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FOOD SELECTION AND CONSUMPTION BY ESTUARINE NEMATODES [1)]

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INTRODUCTION

Nematodes are found all over the world in almost all humid biotopes. In brackish-water biotopes, *e.g.* the mud-flats of the Ems-Dollard estuary in the north-east of The Netherlands, as many as 1500 specimens per cm^2 live in the interstitial spaces of the sediment.

The morphology of nematodes is simple: two concentric tubes, connected at the anterior end by the buccal cavity and posteriorly by the anus. The outer tube mainly consists of an epidermis, the inner tube functions as a digestive tract, composed of a musculated oesophagus anteriorly and the intestine posteriorly (Fig. 1a).

The length of estuarine nematodes varies from 0.5 - 5.0 mm. A wide variation is found in their morphological structures, especially in size and form of the buccal cavity, the armature inside the buccal cavity and the appendages of the head: papillae and setae (Fig. 1b). These structures play a major role in the selection and consumption of food, which consists of bacteria, protozoa, algae, diatoms and small metazoa including nematodes (WIESER, 1953; WARWICK, 1981). WIESER (1953) was the first to arrange marine and brackish-water nematodes according to the size and armature of the buccal cavity, assuming that this classification was also representative of different types of feeding mechanisms. He distinguished four types (Fig. 2), *viz.* 1A) selective deposit feeders; nematode genera with a very small buccal cavity without armature, presumed to feed selectively on small particles such as bacteria; the size of the buccal cavity prohibits the ingestion of larger particles; 1B) non-selective deposit feeders; nematode genera with a buccal cavity of moderate size without armature, which feed less selectively because larger particles can also be ingested; 2A) epigrowth feeders; nematode genera with a medium-sized buccal cavity, provided with small teeth which are used to attack food particles or to scrape them off solid surfaces; 2B) predators/omnivores; nematode genera with wide buccal cavities with large teeth or other powerful structures that are used to destroy relatively large food organisms *e.g.* nematodes and other metazoa; smaller particles can also be ingested, therefore these genera are probably omnivorous. Observations on several species of nematodes, all occurring in the Ems-Dollard estuary (BOUWMAN, 1981, 1983) indicate that food selection and consumption are more complex processes than is suggested by the feeding types WIESER distinguished. In this paper we would like to modify WIESER's classification in the light of our own insights into the food selection and consumption of estuarine nematodes. Our aim is to classify some nematode species according to feeding type, not only on the basis of morphological differences between the species, but also on behavioural differences.

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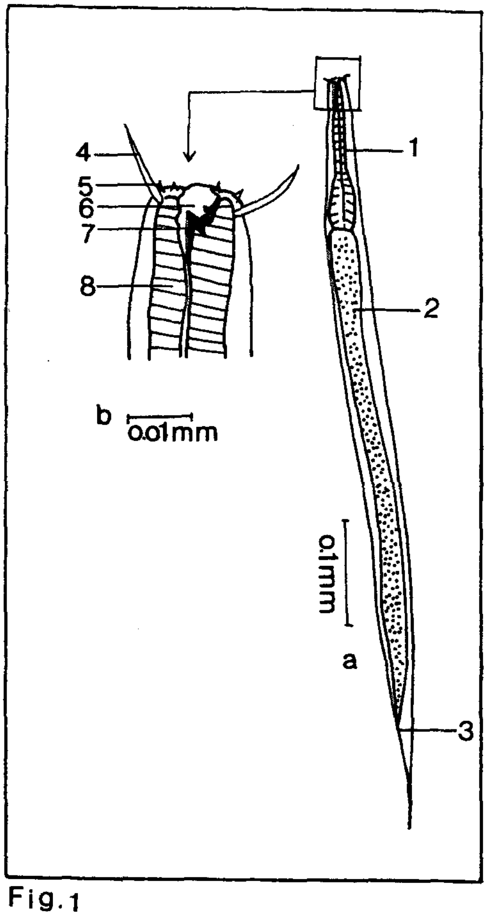


Fig.1

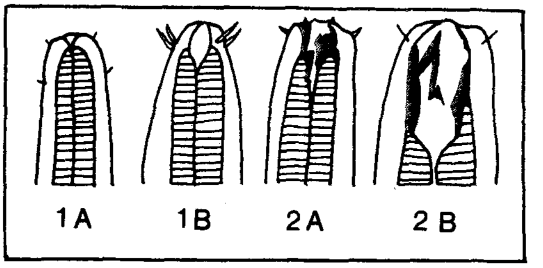


Fig.2

Fig. 1. a. Habitus of a nematode. 1 = oesophagus; 2 = intestine; 3 = anus; b. Head of a nematode. 4 = seta; 5 = papilla; 6 = buccal cavity; 7 = teeth; 8 = oesophagus.

Fig. 2. Feeding types according to WIESER. 1A = selective deposit feeder; 1B = non-selective deposit feeder; 2A = epigrowth feeder; 2B = predator/omnivore.

MATERIALS AND METHODS

Twelve nematode species were studied, all from the Ems-Dollard estuary: *Monhystera disjuncta* BASTIAN 1865, *M.microphthalma* DE MAN 1880, *M.parva* BASTIAN 1865, *Diplolaimelloides bruciei* HOPPER 1970, *Leptolaimus papilliger* DE MAN 1876, *Tripyloides marinus* BÜTSCHLI 1874, *Eudiplogaster pararmatus* W. SCHNEIDER 1938, *Paracyatholaimus proximus* BÜTSCHLI 1874, *Dichromadora geophila* DE MAN 1876, *Chromadorita guidoschneideri* FILIPJEV 1929, *Sphaerolaimus balticus* G. SCHNEIDER 1906, *Adoncholaimus thalassophygas* DE MAN 1876.

The species were cultured in petri dishes with agar, supplied with several types of food: bacteria, protozoa, the algae *Rhodomonas* sp. and *Tetraselmis* sp., the diatom *Navicula salinarum* GRUNOW and the nematode *M.microphthalma* as a prey for the predators. To classify the species in feeding types, several aspects were taken into account and some experiments were carried out.

Morphological aspects.

The size of the buccal cavity indicates the maximum size of food particles that can be ingested; therefore, in fact all nematode species are selective feeders but within the range of potential food items (bacteria, algae, diatoms, protozoa, metazoa) some species are physically able to ingest the whole range and others can only ingest part of it.

The presence and size of sensory organs such as papillae and setae; these are probably used to explore the environment in order to defect potential food organisms and, after detection, to discriminate between edible and similarly sized inedible particles. Nematodes with well developed setae are assumed to feed selectively; by moving their head regularly, while progressing through the sediment or agar, they may collide with a particle that is sensed by the papillae and setae. This triggers off the musculated oesophagus, which starts making contractions that provide the power needed to suck the particle into the buccal cavity, where, if it seems to be edible, the pumping will proceed in order to transport the particle or its contents to the intestine.

Behavioural aspects.

The pumping activity of the oesophagus may be used to determine the degree of selectivity in the feeding strategy. Continuous pumping, more than 60 pulsations per minute, suggests a continuous ingestion of particles and this points to a non-selective way of feeding, although the size of the buccal cavity still prevents too large particles from being ingested. Discontinuous pumping, which means that most of the pulsations are observed only after collision with particles, indicates a more selective feeding strategy.

The intake or the processing by the buccal armature of protozoa, algae, diatoms and nematodes was observed under the microscope in small observation chambers (Type B, MAERTENS, 1975) filled with a thin layer (1 mm) of agar mixed with several types of food; simultaneously, the frequency and timing of the oesophageal pulsations could easily be observed.

Ecological aspects.

The nematode species were isolated from the surface of several littoral macrophytes (*Fucus* sp., *Spartina* sp., *Zostera* sp., *Salicornia* sp.) and from the sediment of the mud-flats. Most species proved to be specific to one of the two habitats sampled (BOUWMAN, 1983). The quality and quantity of food organisms in different biotopes are an indication of the feeding strategies of the species that inhabit these biotopes (WIESER, 1953; WARWICK, 1981).

Experiments.

Experiments with ^{14}C-labelled bacteria and diatoms were used to detect bacteria and to quantify diatom consumption (ADMIRAAL *et al.*, 1983; BOUWMAN, in prep.) All nematode species were cultured for many generations in the laboratory (*S.balticus* excepted) under various food conditions. Growth rate and reproduction success of inoculated populations of nematodes were used to derive information on the specific food requirements of the species investigated.

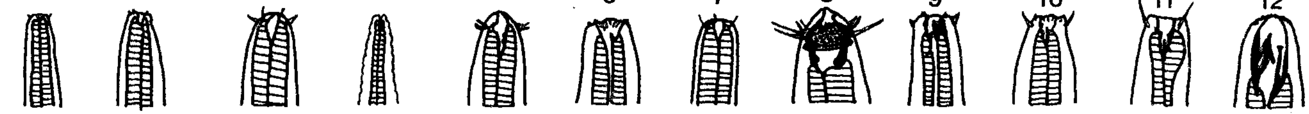
RESULTS AND DISCUSSION

If the classic (WIESER) morphological distinction between nematode feeding types is combined with distinctions based on our observations and experiments and on the habitat preference of the species concerned, a new classification of feeding strategies and techniques is obtained (Table I). This classification is based on physical characteristics of the species and on the feeding strategies that in turn result in specific habitat preferences. Two main categories, the non-selective and the selective feeding strategy, were distinguished.

The non-selective feeding strategy.

Nematode species such as *M.microphthalma* and *D.bruciei* which have almost no sensory organs and buccal cavities, feed on bacteria by means of continuous oesophageal pulsations. Selection of food as an active, behaviourally determined process, does not occur. A passive, physically determined selection, however, takes place, controlled by the dimensions of the

Table 1. Characterization of morphological structure, feeding strategy, ingesting technique, succesful culture, and biotope of origin of 12 nematode species. See Materials and Methods for full species' names. Armature: — = absent; ± = indistinct; + = present; ++ = heavy. Papillae and setae: ± = weakly developed; + = distinct. Enlarged pharyngeal musculature: — = absent; + = distinct. Oesophageal pumping: c = continuous; c/i = continuous series, infrequently interrupted; s = selective. Observed consumption of organisms: bact. = bacteria; Rh. = *Rhodomonas* sp.; Te. = *Tetraselmis* sp.; N.s. = *Navicula salinarum*; prot. = protozoa; nemat. = nematodes. ^{14}C ingestion experiments: + = ingested significantly; — = significantly not ingested; no marks means: not measured. Biotope of origin: m = the surface of macrophytes; s = sediment of tidal flats. Feeding strategy and techniques: non. sel. ingest. = non-selective ingester; sel. destr. = selective destroyer. [1)] from LOPEZ *et al.*, 1979.



	1	2	3	4	5	6	7	8	9	1o	11	12
	Mon. mic.	Dipl. bruc.	Mon. disj.	Lep. pap.	Trip. mar.	Para. prox.	Mon. par.	Sphaer. balt.	Eudip. par.	Dich. geo.	Chrom. guido.	Ado. thal.
size buccal cavity	small	small	small/ medium	small	medium	medium	small/ medium	large	medium	medium	medium	large
armature	—	—	—	—	±	+	—	++	+	+	+	++
papillae and setae	±	±	+	±	+	+	+	+	±	+	+	+
enlarged phar. musculature	—	—	—	—	—	—	—	—	—	—	+	—
oesophageal pumping	c	c	c/i	s	s	s	s	s	s	s	s	s
observed consump. of organ.		Rh.	Rh.Te. N.s.		prot.	Rh.Te. N.s. prot.	N.s.	nemat.	N.s.	N.s.	N.s.	nemat.
^{14}C ingestion experiments												
bacteria	+	+	+			—	—		—		—	— 1)
Nav. sal.			+			+	+		+			
method of consumption	ingestive	ingestive	ingestive	ingestive	ingestive	ingestive	ingestive	ingestive	piercing	piercing	cracking	piercing
successfully cultured on	bact.	bact. Rh.	bact. N.s.	bact.	prot.	N.s.Rh. Te.prot.	N.s.		N.s.	N.s.	N.s.	nemat.
biotope of origin	m	m	m	s	s	s	s/m	s	s	s	s	s
feeding type acc. to WIESER	1A/1B	1A/1B	1B	1A	1B	2A	1B	2B	2A	2A	2A	2B
feeding strategy and techniques	non-sel. ingest.	non-sel. ingest.	non-sel. ingest.	sel. ingest.	sel. ingest.	sel. ingest.	sel. ingest.	sel. ingest. + destr.	sel. destr.	sel. destr.	sel. destr.	sel. destr.

buccal cavity, which prevent larger particles from being ingested. Both species were isolated only from the surface of macrophytes; *D.bruciei* flourishes particularly on *Spartina* sp. whereas *M.microphthalma* was isolated in small numbers from various macrophyte species.

The feeding strategy of *M.disjuncta* is also non-selective but because of its wider buccal cavity diatoms are also ingested; this species prospers on *Fucus* sp.

A high concentration of edible food particles and the low concentration of similarly sized inedible particles in the biotope of the surface of macrophytes, facilitates the non-selective feeding strategy. This strategy is only efficient under these conditions: food selection has already taken place by the habitat; consequently sensory organs are less important and uninterrupted pulsations or series of pulsations (*M.disjuncta*) are not a waste of energy.

The selective feeding strategy.

In the sediment, nematodes have to select edible particles out of a majority of inedible particles. Therefore well-developed sensory organs are necessary. Oesophageal pumping is not continuous but starts after collision with a particle. Within the category of selective strategists, a distinction based on the techniques of consumption can be made, *viz.* the ingestive way, in which food is ingested completely, and the destructive way, in which food particles are first attacked by the buccal armature and consequently their contents are removed through the oesophagus to the intestine. Within the category of the destructive feeders, different mechanisms of destruction can be distinguished, *viz.* piercing and cracking. Some nematode species first pierce their food (*e.g.* diatoms, nematodes) and then swallow the contents. Diatom destroyers of this type first pierce a hole in the diatom, probably just in the raphe (JENSEN, 1982; ROMEYN *et al.*, 1983), the contents of the diatom are subsequently sucked out and the empty frustule remains (Fig. 3b) (*E.pararmatus, D.geophila*). Predatory species of this type pierce a hole in the epidermis of their prey (*e.g.* a nematode) and suck out the contents, leaving the empty epidermis (*A.thalassophygas*). Some nematode species, especially those with enlarged pharyngeal musculature, squeeze part of the diatom cell in their buccal cavity, crack the cell with their teeth, suck out the contents and eject the damaged (*C.guidoschneideri*) or undamaged (*Chromadorita tenuis* in JENSEN, 1982) empty frustule.

In the feeding experiments with ^{14}C-labelled bacteria, none of the selective feeding strategists with obvious buccal cavities, ingested bacteria. It is concluded that these species ignore smaller food organisms while selecting the larger ones. The very small species *L.papilliger*, which has almost no buccal cavity, probably feeds selectively on individual bacteria; however, this species was not used in labelled food experiments though it reproduces already for 1.5 year in agar cultures with bacteria.

The partly overlapping range of food items consumed by a dozen nematode species, led to a preliminary classification (Table 1). Many species do not yet fit into this model and further research will certainly disclose new categories and intermediate forms. For example, the position of the species *P.proximus* is not clear. This species has a well developed buccal cavity equipped with teeth, indicating that diatoms are consumed in the destructive way; however, diatoms, other algae and protozoa are ingested whole, whereas no bacteria are ingested. Therefore, the function of the teeth in this species is not clear. Perhaps they are used to scrape food from solid substrates.

It is obvious that even small, morphologically simply built animals such as nematodes, show a great variety in feeding mechanisms and strategies. This variety is probably as great as that recorded at higher trophic levels. To qualify these feeding strategies, a description and logical ordering of the morphological differences between genera is an important first step. Actual observations on specific food-intake is a necessary second step and it is strange that since WIESER (1953) only little progress has been made. The third step will be the qualification and quantification of specific pathways (specific food items consumed by specific grazers/predators), in the field.

Fig. 3

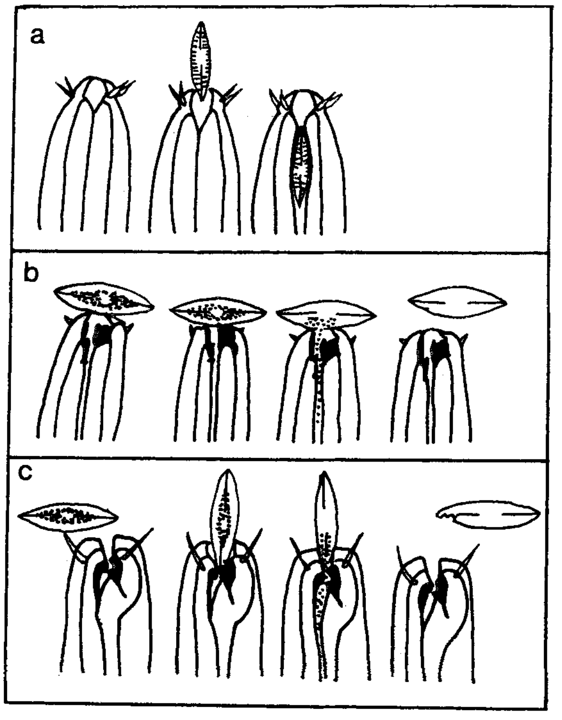


Fig. 3. a. diatom ingestion; b. diatom piercing; c. diatom cracking.

SUMMARY

The feeding strategies and feeding techniques of 12 nematode species, isolated from the Ems-Dollard estuary, were investigated in agar cultures. In the consumption of bacteria, algae, diatoms, protozoa and small metazoa, two main strategies are distinghuished: the non-selective strategy, characteristic of species living on the surface of macrophytes, and the selective strategy, characteristic of sediment-inhabiting species. The selective strategists showed various ingestion techniques, depending on the size and armature of the buccal cavity; food items could be ingested whole, or pierced or cracked and the contents sucked out.

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