8	0.7
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Harpacticoid species									
<i>S. palustris</i>	90			64	+	+	41	12	13
<i>N. palustris</i>	7	+		34	+		25	71	87
<i>H. curticornis</i>				+			33	17	
other species	3			+			+		
number of specimens identified	29	1	0	119	2	1	627	52	18
average number of specimens per cm ²	0.2	+		1.1	+	+	6.0	0.4	0.1

* Number of other species in brackets.

which removed the surface layers of the sediment. The most pronounced changes in the structures of the associations were the increase in the proportion of *Dichromadora geophila* at the stations close to the outfall and of *Sabatieria pulchra* at station 3; the proportion of the other species decreased concomitantly.

Observations on the distribution of specimens over age and sex categories and the trends in the densities of 5 dominant species are shown in figures 5 and 6. The densities of these

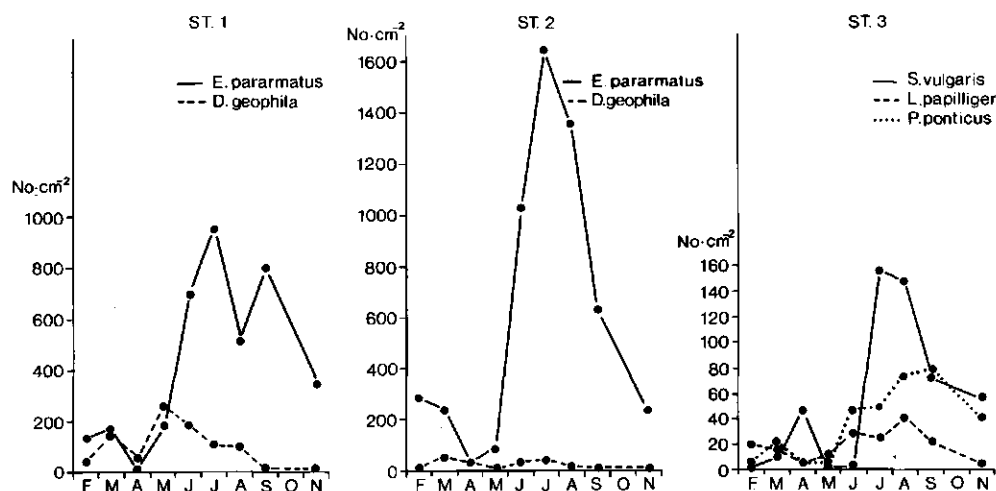


Fig. 5. Development of densities of 5 nematode species.

species rose in spring, peaked in summer and declined in autumn to winter minima. *Eudiplogaster pararmatus*, a species that accounts for c. 70% of all specimens isolated close to the outfall, appears to reproduce throughout the year; this was inferred from the presence of large numbers of larvae and gravid females at all sampling dates. Because this species is ovoviviparous many first stage larvae remained uncounted within the gravid females; up to twelve larvae were observed within these females. Therefore, the proportion of larvae was actually much higher and certainly did not fall below 50% throughout the year. On average most females were gravid, though the ratio gravid/non-gravid changes seasonally, with a conspicuous rise in the proportion of gravid females in early spring. Females outnumbered males by a factor of 2.5 on average; however, in June, when a new, dense population was

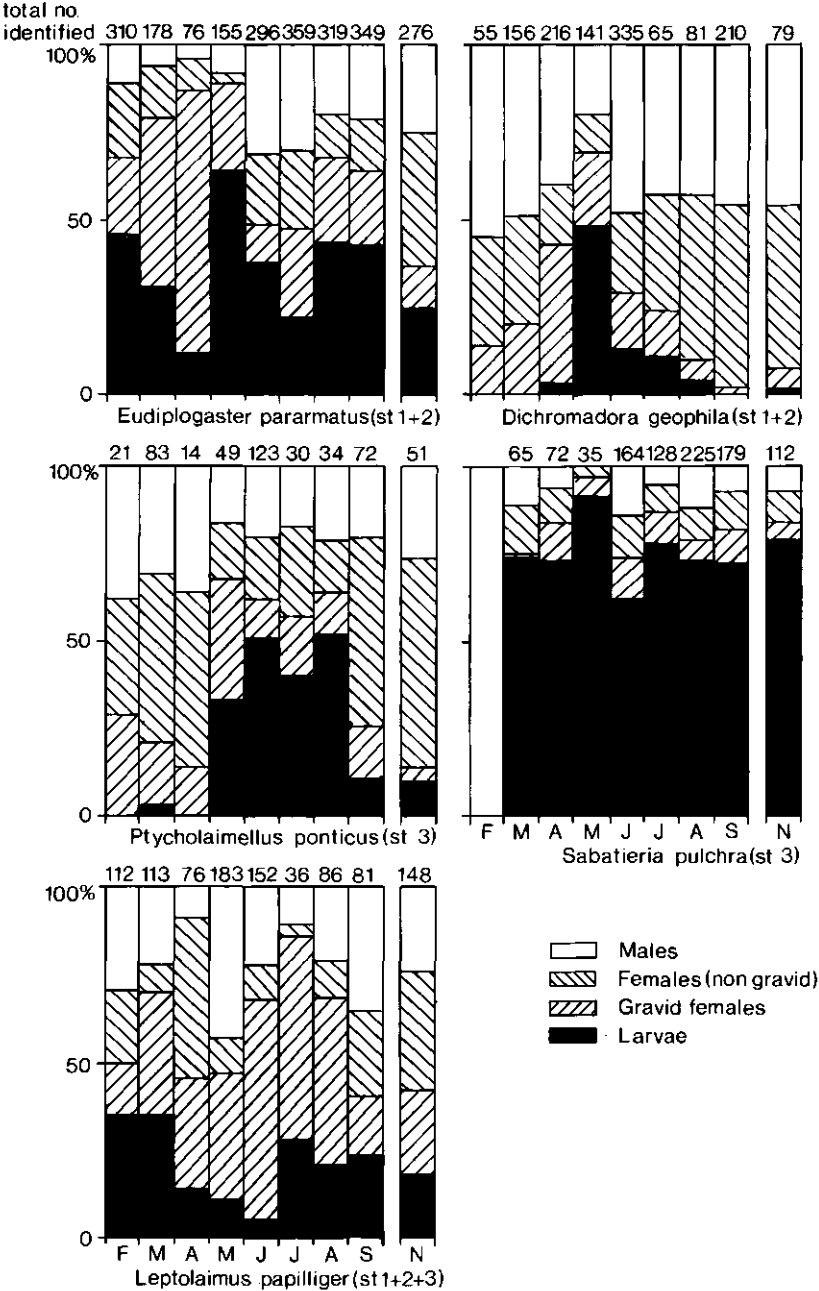


Fig. 6. Distribution of nematode specimens over different sex and age categories.

established, the numbers of both sexes were nearly equal.

Dichromadora geophila showed a different pattern of distribution of specimens over the various categories. Only in May did the proportion of larvae rise to nearly 50%; at all other sampling dates, few or no larvae were counted. It appears that near the outfall this species mainly reproduces during a short period in spring. The non-gravid females outnumbered gravid females throughout the year, except in April and May. The proportion of males was only slightly smaller than that of the females.

Ptycholaimellus ponticus, which is closely related to *Dichromadora geophila* (both are Chromadoridae), dominated in the associations at some distance from the outfall. This species started reproduction in spring and continued to reproduce during the whole summer (the proportion of larvae and gravid females in the samples did not decline drastically until autumn). There were approximately twice as many females as males.

Densities of *Leptolaimus papilliger* changed less markedly; this species was distributed along the whole transect and obviously reproduced throughout the year, as considerable numbers of larvae and gravid females were present at all sampling dates, although in the colder season the numbers of gravid and non-gravid females were approximately equal, whereas in summer c. 85% of the females were gravid. On average the ratio of females/males was 2/1.

Larvae accounted for c. 76% of the population of *Sabatieria pulchra* throughout the year; thus, for the major part of their lifetime the individuals belonging to this species remain immature. The figures for the distribution over the age categories suggest that there was no particular period for reproduction and that this species reproduces throughout the year. However, the summer peak in density suggests particular reproductive activity in the preceding period; as this species also penetrates below 3 cm into the sediment the sampling was not quantitatively reliable and therefore the actual densities of this organism will be different from the figures given.

Information on the food ingestion of nematode species from the transect investigated was obtained in various ways: observations on the gut contents of specimens collected from the field, actual observations through the microscope of food items ingested by nematodes in agar cultures, and population development of species in agar supplied with different

food items. The following feeding categories were distinguished: bacteria ingestion, diatom ingestion, diatom sucking (piercing and cracking), protozoa ingestion, nematode ingestion and nematode sucking.

Leptolaimus papilliger was cultivated in glycine-agar for more than 18 months. As the buccal cavity of this species is very small (width: 1–2 μm), only bacteria could be ingested; absorbed glycine also serves directly as food, but this type of nourishment can only be supplementary, whereas food particles are essential. For indisputable proof that this species ingests bacteria, it has to be offered marked (e.g. ^{14}C -labelled) bacteria; *Leptolaimus papilliger* is supposed to consume bacteria selectively. Of the dominating species, only *Sabatieria pulchra*'s feeding behaviour is still unknown; the fact that the preferred habitat of this species is in the sediment layers along the boundary of the sulphide zone suggests that it probably feeds on bacteria. In the present study no observations of this species were made neither were any data found in the literature. Consequently this species could not be assigned to one of the feeding categories.

Actual ingestion of diatoms was observed under the microscope, within the observation slides, for the species *Daptnema setosum* and *Paracyatholaimus proximus*. The xyalids *Daptnema xyaliforme*, *D. trabeculosum*, *D. procerum* and *D. oxycerca* were isolated from the field with diatoms observable within their intestines. *Eudiplogaster pararmatus* and *Dichromadora geophila* were observed to pinch diatoms to their lips, pierce a hole in the frustule and suck out the cell contents (Romeyn et al., 1983; Romeyn and Bouwman, 1983). *Hypodontolaimus balticus* and *Ptycholaimellus ponticus* took the diatoms partly into their buccal cavities and cracked the frustules by means of transverse movements of their teeth, induced by the heavy pharyngeal musculature that is characteristic of these species. *Tripyloides marinus* fed selectively on protozoa in the laboratory cultures and failed to ingest similarly sized items such as diatoms; *Paracyatholaimus proximus* ingests protozoa and also various types of algae, including diatoms. *Anoplostoma viviparum* is supposed to feed on protozoa (Von Thun, 1968), although this was not observed during this study. Members of the genus *Sphaerolaimus* ingest other nematodes completely whereas the species *Adoncholaimus thalassophygas* was observed to pierce specimens of *Monhystera microphthalma* and *Dichromadora geophila* in agar cultures and then to suck

out the contents. The information on food ingestion of individual species enabled the pattern of food preference of the various nematode associations along the sampled transect, to be established (Table 3). As the overall proportion of species

Table 3. Relative proportion (%) of nematode feeding categories in the associations along the OFP-transect.

food organisms	Station 1	Station 2	Station 3	
	0-1 cm %	0-1 cm %	0-1 cm %	1-3 cm %
bacteria	11.5	3.5	16.5	14
protozoa	0.5	0.5	9	5.5
diatoms ingested	1.5	6	17	11.5
sucked out	82	88.5	22	12
nematodes	3	1	+	+
unknown	1.5	0.5	35.5	58
	100%	100%	100%	100%

with known feeding habits within the associations exceeded 85% (close to the outfall c. 99%; at station 3, c.65% for the upper layer and below c. 50% more deeply), the qualitative feeding requirements of the nematode associations could be ascertained.

The nematode associations can also be divided into feeding categories according to Wieser (1953), who distinguished 4 different feeding types, each with a characteristic buccal morphology: with scarcely any buccal cavity (selective deposit feeders, type 1A); with moderate-sized buccal cavity (non-selective deposit feeders, type 1B); with moderate-sized buccal cavity and small armature (epigrowth feeder, type 2A); with spacious buccal cavity provided with heavy armature (predator, omnivore, type 2B).

The diatom suckers clearly predominated in the associations close to the outfall; diatom consumers (including diatom ingesters) accounted for c. 85% of the nematodes found at these stations. In Wieser's classification the diatom suckers belong to type 2A, the ingesters to type 1B. Close to the outfall the remaining specimens feed on bacteria or prey on other nematodes; part of the small proportion of protozoa

ingesters also ingest diatoms. At station 3 at some distance from the outfall, the distribution of nematodes over the feeding categories was quite different. However, because the feeding preferences of the dominating species *Sabatieria pulchra* are still unknown, a large proportion of the associations could not be classified according to their feeding category. The latter species is thought to consume bacteria and therefore the nematode association from the upper sediment layer probably comprises: c.50% bacteria consumers, c.40% diatom consumers and c. 10% protozoa consumers, with scarcely any predators; in the deeper layers the proportion of assumed bacteria consumers increases, whereas the other categories decrease. At this station the proportions of diatom suckers and ingesters were nearly equal. Feeding type 1B of Wieser's classification dominated at this station, mainly because *Sabatieria pulchra* was classified as a non-selective deposit feeder.

Occurrence of other meiofaunal taxa

The oligochaete fauna in the southeast Dollart is composed of the 3 naiddid species *Amphichaeta sannio*, *Paranaïs litoralis* and *Nais elinguis* and the tubificid species *Tubifex costatus*. On average, the former two species dominated the oligochaete fauna for c. 90%. Seasonal changes in density were greater than among the nematodes (Fig. 3); densities in winter were below 1 ind..cm⁻² and in summer rose to a maximum of c. 50 ind..cm⁻². At station 3 a decrease in numbers was observed in mid-summer, after which densities rose again before decreasing to winter values. Close to the outfall densities remained relatively high after peaking in early summer and also decreased in autumn.

Different species predominated at different parts of the year (Fig. 7; table 2); *Amphichaeta sannio* predominated in spring and late summer and *Paranaïs litoralis* in mid-summer; the proportion of *Tubifex costatus* was most pronounced in the second part of the year. There were also slight differences in dominance of species between the stations. At station 1 *Paranaïs litoralis* generally predominated, whereas at the other stations *Amphichaeta sannio* predominated. *Nais elinguis*, which originates from a freshwater habitat, was almost restricted to the stations close to the outfall and *Tubifex costatus* was nearly equally distributed along the whole transect. The latter species obviously penetrated into the

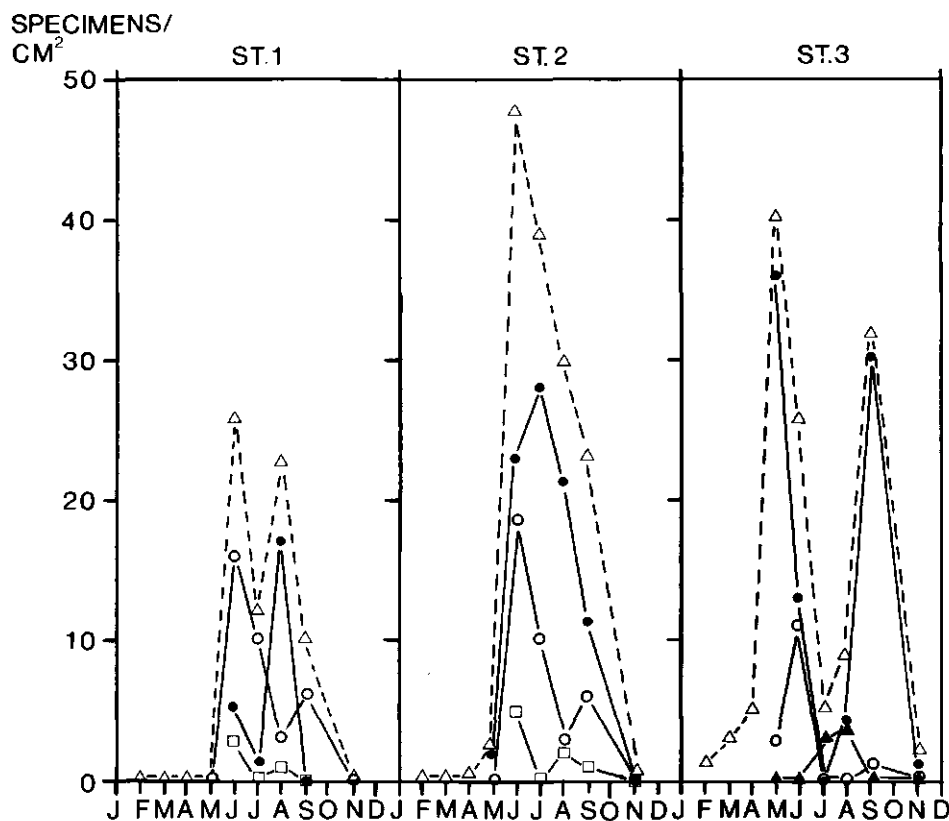


Fig. 7. Development of densities of 4 oligochaete species along the OFP-transect. ●—● *Amphichaeta sannio*; ○—○ *Paranais litoralis*; □—□ *Nais elinguis*; ▲—▲ *Tubifex costatus*; △—△ total number of oligochaetes.

sulphide zone whereas the naidids did not. Diatoms were observed in the intestines of the naidid species, but *Tubifex costatus* did not contain any diatoms.

Harpacticoids were only found in considerable numbers at some distance from the outfall (Fig. 3). Close to the outfall a short rise and fall in densities was observed in early summer. The dominating species were *Stenhelia palustris*, *Nannopus palustris* and *Halectinosoma curticorne* whereas only

small numbers of the species *Tachidius discipes*, *Microarthridion litorale* and *Canuella perplexa* were found. The occurrence of harpacticoids was restricted to the upper one cm layer of sediment (table 2). The dominant species occurred at all 3 stations, with the exception of *Halectinosoma curticorne* which only occurred at station 3.

Turbellarians were not abundant in the sediments of the southeast Dollart (Fig. 3). Winter densities were below 1 ind.. cm^{-2} and in the warmer seasons densities did not exceed c. 15 ind.. cm^{-2} with the exception of station 2 in summer, where densities up to 130 ind.. cm^{-2} were observed; this summer peak was constituted by one species and disappeared again in August.

Nereis diversicolor and *Corophium volutator* occurred at station 3 throughout the year; in summer c. 3 ind.. cm^{-2} of the polychaete and 1 ind.. cm^{-2} of the amphipod were found, most of the specimens being juveniles. In winter, densities of both organisms were below 1 ind.. cm^{-2} . Close to the outfall juveniles were occasionally found.

DISCUSSION

The very thin (3 mm) oxidized upper sediment layer to which most organisms are confined is characteristic of the tidal mudflats close to the outfall (c. 1 km). In this layer diatoms are abundant throughout the year, particularly in the warmer seasons. Macrofauna are absent and meiofauna abundant, especially a few species of nematodes and to a lesser extent some oligochaete species. In winter only the nematode *Eudiplogaster pararmatus* is abundant and in spring densities of nematodes and oligochaetes rise rapidly, remain high in summer and decrease again in autumn. The population structure does not vary much throughout the year, unless severe climatic impacts such as storms occur which removed the upper sediment layer along the whole transect in spring. The meiofauna present mainly feeds on diatoms.

The upper sediment layers of the tidal mudflats at some distance from the outfall (c. 3 km) are oxidized to a depth of several centimetres. Diatom densities and dynamics do not differ very much from densities and dynamics close to the outfall. Several macrofauna species occur throughout the year. Here too, the nematodes are the predominant meiofaunal taxon but their species diversity is much higher here than in the

area close to the outfall. The oligochaete fauna does not differ very much from the fauna close to the outfall. The dynamics of the meiofauna follow the same trend as near the outfall; the density, however, is lower throughout the year. Harpacticoids occur in moderate densities in the warmer season.

It is not very common for nematodes and oligochaetes not to interact with larger faunal organisms; this simplified situation offers an opportunity of studying some aspects of meiofaunal ecology that are not easily studied in more complex systems. In the following pages topics such as the survival strategies of meiofauna and the interaction of meiofauna with macrofauna will be discussed. Finally, attention will be focused on the effects of organic waste on benthic biology.

Survival strategies of meiofauna

Sheltered tidal sediments offer an attractive biotope for meiofaunal organisms. Nematodes in particular occupy all available niches and in the Ems estuary they have been isolated from all the biotopes distinguished (Bouwman, 1983). The other taxa are more discriminating in their biotope and thus the harpacticoids, ostracods, turbellarians and oligochaetes are absent from many estuarine niches. The tidal flats surrounding the outfall in the southeast Dollart are exposed to many different and extreme physical and chemical fluctuations and thus this biotope offers conditions that are adverse to many meiofaunal taxa and species; a few species, however, prosper in that biotope and succeed in creating dense populations. These successful species share the attribute that they all feed selectively on diatoms, either by means of rather sophisticated sucking (*Eudiplogaster pararmatus*, *Dichromadora geophila*) or by ingesting entire cells (*Amphichaeta sannio*, *Paranais litoralis*). As in this biotope bacteria are also abundant, it was rather surprising to find that only the small bacteriafeeding nematode *Leptolaimus papilliger* was numerous. It is assumed that meiofauna in the interstitial biotope feed rather selectively (Bouwman et al., 1983) because non-selective feeding in this environment seems to be uneconomical (in terms of energy) for many species. Bacteria are the smallest food organisms for meiofauna and most individual bacteria are supposed to be too small for selection and ingestion by meiofaunal species. Pro-

bably only those nematode species with very small buccal cavities ingest individual bacteria. In the Dollart *Leptolaimus papilliger* is one such nematode; it measures up to 0.5 mm (adults) with a buccal cavity that is as wide as an average bacterium (1-2 μ m); this species is one of the smallest found in the estuary.

The striking increase in density of nematodes and oligochaetes in spring is supposed to be mainly induced by the temperature. Food (diatoms and also bacteria) is abundant throughout the year and in particular in early spring when diatoms usually bloom (Admiraal et al., 1983). In the laboratory many herbivorous nematode species (Brouwer, in prep.) increase their reproduction rate rapidly when the temperature rises above c. 12 °C. As this happens in April/May in the field, at that time the increase in meiofauna is triggered off. Because the oligochaetes at some distance (station 3) from the outfall have higher densities in winter, oligochaete densities in that area increase earlier (in April) than they do close to the outfall (in May); the opposite was observed for the nematodes and this is probably not induced by the initial densities but because temperature close to the outfall rises faster in spring as a result of the duration of emersion being longer than that of the area further away from the outfall. In June the abundance of a turbellarian species at station 2, and the brief presence of harpacticoids showed that other taxa can also settle, at least temporarily, and even bloom in the vicinity of the outfall, although it is evident that this area is not the appropriate biotope for taxa other than nematodes and oligochaetes; the biotopes in the area at a certain distance from the outfall are much more attractive to other taxa and many other species.

Close to the outfall the nematode fauna was dominated by only two species, *Eudiplogaster pararmatus* and *Dichromadora geophila*. *Eudiplogaster pararmatus* is a halophilic member of the non-marine order of Rhabditida (Diplogasteridae) (Romeyn et al., 1983) and *Dichromadora geophila* is a member of the mainly marine order of the Chromadorida (Chromadoridae). The two species also occur in other parts of the Dollart and were isolated occasionally from the middle and lower reaches of the estuary. *Eudiplogaster pararmatus* is tolerant of limnetic conditions and it also tolerates marine salinities. This species reproduced throughout the various seasons in the south-east Dollart; it protects the first stage larvae by means of

its ovoviviparity. As diatom densities were high throughout the year (Admiraal et al., 1983) the amount of food available is unlikely to limit the densities of this nematode species. As this nematode appeared to consume the diatom *Navicula pygmaea*, which is predominant in summer, with less ease than *Navicula salinarum* which is predominant in winter, the specific structure of the diatom flora probably limits the densities of this nematode species (Romeyn et al., 1983; Admiraal et al., 1983). The inherent properties of this species with respect to salinity tolerance and probably also tolerance to anaerobic conditions and hydrogen sulphide, together with its feeding biology and brood-care appear to enable this species to assume its predominant position under the environmental conditions prevailing near the outfall.

Dichromadora geophila, although numerous too, was obviously less successful than *Eudiplogaster pararmatus* in the area close to the outfall. In its tolerances, feeding biology and life cycle, this species appeared to be similar to *Eudiplogaster pararmatus*; probably the main difference between the two species is the fact that *Dichromadora geophila* is oviparous and thus lacks the possibility of brood-care. Its relative success in the southeast Dollart is probably enhanced by its habit of penetrating more deeply into the sediment, thus sheltering itself from heavy impacts of the weather on the sediment surface layers (storms, ice, dehydration, ect.). As this species reproduced only during a short period in spring, it was not as dominant as *Eudiplogaster pararmatus*.

At some distance from the outfall the nematode *Ptycholaimellus ponticus* reproduced throughout the summer. This species is closely related to *Dichromadora geophila* (both are Chromadoridae) and its feeding biology and life cycle, as observed in laboratory experiments, are similar to those of the latter species. Reproduction throughout the summer seems to be usual for diatom-sucking chromadorids and therefore the failure of *Dichromadora geophila* to reproduce during the greater part of the summer in the area close to the outfall was probably induced by environmental conditions specific to that biotope.

The nematode *Sabatieria pulchra* which was predominant at some distance from the outfall, in particular in the semi-aerobic sediment layers along the boundary of the sulphide system (Bouwman, 1978, 1981, 1983; Jensen, 1981), was nearly absent close to the outfall. In the latter area, the anaero-

bic sediment was covered by only 3 mm thick aerobic surface layers and a boundary layer between the aerobic and anaerobic system had not developed (Schröder and Van Es, 1980); the species *Sabatieria pulchra* failed to colonize this sediment probably because the boundary layer was absent, although single specimens were occasionally isolated there.

The rapid rise of naidid oligochaete species in spring is probably favoured by their asexual reproduction which allows them to react directly to favourable conditions such as rising temperatures and high densities of diatoms in spring (Loden, 1981; Admiraal et al., 1983). Under optimal conditions the population of a species such as *Amphichaeta sannio* doubles in a few days (Admiraal et al., 1983). As the naidid species did not penetrate into the sediment and also because these organisms are probably sensitive to chemical and physical changes in the environment (such as anaerobic conditions), in autumn and winter these oligochaetes disappear close to the outfall, whereas at some distance a few specimens remain per cm² in the colder season. From laboratory experiments in agar it appeared that nematodes such as *Ptycholaimellus ponticus*, *Paracyatholaimus proximus* and *Hypodontolaimus balticus* were less tolerant to lower salinities and this sensitivity probably holds for many other species characteristic of the mudflats at some distance from the outfall. Thus, the disappearance of many species towards the outfall is also caused by lack of tolerance to lower salinities. The decrease in the oligochaete *Nais elinguis* in the reverse direction is, in contrast, the result of a lack of tolerance to higher salinities, as this species originates from limnetic environments, just as the nematode *Eudiplogaster pararmatus*.

Interactions between meio- and macrofauna

The analyses of the survival strategies of various meiofauna species indicate that the biotope close to the outfall particularly favours selective diatom-feeding nematodes and oligochaetes with short life cycles, which are tolerant of low salinities and anaerobic conditions. The density of meiofauna organisms close to the outfall was 3 to 4 times higher than at some distance from the outfall (in summer: c. 1300 ind..cm⁻² close to the outfall versus c. 350 ind..cm⁻² at some distance; c. 2000 mg carbon.m⁻² versus c. 1000 mg carbon.m⁻²) and corresponds with the highest densities of nematodes and oligo-

chaetes reported in the literature (nematodes: Teal and Wieser, 1966; Warwick and Price, 1979; oligochaetes: Dahl, 1960; Arlt and Holtfreter, 1975; Pfannkuche, 1977, 1980, 1981). This success of some meiofauna species contrasts with the absence of larger fauna. The disappearance of macrofaunal organisms close to discharge-points of organic waste is well known from the literature (Anger, 1977; Nichols, 1977; Essink, 1978; Van Es et al., 1980). However, at some distance from outfalls polychaetes such as *Capitella capitata*, *Pygospio elegans* and *Nereis diversicolor* often prosper (Anger, 1977; Essink, 1978). In the Dollart, *Nereis diversicolor* (length up to 20 cm) and the decapod *Corophium volutator* (length up to 0.5 cm) are dominating species at some distance from the outfall and as many as 2300 ind. *Nereis diversicolor*.m⁻² (Essink, 1979) and 16000 ind. *Corophium volutator*.m⁻² (Van Arkel and Mulder, 1982) have been counted.

Nereis diversicolor feeds carnivorously as well as herbivorously, tolerates variations in salinity and in oxygen saturation, tolerates the presence of free sulphide and is not particular about the type of sediment; the herbivorous species *Corophium volutator*, however, is more discriminating. Both species create tunnels within the sediment, the polychaete to depths of 60 cm, the decapod more superficially. In order to feed, the species leave their tunnels and forage over the sediment. The absence of these organisms close to the outfall could be caused by the structure of the sediment, which is very compact below the uppermost few millimetres; this cohesive, anaerobic sediment probably offers much resistance to tube building. As food (diatoms, meiofauna) for both macrofaunal species is abundant close to the outfall, most juvenile specimens survive for a short time; however, the sediment structure could prevent them from settling permanently.

The absence of larger faunal organisms close to the outfall offers those meiofauna organisms present the opportunity of exploiting the abundance of available food without competition and without being consumed by predators. An inverse relationship between the numbers of *Nereis diversicolor* and densities of meiobenthic organisms such as nematodes, oligochaetes and harpacticoids in tidal mudflats has already been observed by Rees (1940) in the Cardiff area. Although the actual consumption pattern of *Nereis diversicolor* in the south-east Dollart is not known, the facts suggest that the absence of such an omnivorous species is at least partly responsible

for the development of high densities of meiofauna.

The effects of organic waste

Effects of organic waste cannot easily be separated from the effects of natural gradients occurring in the estuary.

In spring, the investigated area close to the outfall is probably least affected by discharged waste; at that time the initial meiofaunal populations result from many preceding impacts, of which the waste discharge in the previous autumn is only one whose effects have probably been outstripped in winter by the effects of ice. Thus, the structure and dynamics of meiofauna in spring, as determined by the initial populations, are probably only indirectly affected by the waste discharge in autumn. The development of high densities of diatom-consuming nematodes and oligochaetes results from the high densities of diatoms, the paucity of species with other feeding behaviour (e.g., selective bacteria consumers) and the absence of macrofaunal organisms. The dynamics of briefly blooming turbellarians and harpacticoids must be governed by factors other than waste discharge, as the organisms decrease again in summer. The increase in the numbers of bacteria close to the outfall appears hardly to be utilized as food in a detritivore food chain; the only pathways that were distinguished are relatively unimportant (bacteria → *Leptolaimus papilliger* → *Adoncholaimus thalassophygas*; bacteria → *Tubifex costatus*). A potential bacteria-consuming inhabitant, *Sabatieria pulchra*, which occurs in high densities in other biotopes rich in organic materials in the Ems estuary (Bouwman, 1983), could not settle close to the outfall because the gradual transition layer between aerobic and anaerobic sediment zones failed to develop.

The organic waste discharge in autumn causes a decrease in oxygen saturation in the water and an increase in numbers of sulphur cycle bacteria in the sediment. In autumn, the decline in numbers of meiofaunal organisms, in particular the oligochaetes, is enhanced by the anaerobic conditions. Eventually, only the nematode *Eudiplogaster pararmatus* survives in considerable numbers. It is assumed that severe winters will have the same effect on the biotope as the organic waste. Thus, the effects of waste discharge are limited, in particular because of the time of discharge, which coincides with a natural decrease in faunal populations.

To sum up, it can be stated that the area surrounding the out-fall favours small faunal organisms with life cycles of a few weeks; in spring rapidly reproducing diatom feeders are favoured, in summer these populations remain at approximately the same level and in autumn only *Eudiplogaster pararmatus* survives the anaerobic conditions in considerable numbers. The initial populations in spring are determined by the waste discharge and the winter regime. This sequence of different selective forces does not offer many opportunities for the development of other species and taxa, although the abundant diatoms and bacteria can be exploited by many other organisms too; therefore drastic deviations from the described succession of events (e.g., relatively warm winters, storms and consequent settling of other species, prolonged north-west or south-east winds, etc.) seem to be necessary if the patterns described are to be disrupted. Under such unusual conditions, other species could also exploit the abundance of food and grow in great profusion. This has been observed in other years for the species *Daptonema setosum* and *Anoplostoma viviparum*; for long-term survival in this area the life cycle of these species is probably too long.

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CHAPTER VII

GENERAL DISCUSSION

As most marine nematologists have long concentrated on systematics, the role nematodes play in benthic ecosystems, including estuarine tidal flats, is still obscure. Recent measurements on processes in the benthic environment, such as oxygen consumption (Van Es, 1982) and heat production (Graf et al., 1982; Pamatmat and Findlay, 1983), and observations of the pathways of labelled organic nutrients (Meyer-Reil and Faubel, 1980; Beviss-Challinor and Field, 1982) have contributed suggestions about the way meiobenthos functions within the intricate network of interacting organisms; but because the researchers involved lacked knowledge about the participating organisms, they failed to get to the root of the phenomena. When processes are to be apportioned among the constituent components, the usual practice is to take results from laboratory observations and extrapolate them to situations in the field; e.g., values for oxygen consumption of various nematode species as measured in cartesian divers, are used to quantify the proportion of benthic oxygen consumption due to nematodes: it is not known whether nematode respiration, when the animals are actively moving and grazing in the sediment, is higher than in the artificial environment of the cartesian diver, but extrapolating from the latter situation certainly underestimates the nematodes' share of benthic oxygen consumption. The same caveats apply to the measuring and apportioning of heat production. Following pathways of labelled organic matter remains unsatisfactory as long as actual food relationships are not known.

Therefore, progress in unravelling the various roles of benthic nematodes will be accelerated when the skill of the process measurers is combined with the insights of nematode taxonomists, physiologists and ecologists.

The success of nematodes in colonizing estuarine sediments

In general, nematodes are the most numerous metazoa in estuarine sediments. This predominance can probably be attributed to the following: nematodes are slender and consequently easily adapt to the interstitial spaces of coarse sediments and, if the organisms can burrow, to soft sediments too; wide tolerance of all types of environmental stress (anaerobic

conditions, hydrogen sulphide, hypersalinity, heat, freezing etc.) occurs within the taxon, although these tolerances are species specific; the most sophisticated attribute of nematodes is probably the diversification in buccal structures, which facilitates the exploitation of the manifold food organisms the benthic environment offers. Nematodes have various well-developed sensory organs for exploring the environment for favoured food organisms, e.g. lips with papillae, setae, and sensors for chemical signals (the amphids).

In the following pages we will discuss the relationships between nematodes and their physical environment under estuarine conditions, and with their biological environment with emphasis on food preferences, and the effects of organic pollution on various nematode feeding categories.

Nematodes and their physical environment in estuarine sediments

The presence of free-living nematodes in different biotopes is basically governed by the presence of sufficient amounts of water, oxygen, food and a suitable substratum. In biotopes where these basic conditions are fulfilled, the distribution and species composition of nematode associations depend on the adaptation of species to the specific conditions of the individual biotope, e.g. microstructure of the substratum, salinity, quality and quantity of food, oxygen saturation, concentration of hydrogen sulphide, etc..

The sediment (substratum) in the Ems estuary can be classified into two main types according to structure: solid, sandy sediments with stable, relatively large interstitial spaces containing only little silt and detritus; and soft sediments with small interstitial spaces, filled with silt and detritus, and less stable. Different nematode species inhabit these two biotopes, and their specific behaviour also differs. In the sandy sediment the nematodes move through the interstitial spaces without altering the structure; they adapt to the space present. Nematodes living in silty sediments move by means of burrowing, which is comparable with their movements observed in agar. Nematodes isolated from substrata and put in liquid medium make uncontrolled movements, alternating with periods of immobility, lying curled up or outstretched. In agar most of the isolated nematodes make controlled movements, exploring their environment. The agar suits the nematodes and functions as an artificial substratum. Obviously, the nematodes need an enveloping medium with a certain resist-

ance if properly controlled movements directed towards food exploration are to be triggered off. This requirement probably accounts for the difficulties encountered, when trying to cultivate, in agar, nematode species originating from the sandy margins of the tidal flats in the outer part of the Ems estuary; it must be inferred that the way that these species (e.g. *Metachromadora suecica*, *Monoposthia mirabilis*, *Neochromadora trichophora*) move is not attuned to burrowing through agar. In contrast, many species from soft sediments were easily reared in agar for many generations.

The great diversity of estuarine nematode associations (in the Ems estuary up to 35 species per cm³) is probably primarily attributable to food specialization (Warwick, 1981), which in turn is caused by the great diversity of food organisms. The benthic biotope offers so many different niches on a microscale (Anderson and Meadows, 1978), that colonies of many different microbenthos species develop, coexisting in close proximity but in different microenvironments. These microenvironments in turn result from many physical and chemical gradients existing within the sediments, mainly in the vertical plane, e.g. in the concentrations of oxygen, carbon dioxide, hydrogen sulphide, dissolved organic compounds and in temperature and the penetration of light. The "Farbstreifensandwatt" is an example of four completely different, well-ordered microenvironments, arranged in laminae approximately 1 mm thick in the upper 0.5 cm sediment layer. The thin oxidized sediment layer (0.3 cm), overlying black anaerobic sediments in the area close to the outfall in the south-east Dollart, is another example of easily visible small-scale stratification. Just as different microorganisms dominate in different microenvironments, so do different microorganism-consuming nematode species dominate in response to the microorganisms present (see also Joint et al., 1982).

Estuarine nematodes and their biological environment

Within the benthic network of organisms, nematodes absorb dissolved organic compounds (Chia and Warwick, 1969; Lopez et al., 1979), consume unicellular organisms, regenerate nutrients (Johannes, 1965; Gerlach, 1978), excrete mucus (Riemann and Schrage, 1978; Warwick, 1981), improve gas diffusion and serve as food for other, usually larger organisms, including predators belonging to their own taxon (Gerlach and

Schrage, 1969; Gerlach, 1978). Information (either qualitative or quantitative) about specific relationships between nematodes, their food organisms and their predators is, however, scarce. Microphytobenthic food organisms for nematodes are abundant in the estuarine environment because of the recurrent irradiance of the tidal flats under conditions of ample nutrients; bacteria are abundant because various types of organic substances are imported from the sea and from the fresh water. Interstitial nematodes are assumed to feed rather selectively on microbenthic organisms (Deutsch, 1978; Romeyn and Bouwman, 1983; Chapter V, this thesis), whereas, because of their size, most macrofauna organisms feed less selectively or indiscriminately on microbenthic and meiobenthic organisms.

In the following pages we will discuss the relationship between nematodes and microbenthic food organisms and highlight the effects of organic enrichment on these relationships.

Interactions between nematodes and bacteria

As already argued, controlled movements directed to the exploration of the environment are necessary for the survival of most free-living nematodes. Most nematode species do not consume food organisms offered in liquid media without substrata, but will consume the appropriate food items if they are mixed through agar. Thus, the way food organisms are offered to nematodes is crucial. As the dimensions of benthic bacteria range from 0.5 to 1.5 μm and the width of the buccal cavities of estuarine nematodes range from 5 to 30 μm , the average volume of bacteria is small (less than 1%) compared with the capacity of the buccal cavities. Therefore, selection of individual bacteria in the sediment seems to offer no energy-saving advantage to nematodes, except probably to the very small ones. Our culture experiments (Chapter V) showed that among the c. 25 sediment-inhabiting nematode species tested in agar cultures, only *Leptolaimus papilliger* feeds selectively on individual bacteria. As the buccal cavity of this nematode is very small indeed (width: 1-2 μm), the detection and consumption of individual bacteria is probably advantageous for this species. The small dimensions of the buccal cavities of Oxystominidae, Siphonolaimidae and some other Leptolaimidae suggest that members of these families also consume individual bacteria in the

sediment. However, the great majority of estuarine species probably do not consume individual bacteria (see also Rieper, 1978); this is evident from ingestion experiments with ^{14}C -labelled bacteria in agar (Chapter 5) and agrees, for example, with observations made by Lopez et al. (1979) on the predatory oncholaimid *Adoncholaimus thalassophygus*. As individual bacteria are not consumed, colonies of bacteria, whether or not attached to the surface of solid detritus or sand grains, are likely to be consumed at least by some species that do not ingest individual bacteria: so far this has not been investigated. Useful food items probably have to be a minimum size to be actually used as food by most selective strategists, and while an individual bacterium may be ignored because it is too small, clumps of the same bacteria may be attractive food.

However, on the surface of estuarine macrophytes, nematode species characteristic to that environment (Aufwuchs species) operate with a non-selective feeding strategy. In the interstitial biotope, nematodes select individual food items, including bacteria, by means of occasional oesophageal pulsations that are only triggered off when their lips collide with a probable food particle; the Aufwuchs species, however, pulsate continuously, ingesting large numbers of bacteria indiscriminately and, when their buccal cavity is large enough, also ingesting various types of algae (Chapter V; Romeyn and Bouwman, 1983). These non-selective bacteria consumers need high densities of bacteria in environments that are relatively free from suspended particles by comparison with the sediment (where bacteria are interspersed among a majority of similarly sized inedible particles). Schiemer (1982) observed that the threshold for the growth of larvae of *Caenorhabditis briggsae* in agar supplied with the bacterium *Escherichia coli* as a food organism, was attained when the density of the latter was c. 10^{-8} cells.cm $^{-3}$; for reproduction the threshold was a density of the bacterium of 2.10^8 cells.cm $^{-3}$. He found that 50% of maximum performance was attained at densities of c. 5.10^8 and 8.10^8 cells.cm $^{-3}$ respectively. Our culture experiments (not reported in this thesis) with Aufwuchs species in agar, offered a smaller bacterium (Chapter V), indicated the presence of thresholds at densities of c. 5.10^8 cells.cm $^{-3}$, thus corroborating Schiemer's results. Schiemer's observations indicated that reproduction occurred only at food concentrations higher than the threshold for larval growth, thus redu-

cing the risk of larvae encountering densities of food organisms too low for their growth.

Nothing is known about the threshold densities of bacteria for nematode growth in the interstitial environment. In this environment the bacteria are mixed up with inedible particles and probably the nutritive value per cell is lower than in the Aufwuchs biotope (Schiemer, 1982), which suggests that higher densities of bacteria are needed; but the feeding strategy of the nematode is selective, and is thus adapted to the specific conditions. As a result, the figures for cell density thresholds in the Aufwuchs biotope may also apply in the sediments.

Similarly, nothing is known on the feedback of nematode grazing on bacteria in interstitial biotopes. However, interactions between bacteria and nematodes have been studied under other, probably comparable conditions. Abrams and Mitchell (1980) measured oxygen consumption in decomposing sludge with and without a bacteria-consuming nematode; although the proportion of oxygen consumption by the nematodes in the system was modest (5%), their presence within the system raised the total oxygen consumption by a factor of 6. Comparable results were obtained by Findlay and Tenore (1982) when studying the decomposition of the macrophytes *Gracilaria* and *Spartina* in the presence of various densities of the nematode *Dipholaimella chitwoodi*; the nematode increased maximum rates of carbon mineralization by 300%, at densities of 10^6 nematodes.m⁻². It is assumed that nematode grazing on bacteria prolongs the exponential phase of growing bacterial populations and also stimulates gas diffusion and nutrient regeneration (Anderson et al., 1981; Pamatmat and Findlay, 1983). It is not known whether these two studies of decomposition also accurately reflect mineralization in the sediment; the dynamics of bacteria and of bacteria-consuming nematodes in the sediment are probably weaker than in the organically enriched systems, but at least bacteria-consuming nematodes contribute more than their own metabolism to the total benthic metabolism.

The organic enrichment of the sediments in the southeast Dollart resulting from the waste discharges, and the location in the upper reaches of the estuary, increases the densities of various bacterial groups and the aerobic and anaerobic mineralization (Van Es et al., 1980; Schröder and Van Es, 1980). However, bacteria-consuming fauna, including nematodes, are almost absent in this area; unfortunately, the taxon best

adapted to life under stressed conditions such as those occurring in the organically polluted area, has not provided an adapted bacteria-consuming species except for the tiny nematode *Leptolaimus papilliger*, which is present in modest numbers. No significant numbers of bacteria-feeding nematodes have been found in the upper reaches of other estuaries, either.

Interactions between nematodes and diatoms

Dense populations of benthic diatoms in the surface layers of sandflats and mudflats are characteristic of tidal estuarine areas. These diatoms are favoured as food by many species of chromadorids and monhysterids, which consequently dominate the nematode fauna located in the upper sediment layers of estuarine tidal flats. As the dimensions of estuarine benthic diatoms vary from c. 10 to c. 100 μm , they fit perfectly into the buccal cavities of many estuarine nematode species. Two methods of diatom consumption can be broadly distinguished: the ingestive and the destructive method. Both techniques only operate after the food item has been selected (this does not hold for diatom-consuming Aufwuchsspecies). In laboratory cultures, minimum densities of c. $2 \cdot 10^6$ cells of *Navicula salinarum*. cm^{-3} agar are needed to ensure the growth of the populations of various diatom-feeding nematodes. However, within the sediment, nematodes have to select diatoms out of a majority of inedible particles and this process costs energy; therefore, field densities of diatoms must exceed the densities mentioned for agar cultures, to ensure nematode population growth. Thus, the threshold values in the field are probably in the order of c. 3 to $5 \cdot 10^6$ diatoms. cm^{-3} . Such densities are common in the upper sediment layers of tidal flats in the Ems estuary when sufficient light is available. These diatoms are used as food mainly in the warmer part of the year, as nematode activity increases parallel with the temperature (see also: Admiraal and Peletier, 1980; Colijn and Dijkema, 1981), and consequently selective diatom-consuming nematodes can assume their important position in the benthic estuarine ecosystem.

The proportion of the diatoms consumed by herbivorous meiofauna (nematodes and oligochaetes) in the simple ecosystem close to the outfall in the Dollart is modest, amounting to c. 10% of the daily primary production and of course to a smaller proportion of the standing stock (Admiraal et

al., 1983). These figures are probably generally applicable to meiofauna grazing on microphytobenthos in the other parts of the estuary. The feedback of nematodes grazing on diatom populations is largely unknown but it is assumed that the impact of grazing induces responses that are at least comparable with the response of bacteria being browsed by nematodes. Primary production in dense films of diatoms is thought to be limited by the diffusion rates of oxygen and carbon dioxide (Admiraal et al., 1983) and thus nematodes will stimulate primary production by stimulating gas diffusion. As different diatom species have a different utility as food (Romeyn et al., 1983), grazing nematodes can exercise qualitative selection on the species composition of diatom populations (Admiraal et al., 1983). The latter authors have demonstrated that *Eudiplogaster pararmatus* consumes the diatom *Navicula salinarum* more easily than *Navicula pygmaea*; therefore, it is assumed that the shift from a diatom population dominated by *N. salinarum*, to a population dominated by *N. pygmaea*, following the rise in density of *E. pararmatus* in the Dollart near the outfall in spring, is also stimulated by the nematode's grazing activities (see also: Cuker, 1983). From our laboratory experiments (chapter 5; Romeyn and Bouwman, 1983) it also became clear that there are large differences among algae species in their utility as food for nematodes.

Organic enrichment of the sediments in the southeast Dollart does not cause dramatic short-term changes in species composition or density of diatom populations (Admiraal, 1980). The high densities of diatoms in that area are due to the long duration of irradiance which in turn results from the fact that the flats are high-lying and consequently experience prolonged periods of emersion under conditions of ample nutrients. The herbivorous nematodes are thus not directly affected by organic enrichment; as, however, this enrichment causes the absence of macrofaunal herbivores and also of some meiofaunal competitors for the same food, the herbivorous nematodes are indirectly favoured.

Some remarks on carnivorous nematodes

As protozoa and nematodes consume diatoms and bacteria, nematodes preying on these organisms operate as secondary consumers. In this study little attention was paid to protozoa as food for nematodes. However, some observations of protozoa consumption were made by chance because occasionally protozoa

developed accidentally in agar observation slides with grazing nematodes. The nematode *Tripyloides marinus*, which is distributed all over the estuary (chapter III), was observed to feed selectively on protozoa in agar with diatoms; the nematode *Paracyatholaimus proximus*, which is restricted to the Dollart, ingested protozoa as part of a diverse diet that also comprised various types of diatoms and other algae but that did not include bacteria. These examples indicate that there is probably also a range of feeding strategies and consumption techniques for consumption of protozoa, varying from very exclusive predator/prey relationships to non-specific, incidental consumption of protozoa by nematode species that mainly feed on other food items.

In nearly all the nematode associations distinguished in the Ems estuary, predatory (omnivorous) nematodes participate. In the sandy margins of the tidal flats in the Wadden Sea this feeding category even predominates; however, in all other associations the proportion of this nematode category is small. The abundance of predatory nematodes suggests that their role is essential; as the members of this group have the potential to attack other nematodes, they could act as an internal regulator of nematode densities. However, because their offspring are numerically small and the life cycles are long, it is unlikely that predators react adequately to high densities of the prey organisms available, consequently their role as regulator of nematode densities seems to be merely incidental. The range of feeding strategies and consumption techniques among predatory nematodes probably does not differ from the behavioural variety among diatom consumers; whereas oncholaimids carefully explore their surroundings by continuously moving the head when burrowing through the agar, the sphaerolaimids are mostly immobile, with occasional sudden, fast, decisive actions. Thus, the oncholaimids show the same exploratory behaviour as the diatom-suckers, whereas the sphaerolaimids' strategy is based on surprise. The prey may be pierced and sucked out (oncholaimids) or swallowed whole (sphaerolaimids).

Nothing is currently known about the feedback of the relationship between nematodes, and protozoa and prey-nematodes. Organic enrichment does not affect predatory nematodes directly. Close to the outfall in the Dollart, in the ecosystem dominated by diatoms and diatom-consuming nematodes, the oncholaimid *Adoncholaimus thalassophygas* is present throughout the year but the organism does not succeed in exploiting the

abundance of food and consequently its density remains low.

Suggestions for future research

The new insights reported in the previous chapters of this thesis may be used to design future research. One of the most promising lines of research is undoubtedly the in situ measurement of nematode activities in the benthic environment. For this, certain nematode associations in different parts of the estuary could be used, perhaps beginning with the relatively simple association in the upper reaches of the estuary. Enriching the sediment with ^{14}C -labelled bacteria and diatoms and subsequently measuring the ingestion rates is probably the best method of qualifying and quantifying nematode consumption rates in field situations. Such measurements would clarify the role nematodes play in benthic ecosystems. At present it is unclear whether nematodes and other meiofauna play an essential role in the community metabolism, or whether they merely contribute some biomass to the much greater macrobenthic biomass.

This thesis indicates that thanks to their sophisticated equipment and adapted methods for acquiring food and to their tolerance of environmental stress, nematodes are perfectly suited to the various biotopes of estuarine tidal flats; also that this metazoa taxon is the only one that provides specimens to the most polluted part of the estuary throughout the year; and that in this polluted part of the estuary a well-developed herbivore food-chain has developed that is much more important than the local bacteriovore food-chain.

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SUMMARY

As part of extensive biological and chemical investigations in the Ems estuary, the nematode fauna of this area (mainly located in the sediments of tidal flats) was studied.

First, a new method of isolating nematodes was developed, as none of the existing methods appeared to be quantitatively reliable for the isolation of organisms from silty sediments. The new method is based on differences in specific weight between nematodes (and other meiobenthos), and sediment particles: sediment samples are suspended in Ludox-TM, a colloidal silica, and, whereas organisms float to the surface of this suspension, sediment particles sink to the bottom. The isolation method can be used for either preserved or fresh sediment samples.

In a survey of the estuary 121 nematode species were identified and during subsequent investigations 12 other species were noticed: thus, in all 133 species were identified, 4 of which were new to science. The distribution of species over the estuary was studied and the genesis of species associations was related to environmental conditions. Two main faunas were distinguished: one in the Wadden Sea part of the estuary, the other in the Dollart, both extending into the middle reaches of the estuary. In the lower sediment layers a characteristic nematode fauna was found that consisted of species that were mainly absent from the upper sediment layers. It was concluded that faunal associations from the lower sediment layers originate from marine subtidal locations, whereas the associations from the upper sediment layers of tidal flats are specific to estuarine tidal environments.

Several nematode species were cultured in agar in the laboratory and their feeding-biology was studied. From these investigations it appeared that nematodes, specific to the surface of littoral macrophytes, use non-selective feeding methods, consuming large amounts of bacteria, and, when their buccal cavity is large enough, also diatoms and other algae; the food organisms are ingested by means of continuous oesophageal pulsations. The interstitial nematodes, on the other hand, probably all feed selectively, oesophageal pulsations only being triggered off when a useful food organism is sensed among an overwhelming majority of similarly sized inedible particles. The larger food organisms, diatoms and other algae, protozoa, and small metazoans (including prey-nematodes) may be ingested whole or punctured and subsequently sucked out;

specific buccal structures determine which consumption technique is used: when armature is absent food items are ingested whole, when armature is present food items are attacked and sucked out. Individual bacteria are probably too small for most interstitial nematodes and consequently are ignored as food.

Special attention was focused on the ecosystem of the tidal flats close to the outfall in the southeast Dollart. It appeared that in that area the benthic ecosystem was dominated by a herbivorous food-chain, comprising diatoms and diatom-consuming nematodes (throughout the year) and oligochaetes (only in the warmer part of the year).

It is concluded that the success of nematodes in colonizing almost all estuarine biotopes is due to their size, their sophisticated methods of food acquisition and their tolerance of environmental stress. The discharge of organic waste enhances the effects of natural gradients occurring in the estuary. The main effect is the overall decrease of species diversity and the indirect promotion of a herbivorous food-chain in which nematodes predominate the grazing fauna.

SAMENVATTING

De nematodenfauna van het Eems estuarium (grotendeels gelocaliseerd in het oppervlakkig sediment van droogvallende platen) werd bestudeerd als onderdeel van meer uitgebreid biologisch en chemisch onderzoek in dit gebied.

Het onderzoek begon met de ontwikkeling van een nieuwe methode om nematoden uit het wadsediment te isoleren. Dit was noodzakelijk omdat geen van de bestaande methoden kwantitatief betrouwbaar leek, vooral met betrekking tot isolatie uit slikkige sedimenten. De nieuwe methode is gebaseerd op verschil in soortelijk gewicht tussen nematoden en overig meiobenthos enerzijds en sediment partikels anderzijds. Bij gebruik van deze scheidingswijze worden sediment monsters gesuspenderd in Ludox-TM, een silicium colloïd, en na centrifugering of een nacht wegzetten drijven de nematoden, oligochaeten en harpacticiden aan het oppervlak van de vloeistof terwijl de sediment deeltjes naar de bodem zijn gezakt. Na zeping van de afgezogen organismen is ook het fijnere detritus verwijderd zodat de organismen zich, uitsluitend verontreinigd met eventueel aanwezig grof detritus, op de zeef bevinden. De isolatie methode is zowel te gebruiken voor verse als voor geconserveerde sediment monsters.

Een inventarisatie, uitgevoerd over het gehele estuarium, leverde 121 soorten nematoden op, waaraan later onderzoek nog 12 soorten toevoegde (totaal 133 soorten); hiervan waren er 4 nieuw voor de wetenschap. De verspreiding van de soorten over het estuarium en de gemeenschappen die door soorten werden gevormd, waren onderwerp van studie en werden gerelateerd aan de karakteristieke hoedanigheden van de onderscheiden biotopen. Twee hoofd-faunas werden onderscheiden: één in het Waddenzee-gedeelte van het Eems estuarium, de andere in de Dollard, terwijl vertegenwoordigers van beiderlei herkomst het midden-gebied bevolken. De diepere sedimentlagen bleken vooral gekoloniseerd door soorten die specifiek aldaar voorkomen en niet of vrijwel niet in de oppervlakkige sedimentlagen; deze soorten bleken merendeels van sublittorale herkomst te zijn, terwijl de soorten-gemeenschappen uit de oppervlakkige sedimentlagen karakteristiek zijn voor droogvallende platen in estuariene gebieden.

Een aantal nematoden soorten werd in het laboratorium gekweekt in agar cultures en bestudeerd, in het bijzonder met betrekking tot hun voedings-biologie. Uit dit onderzoek bleek dat nematoden die specifiek voorkomen aan het oppervlak van

estuariene macrophyten, niet-selectieve voedselopname-methoden hanteren, waarbij vooral aanzienlijke aantallen bacteriën worden geconsumeerd, en, wanneer hun bekholte ruim genoeg is, ook diatomeeën en andere algen; deze voedselorganismen worden opgenomen door middel van voortdurend pulseren van de slokdarm. De interstitiele nematoden daarentegen, nemen waarschijnlijk uitsluitend selectief voedsel op; het pulseren van de slokdarm vindt alleen plaats wanneer met behulp van diverse sensoren (lippen met papillen, borstelharen, chemoreceptoren) een mogelijk bruikbaar voedselorganisme is gelocaliseerd temidden van een overmaat aan even grote partikels die niet geschikt zijn als voedsel. De grotere voedselorganismen zoals diatomeeën en andere algen, protozoën en kleine metazoën, inclusief prooi-nematoden, kunnen in hun geheel worden ingeslikt, of aangeboord en leeggezogen; soort-specifieke bekstructuren bepalen welk type consumptie-techniek wordt toegepast: wanneer er geen bewapening aanwezig is worden de voedselorganismen in hun geheel ingeslikt en wanneer de bekholte wel bewapend is worden voedselorganismen doorboord of gekraakt en vervolgens leeggezogen. Individuele bacteriën zijn waarschijnlijk te klein voor de meeste interstitiele nematoden en worden niet als voedsel opgespoord.

Speciale aandacht werd gewijd aan het ecosysteem van de droogvallende platen nabij de spuisluis in de zuidoost Dollard. Het bleek dat in dat gebied het benthische ecosysteem wordt gedomineerd door een herbivore voedselketen, grotendeels bestaande uit diatomeeën en diatomeeën-etende nematoden (het hele jaar) en oligochaeten (lente en zomer); de ook in grote dichtheden voorkomende bacteriën vormen geen deel van een voedselketen van vergelijkbare betekenis.

Geconcludeerd wordt dat het succes van nematoden in estuariene biotopen mogelijk wordt gemaakt door hun vorm, hun verfijnde vermogen uiteenlopende soorten voedselorganismen op te sporen en te consumeren en door hun tolerantie ten opzichte van de voorkomende fysische en chemische extremen, van zowel natuurlijke als door de mens veroorzaakte herkomst. Mede ten gevolge van deze hoedanigheden komen de hoogste dichtheden nematoden voor in het meest vervuilde, soortenarmste deel van het estuarium.

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