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Tracing organic matter sources of estuarine tidal flat nematodes with stable carbon isotopes

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ABSTRACT: The present study explores the use of stable carbon isotopes to trace organic matter sources of intertidal nematodes in the Schelde estuary (SW Netherlands). Stable carbon isotope signatures of nematodes from a saltmarsh and 4 tidal flat stations were determined in spring and winter situations, and compared to isotope ratios of organic matter sources within the estuary. Nematodes collected from fine sandy tidal flat sediments in late spring and during mild and sunny late winter weather had $\delta^{13}C$ values consistent with microphytobenthos as their prime carbon source. Nematodes from a silty station and individuals sampled under cold and dark winter conditions had $\delta^{13}C$ values intermediate between those of microalgae and particulate organic matter. The isotopic signatures of nematodes from the saltmarsh station were intermediate between those of microalgae, *Spartina anglica*-litter and particulate organic matter. An *in situ* $H^{13}CO_3^-$ spike experiment at 2 tidal flat stations corroborated the importance of microphytobenthos as a carbon source for nematodes, yet at the same time contradicted the hypothesis that direct grazing would be the main pathway of microalgal carbon to nematode consumers. A laboratory experiment adding ^{13}C-labeled algal detritus to sediment microcosms demonstrated the nematodes' ability to rapidly utilize settling organic matter too. Incorporation of carbon from phytodetritus by subsurface nematodes in both enrichment experiments was high, but, compared to carbon utilization by surface individuals, showed time-lags largely consistent with sediment mixing rates. A combination of observed natural isotope signatures and experimental results suggests that tidal flat nematodes preferentially utilize labile organic carbon derived from microphytobenthos or settling phytoplankton; organic matter from terrestrial or riverine origin does not contribute significantly to the diet of nematodes at our study sites.

KEY WORDS: Food web · Nematodes · Microphytobenthos · Phytoplankton · Intertidal estuarine ^{13}C

INTRODUCTION

Several authors have suggested a potentially crucial role for the meiofauna in benthic energy fluxes (Gerlach 1971, Fenchel 1978, Coull & Bell 1979, Kuipers et al. 1981), but detailed knowledge on their trophic position is lacking. Nematodes are consistently the most abundant meiobenthic taxon in estuarine sediments. In the meso- and polyhaline reaches of the Schelde estuary (SW Netherlands), they comprise on average more than 90% of the total metazoan meiofauna (Li & Vincx 1993, Soetaert et al. 1994, Moens et al. 1999b).

Nematode communities are generally looked upon as grazers of microalgae and bacteria (Montagna 1995). Other feeding modes have, however, been proposed for many nematode taxa (Moens & Vincx 1997 and references therein). Omnivores or facultative predators (sensu Moens & Vincx 1997) are highly abundant in the meso- and polyhaline reaches of the Schelde estuary (Li & Vincx 1993, Soetaert et al. 1994). These nematodes are known to aggregate on organic deposits (Lopez et

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al. 1979, Lorenzen et al. 1987, Prein 1988), where they probably utilize a mix of microbiota and particulate and dissolved organic matter (Moens et al. 1999c). Other nematodes, especially deposit-feeders, graze on microalgae but equally ingest other, similarly sized particles (Jensen 1987, Moens & Vincx 1997).

In addition to microphytobenthic production (typically ≅100 g C m^{-2} yr^{-1} on intertidal flats: De Jong & de Jonge 1995, Heip et al. 1995, MacIntyre et al. 1996), organic matter of terrestrial, riverine, estuarine and marine origin may serve as carbon sources for estuarine food webs. Deegan & Garritt (1997) demonstrated significant spatial variability in the estuarine food webs of the Plum Island Sound system, Massachusetts, USA. They concluded that (1) macrofaunal consumers primarily depend on autochthonous sources of organic matter, and (2) benthic and pelagic organisms largely utilize different organic sources, the former relying on benthic microalgae and saltmarsh vegetation, the latter on phytoplankton. Riera & Richard (1996) also found a strong spatial variability in carbon sources used by the oyster *Crassostrea gigas* along an estuarine gradient in the Bay of Marennes-Oléron, France. Herman et al. (2000) used natural isotope ratios of carbon and nitrogen and isotope labeling approaches, and observed that intertidal macrobenthos relies primarily on microphytobenthos and suspended particulate organic matter, with little dependence on allochthonous carbon. No meiobenthos was, however, included in either of these studies.

We used stable isotopes to trace carbon sources for tidal flat nematodes in the lower part of the Schelde estuary. Natural stable isotope ratios are presented on a community level as well as for abundant species or genera belonging to different trophic types, and compared to isotope ratios of a range of organic sources in the Schelde estuary. An *in situ* $NaH^{13}CO_3$ enrichment experiment was performed to trace uptake of microphytobenthic carbon by tidal flat nematode communities. Finally, the nematodes' capacity to utilize freshly settled organic matter was assessed after addition of ^{13}C-enriched algal detritus to sediment microcosms. Previous studies on meiobenthos from different marine and estuarine habitats and focusing on a variety of response times have yielded conflicting conclusions as to whether nematode communities utilize, and respond to, inputs of fresh algal detritus from the water column (see, e.g., Rudnick 1989, Gooday et al. 1996, Olafsson & Elmgren 1997, Olafsson et al. 1999).

MATERIALS AND METHODS

Study sites. Samples were taken at 2 stations on the Molenplaat (MP 2 and MP 4), an intertidal flat at the meso-/polyhaline boundary in the turbid, nutrient-rich and heterotrophic Schelde estuary (average salinity between 20 and 25), and at 3 sites in and adjacent to the Paulina saltmarsh (average salinity between 24 and 32) (Fig. 1).

Most of the Molenplaat is located between –1 m and +1 m relative to mean tidal level. Mean tidal range is approximately 5 m. The period of emersion is about 7 h per tidal cycle. The 2 MP stations are characterized by contrasting sediment characteristics (Table 1). Diatoms largely dominate the microphytobenthos at both stations (Lucas & Holligan 1999), as is the case along most of the Schelde estuary (Sabbe & Vyverman 1991). Samples were collected from both stations during emersion in June 1997 in a period of bright summer weather near the end of a spring microphytobenthos and phytoplankton bloom; further samples were taken at MP 4 in March 1999 during a period of cold and rainy weather.

At Paulina, samples were taken at 3 stations (see Table 1 for sediment characteristics): Stn A (PS A) was located at the edge of a drainage gully in a small saltmarsh, in the lower vegetation zone, dominated by *Spartina anglica*. Stn B (PS B) was located ca. 500 m upstream from the marsh on an intertidal flat. Stn C (PS C)

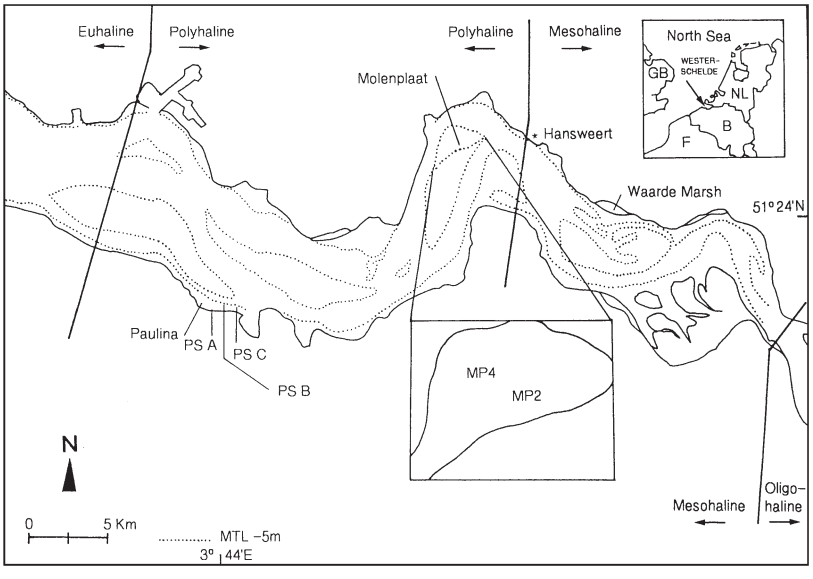

Fig. 1. Map of the Schelde estuary with indication of sampling stations chosen in the present study and those referred to in Table 4

was located more than 1 km upstream of PS B on the same tidal flat, without direct influence of upstream saltmarsh vegetation. The Paulina sites were sampled in February 1998, during a period of relatively mild and sunny weather, with large diatom patches at PS A and B. Station B was also sampled in March 1999 when virtually no microphytobenthos patches were detectable.

Natural stable carbon isotope signatures of nematodes. First, we assessed small-scale horizontal heterogeneity of nematode carbon isotope ratios. Carbon isotope ratios of *Enoploides longispiculosus* from 10 cores at MP 4 were compared. In addition, we collected groups of 5 adults of the large facultative predator *Adoncholaimus fuscus* from each of 5 cores taken within a 1 m^2 frame at PS A, as well as 5 individual adults taken from a single core. *A. fuscus* were separated live from freshly collected sediment after dispersion of sediment aliquots with artificial seawater (ASW: Dietrich & Kalle 1957). All other nematode samples were stored frozen at −20°C until treatment. Nematodes were collected from thawed samples via density centrifugation (Heip et al. 1985) with the colloidal silicagel Cecasol 40C (Sobrep) and subsequently rinsed with tap water. In a preliminary analysis, we checked whether sample treatment with 4% formaldehyde (as in the $H^{13}CO_3^-$ spike experiment) and colloidal silica affected nematode natural carbon isotope signatures. For this purpose, we compared isotope signatures of 5 groups of 3 *A. fuscus* which were handpicked live from untreated sediment with ratios of *A. fuscus* elutriated with colloidal silica from (1) frozen and (2) formaldehyde-preserved samples. We also compared isotope signatures of 3 untreated PS B nematode (whole-community) samples with those of frozen or formaldehyde-preserved samples elutriated with colloidal silica.

Table 1. Summary of the most important characteristics of the Molenplaat (MP) and Paulina (PS) sampling stations. PS A is a saltmarsh station, all others are on bare tidal flats. MPB: microphytobenthos. Sediment grain size and organic carbon data for MP 2 and MP 4 are from 9 June 1996. nd: not determined

Stn Depth range (cm)	% mud	Median grain size (µm)	Organic carbon (wt %)	MPB production (mg C m^{-2} h^{-1})
MP 2				
0–1	43	77	0.64	105
0–25	30	94	0.41	
MP 4				
0–1	4	170	0.06	131
0–25	5	167	0.07	
PS A				
0–1	29	93	1.17	nd
0–10	25	98	1.44	
PS B				
0–1	9	166	0.24	nd
0–10	6	171	0.18	
PS C				
0–1	0	231	0.08	nd
0–10	0	229	0.07	

Nematodes were handpicked with a fine needle, rinsed twice in sterile ASW to remove adhering particles, and finally transferred to a drop of distilled water in 2.5 × 6 mm aluminium cups (Van Loenen Instruments). Pretreatment of the aluminium cups for 4 h at 550°C ensured that they were not contaminated with exogenous organic carbon. Nematodes which did not appear clean after 2 transfers were discarded. The aluminium cups were oven-dried, pinched closed, and stored in screw-cap glass tubes until analysis. The number of nematodes $sample^{-1}$ depended on crude biomass estimates based on observations of length and width of selected specimens. Carbon was conservatively estimated at 10% of nematode wet weight (Sikora et al. 1977, Heip et al. 1985). Except for some samples from the enrichment experiments, we always collected at least 10 µg C $sample^{-1}$, corresponding to 50 to 200 specimens in whole-community samples and to 20 or more *Enoploides longispiculosus*. Adult *Adoncholaimus fuscus* yielded ≥5 µg C $individual^{-1}$, sufficient for reproducible measurements.

The carbon isotopic composition of the samples was determined with a Fisons CN-analyser coupled online via a con-flo 2 interface to a Finnigan Delta S mass spectrometer. Results are reported in the δ notation relative to Vienna PDB and expressed in units of ‰, according to the standard formula:

$$\delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 10^3$$

Reproducibility of $\delta^{13}C$ values was better than 0.2‰.

Differences between sampling sites and sampling times were compared by 1-way analysis of variance (ANOVA); unplanned pairwise comparisons were based on Hochberg's GT2-method for unequal sample sizes as recommended by Sokal & Rohlf (1995), with Bonferroni correction for multiple pairwise tests. Data were normally distributed and homoscedastic, and hence not transformed prior to analysis.

Consumption of microalgal carbon by nematodes. In the field experiment, conducted at MP 2 and MP 4 in June 1997, we introduced $NaH^{13}CO_3$ *in situ* in a final concentration of 1 g ^{13}C m^{-2}, by spraying the sediment surface of two 0.25 m^2 frames at the beginning of low tide. A detailed description of this experiment is given by Middelburg et al. (2000). The introduced ^{13}C was incorporated by the microphytobenthos, and its fate recorded over a period of 3 d (MP 4) or 4 d (MP 2). Duplicate 2.4 cm diam. cores for nematode C-isotope analysis were taken after 1, 2, 4, 24, 48, 72 and 96 h. The upper 3 centimetres were vertically subdivided

per cm and preserved with hot (70°C) neutral formaldehyde in a final concentration of approximately 4%. Nematodes were extracted from these samples as already described.

In the laboratory experiment, we used two 14 cm diam. Perspex cores with sediment collected from PS B in March 1999. Ambient temperature at the time and site of sampling was approximately 10°C. Cores were transported to the laboratory within 2 h of collection and incubated with 3 cm of overlying habitat water in a dark room at 14°C. After an acclimatisation period of 24 h, the overlying water was gently siphoned off, taking care to minimize sediment disturbance, and replaced by 154 ml of ASW containing 77 mg of ^{13}C-enriched lyophilised algal material (98% ^{13}C: Cambridge Isotope Laboratories). Thus, average sediment water cover was 1 cm and organic matter enrichment 0.5 mg cm^{-2} (i.e. approximately 1.5 g C m^{-2}). Added algal carbon represented 1 to 2% of the total particulate organic carbon in the upper 1 cm interval of the sediment. The phytodetritus was allowed to settle for 1 h, and this moment is referred to as Time zero for the experiment. 3.6 cm diam. perspex cores were inserted at time zero and single cores (1 from each 14 cm diam. core) were withdrawn after 0.5, 3, 24 and 72 h for nematode carbon-isotope analysis. Small sediment fractions were oven-dried and used for the determination of sedimentary organic carbon-isotope signatures after acidification with HCl. Nematodes were elutriated and treated as in the previous experiment.

The amount of ^{13}C incorporated by nematodes in both enrichment experiments was calculated as the product of excess ^{13}C (E) and nematode biomass for each depth layer. Excess ^{13}C is the difference between the fraction ^{13}C (F) of control and sample, i.e.

$$E = F_{sample} - F_{control}$$

with $F = {}^{13}C/({}^{13}C + {}^{12}C) = R/(R+1)$, and $R = (\delta^{13}C/1000 + 1) \times R_{VPDB}$, where $R_{VPDB} = 0.0112372$ = the carbon isotope ratio of the reference material (Vienna PDB).

RESULTS

Natural stable carbon isotope signatures of nematodes

Small-scale horizontal heterogeneity typically spanned a range of 2 to 3‰. It was smaller for samples containing higher nematode numbers, e.g. whole-community samples and most samples of specific genera. As an example, δ^{13}C of 10 *Enoploides longispiculosus* samples from MP 4 in March 1999 averaged –15.43 ± 0.68‰ (SD), with highest and lowest values of –14.09 and –16.14‰, respectively. In a pool of 10 samples of the facultative predator *Adoncholaimus fuscus* (PS A, February 1998), δ^{13}C ranged from –16.22 to –19.20‰ with a mean of –17.64‰. Nematodes collected live from sediments (1) did not show significantly different δ^{13}C values compared to nematodes elutriated with Ludox from frozen (2) or formaldehyde-preserved (3) samples (–18.5, –18.4 and –16.5, respectively, in *A. fuscus*, and –14.7, –14.3 and –13.4 in whole-community samples). The general tendency of formaldehyde-preserved samples to be heavier does, however, warrant caution with the use of chemical preservatives when studying natural (i.e. non-enriched) carbon-isotope ratios.

Nematodes collected at different sites and/or times had significantly different isotopic signatures ($p = 0.000$, $df_{among} = 7$, $df_{within} = 48$, $F_s = 17.05$). Nematodes from PS A, i.e. in the saltmarsh, were significantly more depleted in ^{13}C compared to Stns B and C ($p < 0.01$); the latter 2 did not differ (Table 2). In June 1997, nematodes at MP 2 were slightly but signifi-

Table 2. Nematode δ^{13}C signatures (mean ‰). Comparison for different intertidal stations and different sampling times. MP: Molenplaat station; PS: Paulina station; PS A is a saltmarsh station, all others are on bare tidal flat sediments; a,b: whole nematode communities (excluding predacious *Enoploides longispiculosus*) and *E. longispiculosus* samples, respectively; x: significant ($p < 0.01$) pairwise difference as calculated *a posteriori* with Hochberg's GT2-method for unequal N (Sokal & Rohlf 1995) after a significant ($p = 0.000$, $df_{among} = 7$, $df_{within} = 48$, $F_s = 17.05$) 1-way ANOVA; ns: not significant

Stn Date	MP 2 June 1997	MP 4 June 1997a	MP 4 June 1997b	MP 4 Mar 1999a	MP 4 Mar 1999b	PS A Feb 1998	PS B Feb 1998	PS C Feb 1998
MP 2 Jun 1997	–17.36	x	x	ns	ns	ns	x	x
MP 4 Jun 1997a	x	–15.21	ns	x	ns	x	ns	ns
MP 4 Jun 1997b	x	ns	–14.28	x	ns	x	ns	ns
MP 4 Mar 1999a	ns	x	x	–18.48	x	ns	x	x
MP 4 Mar 1999b	ns	ns	ns	x	–15.43	x	ns	ns
PS A Feb 1998	ns	x	x	ns	x	–17.19	x	x
PS B Feb 1998	x	ns	ns	x	ns	x	–14.69	ns
PS C Feb 1998	x	ns	ns	x	ns	x	ns	–14.03

Table 3. Natural $\delta^{13}C$ ratios (‰) of nematode genera collected from stations at Paulina. Stn A is a saltmarsh station, Stns B and C are unvegetated tidal flat stations. DF: deposit feeder (mainly herbivorous); CF: ciliate feeder; EF: epistrate feeder (mainly herbivorous); P: predator; FP: facultative predator

Nematode	Stn A	Stn B	Stn C
Whole community	−17.39	−14.42	−14.12
Whole community	−17.47	−15.45	−14.42
Daptonema (DF)		−13.90	
Tripyloides (CF)		−14.84	
Sphaerolaimus (P)	−16.10	−14.53	
Enoplus (P or FP)	−19.09	−14.52	−13.39
Adoncholaimus (FP)	−17.20	−15.14	−14.53
Metachromadora (EF)	−15.07		
Calyptronema (P)	−15.97		
Axonolaimus (DF)	−17.95		
Praeacanthonchus (DF)	−17.02		
Halichoanolaimus (P)	−18.66		
Unidentified			−14.83
Oncholaimus (FP)			−14.18
Enoploides (P)			−12.73
Average	−17.194	−14.686	−14.029
SD	1.169	0.509	0.727

cantly ($p < 0.01$) more depleted in ^{13}C than individuals at MP 4, but had $\delta^{13}C$ values overlapping with MP 4 nematodes collected in March 1999. The predacious *Enoploides longispiculosus* was isotopically heavier than other nematodes at MP 4 ($p < 0.01$ in June 1997). $\delta^{13}C$ of *E. longispiculosus* did not differ between June 1997 and March 1999, but $\delta^{13}C$ of other nematodes did (being isotopically heavier in June: $p < 0.01$) (Table 2).

Table 3 presents $\delta^{13}C$ signatures of different nematode genera and trophic types at the Paulina stations. Adequate replication was not possible due to lack of material; consequently no significance could be attributed to the observed trends. At Stn A, the epistrate-feeding nematode *Metachromadora* and the predatory nematode genera *Sphaerolaimus* and *Calyptronema* were isotopically heavier than whole-community samples, dominated by deposit-feeding and facultatively predatory genera. This did not, however, hold for other supposedly predatory or facultatively predatory nematodes. No trends were found for PS B samples. At Stn C, predatory genera again appeared isotopically heavier than other nematodes.

Two genera, *Adoncholaimus* and *Enoplus*, were common to all 3 Paulina stations, and clearly showed the same trend as revealed by the comparison of all samples per station: specimens from the saltmarsh station PS A were more depleted in ^{13}C than specimens from the other stations. *Sphaerolaimus* was obtained from 2 of the 3 stations; here too, saltmarsh *Sphaerolaimus* were isotopically lighter than their congeners from PS B.

Consumption of microalgal carbon by nematodes

In the $H^{13}CO_3^-$ enrichment experiment on the Molenplaat, nematodes at both stations rapidly incorporated microphytobenthic ^{13}C (Fig. 2). Uptake kinetics and excess ^{13}C-levels were similar for both stations, except for the return to near natural values at MP 4 after 24 h, for which we have no other explanation than horizontal heterogeneity in label administration to the sediment. Total carbon assimilated by the nematodes was roughly proportional to nematode biomass, but did not relate to trophic structure of the nematode community, which was largely dominated by the predacious *Enoploides longispiculosus* at MP 4, and by a mix of ciliate-feeders, deposit-feeders, epistrate-

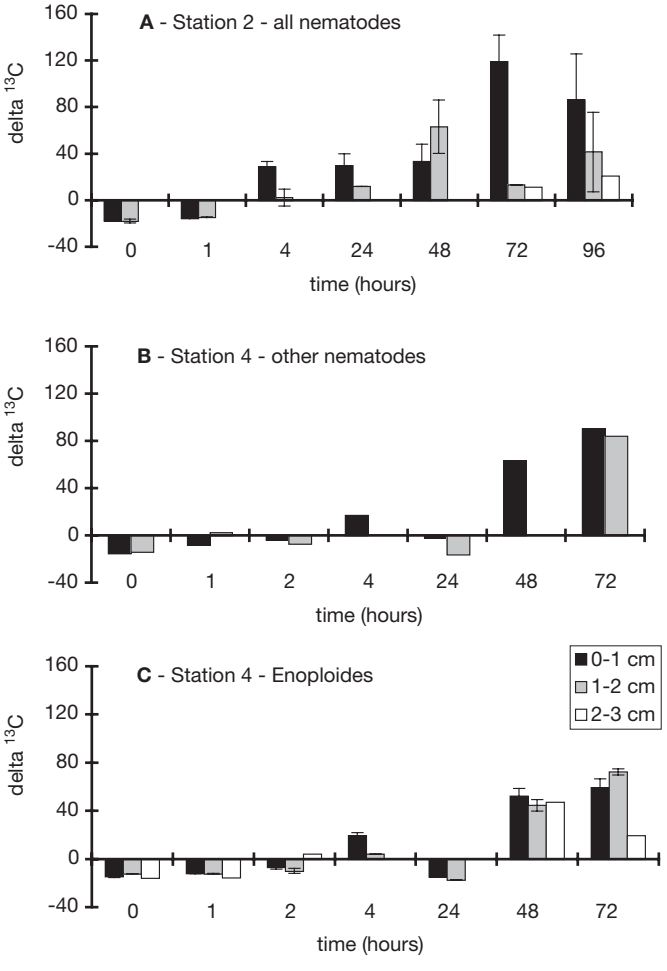

Fig. 2. $H^{13}CO_3^-$ pulse-chase experiment: stable carbon isotope ratios of the nematode fauna at MP 2 (A, all nematodes) and MP 4 (B, all nematodes except *Enoploides longispiculosus*; C, *E. longispiculosus*), as a function of time and sediment depth. Data are means ± SD of 2 replicates. Data without error bars are measurements on pooled nematofauna of 2 replicate samples

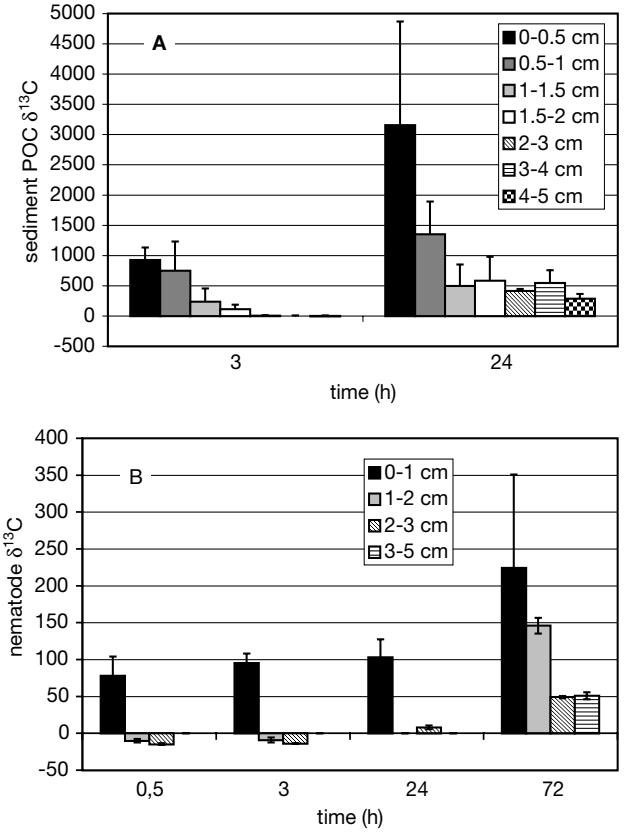

Fig. 3. Labeled algae experiment: stable carbon-isotope ratios of bulk sedimentary organic carbon (A) and of 'total nematodes' (B) as a function of time and depth. In (B), depth layers of 1–2, 2–3 and 3–5 cm have been pooled. Data are means + SD of 2 replicates

feeders and facultative predators at MP 2. At MP 4, nematodes from below 1 cm became more rapidly enriched in ^{13}C than at MP 2.

In the detritus sedimentation experiment, tidal effects were excluded. ^{13}C uptake by nematodes below 1 cm depth remained low until at least 24 h; after 72 h, enrichment in nematodes between 1 and 2 cm was comparable to ^{13}C enrichment in upper 1 cm nematodes after 24 h, and twice as high as enrichment in nematodes below a depth of 2 cm (Fig. 3). Total particulate organic matter analyses on sediment showed that the algal detritus initially (up to 3 h) remained on or near the sediment surface. After 24 h, however, algal carbon had penetrated down to a depth of 5 cm (the deepest layer analyzed: Fig. 3A). This is reflected, albeit with a time-lag, in the $\delta^{13}C$ depth profile of nematodes (Fig. 3B). Hence, nematodes in subsurface layers utilized sedimented algal detritus, but less rapidly than did surface nematodes.

The total amount of ^{13}C incorporated by nematodes was similar for both enrichment experiments (0.54 and 0.25 mg ^{13}C m^{-2} at MP 4 and 2, respectively, and 2 mg ^{13}C m^{-2} at PS B), differences being attributable to differences in (1) nematode biomass between sites (averaging 0.67, 0.18 and 1.2 g C m^{-2} at MP 4, MP 2 and PS B, respectively) and (2) ^{13}C enrichment of substrates.

DISCUSSION

This study used stable isotopes of carbon to infer food sources of estuarine tidal flat nematodes. Many authors have advocated a multiple stable-isotope approach to trace food sources for heterotrophic organisms, including nitrogen and sulphur isotopes (e.g. Peterson & Fry 1987, Deegan & Garritt 1997). However, the amount of biomass available for the taxonomic and vertical resolution aimed at in this study was not sufficient for additional N and S isotope analyses. Carbon isotope fractionation during heterotrophic processing is limited (DeNiro & Epstein 1978, Rau et al. 1983); hence, the resolution power of the technique depends on the magnitude and consistency of isotopic differences of potential substrates. In the Schelde estuary, the isotope signatures of the main organic matter sources considered were sufficiently different, except for the discrimination between phytoplankton and other suspended particulate organic matter (Middelburg et al. 1997, Middelburg & Nieuwenhuize 1998, Herman et al. 2000).

Isotope ratios of potential food sources

Table 4 summarizes the available information on carbon isotope ratios of the main organic matter sources in the Schelde estuary. Macroalgae and seagrasses are not considered here because they represent but a very small carbon input (macroalgae) or are absent (seagrasses) from the estuary. Microphytobenthos $\delta^{13}C$ at our study sites is in the range typical of saltmarsh and tidal flat benthic microalgae (Currin et al. 1995, Riera et al. 1996, Deegan & Garritt 1997). Unfortunately, the data on microphytobenthos and sedimentary POM at the Paulina sites were not obtained at the same time as the nematode samples. Available data on MP 4 and PS B indicate that seasonal variability in sedimentary POM carbon-isotope ratios is limited. While seasonal shifts in microalgal $\delta^{13}C$ have been documented (e.g. Schwinghamer et al. 1983), they appear to be relatively small on a 'community basis' (Currin et al. 1995, Riera et al. 1996, Deegan & Garritt 1997). Phytoplankton $\delta^{13}C$ in this section of the estuary is not much different from bulk suspended POM (J.J.M. unpubl. data). $\delta^{13}C$ of bulk sedimentary POM on the Molenplaat in June 1997 averaged –23‰ (Herman et al. 2000).

Nematodes from PS A, in a saltmarsh gully, were collected near a *Spartina anglica*-dominated vegetation. The carbon-isotope signature of *Spartina* spp. is typically in the order of –12 to –13‰ (Currin et al. 1995, Créach et al. 1997, Deegan & Garritt 1997, Middelburg et al. 1997). Preferential decomposition of relatively heavy, labile components generally leads to only a small ^{13}C depletion (1 to 2‰) in *Spartina* spp. detritus relative to fresh tissue (Ember et al. 1987, Benner et al. 1991, Middelburg et al. 1997). However, bulk sediment organic matter in saltmarshes is generally ^{13}C depleted by 9 to 12‰ relative to fresh *Spartina* spp. tissue, probably as a result of input and retention of lighter allochthonous carbon (Middelburg et al. 1997). In the Waarde saltmarsh in the Schelde estuary, sedimentary $\delta^{13}C$ was –22‰ in the upper 5 cm (Middelburg et al. 1997), close to the value at PS A (–23‰).

Table 4. Stable carbon isotope signatures of organic carbon sources in the Schelde estuary (locations as in Fig. 1). Present study data are from single analyses (February 1998) or are means and standard deviations of 2 replicate cores (June 2000)

Carbon source	Location	Date	$\delta^{13}C$	Source
Microphytobenthos	MP 2	Jun 1997	–16 ± 2	Middelburg et al. (2000)
	MP 4	Jun 1997	–14 to –15	Herman et al. (2000)
	PS A	Jun 2000	–17,42	Present study
	PS B	Jun 2000	–18,19	Present study
	PS C	Jun 2000	–21,09	Present study
Bacteria (upper mm)	MP 2	Jun 1997	–14.5 ± 2	Middelburg et al. (2000)
Bulk sediment POC	MP 2: top 10 cm	Jun 1997	–23	Herman et al. (2000)
	MP 2: top mm	Jun 1997	–22,3	Herman et al. (2000)
	MP 4: top 10 cm	Jun 1997	–21,8	Herman et al. (2000)
	MP 4: top mm	Jun 1997	–19,3	Herman et al. (2000)
	MP 4: top 10 cm	Mar 1999	–21,8	J.J.M. (unpubl. data)
	MP 4: top cm	Mar 1999	–22,7	J.J.M. (unpubl. data)
	MP 4: top mm	Mar 1999	–23,8	J.J.M. (unpubl. data)
	PS A: upper cm	Jun 2000	–22.54 ± 0.61	Present study
	PS A: 1–2 cm	Jun 2000	–23.23 ± 0.06	Present study
	PS A: 2–3 cm	Jun 2000	–22.95 ± 0.12	Present study
	PS A: 3–5 cm	Jun 2000	–23.41 ± 0.23	Present study
	PS B: upper cm	Jun 2000	–19.60 ± 0.43	Present study
	PS B: 1–2 cm	Jun 2000	–22.47 ± 0.59	Present study
	PS B: 2–3 cm	Jun 2000	–19.20 ± 1.13	Present study
	PS B: 3–5 cm	Jun 2000	–22.25 ± 0.42	Present study
	PS C: upper cm	Jun 2000	–20.50 ± 0.85	Present study
	PS C: 1–2 cm	Jun 2000	–21.52 ± 0.48	Present study
	PS C: 2–3 cm	Jun 2000	–18.32 ± 1.32	Present study
	PS C: 3–5 cm	Jun 2000	–21.78 ± 0.20	Present study
	PS B: upper cm	Feb 1998	–20.52	Present study
	PS B: 1–2 cm	Feb 1998	–21.28	Present study
	PS B: 2–3 cm	Feb 1998	–22.20	Present study
	PS B: 3–5 cm	Feb 1998	–22.78	Present study
Spartina	Waarde marsh	Aug 1994	–12.2 to –13.1	Middelburg et al. (1997)
Sediment	Waarde marsh	Aug 1994	–23.3±0.8	Middelburg et al. (1997)
Sediment	Waarde flat	Aug 1994	–25,5	Middelburg et al. (1997)
Sediment	Waarde flat	Aug 1996	–24.8± 0.9	Boschker et al. (1999)
Sediment	Waarde marsh	Aug 1996	–22.2± 1.1	Boschker et al. (1999)
Bacteria	Waarde marsh	Annual	–19.6± 1.2	Boschker et al. (1999)
Pelagic bacteria	Hansweert	Apr 1997	–14.3± 1.7	H. T. S. Boschker (unpubl. data)
Algae	Hansweert	Apr 1997	–19.1± 1.4	J.J.M. (unpubl. data)
POC (bulk SPM)	Hansweert	Apr 1997	–22.1± 0.5	J.J.M. (unpubl. data)
POC (bulk SPM)	Molenplaat	Jun 1996	–24,2	J.J.M. (unpubl. data)
POC (bulk SPM)	Molenplaat	Jun 1998	–23.9± 0.1	J.J.M. (unpubl. data)
POC (bulk SPM)	Salinity 20–25[a]	Aug 1994	–20.1± 1.7	Middelburg & Nieuwenhuize (1998)
POC	Marine end-member	Feb 1999	–22.6	Hellings et al. (1999)
POC	Marine end-member	Apr 1999	–23.2	Hellings et al. (1999)
POC	20–35 km range[b]	Feb 1999	–24.9± 0.5	Hellings et al. (1999)
Terrestrial matter	End-member	Aug 1994	–26	Middelburg & Nieuwenhuize (1998)

[a]Different sampling stations in salinity range 20 to 25
[b]Different sampling stations in zone from 20 to 35 km upstream of mouth of estuary

Site differences

Our results for the natural stable carbon-isotope ratios of whole nematode communities on the sandy tidal flats (MP 4, PS B and PS C) are in accordance with the hypothesis that the microphytobenthos (MPB) constitutes an important carbon source for tidal flat nematodes (Riera et al. 1996). Application of a simple 2-source mixing model with microphytobenthos and either sedimentary POM or bulk suspended POM (SPM) as potential carbon sources allows an estimate of the relative dependence of the nematode community on MPB. We used the isotope ratios for MPB and sediment POM (top 10 cm) listed in Table 4 and a bulk SPM value of –24 (J.J.M. unpubl. data); nematode isotope signatures were obtained from Table 2, but with a 1‰ correction for fractionation with trophic level (DeNiro & Epstein 1978). Such calculations indicate a 66 to 70.5% dependence of MP 2 (total) nematodes on MPB in June. The respective values for MP 4 in June and March are 80 to 82% and 34 to 48%, respectively. The March values have to be interpreted with caution, because MPB and SPM signatures for this period are not available. Similar calculations for the 3 Paulina sites indicate even higher nematode dependence on MPB, but again should be treated with caution for the same reason as for MP 4 in March.

These results are surprising, because a clear dominance of herbivorous nematodes has been reported in but very few studies conducted in temperate tidal estuaries (Bouwman et al. 1984), and such dominance does not apply to the current study sites. This discrepancy suggests that microphytobenthos carbon is routed to nematodes via other pathways than mere grazing, in accordance with results from the enrichment experiments (see below). The microphytobenthos is usually an assemblage of species, with potentially slightly different $\delta^{13}C$ signatures. Such differences may in turn be reflected in small within-site interspecific variation in $\delta^{13}C$ among supposedly herbivorous nematode species (e.g. species of *Metachromadora*, *Axonolaimus* and *Praeacanthonchus* at PS A: Table 3). A high feeding selectivity has been suggested for estuarine nematodes grazing on bacteria and microphytobenthos (Moens et al. 1999a,b).

An increased relative importance of POM at Stn 2 compared to Stn 4 is in line with extant organic matter concentrations (1 order of magnitude higher at MP 2 than MP 4) (Herman et al. 2000, Middelburg et al. 2000), as well as with the trophic structure of the respective nematode assemblages. Facultative predators and deposit-feeders dominate at MP 2, and both are capable of ingesting several types of POM (Moens & Vincx 1997, Moens et al. 1999c). These feeding guilds are relatively rare in the upper sediment layers at MP 4.

It is worth noting that microphytobenthos biomass at MP 2 in June 1997 was several times higher than at MP 4 (Middelburg et al. 2000), and it may seem odd that this would not be reflected in nematode isotope signatures. However, contrary to standing stock, primary productivity does not differ between the 2 stations (Hamels et al. 1998). This apparent contradiction relates to the depth of the photic zone (2.6 vs 1 mm at MP 4 and 2, respectively: Barranguet & Kromkamp 2000). Our data thus suggest that production rather than standing stock governs benthic consumer biomass, in accordance with observations on deposit-feeding macrofauna at the same sites (Herman et al. 2000).

Meiofauna isotope ratios in the North Inlet Estuary, USA, reflected *Spartina anglica* as well as microphytobenthos, but ratios of both organic sources overlapped, precluding unequivocal interpretation (Couch 1989). In our study, isotope ratios of nematodes from an *S. anglica*-dominated site (PS A) did not reflect *S. anglica*, suggesting they derive their carbon from allochthonous organic matter, microphytobenthos, or both. Two-source mixing models with MPB and either *S. anglica* or sedimentary POM as carbon sources yield a dependence of nematodes on MPB carbon of (more than) 100 and 86%, respectively. Interestingly, bacteria from another *Spartina anglica*-dominated mineral marsh in the Schelde estuary had an average $\delta^{13}C$ of –19.6 with a range of –21.8 to –17.6 (Boschker et al. 1999), similar to the nematode values at Stn PS A. These isotope signatures are consistent with observations of significant non-macrophyte inputs and of relatively small transfers of *Spartina* sp. organic matter to sediments and heterotrophic organisms in Schelde saltmarshes (Middelburg et al. 1997, Boschker et al. 1999). They are also in line with data showing but a limited contribution of *Spartina* sp. to the diet of several saltmarsh invertebrates (Riera et al. 1999). However, a combination of *S. anglica* and allochthonous carbon could also explain the saltmarsh nematode $\delta^{13}C$ observed in the present study (nematodes then deriving ca. 46.5% of their carbon from *S. anglica* and 53.5% from sediment POM).

Consumption of microalgal carbon by nematodes

Nematodes at MP 2 and MP 4, including the predacious *Enoploides longispiculosus*, rapidly incorporated microphytobenthic carbon, suggesting that the benthic microbial food web rapidly utilized the freshly produced microphytobenthic carbon. In view of the high relative abundance of *E. longispiculosus* at MP 4, it is unlikely that predation on other nematodes constituted the main pathway of ^{13}C to this predacious nematode. Predation on ciliates has recently been shown to be an

important feeding strategy of *E. longispiculosus* at MP 4 (Hamels et al. 2001). Direct utilization of microphytobenthic exopolymer secretions (see below) is another possible food-web link. The trophic structure of nematode communities of MP 2 and MP 4 also indicates that direct grazing on microalgae was not the predominant route of ^{13}C to nematodes. The amount of carbon assimilated by nematodes at MP 2 remained more or less constant from 4 to 48 h, but increased thereafter, suggesting that basically different carbon sources were being utilized. Over the first 48 h these may have consisted of microphytobenthos and its extracellular secretions via direct grazing and via predation on herbivores, while later on recycled carbon may have become a prominent source for the nematode community. Utilization of microbial exopolymer secretions by meiofauna has been documented, but its ecological significance remains poorly understood (Lopez et al. 1979, Decho 1990, Decho & Moriarty 1990).

Montagna (1995) suggested that nematode grazing on microphytobenthos may have a significant impact on primary production. Some authors have even found grazing to (temporarily) exceed primary productivity (Blanchard 1991, Montagna & Yoon 1991). The results of our $H^{13}CO_3^-$ spike experiment do not support this conclusion. Nematodes at MP 2 and MP 4 incorporated less than 1% of the total amount of ^{13}C fixed by microphytobenthos (150 and 250 mg ^{13}C m^{-2} at Stns MP 2 and MP 4, respectively: Middelburg et al. 2000). The observed data, of course, represent assimilation rather than grazing, and do not account for label losses due to respiration and excretion/defecation. However, even taking into account all these factors, nematode carbon utilization probably never constituted more than a few percent of primary production.

Uptake of phytodetritus ^{13}C by nematodes in the second enrichment experiment was almost instantaneous, but leveled off after 3 h and remained constant up to 24 h. After 72 h, a sharp increase in nematode $\delta^{13}C$ was found. It is plausible that the rapid initial carbon utilization mainly reflects ingestion of detritus, while labeling during longer incubations again may result from different pathways, involving intermediate trophic steps between algal detritus and nematodes. In an experiment with ^{14}C-labelled diatoms, Olafsson et al. (1999) found carbon uptake by nematodes capable of grazing diatoms as well as by species incapable of direct grazing. These authors, however, analyzed carbon uptake after a much longer incubation (4 wk) than in our experiments. A combination of their species-level approach with a determination of short-term uptake kinetics will be indispensible to unravel the different pathways of algal/detrital carbon through the meiobenthos. In a similar experimental setup, Moodley et al. (2000) demonstrated rapid uptake of settled *Chlorella* sp. by the dominant foraminifer *Ammonia* sp. in estuarine tidal flats. They also observed resource partitioning among different foraminiferal genera within the upper 1 cm.

In contrast to Rudnick's (1989) suggestion that different carbon sources are utilized by surface and subsurface living nematodes, our results demonstrate that algal carbon produced on or administered to the sediment surface is rapidly incorporated by surface as well as subsurface nematodes. The different habitats sampled (subtidal vs intertidal in our study) may be a reason for this discrepancy. However, Olafsson et al. (1999) also found that carbon utilization by subtidal nematodes was unrelated to their vertical distribution in the sediment. In the $H^{13}CO_3^-$ pulse-chase experiment at MP 4, label uptake by subsurface nematodes almost coincided with uptake by surface individuals, while at MP 2 incorporation by subsurface nematodes lagged behind that of surface individuals. This is (to some extent) consistent with sediment mixing rates at both sites (Middelburg et al. 2000). However, the observation that nematodes below 1 cm at MP 4 became ^{13}C-enriched before label penetration was observable at that depth corroborates vertical migration of *Enoploides longispiculosus* and several other nematode species during ebb tide at MP 4 (Steyaert et al. 2001). Vertical transport of fresh detritus by deposit-feeding macrofauna (see, e.g., Levin et al. 1997) may proceed at rates of >1 cm d^{-1} (Graf 1989) and may further facilitate its utilization by subsurface nematodes. Thus, in continental slope sediments, some deeper-dwelling fauna more readily assimilated settled phytodetritus than did near-surface forms (Blair et al. 1996, Levin et al. 1999).

In conclusion, this paper demonstrates that labile organic carbon, as derived from microphytobenthos and settled phytoplankton, constitutes an important carbon source for tidal flat nematode communities in the lower part of the Schelde estuary, albeit the pathways whereby microalgal organic matter is utilized remain as yet unclear. We found no indications that organic matter from terrestrial or riverine origin (with $\delta^{13}C$ of end-member particulates of −26 and −30‰, respectively: Middelburg & Nieuwenhuize 1998) contributes significantly to the benthic food webs of our study sites. Apparently, tidal flat nematodes preferentially utilize labile, locally produced organic matter. This holds for surface- as well as subsurface-dwelling nematodes, time-lags between deposition/production on the sediment surface and assimilation of organic matter by subsurface individuals probably being determined by sediment mixing rates.

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