OCCURENCE AND FEEDING BIOLOGY OF SOME NEMATODE SPECIES IN ESTUARINE AUFWUCHSCOMMUNITIES (1)

by

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Résumé

Les peuplements de nématodes estuariens, vivant à la surface des macrophytes littoraux, des cyanophytes et dans l'alluvion organique de l'estuaire de l'Ems dans le nord-ouest des Pays-Bas, sont dominés par quelques espèces. Ces espèces sont absentes ou très rares dans le sédiment ; on les appelle : « Aufwuchs ».

Le comportement alimentaire de ces espèces « Aufwuchs » diffère de façon très nette de celui des espèces colonisant le sédiment en permanence. Ces dernières doivent sélectionner les particules de nourriture à partir d'un ensemble d'éléments de taille similaire et non comestible. Les espèces « Aufwuchs », elles, peuvent se nourrir de façon non sélective du fait de l'abondance de la nourriture clans leur biotope et de sa qualité relativement « pure ».

Introduction

In estuarine environments, nematodes occupy almost all available niches (Bouwan, 1983). Some species only occur in very specific biotopes, others are more widely distributed. Several authors, listed in Table 1, noticed the predominance of members of the families of the Monhysteridea, Rhabditidae and Chromadoridae in nematode associations found on the surface of littoral macrophytes, mats of cyanophytes and decaying material drfited ashore (debris). From henceforth we will refer to species found in these biotopes as Aufwuchs species. Some are restricted to Aufwuchs communities and do not occur in the adjacent sediment (Warwick and Price, 1979; Bouwman, 1981, 1983). Species must be adequately adapted to survive in a specific biotope, but knowledge about these adaptations in scarce.

Aim of this study was to survey the nematode associations in Aufwuchs communities and in the adjacent sediment and to analyse the various survival strategies of the nematode species found. The feeding biology of specific Aufwuchs species was compared to that

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

TABLE 1
Literature reporting on the occurrence of typical Aufwuchs species.

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

Materials and methods

1) 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	***Spartina* sp.** ***Fucus*** ***Ulva***	***Zostera* sp.**	***Salicornia*** ***Enteromorpha* sp.**	
cyanophytes			***Oscillatoria* sp.**	***Oscillatoria* sp.**
debris	+			
sediment	+	+	+	+

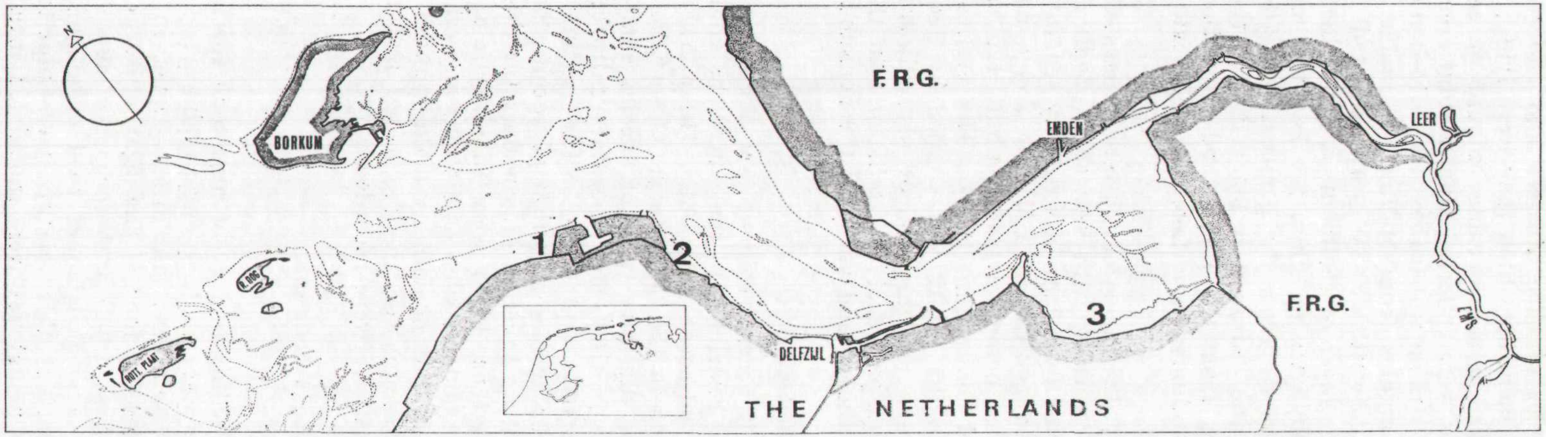

FIG. 1

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. 60cm 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. 3mm thick), covering a compact mat of cyanophytes (c. 2mm); 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 (0 2.4cm).

In the laboratory the nematodes were separated from plant material 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 8cm. The compact mat of *Oscillatoria* in the FSSW was separated from the sediment and analysed for nematodes separately.

2) 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 a 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 muscular oesophagus; the frequency and the degree of continuity of the pulsations were recorded.

3) Cultivation and feeding experiments

a) *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, 5g/l, salinity 25 p. 1000) 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 16h daylight period. The food organisms used were the diatom species *Navícula salinarum* and *Nitzschia* cf *closterium* (Baccillariophyceae), 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 culture was c. 2.10^6 cells/cm^3. To establish agar cultures with bacteria as food organisms, the amino acid glycine was added: final concentration in the cultures was 0.125g/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 for many nematode species.

The nematode species *Rhabditis marina* Bastian 1865, *Monhystera parva* Bastian 1865, *Monhystera microphtalma* De Man 1880, *Diplolaimelloides brucici* 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.

b) Feeding experiment

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 experimens with ^{14}C-labelled diatoms as food, the following procedure was used. Exponentially growing cultures of *Navícula salinarum* (Grunow) were labelled by adding $H^{14}CO_3$. After 24h incubation in light (100µE/m^2/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; homogenous labelling was not ensured. Agar droplets of 0.5cm^3 containing c. 5.10^6 diatom cells/cm^3, were inoculated with 15-20 nematodes. After various incubation periods of 2, 4 and 20h, 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 0.5ml demineralized water and 7ml 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. 1.3µm long, motile and it was isolated from the Ems estuary. Several samples of 1ml from a batch culture in exponential phase, were frozen in liquid nitrogen and stored. For the ingestion experiments, ^{14}C-labelled glucose (50mCi) was added to the samples in a 30ml serum bottle, containing 9ml nutrients medium. After 22h of incubation at room temperature, the cultures reached the stationary phase as assessed by spectrophotometric measurements at OD^{430}. The degree of labelling of the cells was 0.015-0.018 dpm/cell at a cell density of $0.3\text{-}0.4.10^9$ cells/ml, OD^{430}: 0.25-0.28. Densities of $0.9\text{-}1.2.10^9$ 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 homogenous distribution of bacteria in the agar. Incubation, and measurements of radioactivity were carried out in the same was 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 24h 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 lost 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

1) Survey of nematodes

Several nematode species that had not been isolated from the Ems estuary previously, were found (Table 2).

TABLE 2

Nematode species not isolated previously from the Ems Estuary.

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

TABLE 3

Occurrence of dominant nematode species on the surface of macrophytes, mats of cyanophytes, debris and in the surface layer of the sediment.

*=number of other species, ** = *Chromadora nudicapitata* dominant in the upper sediment layer, *Diplolaimelloides oschei* dominant in the cyanophyte layer, *** = *Monhystera microphthalma*, ****=no of specimens per 8cm^3 of sediment.

Sample station Eemshaven **nematode species**	***Fucus*-sediment**		***Spartina*-sediment**		***Ulva***	**debris**
Rhabditis marina	2		4			10
Monhystera disjuncta	113		1			1
Monhystera parva	4	5	32	4	1	72
Diplolaimelloides bruciei			57			1
Chromadora nudicapitata			2		1	7
Daptonema normandicum		3		16		
Daptonema oxycerca		12	1	4	13	2
Daptonema setosum		29	1	12		12
Monoposthia costata			1	10		
Atrochromadora microlaima		32	3	17	75	3
Innocuonema tentabundum		3	3	15	4	4
Praeacanthonchus punctatus	1		1		14	
other species		36(11)*)	14(10)	42(12)	12(7)	8(8)
	—	—	—	—	—	— +
	120	120	120	120	120	120

Sample station Mellum **nematode species**	**Farbstreifensandwatt (FSSW)** **0-1cm**	**1-2cm**	**2-3cm**	**3-4cm**	**4-5cm**	**5-6cm**	**6-7cm**
Chromadora nudicapitata	68**)	0	0	0	0	0	0
Diplolaimelloides oschei	29**)	0	1	5	9	13	0
Syringolaimus striatocaudatus	8	0	0	0	0	0	0
other species	15(8)		0	1***)	0	0	0
	—	—	—	—	—	—	— +
	120	0****)	1	6	9	13	0

Sample station Hoogwatum **nematode species**	***Zostera*-sediment**	
Monhystera parva	13	
Chromadora nudicapitata	16	
Daptonema normandicum	2	6
Daptonema oxycerca	6	12
Atrochromadora microlaima	6	16
Dichromadora geophila	7	5
Innocuonema tentabundum	1	8
Paracanthonchus caecus	13	3
Axonolaimus paraspinosus	6	
Halalaimus gracilis	17	42
Viscosia viscosa	7	8
other species	26(13)	20(12)
	—	— +
	120	120

Sample station Reide nematode species	*Salicornia*-sediment		*Oscillatoria*-sediment		*Enteromorpha*
Rhabditis marina	6				
Monhystera disjuncta	8				
Diplolaimelloides bruciei	26				
Monhystera sp.		8	1		
Eleutherolaimus stenosoma		20			17
Daptonema normandicum		7	27	1	
Daptonema setosum	1		48	25	
Theristus flevensis	66	8	12	73	3
Chromadorita supralitoralis	2	8	8	5	
Ptycholaimellus ponticus			1	1	14
Paracanthonchus sp.		12		1	10
Microlaimus globiceps		8			3
Tripyloides marinus		11	7	5	7
Anoplostoma viviparum		12	4	2	35
Syringolaimus striatocaudatus		12		1	
other species	11(6)	14(9)	12(3)	6(5)	31(11)
	120	120	120	120	120

A limited number of species was found that dominated the Aufwuchs communities (Table 3). 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 bruciei* (on *Spartina), Diplolaimelloides oschei* (in *Oscillatoria* mats from the FSSW); the chromadorid species *Chromadora nudicapitata* 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: *Atrochomadora microlaima* (on *Ulva), Anoplostoma viviparum* (on *Enteromorpha), Theristus flevensis* (on *Salicornia)* and several *Daptonema* species (in particular on debris and on *Oscillatoria).* The 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.

2) 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 4).

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 bruciei* ingested the alga *Rhodo-*

TABLE 4

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* sp., R—*Rhodomonas* sp.

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

monas; 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.

3) 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 5).

TABLE 5

Pumping activity (pulsations/minute) of Aufwuchs species and of interstitial species as observed in agar cultures with various food organisms. A=Aufwuchs, S=Sediment, ?=no data, N=*Navicula salinarum,* Ni=*Nitzschia* cf *closterium,* T=*Tetraselmis* sp., B=Bacteria, sa=sterile agar.

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

Rhabditis marina pulsated continuously with a high frequency in the presence of different food items offered (c. 90 pulses/minute). *Diplolaimelloides bruciei* also pulsated with a high frequency but not continuously and therefore on average less frequent (c. 40p/m).

Monhystera disjuncta pulsated very irregularly, sometimes with a high frequency (c. 60p/m) and sometimes not at all; the species always pulsated when colliding with an algal cell but also when not colliding (average frequency 6p/m). *Chromadora nudicapitata* and *Monhystera parva* pulsated after collision with an algal cell and occasionally at other times. The sediment inhabiting species *Daptonema setosum* and *Chromadorita guidoschneideri* only pulsated after colliding with a particle, which in the agar cultures usually means a food item.

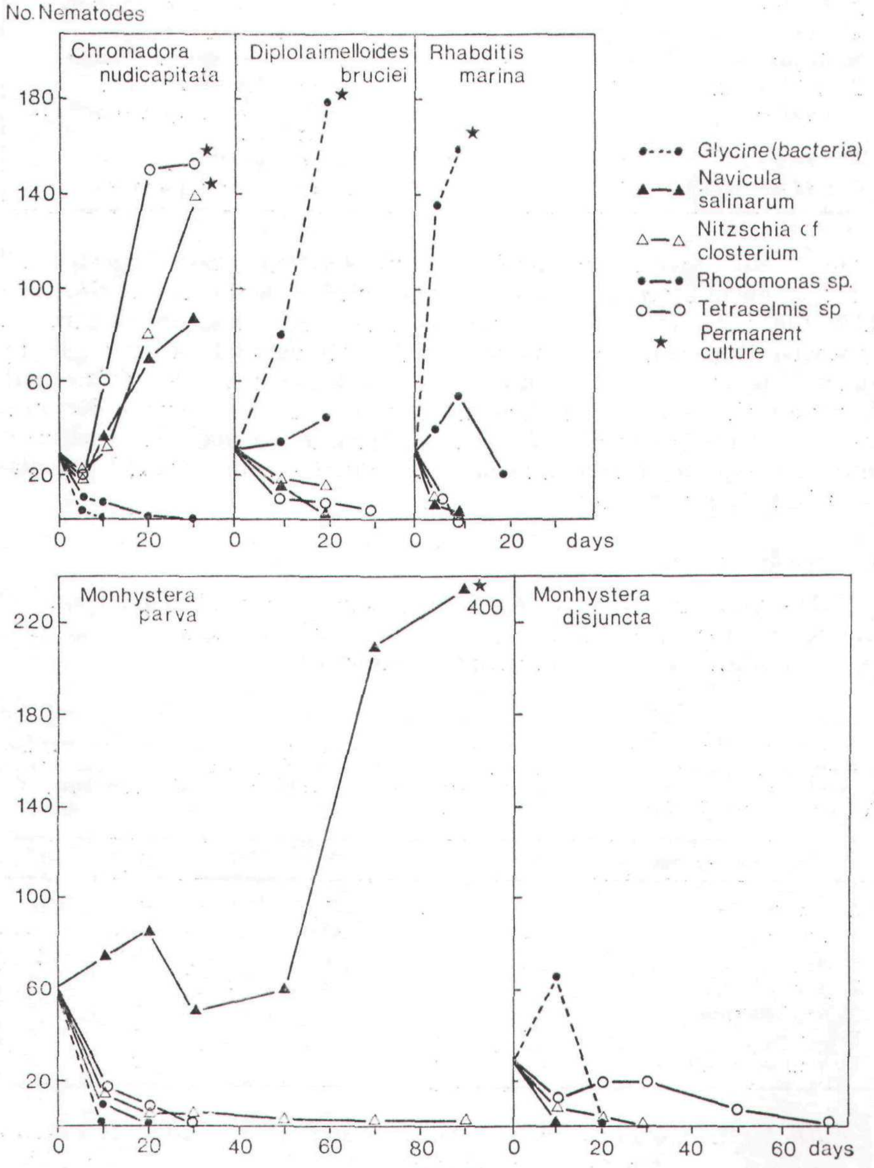

Fig. 2

Development of populations of some nematode species in agar cultures with various food organisms.

4) Culture experiments

From the results of culture experiments with 5 nematode species on different types of food (Fig. 2) it is clear that *Rhabditis marina* and *Diplolaimelloides bruciei* are only able to increase their numbers in glycine enriched (bacteria) agar; in all other cultures *Rhabditis marina* died out rapidly. The same results were obtained when culturing *Diplolaimelloides bruciei,* 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 easily be 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 died out. *Chromadora nudicapitata* could be raised on the various types of algae offered, with the exception of *Rhodomonas.*

5) Feeding experiments with labelled food

The results of feeding experiments with 7 nematode species suplied with labelled diatoms and labelled bacteria, support the information already gained from observations on food intake and culture experiments. *Rhabditis marina, Diplolaimelloides bruciei* and *Monhystera disjuncta* ingested significant numbers of bacteria, 1700, 500 and 300 cells/h respectively (Table 6). *Monhystera disjuncta* ingested diatoms too, c. 18/h. *Daptonema setosum* hardly ingested 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

TABLE 6

Ingestion and incorporation of ^{14}C-labelled bacteria and diatoms by some Aufwuchs and some interstitial nematode species. (+=ingestion observed.)

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

incubation showed that numerous diatoms were ingested or sucked out. Under the prevailing experimental conditions, the incorporation of labelled carbon amounted 20-50 per cent of the total amount of labelled carbon ingested in the experiments with bacteria and c. 20 per cent 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.

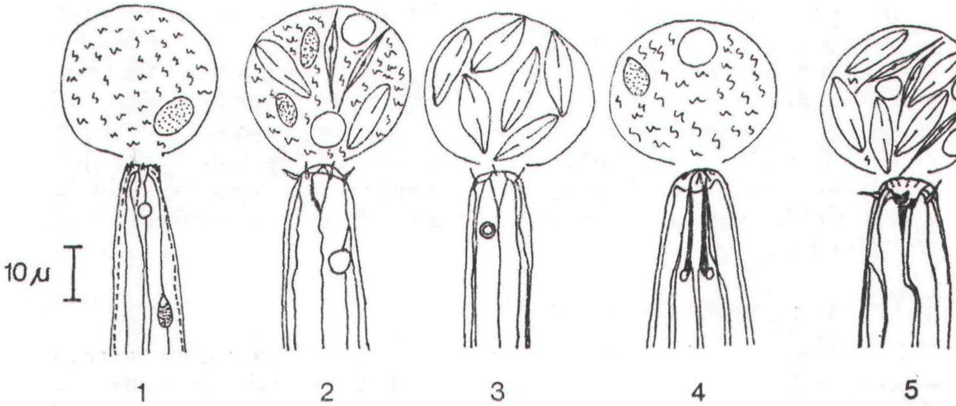

Fig. 3

Menu of five nematode species.

1=*Diplolaimelloides bruciei*
2=*Monhystera disjuncta*
3=*Monhystera parva*
4=*Rhabditis marina*
5=*Chromadora nudicapitata*

∽ **=bacteria**
▨ **=*Rhodomonas***
○ **=*Tetraselmis***
⬭ **=*Navicula salinarum***
⟋ **=*Nitzschia* cf *closterium***

DISCUSSION

The feeding behaviour of characteristic Aufwuchs species such as *Rhabditis marina* and *Diplolaimelloides bruciei*, 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 bruciei* 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 œsophagal 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 bruciei)* 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 by means of a very selective way *(Daptonema setosum, Chromadorita guidoschneideri). Monhystera disjuncta* fits in between the non-selective Aufwuchs strategists and the other groups mentioned.

The 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 *Diplolaimelloides bruciei* is also high (Warwick, 1981) and assumed to be as high as that of the closely related species *Monhystera microphthalma,* females of which 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 but one specimen 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 outcompete species from the intertitial biotope, thus forming almost monospecific populations on *Fucus* and *Spartina.* *Monhystera parva* and *Chromadora nudicapitata* obviously operate in a way intermediate 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 a slightly lower reproductive effort than the monhysterid opportunists and that *Chromadora nudicapitata* had a least the same reproductive effort as its interstiial relatives.

Culture experiments underline the relation between the different species and their biotope. The characteristic Aufwuchs species *Rhabditis marina* and *Diplolaimelloides bruciei* could be raised only on bacteria which probably form the bulk of food in various Aufwuchs biotopes. The more selectively feeding *Monhystera parva* could 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 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 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* and also *Enteromorpha* (Pregnall, 1983) produces exudates, resulting in a mucous layer rich in bacteria and protozoa; on the *Fucus* sampled from the breakwaters, however, diatoms were missing. The exudates probably prohibit the growth of these epiphytes (as described for *Zostera marina* by Harrison, 1982). This explains the absence of diatoms in the intestines of the species *Monhystera disjuncta* which is predominant on *Fucus.* The nematode species *Diplolaimelloides bruciei* 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 bruciei* 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. According to Koop and Griffiths (1982) the distribution of meiofauna in these biotopes is probably governed by the distribution of dissolved organic matter. Gerlach (in Koop and Griffiths, 1982) mentioned dense nematode populations under kelp debris. The high temperatures occurring in the decaying material, probably favour the development of species such as *Rhabditis marina* which belong 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 *Anoplostomo viviparum* on *Entcromorpha* is not well understood because these species are also numerous in various interstitial biotopes (Bouwman, 1982). 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 ovoviparous. 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 occuring in his cultures. Probably the ovoviviparity is a reaction on the presence of free 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 interstitial biotopes; not only in their morphology (Wieser, 1953) but also in their behaviour (Romeyn and Bouwman, 1983). The feeding methods of Aufwuchs species are quite different from those of interstitial species.

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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. Feeding behaviour of these 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.

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