Carbon partitioning within meiobenthic nematode communities in the Exe Estuary, UK

Andrew D. Kennedy [*]

Department of Biological Sciences, Hatherly Laboratories, University of Exeter, Exeter EX4 4PS, United Kingdom

ABSTRACT: Acknowledging the importance of free-living nematodes to the trophic dynamics of marine benthic systems, a study was performed in the Exe Estuary, southwest England, to estimate the magnitude and partitioning of carbon flow through Wieser's (1953; Ark. Zool. 4: 439–484) classification of nematode feeding groups. Quarterly sampling over a 12 mo period of mud and sand substrata revealed mean nematode densities of 2.06×10^6 and 1.69×10^6 m^{-2} respectively, with highest populations in July. Species identities and dimensions were determined using image processing techniques: 21 species were recorded from the mud habitat and 30 species from the sand. Non-selective deposit feeders (Group 1B) dominated the mud community and epigrowth feeders (Group 2A) the sand. Literature conversion factors were used to calculate respiration, production and carbon consumption by each of the feeding groups; a model describing the partitioning of carbon flow was thus achieved. The model reveals that, despite the numerical dominance of mud and sand communities by Groups 1B and 2A respectively, in terms of carbon flow the omnivore-predators (Group 2B) play an important role. Whole nematode community production estimates of 1.4 and 1.0 g C m^{-2} yr^{-1} are exceeded by the carbon consumption of this group, viz. 2.0 and 3.1 g C m^{-2} yr^{-1} Assuming that omnivore-predator nematodes derive a significant proportion of their diet from Metazoa, the model reveals that nematodes play a more important role in the 'small food web' than has hitherto been acknowledged.

KEY WORDS: Trophic pathways · Nematoda · Feeding groups · Consumption · Small food web

INTRODUCTION

Meiofauna comprise one of the most numerous groups of organisms in marine soft bottom communities. In littoral sediments, densities generally range from 10^5 to 10^7 individuals m^{-2} (Tietjen 1969, Coull & Bell 1979). Although their biomass is small, according to the basic principle that metabolism is a function of body surface area rather than of body weight, their energetic significance is relatively great. Gerlach (1971), Fenchel (1978) and Kuipers et al. (1981) all emphasize the importance of meiofauna in marine energetics.

The trophic position of meiofauna in benthic communities is a subject of considerable controversy. An open question is the extent to which they are either a self-contained 'energy sink' or, alternatively, facilitate the transfer of primary food resources up the size spectrum, ultimately to commercially important food species for man. Meiofaunal populations may be controlled either by internal predation by carnivorous meiofauna or by infaunal predation by macrobenthos and by small epibenthic predators. No conclusion has yet been reached as to which trophic pathway accounts for a greater proportion of meiofaunal yield.

This paper describes a combined field and modelling approach used to assess the potential of a single meiofaunal phylum to contribute to the energy sink hypothesis. Nematoda is the most ubiquitous, abundant and diverse meiofaunal component of most benthic communities (Platt & Warwick 1980, Warwick 1981, Heip et al. 1982, Vranken & Heip 1986, Vranken et al. 1986); it is thus likely to play an important role in marine benthic trophic dynamics.

[*] Present address: Division of Fisheries, CSIRO Marine Laboratories, PO Box 20, North Beach, Western Australia 6020, Australia

Nematodes possess a wide range of buccal structures which are believed to reflect their diet (Wieser 1953). The purpose of the study was to calculate total nematode community consumption and its partitioning between different feeding modes. Of particular interest were the omnivore-predator feeding nematodes since this group, through preying on other metazoa, is expected to play a central role in the small food web.

MATERIALS AND METHODS

The investigation was carried out in the Exe Estuary, southwest England (Fig. 1). A detailed description of the physical, chemical and biological nature of the estuary is given by Boalch (1980). Earlier work on the trophic dynamics of its meiobenthos is described by Warwick (1982), Gee (1987) and Kennedy (1993).

At quarterly intervals between October 1989 and July 1990, 12 sediment samples were taken on a stratified random basis from 2 contrasting intertidal sample

Fig. 1. Map of Exe Estuary (SW England), showing location of sample sites

Table 1 Population densities of nematodes at sand and mud sites in the Exe Estuary (ind. $\times 10^6$ m^{-2} sediment surface)

	January	April	July	October	(Mean)
Mud site	2.51 ± 0.04	1.36 ± 0.13	2.90 ± 0.17	1.47 ± 0.12	(2.06)
Sand site	1.37 ± 0.02	1.85 ± 0.04	2.42 ± 0.08	1.10 ± 0.02	(1.69)

stations, one mud and one sand. Sampling was achieved using simple corers constructed from surgical syringes. To reflect the greater abundance of meiofauna in mud than in sand, syringes of dimensions 50 mm length by 16 mm internal diameter were used for sampling the mud substratum while syringes of dimensions 100 mm length by 26 mm diameter were used for the sand. These dimensions conform with the recommendations of McIntyre & Warwick (1984). The samples were fixed using 10 % formalin and preserved in 4 % formalin for laboratory analysis. Meiofauna were extracted using a modified version of the Ludox density separation technique (Jonge & Bouwman 1977) described by Austen (1986). Extracted meiofauna were slide-mounted in glycerol for subsequent microscopy examination.

The meiofauna thus obtained were analysed for 2 criteria: (1) the total number of nematodes present, and (2) the species identity, feeding group and dimensions of the first 50 nematodes encountered for each quarter from each sample site by random scanning of the slides. Dimensions were determined using a KONTRON-M15 image processing system; each measurement was repeated 3 times and the mean taken as the best estimate.

RESULTS AND ANALYSIS

The population densities of nematodes calculated from samples for each quarter at the 2 sample sites are given in Table 1. The relative abundance of nematode species encountered by random scanning is given in Table 2. Their allocation to trophic groups is included. For the purpose of this study, Wieser's (1953) feeding classification is used. This divides nematodes into (1A) selective deposit feeders, (1B) non-selective deposit feeders, (2A) epigrowth feeders, and (2B) omnivore-predators, on the basis of buccal morphology.

Individual nematode volumes were calculated using the formula $V = KLW^2$, where V = volume (nl), K is a constant (530), and L and W are respectively length and maximum width (mm). The derivation of this formula is explained by Warwick & Price (1979). This technique was felt to be more accurate than that of Bovée (1987), which takes no account of nematode
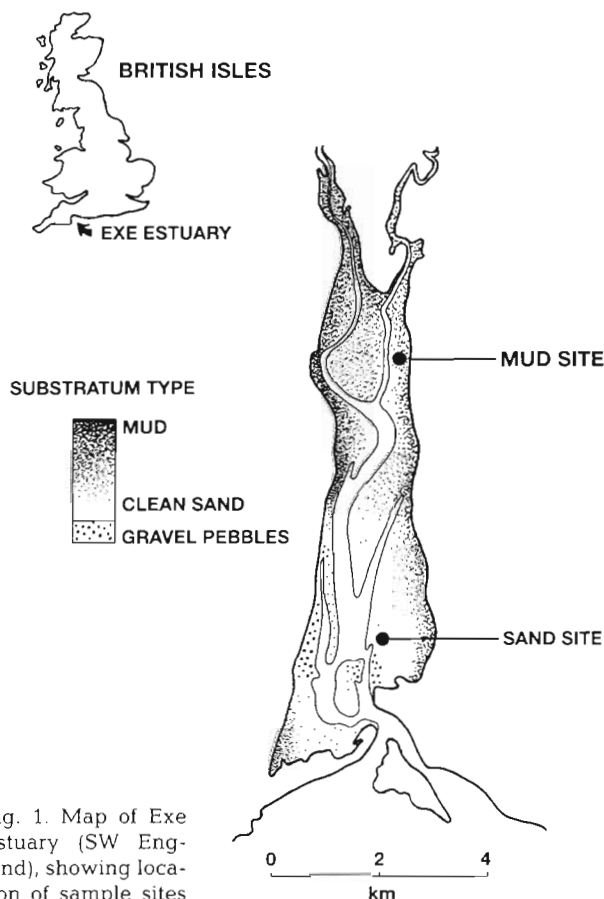
Table 2. Relative abundance of nematode species (expressed as percentage of total). Feeding groups also shown

Number	Species	January	April	July	October	Mean	Feeding group
Mud site							
1	Metalinhomoeus filiformis	16	48	48	30	35.5	1B
2	Sabatieria pulchra	46	36	8	26	29.0	1B
3	Ptycholaimellus ponticus	8	0	12	14	8.5	2A
4	Viscosia viscosa	12	4	2	2	5.0	2B
5	Dichromadora cephalata	2	2	6	2	3.0	2A
6	Halalaimus gracilis	2	2	4	4	3.0	1A
7	Anoplostoma viviparum	2	2	2	4	2.5	1B
8	Dichromadora geophila	2	0	8	0	2.5	2A
9	Sphaerolaimus hirsutus	4	0	0	4	2.0	2B
10	Metachromadora vivipara	0	0	4	2	1.5	2A
11	Calyptronema maxweberi	0	2	0	2	1.0	2B
12	Camacolaimus barbatus	0	2	0	2	1.0	2A
13	Praeacanthonchus punctatus	0	0	2	2	1.0	2A
14	Thalassoalaimus tardus	2	0	0	2	1.0	1A
15	Adoncholaimus thalassophygas	0	2	0	0	0.5	2B
16	Antomicron elegans	2	0	0	0	0.5	1A
17	Chromadora macrolaima	0	0	0	2	0.5	2A
18	Daptonema normandicum	0	0	0	2	0.5	1B
19	Hypodontolaimus balticus	0	0	2	0	0.5	2A
20	Onyx sagittarius	0	0	0	2	0.5	2A
21	Paralinhomeus tenuicaudatus	2	0	0	0	0.5	1B
22	(Unidentified species)	(0)	(2)	(2)	(0)	(1.0)	(–)
Sand site							
1	Chromadora nudicapitata	12	2	20	10	11.0	2A
2	Leptolaimus ampullaceus	6	12	4	18	10.0	1B
3	Microlaimus spp.	10	14	8	6	9.5	2A
4	Enoplolaimus proprinquus	10	8	8	6	8.0	2B
5	Xyala striata	10	6	8	8	8.0	1B
6	Neochromadora tricophora	6	8	10	4	7.0	2A
7	Pomponema sedecima	6	4	4	8	5.5	2A
8	Neochromadora tecta	4	6	4	4	4.5	2A
9	Gammanema conicauda	2	6	4	2	3.5	2B
10	Onyx perfectus	2	6	0	4	3.0	2A
11	Sigmophoranema litorale	0	0	4	4	2.0	2A
12	Theristus denticulatus	4	2	0	2	2.0	1B
13	Ascolaimus elongatus	2	2	0	2	1.5	1B
14	Trefusia longicaudata	2	2	0	2	1.5	1A
15	Enoploides brunetti	0	0	2	2	1.0	2B
16	Eumorpholaimus sabuliculous	0	4	0	0	1.0	1B
17	Chromadorella filiformis	0	0	4	0	1.0	2A
18	Chromadorina germanica	0	0	0	4	1.0	2A
19	Chromodorita tenuis	0	0	2	2	1.0	2A
20	Oncholaimus brachycercus	2	0	2	0	1.0	2B
21	Sigmophoranema rufum	2	0	0	2	1.0	2A
22	Adoncholaimus fuscus	0	2	0	0	0.5	2B
23	Enoplolaimus denticulatus	0	2	0	0	0.5	2B
24	Gerlachius novusetosus	2	0	0	0	0.5	1A
25	Ptycholaimellus ponticus	0	0	2	0	0.5	2A
26	Stephanolaimus elegans	0	0	0	2	0.5	2A
27	Tarvaia angusta	0	2	0	0	0.5	1A
28	Trichotheristus mirabilis	0	2	0	0	0.5	1B
29	Viscosia cobii	0	0	0	2	0.5	2B
30	Viscosia viscosa	0	0	2	0	0.5	2B
31	(Unidentified species)	(18)	(10)	(12)	(6)	(11.5)	(–)

Table 3. Integrated biomass of feeding groups (mg m^{-2} sediment surface)

	1A	1B	2A	2B
Mud site				
January	11.49	217.86	41.96	240.14
April	2.07	149.46	7.54	80.89
July	9.01	225.11	139.79	35.28
October	6.73	112.02	57.29	70.25
(Mean)	(7.32)	(176.11)	(61.65)	(106.64)
Sand site				
January	3.92	32.31	64.04	91.23
April	7.75	49.75	69.43	171.96
July	3.39	32.60	130.54	202.81
October	1.57	32.30	47.56	72.96
(Mean)	(4.16)	(36.74)	(77.89)	(134.74)

width, and that of Andrassy (1956), which assumes a conical tail shape. Nematode volume was converted into biomass by assuming a specific gravity of 1.13 (Wieser 1960), an estimate of dry weight as 22.5% of wet weight [midway between the values of 20% and 25% reported by Myers (1967) and Wieser (1960)], and carbon content as constituting 40% of dry mass (Steele 1974, Feller & Warwick 1988). The integrated biomass of feeding groups per quarter per m^2 of sediment surface at each site are shown in Table 3.

Nematode community respiration was estimated using literature values for the regression of size on oxygen consumption. These were derived by plotting respiration rate (measured using Cartesian Diver or oxygen electrode techniques) against body volume, and expressing the results in the form: $R = aV^b$ where R = oxygen consumption, V = volume, and a and b are constants. As for other poikilotherms, b is taken as being 0.75 (Teal & Wieser 1966). The value for log a is considered to be an indication of metabolic intensity (Schiemer & Duncan 1974) and to correlate with feeding group (Wieser & Kanwisher 1961, Teal & Wieser 1966). Warwick & Price (1979) provide estimates for 48 nematode species based on a synthesis of experimental data and literature values. By using their mean values assigned for each feeding group (Table 4)

Table 4. Log a values for nematode feeding groups. Data derived from Warwick & Price (1979)

Feeding group	Log a ± 1 SE
Selective deposit feeders (1A)	-0.344 ± 0.095
Non-selective deposit feeders (1B)	0.018 ± 0.059
Epigrowth feeders (2A)	-0.258 ± 0.076
Predator-omnivores (2B)	0.101 ± 0.076

the oxygen requirements at 20°C of the nematodes recorded in this study were calculated.

To convert these figures into field values, sediment temperatures recorded at the time of meiofaunal sampling and a Q_{10} of 1.8 were used. The Q_{10} figure is intermediate between reported values for nematodes (see Wieser & Schiemer 1977, Zaika & Makarova 1979, Atkinson 1980, Price & Warwick 1980). To produce an estimate of average daily temperature, 2°C has been deducted from the recorded sediment temperatures to compensate for sampling always being performed during daylight hours. By substituting these values into the classical Q_{10} equation (Hoff 1896) the total oxygen consumed by each group was estimated. Oxygen respired was converted into carbon metabolized using the relationship 1 ml O_2 respired = 0.4 mg carbon metabolized (Crisp 1984) (Table 5).

Table 5. Summary of nematode community energetics (all values mg C m^{-2} yr^{-1}) for the 4 feeding groups

Parameter	1A	1B	2A	2B
Mud site				
Respiration	34.9	1660	380	746
Production	29.3	704	247	427
Consumption	107	3940	1040	1960
Sand site				
Respiration	20.7	376	505	1340
Production	16.6	147	312	539
Consumption	62.3	872	1360	3120

To calculate nematode production the P/B technique was employed (Waters 1977). This relies upon the relatively predictable relationship between annual production and mean annual biomass of a population (Dickie 1972, Banse & Mosher 1980), a function of its life-history characteristics. For the purpose of this study a P/B ratio of 10 was employed, considered adequate by Bodin et al. (1984) for the assessment of meiofaunal production. The value conforms with the findings of von Thun (1968) and Warwick & Price (1979) and with the recommendations of Gerlach (1971) and McIntyre (1969). However, it differs from the conclusions of Vranken et al. (1986) who consider it to be too low. To convert from dry weight to carbon the relationship carbon content = 40% of dry weight (Steele 1974, Feller & Warwick 1988) was used.

Conventional energy budget principles were employed to calculate nematode consumption. The energy flow through a nematode population can be written as: $C = P + R + G + U + F$ where C = consumption, P = production, R = respiration, U = soluble waste products, F = particulate waste products and G =

gonad output. Since nothing is known about excretion in marine nematodes (Heip et al. 1985, Feller & Warwick 1988) an assimilation efficiency of 60% was assumed, demonstrated by Marchant & Nicholas (1974) for the bacteria-feeding *Pelodera* and adopted by Warwick et al. (1979) for their description of secondary production in the Lynher estuary. This allows the unassimilated energy factors $(U + F)$ to be discounted. Gonad output is the only unquantifiable component of the equation, and for the sake of this study energy bound up in the form of eggs and other reproductive products has been ignored; consumption figures should therefore be viewed as a minimum.

DISCUSSION

The total biomass figures calculated for the combined nematode feeding groups, although low for an estuarine system, are within the range of values quoted in the literature (see review by Lasserre et al. 1976); published values have often been formulated using data gathered during only one (usually summer) season, when standing stocks are likely to be high. The greater biomass from the Exe Estuary mud site reflects the higher productivity of this habitat when compared with coarser sand. The diversity of the system is lower (21 species as opposed to 30) and the species dominance more marked (Fig. 2), confirming what is already known about the community composition of such systems (Wieser 1960, Warwick 1971). The total
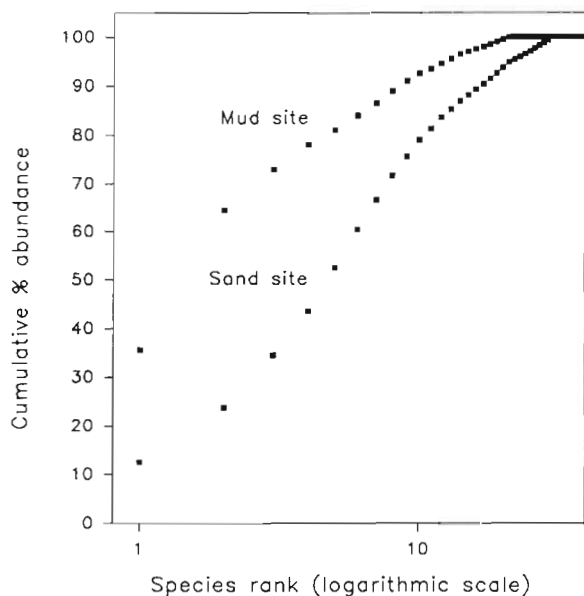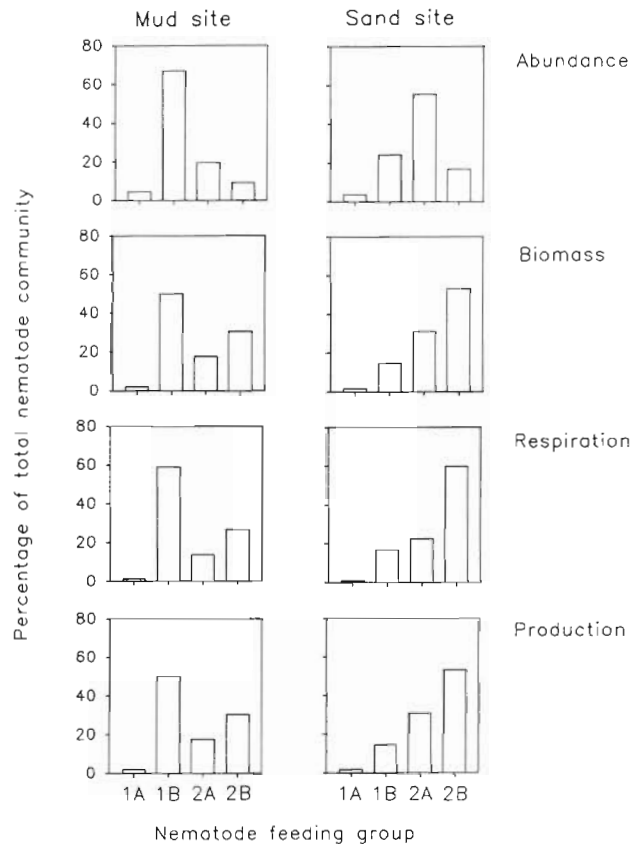

Fig. 3. Percentage importance, in terms of abundance, biomass, respiration and production, of Wieser's (1953) 4 nematode feeding groups at sand and mud sites in the Exe Estuary

Fig. 2. *K*-dominance curves for Exe Estuary nematode communities

community consumption figures of 7.05 (mud) and 5.41 (sand) g C m^{-2} yr^{-1} compare realistically with a value of 29.71 g C m^{-2} yr^{-1} obtained for the total meiofaunal community from a more densely populated estuary (Warwick et al. 1979).

The purpose of this study was to model the partitioning of carbon flow between nematode feeding groups. Carbon sources for nematode community nutrition could then be identified. If detritus and algae comprise the bulk of their diet then nematodes are unlikely to contribute significantly to the small food web. Conversely, if the energetic demand of omnivorous predatory nematodes is great, a significant role in the small food web may be predicted.

A summary of carbon partitioning in abundance, biomass, respiration and production terms is given in Fig. 3. The relative consumption of each feeding group in sand and mud substrata is shown in Fig. 4. The contrast between the importance of each group in abundance and energetic terms is considerable. For example, while in abundance terms epigrowth feeders comprise 55.6% of the sand nematode fauna, in con-
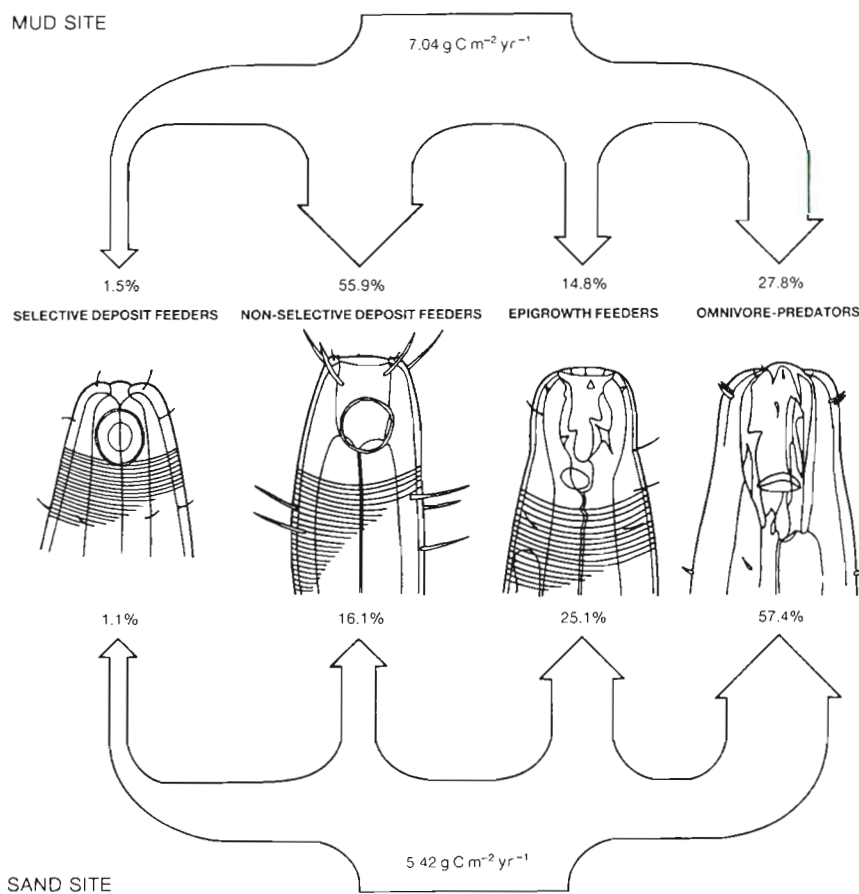
MUD SITE

Fig. 4. Summary of partitioning of carbon consumption between nematode feeding groups in Exe Estuary sand and mud substrata (representative species redrawn from Platt & Warwick 1980)

sumption terms they account for only 25.1 % of the carbon flow. Conversely omnivore predators, which comprise 16.7 % of the sand nematode fauna, account for 57.4 % of its consumption. These community patterns are reflected at the species level (Table 6). *Enoploides brunetti*, a sand-dwelling omnivore predator, although only 15th in importance in numerical terms, is 2nd in importance in consumption terms. Conversely *Halalaimus gracilis*, a mud-dwelling non-selective deposit feeder, is 6th in numerical importance and 16th in consumption terms. By plotting the feeding modes of individual nematode species by their ranked contribution to total community consumption (Fig. 5) it can be seen that 2 omnivore-predator species (*Enoplolaimus proprinquus* and *Enoploides brunetti*) dominate the sand system, each with over 15 % of the total consumption, while at the mud flat, although a single non-selective deposit feeder (*Sabatieria pulchra*) is dominant, omnivore-predators also play an important role.

These findings are of significance to whole-community benthic trophic dynamics. Where traditionally the functional role of nematodes has been thought to reflect the numerical domination by non-selective deposit feeders and epigrowth feeders in mud and sand substrata respectively, the present study suggests that, in energetic terms, the omnivore-predators, despite their low abundance, play an important role in both communities. This supports the findings of Warwick

Table 6. Ten most important nematode species, in consumption terms, at sand and mud sites in the Exe Estuary (values = percentage of total carbon consumed)

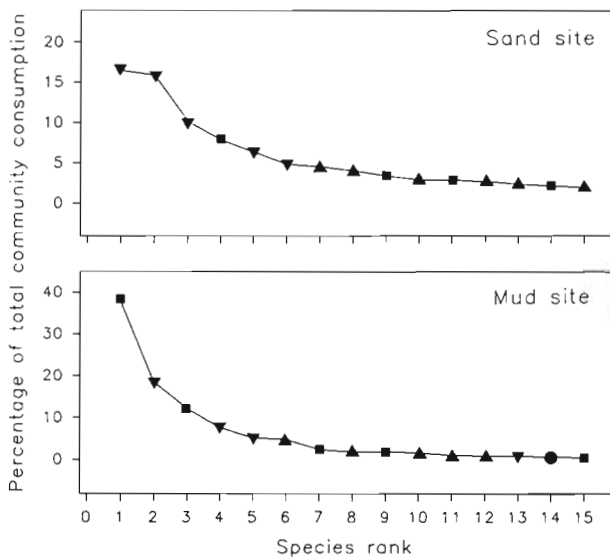| Sand site		Mud site	
Enoplolaimus proprinquus	16.5	*Sabatieria pulchra*	38.2
Enoploides brunetti	15.9	*Sphaerolaimus hirsutus*	18.5
Gammanema conicauda	10.2	*Metalinhomoeus filiformis*	12.2
Xyala striata	7.9	*Viscosia viscosa*	7.6
Oncholaimus brachycercus	6.4	*Calyptronema maxweberi*	5.3
Enoplolaimus denticulatus	4.9	*Ptycholaimellus ponticus*	4.8
Pomponema sedecima	4.6	*Anoplostoma viviparum*	2.4
Chromadora nudicapitata	4.1	*Praeacanthonchus punctatus*	1.9
Leptolaimus ampullaceus	3.4	*Paralinhomeus tenuicaudatus*	1.9
Neochromadora tecta	3.0	*Dichromadora cephalata*	1.7

Fig. 5. Consumption-rank curves (% of total consumption) for nematode species at sand and mud sites in the Exe Estuary. Key: (●) Group 1A; (■) Group 1B; (▲) Group 2A; (▼) Group 2B

(1982) and counters the traditional belief that detritus and sand-adhered algae provide the majority of nematode sustenance (see e.g. Mare 1942, Perkins 1958, Swedmark 1964). In energetic terms, small metazoa now seem likely to provide a significant meiofaunal food source. Wieser's omnivore-predator nematodes consume approximately 1.96 and 3.12 g C m^{-2} yr^{-1} in the mud and sand substrata respectively. This is more than total nematode community production. Carbon cycling within the meiofauna must thus account for a significant proportion of benthic production. As Kuipers et al. (1981) suggest, this trophic pathway will not yield a considerable amount of secondary biomass but instead produce mainly heat and release nutrients.

One qualification is required to these conclusions: a central tenet of the study, resulting from the adoption of Wieser's (1953) classification scheme, is that a relationship exists between nematode buccal structure and diet. Nematode species with no buccal cavity (Group 1A) are predicted to consume only free particles of bacterial size. Species with unarmed buccal cavities (Group 1B) may ingest free particles of a larger size provided they require no mastication. Epigrowth feeders (Group 2A) with small rasping or piercing teeth may feed on algae, including diatoms. Omnivore predators, by virtue of their large powerful denticles (Group 2B), may prey upon other small metazoa. While substantial evidence exists to support this relationship (see e.g. von Thun 1968, Tietjen & Lee 1975, Heip et al. 1978, Jensen 1982, Romeyn et al. 1983), including

observations of the predatory habits of 2B nematodes (see Lopez et al. 1979, Heip et al. 1985), the validity of the buccal morphology/diet relationship has recently been questioned (see Romeyn & Bouwman 1983, Jensen 1987). Detailed research is required to evaluate the true nature of nematode diet so that the validity of modelling approaches, such as that used here, may be critically assessed.

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