OBSERVATIONS ON THE FEEDING ECOLOGY OF ESTUARINE NEMATODES

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Observations on living estuarine nematodes show that previous feeding type classifica-tions do not accurately represent the trophic structure of an intertidal mudflat in the Westerschelde Estuary (Netherlands). A new scheme with six major nematode feeding guilds is proposed: (1) microvores; (2) ciliate feeders; and (3) deposit feeders *sensu stricto* are all nematodes without a distinct buccal armature. In the first two groups bacteria and protozoa, respectively are the major particulate food sources, while other items are included in the diet of the third. The three other categories are recognized among the nematodes with a buccal armature: (4) epigrowth feeders; (5) facultative predators; and (6) predators. Diatoms and other microalgae are an important particulate food for many epigrowth feeders. The importance of bacteria as a food source for these nematodes remains poorly documented. A strictly or mainly predatory behaviour has been described for only few species from the study area. Several nematodes, however, are facultative predators. The predatory strategy of *Calyptronema maxweberi*, as described in this paper, suggests the use of a paralysing or lethal secretion in prey capture, which, to our knowl-edge, is the first report for aquatic nematodes. Furthermore, the importance of sources other than particulate food in free-living aquatic nematodes is stressed. Our observatior s show that many aquatic nematodes are in fact opportunistic feeders, which may change feeding strategies in response to available food.

INTRODUCTION

Nematodes are the most abundant meiofaunal component of marine and estuarine soft sediments. They can reach densities up to several million individuals m^{-2}, repre-senting an average biomass of 0·2–0·5 g carbon m^{-2}. In coastal areas, this is but a small fraction of the total carbon input, but it by far exceeds the contribution of other meiofauna (Vranken & Heip, 1985), especially in estuaries with a high carbon input (Heip et al., 1982). In organically polluted sites with a predominance of large nema-todes, biomass values of up to 50 g wet weight m^{-2} have been reported (Bett & Moore, 1988). In terms of adenosine triphosphate (ATP), nematodes may comprise up to 92% of living carbon in intertidal sediments, a contribution over ten times more important than that of bacteria (Sikora et al., 1977). Bouwman (1983) attributed nematode dominance in estuarine sediments to three main factors: (i) their burrowing capacity, in combination with their small and slender shape, allowing the occupation of interstitial spaces in coarse grained sediments as well as the invasion of soft sediments; (ii) their tolerance, as a taxon, of a variety of environmental stresses; (iii) the diversification in buccal struc-tures, enabling nematodes to exploit a broad range of food items present in the benthos.

Wieser (1953) linked buccal morphology of free-living aquatic nematodes to feeding ecology. His feeding type classification discriminated between group 1: without a buccal armature, with 1A: the selective deposit feeders and 1B: the nonselective deposit feeders; and group 2: with a buccal armature, with 2A: the epistrate feeders and 2B: the predators (Wieser, 1953) or omnivores (Wieser, 1960). Further qualitative information on the feeding biology of marine nematodes was gained from occasional observations of gut contents (e.g. Perkins, 1958; Hopper & Meyers, 1967; von Thun, 1968; Deutsch, 1978). Wieser's (1953) feeding type classification has been widely used since, and only few significant alterations have subsequently been proposed. Romeyn & Bouwman (1983) discriminated between two major feeding strategies, the selective and the nonselective, and included cephalic setation in the selection mechanism. Jensen (1987a) omitted the subdivision between selective and nonselective deposit feeders. While Wieser's (1953) class 2A was confirmed, he subdivided the 2B group into real predators and scavengers.

This paper presents new and additional qualitative information on the feeding ecology of free-living estuarine nematodes, based on observations of living animals from the Westerschelde Estuary.

MATERIALS AND METHODS

Nematodes were sampled from an intertidal mudflat in the mesohaline zone of the Westerschelde Estuary, in the south-western part of the Netherlands (Figure 1). Samples were taken at random along a transect from high to low tide level. Along this transect, sediment varies from very muddy, fine sand at the high tide level to a coarser grained sediment with smaller silt fraction at the low tide level. The temporal variability of the nematode community from a station at the high tide level (WO22) and from a subtidal station (WS22) has already been studied (Li, 1993). Table 1 lists the 22 most abundant species at station WO22 (data from Li, 1993), and species not previously reported from this site. Additional observations on nematodes from a sampling site near Terneuzen (Figure 1) were made.

Nematodes were collected from the samples by simple decantation or by the Ludox centrifugation-flotation technique, modified after de Jonge & Bouwman (1977), using a nontoxic silica gel Cecasol 40C (SOBREP).

Living nematodes were observed under a Leitz Dialux inverted microscope in agar plates with different nutrient enrichments, sustaining one or more of a variety of possible food items, such as bacteria, diatoms, green algae, cyanophytes, ciliates, oligochaetes, and other nematodes. For the majority of our observations, small spots of sediment or plant detritus were inoculated on agar to form spot plates.

RESULTS

A summary of the particulate food sources of the estuarine nematodes observed, is given in Table 2. This information is neither complete nor conclusive in listing the relative importance of different food items.
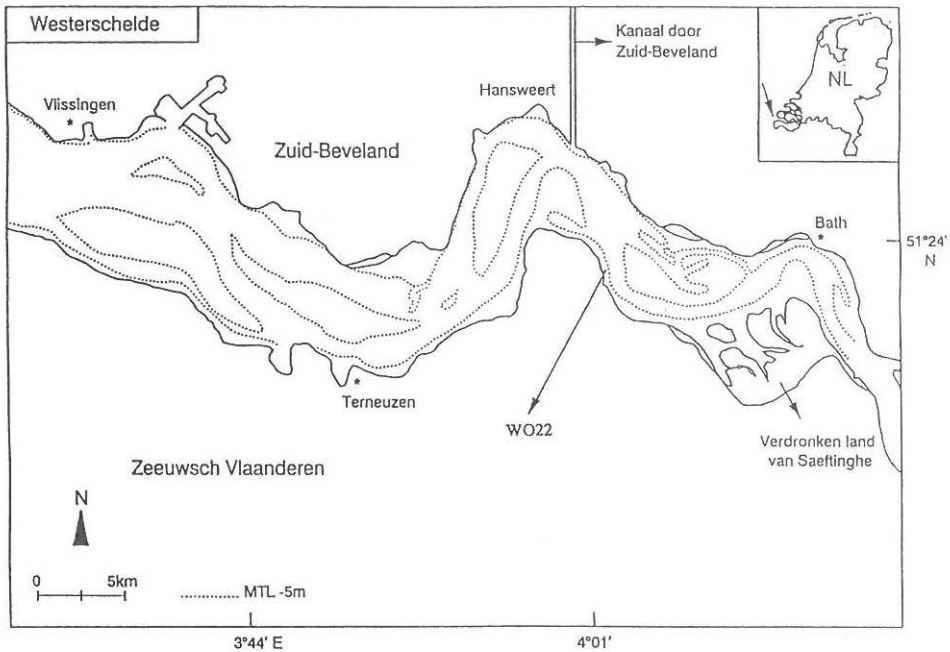
Figure 1. Location of the sampling station WO22 in the Westerschelde Estuary.

Observations

The rhabditid nematodes *Pellioditis marina* (Bastian, 1865) and *Panagrolaimus* sp. Fuchs, 1930 almost continuously ingest bacteria and other microbenthal components, including small green algae. Almost all particles which fit into the buccal cavity are ingested, hinting at a selection mechanism based primarily on particle size. Several monhysterids also feed on bacteria, but their food ingestion is more discontinuous. They do, however, have a broader food range. *Diplolaimelloides meyli* Timm, 1966 and *Monhystera disjuncta* Bastian, 1865 were both observed ingesting several algae and diatoms. Since diatoms and algae can be omitted from laboratory cultures (T.M. & M.V., personal observations), they probably do not make up an important part of the diet of these nematodes, but uptake can be significant: juvenile stage 4 (J4) and adult *D. meyli* ingested up to 15 *Cylindrotheca closterium* (Ehrenberg) Reimann & Lewin in 10 min, while smaller juveniles failed to ingest any diatom or similarly sized particle. Diatoms make up a substantial part of the diet of *M. parva* (Bastian, 1865), size of a particle being the major, if not the only criterion for successful uptake. Many diatoms are sucked into the mouth but not ingested, as they do not fit into the nematode's widened buccal cavity. *Monhystera disjuncta* occasionally feeds on ciliates (*Euplotes* sp.), both by ingesting individuals entirely and by opening them: probably using the slight cuticularization of the mouth, and sucking out the contents. *Daptonema setosum* (Bütschli, 1874) sometimes swallows small ciliates (see also Nehring, 1992b), but this seems merely to be part of a nonselective feeding strategy.

Table 1. *Occurrence, abundance and results from observations and culture experiments of nematode species collected from station WO22.*

Species	Density (%)	Biomass (%)	Observations	Culture
Species from station WO22 (cf. Li, 1993)				
Viscosia viscosa	21·66	22·83	+	−
Daptonema setosum	14·03	29·19	+	−
Tripyloides gracilis	13·14	9·74	+	++
Halalaimus gracilis	12·47	2·84	+	−
Chromadora macrolaima	10·22	8·90	+	−
Dichromadora cephalata	9·41	7·07	+	++
Theristus pertenuis	5·21	2·19	+	−
Anoplostoma viviparum	3·64	6·10	+	−
Thalassoalaimus septentrionalis	2·62	2·88	−	−
Dichromadora geophila	1·24	1·59	+	++
Leptolaimus elegans	1·11	0·12	+	+++
Daptonema normandicum	0·95	0·64	+	−
Hypodontolaimus balticus	0·86	1·18	+	+
Deontolaimus papillatus	0·55	0·09	−	−
Viscosia sp.	0·54	0·12	−	−
Daptonema sp.	0·54	0·10	+	−
Sabatieria pulchra	0·51	1·00	−	−
Sphaerolaimus gracilis	0·39	0·52	+	+
Chromadorita tentabunda	0·31	0·09	−	−
Calyptronema maxweberi	0·27	0·64	+	+
Ptycholaimellus sp.	0·27	0·17	+	−
Species from subtidal WS22 (cf. Li, 1993)				
Enoploides spiculohamatus	8·53		+	−
Oncholaimus oxyuris	4·55		+	++
Species not previously reported for WO22 or WS22				
Pellioditis marina			+	+++
Panagrolaimus sp.1			+	+++
Panagrolaimus sp.2			+	++
Diplolaimelloides meyli			+	+++
Diplolaimella dievengatensis			+	+++
Monhystera parva			+	++
Monhystera disjuncta			+	+++
Monhystrella macrura			+	+
Monhystrella parelegantula			+	++
Adoncholaimus fuscus			+	+

+ and -, indicate presence and absence, respectively, for observations of feeding behaviour of living nematodes. + and -, relates to presence and absence of successful culture experiments. +, ++ and +++, indicate the rearing of one and more than one (consecutive) generation and permanent culture.

For other nematodes, however, protozoa are a major food source. Adult females of *Tripyloides gracilis* (Ditlevsen, 1918) (Tripyloididae) were observed ingesting up to 70 unidentified parameciform ciliates (40–80 µm in size) in 5 min. Similarly sized diatoms, however, were not ingested, indicating a selection mechanism where size is not the

Table 2. *Particulate food sources of nematodes from station WO22 in the Westerschelde Estuary.*

	Bac	Pro	Dia	Alg	Scav	Nem	Oli	Det
Microvores								
Halalaimus gracilis	+++							
Leptolaimus elegans	+++							
Ciliate feeders								
Trypiloides gracilis	+	+++						
Anoplostoma viviparum	+	+[3]						
Deposit feeders								
Pellioditis marina	+++			+[1]				
Panagrolaimus sp.	+++							
Monhystrella parelegantula	+++							
Monhystrella macrura	+++		+	+				
Monhystera disjuncta	+++	+		+[2]				
Diplolaimella dievengatensis	+++	r						
Diplolaimelloides meyli	+++		+	+				
Monhystera parva	+		+++	++				
Daptonema setosum	+	+	+++	+		r		+
Epigrowth feeders								
Dichromadora cephalata	+?	r	+++	++	r[5]			
Chromadora sp.	+?		+++	++				
Hypodontolaimus balticus	+?		+++	+				
Ptycholaimellus sp.			+++					
Facultative predators								
Viscosia viscosa					++	+		++
Oncholaimus oxyuris	+[4]	r		+[4]	+[4]	++		++
Adoncholaimus fuscus					++	+		+
Predators								
Calyptronema maxweberi						+++		
Sphaerolaimus gracilis						+++		
Enoploides spiculohamatus						+++	+++	

+, ++, and +++, indicate relative importance; r, occasional food sources. Alg, other algae/cyanophytes; Bac, bacteria; Dia, diatoms; Det, detritus; Nem, nematodes; Oli, oligochaetes; Pro, protozoa; Scav, scavenging on dead nematodes. References: [1], Tietjen et al., 1970; [2], Romeyn & Bouwman, 1983; [3], von Thun, 1968; [4], Heip et al., 1978; [5], only one observation and not certain whether predation or scavenging was involved.

major criterion for uptake. Moreover, cultures of this species thrived well as long as ciliates were abundant, whereas mortality increased with decreasing ciliate numbers.

Unlike previously mentioned nematodes, which continuously glide through the sediment or over a substrate 'probing the environment for food' (von Thun, 1968), *D. setosum* has a restless and erratic feeding behaviour, interrupting periods of immobility or slow gliding with abrupt activity. Among others, diatoms are clearly an important food, since freshly sampled individuals commonly have up to 40 or more diatom frustules in their intestine. Other items, including sand particles and small ciliates, are also ingested. Juveniles, from J2 onwards, swallow diatoms, but in J2 and J3 the gut is rarely filled with them.

Dichromadora cephalata (Steiner, 1916) (Chromadoridae) occasionally pierces and empties dead ciliates, yeasts, or smooth bacterial colonies, but like most other epigrowth

feeders (Wieser, 1953) observed, it feeds primarily on diatoms and other microalgae. Having encountered a diatom, *D. cephalata* will suck it into the mouth by oesophageal contractions. The diatom is then pierced and emptied, or, if unsuitable, discarded. *Dichromadora cephalata* empties a thin *C. closterium* with only two to six oesophageal contractions, whereas emptying a larger *Navicula* sp. Bory requires 20–40 contractions, often spread over two or three attacks. Apparently, the orientation of a diatom is of some importance: *D. cephalata* will attack a larger *Navicula* sp. from different angles, but it will only empty a *C. closterium* when its attacks are directed at the thicker central part of the diatom. *Dichromadora cephalata* also feeds on filamentous green and blue-green algae in much the same way as it does on diatoms. One observation of an adult female *Dichromadora* sp. piercing and partly emptying a *Monhystrella parelegantula* (De Coninck, 1943), shows that carnivorousness can occasionally occur in epigrowth feeders. Whether or not this was a case of direct predation rather than of scavenging, is unclear.

Hypodontolaimus balticus (Schneider, 1906) (Chromadoridae) opens a diatom by one or a few rapid, woodpecker-like knocks with its dorsal tooth. It either directs the slender diatom *C. closterium* into its mouth by the thin end, or, after an encounter from the side, brakes it by forceful oesophageal contractions, and then further handles it in much the same way as it does with other diatoms. In the latter case, the nematode often has difficulties removing the empty frustule from the mouth. *Hypodontolaimus balticus* individuals were regularly observed with two additional, stiff 'setae', the thin edges of an empty *C. closterium* emanating from the mouth. In addition, *H. balticus* can swallow very small diatoms entirely (T.M. & M.V., personal observations).

In *Dichromadora* sp., *Chromadora* sp., *Hypodontolaimus* sp., and *Ptycholaimellus* sp., oesophageal contractions are frequently observed in the absence of solid food particles. *Dichromadora* sp. and *Hypodontolaimus* sp. show this nonparticle-induced pumping especially in spots where mucus threads, fungal hyphae, filamentous algae or cyanophytes, and other items, form a web or mat, probably stuffed with adhering microbiota (Riemann & Schrage, 1978). *Dichromadora cephalata* sometimes probes the cuticle of living *Oncholaimus oxyuris* Ditlevsen, 1911. *Hypodontolaimus balticus* forms clumps of up to six individuals, which actively forage on each other's body surfaces. *Dichromadora cephalata* and *Chromadora macrolaima* De Man, 1889 sometimes develop in considerable numbers in spot plates containing only low diatom densities, suggesting other components are also important food. This is further supported by a lack of positive correlation of peak abundance of epigrowth feeders in station WO22 to peak microalgal abundance (data from Li, 1993).

Sphaerolaimus gracilis De Man, 1876 (Sphaerolaimidae) attacks other nematodes from the side or from the rear or front, anchoring its prey with its buccal armature. Apparently, *S. gracilis* at least partly digests its prey extracorporally, since small portions of the contents of the body of the prey can be observed being ingested as fluid at regular intervals. During feeding, *S. gracilis* alternates periods of immobility with short, energetic jumps or fierce movements of the head, while the prey continues to struggle vigorously, sometimes resulting in the escape of a partly devoured nematode. *Sphaerolaimus gracilis* adults and J4 require 5–25 min to ingest an entire J4 *Diplolaimelloides*

meyli. Small juvenile *Daptonema* sp. are swallowed within a few minutes. Often, *S. gracilis* sampled from the field still had recognizable prey in their mouth, frequently identified as *Viscosia viscosa* (Bastian, 1865). Juvenile stage 1 and J2 exhibit the same predatory behaviour as adults, but as prey range is apparently limited by the size of the widened buccal cavity of *Sphaerolaimus*, they frequently do not manage to eat a captured prey. On one occasion, two adult *S. gracilis* were observed scavenging on an adult female *Adoncholaimus fuscus* (Bastian, 1865).

Adult and juvenile *O. oxyuris* and *A. fuscus* (Oncholaimidae) were regularly observed foraging on living (monhysterid) prey in a way similar to *S. gracilis*. A prey nematode is tackled from one side and then slowly ingested. A J4 *V. viscosa* (Oncholaimidae) was seen ingesting two juveniles of the tiny *M. parelegantula*.

Enoploides spiculohamatus Schulz, 1932 (Enoplidae) not only attacks and ingests a variety of nematodes, but also oligochaetes. When encountering an oligochaete, *E. spiculohamatus* first retreats, then returns for a fierce attack. The nematode bites a route to the intestine of its prey, which is then emptied by oesophageal contractions. Upon withdrawal from the prey, the nematode usually forages on the spilled remains of its prey's intestinal contents. One successful attack takes 10–30 min.

When freshly hatched juveniles (this behaviour has not yet been observed in adults) of the enchelidiid *Calyptronema maxweberi* (De Man, 1922), maintained in agar plates together with the monhysterid *Diplolaimelloides meyli*, encounter living *D. meyli*, they push their heads once or twice against the prey, and then retreat for a short while. Immediately after the first contact, the prey is entirely immobilized. The predator then returns, pierces the body and intestinal wall of its prey and sucks out the contents. It thereby crawls into the prey to empty it almost completely. The remaining 'nematode ghosts' can be found in significant numbers in cultures containing only few *C. maxweberi*, indicating that this predatory behaviour may be quantitatively important.
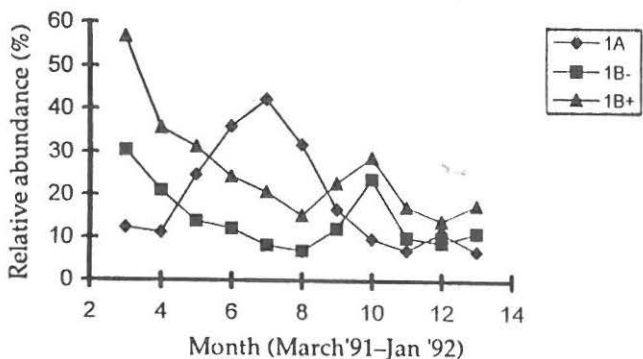

Figure 2. Monthly abundance data of selective (1A) and non-selective (1B) deposit feeders *sensu* Wieser (1953) at station WO22 during March 1991 – January 1992. 1B+, denotes deposit feeders *sensu* Moens & Vincx (present study) together with ciliate feeders, 1B-, denotes deposit feeders only.

DISCUSSION

The subdivision of deposit feeders into a selective and a nonselective group (Wieser, 1953) was rejected by Jensen (1987a), both for lack of experimental evidence and because the size ranges of buccal cavities in the two categories are comparable. However, we suggest the reinstatement of such a subdivision fɔ: the following reasons. The difference in maturity index (Bongers et al., 1991) between selective and nonselective deposit feeders, as well as their relative proportion in organically enriched as opposed to unenriched sediments (Vincx, 1989; Smol et al., 1991), suggests significant ecological differences. Moreover, in station WO22 selective and nonselective deposit feeders have clearly different seasonal abundance patterns (Figure 2). An ecologically relevant subdivision between Wieser's (1953) groups 1A and 1B is further supported by the analysis of functional groups in deep-sea nematode communities (Thistle et al., 1995). Regardless of difficulties in assigning species to either feeding type, merely lumping them together (Ferris & Ferris, 1979; Jensen, 1987a) may devalue the possible importance of Wieser's (1953) selective deposit feeders in biomonitoring. To avoid confusion with previously used terminology (Wieser, 1953; Jensen, 1987a), we propose the terms microvores and deposit feeders *sensu lato* as opposed to selective and nonselective deposit feeders, respectively. Within the deposit feeders *sensu lato*, a distinction is made between ciliate feeders and deposit feeders *sensu stricto* for reasons argued below.

In view of their small buccal cavities, microvores are automatically restricted to small particulate food or dissolved organic matter. For these nematodes, picking out bacteria on an individual basis may prove to be energetically favourable compared to nonselective oesophageal pumping.

Selectivity in deposit feeders *sensu lato* appears to be mainly a function of particle size. Obtainable food should, however, not be narrowed down on the mere basis of nematode mouth size. *Theristus* sp. (mouth size 10 μm) was reported ingesting diatoms with a diameter of 24 μm and a length up to 220 μm (Boucher, 1973). The nematodes' ability to widen their mouth during feeding clearly broadens their food range. In addition to a maximum, however, there might also be a minimum size necessary for particles to induce food uptake (Cheng et al., 1979; Nuß, 1985).

Selectivity between different bacteria may reside at the level of digestion rather than of ingestion, since food sometimes passes undigested through the gut of a nematode (Tietjen et al., 1970). Additionally, bacteria of different strains or age may differentially attract consumers of nematodes (Grewal & Wright, 1992).

It has been argued that the almost continuous food ingestion by rhabditids and several monhysterids as opposed to the irregular feeding action of e.g. several xyalid nematodes, may reflect adaptations to epiphytic and benthic environments, respectively (Bouwman et al., 1984). According to Romeyn & Bouwman (1983), its well-developed cephalic setation would make *Daptonema* sp. a selective feeder. However, at present little evidence seems to support the involvement of cephalic setation in food selection. In fact, present observations suggest that in deposit-feeding nematodes, cephalic setation will merely be involved in a probing of size, shape, and possibly rigidity of a particle, rather than in the actual discrimination between edible and nonedible. The observation of a *D. setosum* partly ingesting a juvenile *Diplolaimelloides*

meyli by the tail, similarly shaped as the most abundant diatoms present in the agar plate, may be illustrative here. Suddenly, the *Daptonema setosum* seemed to detect the mistake and regurgitated the prey. Similarly, a *Sabatieria* sp. De Rouville, 1903 (Comesomatidae) with a juvenile *Daptonema* sp. in its gut (North Sea sample), and an adult *Gonionchus* sp. Cobb, 1920 (Xyalidae) containing a juvenile microlaimid (Antarctic sample, S. Vanhove, personal communication), indicates that a predominantly size-based particle selection can occasionally lead to ingestion of small nematode prey.

One should not infer from the foregoing a minor role for selective uptake by deposit feeders. Nematode communities are often very diverse and considerable habitat over-lap between species with supposedly similar food ranges occurs. It is thus possible to find three or four species of *Daptonema* (*D. setosum*, *D. normandicum* (De Man, 1890), *D. tenuispiculum* (Ditlevsen, 1919), and *Daptonema* sp.) (Li, 1993) in our sampling site, which suggests a high degree of specificity in either microhabitat choice (Jensen, 1981, 1987b), food selection (Jensen, 1986, 1987a; Trotter & Webster, 1984), or both. The question remains whether digestive selectivity combined with microhabitat specificity can account for such a complex congeneric coexistence.

Within the deposit feeders *sensu lato*, some species have a food selection mechanism which is not mainly based on particle size; diatoms and algae, which would fit into their buccal cavity, are not ingested, while similarly sized protozoa are. As yet, our observa-tions on *Tripyloides gracilis* and *T. marinus* (Bütschli, 1874) and those of Von Thun (1968) on *Anoplostoma viviparum* (Bastian, 1865) (Anoplostomatidae) are the only ones impli-cating marine nematodes in significant predation on ciliates. In view of their relative abundance (they comprise ≤25% of nematodes in station WO22 (Li, 1993)) and because of the different selection mechanism involved, the phenomenon is significant enough to erect another category within the traditional deposit feeders. Protozoa are a food source, the importance of which for nematodes might have been underestimated up to now. Bacteria probably make up part of the diet of ciliate feeders as well, their importance possibly being greater in juvenile stages.

Diatoms are an important food source for several representatives of the deposit feeders *sensu stricto*. These nematodes have no buccal armature; diatoms are ingested entirely and (partly) digested during passage through the intestine (Nehring, 1992b). Epigrowth feeders, however, are characterized by the presence of a buccal armature, supposedly used to either scrape off particles from a substrate, or to damage and open food items before emptying them. Diatoms and other microalgae are an important food for many representatives of this group. There are two strategies in which diatoms are preyed upon: cracking and piercing (Nehring, 1992a). However, several diatom species were occasionally attacked in a rather piercer-like way by the crackers *Hypodontolaimus* sp. and *Ptycholaimellus* sp.; the reverse, a cracker-like behaviour in piercing nematodes has not yet been observed. Not all presumed epigrowth feeders belong to either of the two major diatom-feeding strategies. *Paracyatholaimus proximus* (Cyatholaimidae) in-gests diatoms and ciliates in a deposit feeder-like way (Romeyn & Bouwman, 1983). The qualitative feeding pattern of epigrowth feeders is found throughout all life stages, from freshly hatched juveniles to adults. Obviously, the range of diatoms available as prey will at least in part depend on their size, thus confining smaller juveniles to a more limited diet.

Diatoms are clearly an important food for epigrowth feeders. However, the high abundances of these nematodes at several deep-sea locations (e.g. Vincx et al., 1994; Thistle et al., 1995) are but one indication for the involvement of other components in their diets. Although it has been suggested that epigrowth feeders do not significantly feed on bacteria (Tietjen & Lee, 1973; Jennings & Deutsch, 1975; Deutsch, 1978), their teeth may be used to scrape off microbiota from solid surfaces or from mucus threads (cf. Boucher, 1973; Jensen, 1982). Alongi & Tietjen (1980) cultured *Chromadorina germanica* on a diet of bacteria, provided that enough bacteria were attached to a solid substrate. Riemann & Schrage (1978) argue that nonparticle-induced oesophageal pumping is a mechanism employed to feed on all sorts of small particles entrapped in the nematodes' mucus threads. The buccal apparatus would thereby act as a filter to prevent the oesophagus from becoming clogged, rather than as an actual scraping device.

The mechanisms involved in discriminating between edible and nonedible particles, and among the edible ones, in preferring some to others, are at present unknown. Particle size (Tietjen & Lee, 1973) and rigidity (Romeyn et al., 1983) may play a role in food selection. *Dichromadora cephalata* was often more successful in preying on several diatom species within the agar than on the agar surface, especially when the diatoms had not firmly settled (T.M. & M.V., personal observations), raising the question whether all diatoms in the sediment are equally available to the nematodes. Epipsammic species, attached to sand grains, could for example be more readily available to epigrowth feeders than epipelic ones (see also Boucher, 1973). Orientation of a diatom may also be important, since many collisions of several chromadorid species with suitable food items did not result in any feeding response at all.

Nematodes belonging to Wieser's (1953) group 2B have diverse feeding habits and candidate food sources. Wieser (1960) therefore used the name omnivores rather than predators, but this too is misleading in that it suggests additional food for species which indeed are strictly or mainly predatory. *Sphaerolaimus gracilis* is a predator which apparently forages exclusively on other nematodes, prey range being determined by size. Juveniles, from J1 onwards, feed in much the same way as adults. The presence of diatom frustules in the intestine of juvenile *S. dispar* (Boucher, 1973) may be a consequence of the ingestion of diatom-containing prey. *Enoploides spiculohamatus* and *E. longispiculosus* Vitiello, 1967 not only feed on nematodes, but also on oligochaetes and maybe still other meiofauna. The long survival periods of *E. spiculohamatus* on agar plates deficient in suitable prey suggest that microbiota too may, directly or indirectly, contribute to the diet of a predator (see also Yeates, 1970, 1987, for culture of terrestrial predatory nematodes on bacteria).

The remainder of Wieser's (1953) group 2B are commonly considered as omnivorous. The nature of this 'omnivorousness' is, however, poorly understood. Oncholaimids and enchelidiids scavenge on dead animals, as illustrated by several observations (T.M. & M.V., personal observations on *Adoncholaimus fuscus* and *Viscosia* sp., feeding on dead foraminiferans; *A. thalassophygas* (Lopez et al., 1979; Riemann, 1986); *Oncholaimus oxyuris* (Heip et al., 1985); *Metoncholaimus scissus* (Meyers & Hopper, 1973); *Pontonema vulgare* (Rasmussen, 1973; Lorenzen et al., 1987; Jensen, 1987a; Prein, 1988)). Jensen (1987a) therefore named these nematodes scavengers, but other feeding strategies may be

equally or predominantly important. *Metoncholaimus scissus* forages by random inges-tion of fine sediment and detrital material (Meyers et al., 1970), the presence of mat-forming organisms being an important factor to render a substrate attractive (Meyers et al., 1970; Meyers & Hopper, 1966; Hopper & Meyers, 1966). This mode of feeding was also alluded to in early studies on *M. pristiurus* (Cobb, 1932), and observed by the present authors in *Viscosia viscosa* in mats of epipelic diatoms. Significant label uptake by *A. fuscus* in ^{3}H-adenine impregnated sediment devoid of living nematode prey and bacteria indicates that, although the presence of mud or detritus in its gut may in part derive from the intestinal contents of prey animals, sediment particles are also ingested directly (L. Verbeeck & T. Moens, unpublished data). It would be interesting to know whether the nonselective particle ingestion of oncholaimid nematodes aims at the adhering microbiota, or rather at adsorbed organic carbon, or whether particles are merely ingested in the process of nonselective ingestion aiming at dissolved organic matter. Microbiota often pass through the gut of *A. thalassophygas* undigested and label from ^{14}C-glucose impregnated bacteria was not incorporated by this nematode (Lopez et al., 1979). Label from dissolved glucose, however, was readily incorporated, and it was therefore concluded that juvenile *A. thalassophygas* benefit primarily from dis-solved organic carbon (DOC), a food source still obtainable for older juveniles and adults, which further feed by predation and scavenging. A shift from juvenile omnivorousness to adult carnivorousness has also been documented for an enoplid nematode (Hellwig-Armonies et al., 1991). The extent to which nematodes 'garden' their own organic food source, i.e. by the copious oral mucus secretions in *A. thalassophygas* (Riemann & Schrage, 1978), still remains unknown.

The only character common to all scavengers *sensu* Jensen (1987a) observed, is the ability to forage on living nematode prey. Prey is ingested, not pierced, and in *A. fuscus* and *O. oxyuris* predation can be commonly observed in juveniles, from J1 onwards, as well as in adults. The quantitative importance of predation in these nematodes is unclear, but *A. fuscus* adults and J4 were able to significantly reduce numbers of *Diplolaimelloides meyli* on agar plates deficient in other food items, though to a lesser extent than *E. longispiculosus*. In organically enriched medium, however, *A. fuscus* was never observed ingesting prey, whereas *E. longispiculosus* actively preyed on oligochaetes and a variety of nematodes (L. Verbeeck & T. Moens, unpublished observations). It seems plausible that oncholaimid nematodes are very opportunistic feeders, and that predation is merely a facultative mechanism to obtain extra food. It is therefore pro-posed that the term facultative predators is used instead of omnivores (Wieser, 1953) or scavengers (Jensen, 1987a).

Our observations on *Calyptronema maxweberi* demonstrate that any enchelidiid or oncholaimid nematode cannot automatically be considered a facultative predator, predation clearly constituting a significant fraction of its juvenile feeding ecology. There are as yet no data on the feeding behaviour of adults, and it is obvious that males, in view of their minute buccal cavity, will feed in a different way, if at all. Observations suggest the involvement of some 'chemical warfare' in prey capture by this nematode. To our knowledge, no other reports on the use of paralysing or lethal substances in predation of aquatic nematodes have hitherto been published. Enoplid nematodes, on
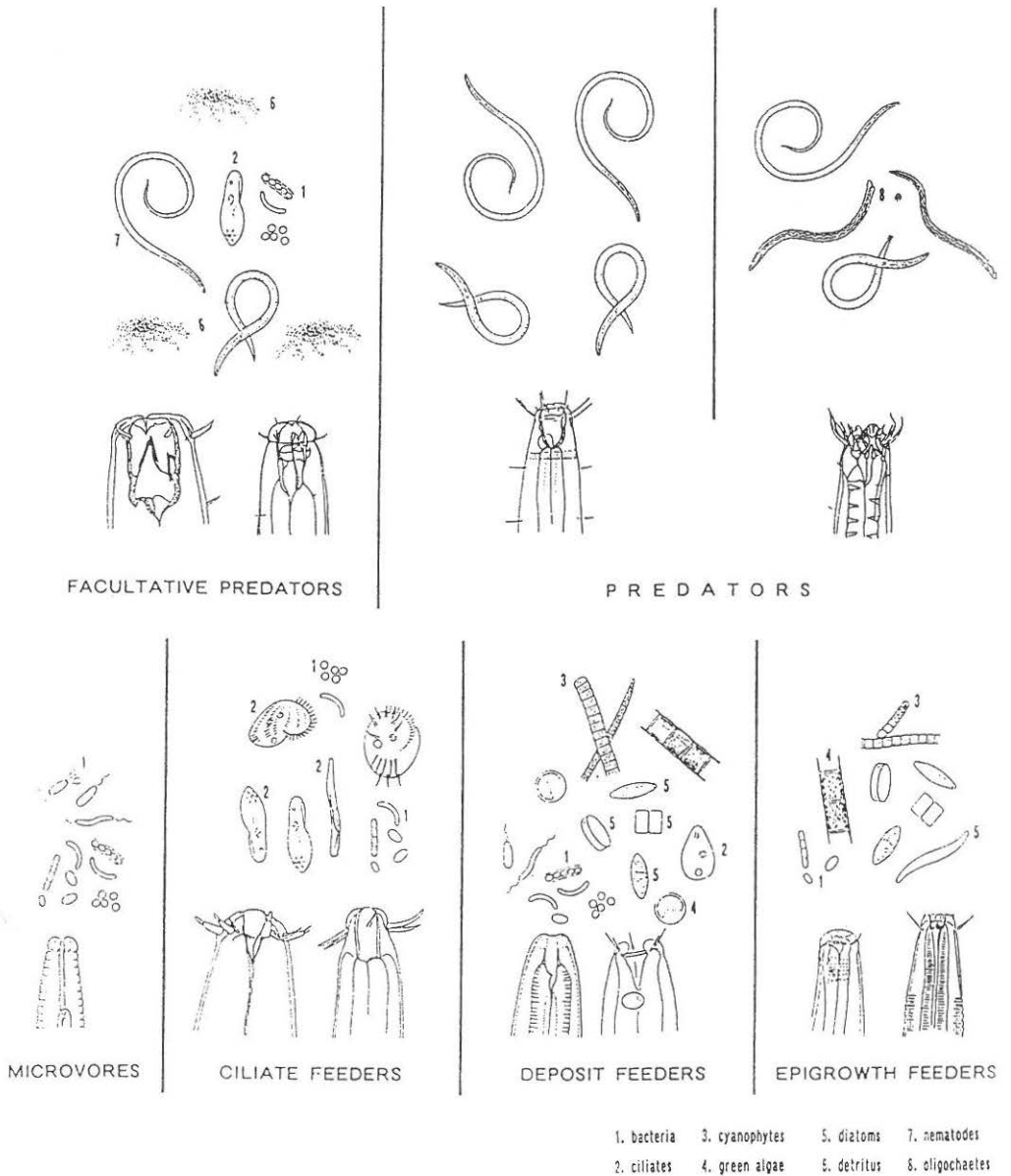
Figure 3. Estuarine nematode feeding guilds and their particulate food sources, as derived from observations on representatives from an intertidal mudflat in the Westerschelde Estuary (south-west Netherlands). Food items have been redrawn after Fitter & Manuel, 1986. Some of the nematodes have been redrawn after Platt & Warwick, 1983.

the other hand, should not automatically be considered strictly predatory. *Enoplus brevis* not only ingests other nematodes and oligochaetes, but also cyanophytes, diatoms, rotatoria, and detritus (Hellwig-Armonies et al., 1991). In fact, although its buccal morphology would classify it as a predator, its feeding behaviour apparently is much like that of a facultative predator.
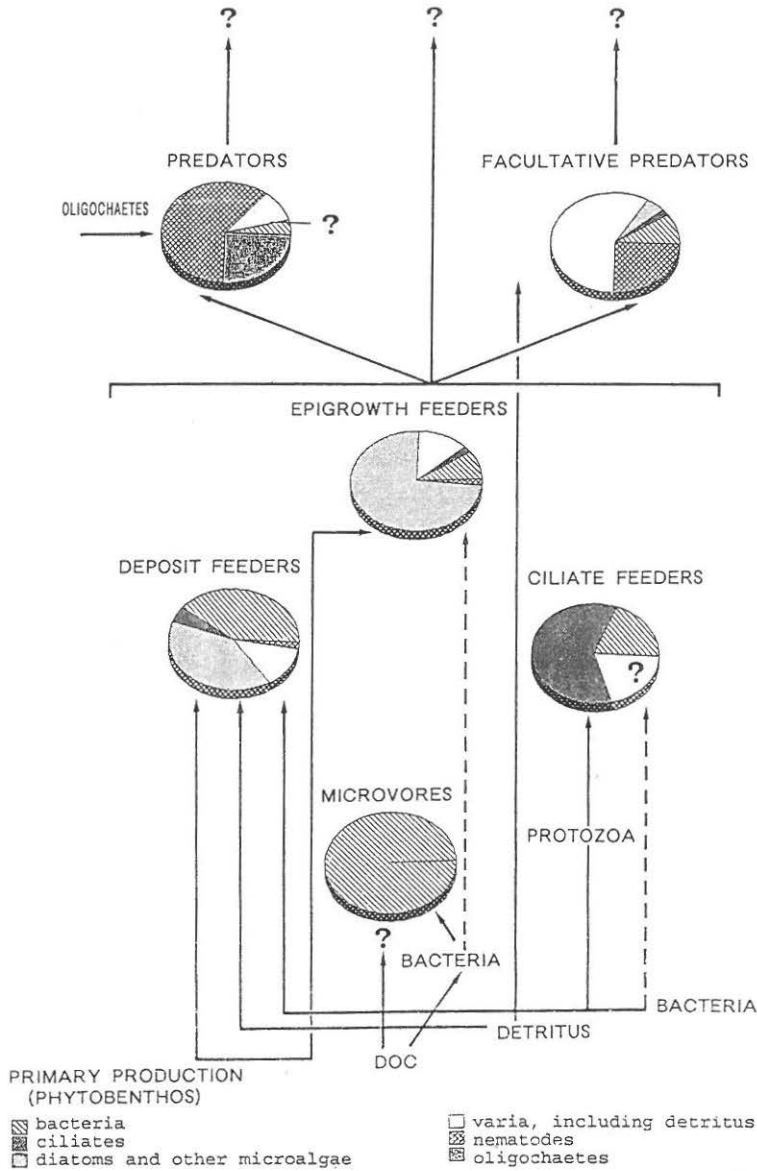
Figure 4. A tentative scheme of patterns of carbon flow into and through different nematode feeding guilds.

Observations illustrate major relations between (groups of) nematode species and particular food sources, which offer a more direct basis for assigning the six feeding guilds proposed in Figure 3 than mere morphological characters, which give information on a nematode's ability to handle food rather than on any actual feeding preference. However, quoting Yeates et al. (1993), it is clear from the opportunistic feeding behaviour of many nematodes observed in the present study that 'ideally the feeding habits of each nematode species should be determined in each particular ecological

setting'. Due to major difficulties in long-term maintenance of most marine species, no such detailed account of nematode feeding can be given at present. However, as the role of nematodes in sediments is still poorly understood, ecologists and modellers have a dire need of schemes which illustrate the possible pathways of carbon flow through this component of the benthos, and the present data may allow a more refined interpretation of nematode feeding ecology than previous schemes. A tentative scheme, based on the qualitative data derived from our observations, is proposed in Figure 4.

A major flaw in our understanding of the trophic position of nematodes in marine sediments is the virtually complete lack of information on the role of dissolved organic carbon (DOC) in their nutrition. Jensen (1986, 1987a,b) demonstrated significantly lower body volume to body surface ratios in thiobiotic nematodes as opposed to oxybiotic species, and hinted at the possible involvement of transepidermal uptake of DOC in their survival strategy. Experimental evidence for uptake of DOC by a meiofaunal community with nematode predominance was given by Montagna (1984). Dissolved organic carbon uptake was demonstrated for two oncholaimid and one comesomatid nematode species by Chia & Warwick (1969), Lopez et al. (1979), and Riemann et al. (1990), but found to be of lesser importance for the rhabditid *Pellioditis marina* (Tietjen & Lee, 1975). Riemann & Schrage (1988) showed attraction of *A. thalassophygas* to CO_2, thus indicating that motile oxybiotic species might react to and benefit from the release of fermentation products from anaerobic sediment layers. The age- and sex-specific distribution pattern of *Anoplostoma viviparum* (Surey-Gent, 1981) adds to this hypothesis. These observations become even more interesting in view of the presence of the enzyme carbonic anhydrase in the intestine of another oncholaimid nematode, *Pontonema vulgare* (Jennings & Colam, 1970). Uptake of DOC is mainly through the intestine (Chia & Warwick, 1969). Nonparticle-induced oesophageal action might thus be a strategy for obtaining dissolved organic compounds, released by microbial activity. Microbial and microphytobenthal exopolymer secretions (EPS), which by themselves can offer an easily assimilable organic food source for meiobenthic animals (Decho & Moriarty, 1990) are known to trap DOC (Decho, 1990; Decho & Lopez, 1992), so any EPS-covered particle may be a strongly nutrient enriched food source. Hence, uptake of DOC may be enhanced by nonselective particle ingestion.

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