

## Carbon flows through meiobenthic nematodes in the Westerschelde Estuary

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**Summary** – A time dynamic model was used to estimate carbon flows through nematodes in an intertidal benthic ecosystem in the Westerschelde Estuary, The Netherlands. The model calibrated the nematode biomass observed from March 1991 to February 1992. The forcing functions of the model included meiobenthos biomass, macrobenthos biomass, bacterial density, chlorophyll-a concentration, and other abiotic data such as temperature and day length. We estimate that the nematode population had a low level of standing stock,  $249 \text{ mg C m}^{-2}$ , but a high level of carbon flow. It consumed  $98 \text{ mg C m}^{-2} \text{ d}^{-1}$  and produced  $22 \text{ mg C m}^{-2} \text{ d}^{-1}$ . Defecation was  $73 \text{ mg C m}^{-2} \text{ d}^{-1}$ . Losses in respiration, excretion and natural death were only  $3 \text{ mg C m}^{-2} \text{ d}^{-1}$ . The annual P/B was 32 for local nematode community. These data show the importance of nematodes in the decomposition of particles of organic matter, and as a pathway from organic detritus to higher trophic levels in the benthic ecosystem.

**Résumé** – *Le flux de carbone chez les nématodes meiobenthiques de l'estuaire de l'Escaut Occidental* - Un modèle en temps dynamique a été utilisé pour évaluer le flux de carbone chez les nématodes appartenant à un écosystème benthique intertidal de l'estuaire de l'Escaut Occidental, aux Pays-Bas. Le modèle a permis de calibrer la biomasse des nématodes de mars 1991 à février 1992. Les fonctions de contrainte du modèle incluent la biomasse du meiobenthos, celle du macrobenthos, la concentration en bactéries, la concentration en chlorophylle a, et d'autres paramètres de l'environnement, tels la température et la photopériode. Il est estimé que la population de nématodes présente un faible niveau de stock,  $249 \text{ mg C m}^{-2}$ , mais un niveau élevé de flux de carbone. Les nématodes consomment  $98 \text{ mg C m}^{-2} \text{ d}^{-1}$  et produisent  $22 \text{ mg C m}^{-2} \text{ d}^{-1}$ . La défécation est de  $73 \text{ mg C m}^{-2} \text{ d}^{-1}$ . Les pertes dues à la respiration, l'excrétion et les morts naturelles sont seulement de  $3 \text{ mg C m}^{-2} \text{ d}^{-1}$ . Le rapport P/B annuel est de 32 pour la communauté locale de nématodes. Ces données démontrent l'importance des nématodes dans la décomposition de la matière organique particulaire et dans le cheminement des détritiques organiques aux niveaux trophiques supérieurs dans un écosystème benthique.

**Key-words:** carbon flow, marine nematodes, meiobenthos.

Nematodes are the most abundant component of the meiofauna in benthic systems (Coull, 1988), and consist primarily of organic detritus feeders and diatom feeders (Montagna, 1980; Findlay & Tenore, 1982; Alkemade *et al.*, 1993). The annual turnover of the biomass (P/B) of nematodes has been estimated as high as nine (Gerlach, 1971), and even up to 69 (Vranken & Heip, 1986). Nematodes are consumed by other members of the meiobenthos such as *Protohydra* (Heip & Smol, 1975; Elmgren, 1976), other large nematodes (Weiser, 1953), or by members of the epibenthos such as goby (Hamerlynck & Vanreusel, 1993). Thus, nematodes may constitute an important energy pathway from the primary production and detritus to higher trophic levels.

In the past, energetics studies of nematodes have been based on populations of single species (Tietjen, 1980; Warwick, 1981; Schiemer, 1982; Herman & Vranken, 1988). Because of the difficulty in culturing nematodes, energetics has been studied in only a few species, in particular species feeding on bacteria or diatoms, such as *Monhystera disjuncta* (Tietjen, 1980; Vranken & Heip, 1986; Herman & Vranken, 1988), *Diplolaimelloides brucei* (Warwick, 1981), or *Caenorhabditis briggsae* (Schiemer *et al.*, 1980; Schiemer, 1982). Energy flow of a nematode community is often estimated based on indirect methods, *e.g.*, by estimating respiration rates or assuming an annual P/B of nine (Van Damme *et al.*, 1980; Heip *et al.*, 1984, 1990). The defecation rate was unknown and the

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variation of P/B was not considered. Modeling ecosystems in energetics are often based on a whole marine ecosystem rather than by focusing on a single compartment (Steele, 1974; Warwick *et al.*, 1979; Carrada *et al.*, 1983; Baretta *et al.*, 1988; Fransz *et al.*, 1991; Chardy & Dauvin, 1992). All nematodes, all members of the meiobenthos, or all members of the benthos, are set as one state variable. Little information within the compartment is provided by such models. Modeling nematodes at the feeding type level may provide significant information, which would be different from that obtained from modeling single species or from modeling the whole benthos.

In the Westerschelde Estuary, nematodes represent more than 95 %, in density, and more than 85 %, in biomass, of the total meiobenthos (Van Damme *et al.*, 1980). Nematode abundance decreases from the sea to a brackish zone. Nematode communities in brackish zones have a higher temporal variation than communities in the mouth area (Li & Vincx, 1993). Predation pressure from the deposit-feeding macrofauna is the main source of this temporal variation (Li *et al.*, 1996). A detritus food chain system is suggested for the brackish zone, which is distinguished from a producer food chain system with higher abundance of nematodes in the mouth area (Hummel *et al.*, 1988). We will model carbon flows through nematodes in this "predator controlled" and "detritus food chain" system.

## Materials and methods

The model consists of several mathematical equations that calculate the variation of nematode biomass in response to variation in the environment. The model input were observed environmental data, and its output was a simulated nematode biomass. The model used FORTRAN 77 and was facilitated by the

PC software SENECA (De Hoop *et al.*, 1992). SENECA is designed to process and develop simulation models of time-dependent processes such as ecosystem models. It simplifies the model setup and supports calibration techniques.

The study site was the brackish intertidal zone of the Westerschelde Estuary (Fig. 1). Nematodes were sampled from March 1991 to February 1992 and classified into four feeding types (Weiser, 1953), *i.e.*, selective deposit feeders (1A), non-selective deposit feeders (1B), epigrowth feeders (2A), and polyphage/predators (2B). Two replicates were taken each time to reduce the spatial variation of nematodes within m-scale (Li *et al.*, unpubl.). Significant differences ( $P \leq 0.05$ ) among time samples were found for each feeding group. Average data were used in the model. Environmental data include total meiobenthos biomass, macrobenthos abundance and biomass, bacterial density, TOC (Total Organic Carbon) contents, and sedimentary chlorophyll-a concentration.

The development of the model included four processes: consumption, assimilation, losses (including respiration, excretion and natural death), and predation (Fig. 2). The food source system was based on the hypothesis of a detritus food chain system at the study site (Hummel *et al.*, 1988). In such case, POC (Particle Organic Carbon) is the main food source for nematodes and it can be calculated from TOC. Other food sources include diatoms, bacteria and nematode preys. The model included four types of predators: protohydra, turbellarians, polychaetes, and epi-benthic predators. The values of the model parameters were estimated based on the observed nematode biomass. The simulation of carbon flows through nematode standing stocks was based on repeating the cyclic observed environmental condition. So the output of the model was stable fluctuation. The detailed structure of the model was described by Li *et al.* (1996 *a*), and it can be summarized by a list of mathematical equations (Table 1). The model was validated according to the following three points: *i*) the model as calibrated by the nematode biomass observed during the first 3 months fits the observations for a whole year; *ii*) the simulations based on one year data predict that group 2B has the highest stock, followed by groups 1B, 2A, and 1A; these results are similar to those obtained during a seven year observation study made at a nearby station (Li & Vincx, 1993); *iii*) the result of the calibration showed that small nematodes have a higher respiration rate than large nematodes, which agrees with biological knowledge.

## Results

The predicted nematode standing stock was  $249 \text{ mg C m}^{-2}$  (Table 2, Fig. 3). Nematodes consumed  $98 \text{ mg C m}^{-2} \text{ d}^{-1}$  and defecated  $73 \text{ mg C m}^{-2} \text{ d}^{-1}$  of decom-

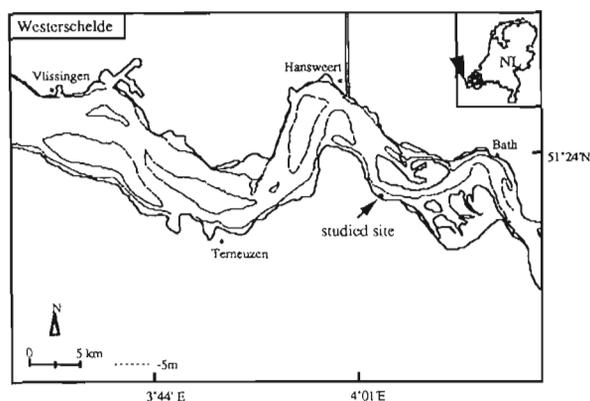


Fig. 1. The location of the studied station at the intertidal brackish zone of the Westerschelde Estuary (NL = The Netherlands).

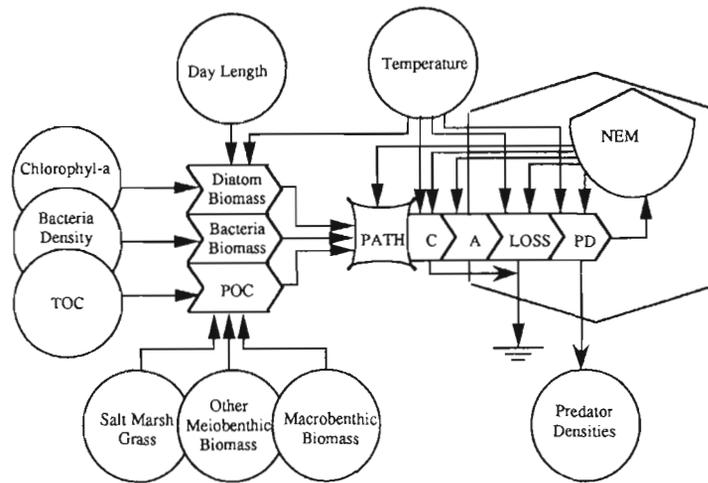


Fig. 2. The model structure with the energy-circuit language (Odum 1972).

88 % of what was assimilated. Losses, including respiration, excretion and natural death, were  $3 \text{ mg C m}^{-2} \text{ d}^{-1}$ , which represents only 3% of consumption and 12 % of assimilation. Annual biomass turnover (P/B) was 32 and the production efficiency was up to 88 %.

The assimilation efficiencies ( $p_{(4,i)}$  in Table 2) of nematodes were different with different food sources. Carbon assimilation was lower when nematodes fed on POC (18-36 %) than when they fed on bacteria (24-64 %), diatoms (63-78 %), or preys (55-80 %). The average assimilation efficiency for nematodes in the Westerschelde was low (24-26 %).

## Discussion

### STANDING STOCK

The predicted nematode standing stock in the brackish zone of the Westerschelde Estuary was  $249 \text{ mg C m}^{-2}$ . This is lower than in other areas. For example, the standing stock is 120-190  $\text{mg C m}^{-2}$  in the Belgian coastal zone of the North Sea (Vincx, 1989), but 412  $\text{mg C m}^{-2}$  in the mouth of the Westerschelde (Van Damme *et al.*, 1980), and 788  $\text{mg C m}^{-2}$  in the Lynher Estuary (Warwick *et al.*, 1979). Three factors contribute to the low standing stock in the brackish zone compared to the marine zone of the Westerschelde (Li & Vincx, 1993). Firstly, detritus is the major food in the brackish zone (Hummer *et al.*, 1988), which means that food quality and assimilation efficiency in the brackish zone are lower than in the marine zone where the primary production is much higher (Hummel *et al.*, 1988). Secondly, the sediment size is smaller in the brackish zone (mean diameter: 74-98  $\mu\text{m}$ ) than in the marine zone (mean diameter: 138-167  $\mu\text{m}$ ). Smaller sediments select for smaller

**Table 1.** Formula used in the model. Variables:  $B_j$  = nematode biomass ( $j = 1-4$  for the four feeding groups),  $C_j$  = consumption,  $A_j$  = average assimilation efficiency,  $D_j$  = predation death,  $S_j$  = total food source,  $L_j$  = loss in respiration, excretion and natural death). Forcing function:  $T$  = temperature  $^{\circ}\text{C}$ ,  $M_k$  = predator density ( $k = 1-4$  for protohydra, turbellarians, polychaetes, and epibenthos),  $F_{(ij)}$  = single food source ( $i = 1-7$  for the four nematode feeding groups, bacteria, diatom, and particle organic matter). Parameters:  $p_{(1)}$  = maximum consuming rate of nematodes,  $p_{(2)}$  = temperature effects  $Q_{10}$  for nematodes,  $P_{(3)}$  = food concentration that nematodes reach half of  $p_{(1)}$ ,  $p_{(4,i)}$  = assimilation efficiency for single food source  $i$ ,  $p_{(5)}$  = loss rates from respiration, excretion and natural death of nematodes,  $p_{(6,k)}$  = grazing rates of predator  $k$ ,  $p_{(7j)}$  = effect of aggregated distribution of nematodes  $j$  on their predation death,  $p_{(8,k)}$  = temperature effects  $Q_{10}$  for predator  $k$ .

$$\frac{D(B_j)}{d(t)} = C_j \cdot A_j - L_j - D_j \quad (1)$$

$$C_j = \frac{B_j \cdot p_{(1)} \cdot S_j \cdot P_{(2)}^{\frac{T-20}{10}}}{S_j + P_{(3)}} \quad (2)$$

$$S_j = \sum F_{ij} \quad (3)$$

$$A_j = \sum \frac{p_{(4,i)} \cdot F_{(i,j)}}{S_j} \quad (4)$$

$$L_j = B_j \cdot p_{(5)} \cdot P_{(2)}^{\frac{T-20}{10}} \quad (5)$$

$$D_j = \sum M_k \cdot P_{(6,k)} \cdot e^{-\frac{P_{(7,j)}}{B_j}} \cdot P_{(8,k)}^{\frac{T-20}{10}} \quad (6)$$

**Table 2.** Mean values of energy data for total nematodes. The values are based on a simulation made from 1991 to 1995 that used the environmental data obtained from 1991 to 1992.

	Related to Table 1	Estimations
Standing stock (mg C m <sup>-2</sup> )	B	249.2
Available food source (mg C m <sup>-2</sup> )	S	867384
Consumption (mg C m <sup>-2</sup> .d <sup>-1</sup> )	C	97.6
Daily consumption rate %	C/B .100	39
Defecation (mg C m <sup>-2</sup> .d <sup>-1</sup> )	C- C . A	72.5
Average assimilation efficiency %	A 100	26
Assimilation efficiency (%) of POM feeders	p <sub>(4,1)</sub> 100	23
Assimilation efficiency (%) of bacteria feeders	p <sub>(4,2)</sub> 100	55
Assimilation efficiency (%) of diatom feeders	p <sub>(4,3)</sub> 100	72
Assimilation efficiency (%) of predators	p <sub>(4,4)</sub> 100	73
Loss* (mg C m <sup>-2</sup> .d <sup>-1</sup> )	L	3
Loss rate (d <sup>-1</sup> )	L/B	0.012
Production or predation (mg C m <sup>-2</sup> .d <sup>-1</sup> )	C A - L or D	22
Production efficiency %	(C.A-L)/(C.A)	88
Annual P/B(y <sup>-1</sup> )	C.A/B	32
Ecological efficiency %	D/C.100	23

\* Include: respiration, excretion and natural death.

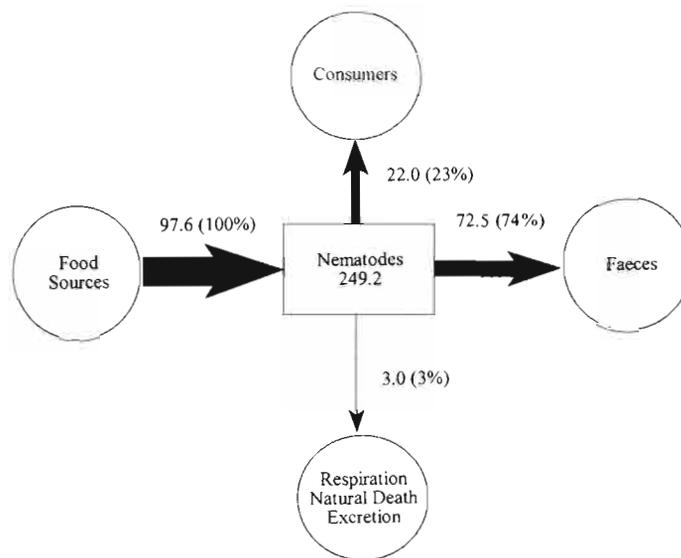
nematodes. As animal body size is negatively correlated with respiration rate, the smaller nematodes of the brackish zone have a higher respiration rate than those in the marine zone. This higher respiration rate in turn lowers production efficiency. The low production efficiency of the nematode community in the brackish zone is one of the factors of its low standing stock. Thirdly, the populations of the main predator of nematodes, *Heteromastus filiformis* (polychaete), decrease from brackish zones to the sea (Meire *et al.*, 1991). The lower standing stock of the nematode community in the brackish zone may be due to high predation mortality. To sum, food quality, sediment size, and predation pressure are the key factors of the level of nematode standing stock in the Westerschelde.

#### PRODUCTIVITY

Although the biomass is low in the Westerschelde Estuary, production can be as high as 8 g C m<sup>-2</sup> y<sup>-1</sup>, which is almost twice previously reported values. Van Damme *et al.* (1980) reported a production of 4.1 g C m<sup>-2</sup> y<sup>-1</sup> for nematodes in the mouth of the Westerschelde and Heip *et al.* (1984) reported a production of 1.5-2.0 g C m<sup>-2</sup> y<sup>-1</sup> for the total meiobenthos in the Southern Bight of the North Sea. In the present study, the estimated production efficiency ranged from 53 to 95% for the four feeding groups (Table 3). The total production efficiency was 88 % because the

group of polyphages (2B) was dominant. This production efficiency level is high compared to levels observed in studies on individual species in the laboratory (Table 3). The species studied in the laboratory were different from the species observed here, but it is also possible that production efficiency of a nematode is higher in the field than in the laboratory. Chardy and Dauvin (1992) simulated the carbon flows in the western English Channel by including the total meiofauna as one compartment in their system. Although nematodes composed up to 85 % of biomass, the total assimilation efficiency (46 %) was much higher and the total production efficiency (31 %) much lower than those observed for nematode species in the laboratory (Table 3). This shows that nematodes have a much higher productivity than other components of the meiofauna. Published results also show that productivity varies among various nematode species.

The present model gives an estimate of 32 for the biomass turnover (the annual P/B). This value is three times higher than values from previous studies. Gerlach (1971) estimated an annual P/B equal to 9 for nematodes, and this value has been used to calculate the production in many studies. The annual P/B is the product of the number of generation per year by the life cycle turnover (P/B<sub>generation</sub>). For nematodes, a P/B<sub>generation</sub> equal to 3 was estimated by Herman and Vranken (1988) but they studied juvenile stages only.



**Fig. 3.** The carbon flow ( $\text{mg C m}^{-2} \text{d}^{-1}$ ) through nematode standing stock ( $\text{mg C m}^{-2}$ ) according to the simulation (1991-1995) of the model for nematodes in the brackish tidal flat of the Westerschelde.

**Table 3.** The comparison of estimated assimilation efficiency (A.E.) and production efficiency (P.E.) to the previous studies.

Authors	Nematodes	A.E. (%)	P.E. (%)
Present study	Group 1A ( <i>Halalaimus gracilis</i> <sup>a</sup> )	24	53
Present study	Group 1B ( <i>Daptonema seiosum</i> <sup>a</sup> )	26	86
Present study	Group 2A ( <i>Chromadora macrolaima</i> <sup>a</sup> )	26	77
Present study	Group 2B ( <i>Viscosia viscosa</i> <sup>a</sup> )	26	95
Marchant & Nicholas (1974)	<i>Pelodera</i> sp. (1A)	n/a	38
Warwick <i>et al.</i> (1979)	Nematodes <sup>b</sup>	60 <sup>c</sup>	38 <sup>c</sup>
Tietjen (1980)	<i>Chromadorina germanica</i> (2A)	6	79
Tietjen (1980)	<i>Monhystera disjuncta</i> (1B)	18	80
Tietjen (1980)	<i>Rhabditis marina</i> (1A)	26	97
Schieemer <i>et al.</i> (1980)	<i>Plectus palustris</i> (1A)	12-52	35-87
Warwick (1981)	<i>Diplolaimelloides brucei</i> (1B)	n/a	71-87
Schiemer (1982)	<i>Caenohabditis briggsae</i> (1B)	n/a	48-63
Woombs & Laybourn-Parry (1985)	<i>Diplogasteritus nudicaptatus</i> (1A)	16-34 <sup>c</sup>	54-78 <sup>c</sup>
Woombs & Laybourn-Parry (1985)	<i>Paroigolaimella bernensis</i> (1A)	12-28 <sup>c</sup>	48-78 <sup>c</sup>
Woombs & Laybourn-Parry (1985)	<i>Rhabditis curvicaudata</i> (1A)	9-13 <sup>c</sup>	24-49 <sup>c</sup>
Herman & Vranken (1988)	<i>Monhystera disjuncta</i> (1B)	18-27	60
Chardy & Dauvin (1992)	Meiofauna (65-86% nematodes <sup>d</sup> in biomass)	46 <sup>c</sup>	31 <sup>c</sup>

<sup>a</sup> dominant species within the group; <sup>b</sup> all 40 species include: 27 % 1A, 27 % B, 44 % 2A and 1 % 2B; <sup>c</sup> calculated according to the published data; <sup>d</sup> dominant species include *Richtersia kreisi* (1B), *Microlaimus conspicuus* (2A), *Chromaspirina renaudae* (2B), *Cylindrotheristus divertens* (1B), and *Prochromadorella dilvevsi* (2A).

Adult nematodes in the Westerschelde varied greatly in body size. Table 4 shows that growth occurs during the adult stage and so this stage probably has a  $P/B_{\text{generation}}$  higher in most nematode species in the Westerschelde Estuary. The maximum  $P/B_{\text{generation}}$  may be as high as 5, as postulated by Sanders (1956) for short-lived benthic species and by Waters (1969) for freshwater invertebrates. The average minimum generation time of nematodes being often less than 1/3 year (see review by Heip *et al.*, 1985), an annual  $P/B$  equal to 9 is an underestimate for nematodes. Table 5 gives some examples of annual  $P/B$  of nematodes that are larger than 9. Heip *et al.* (1990) suggested that, in the Southern Bight of the North Sea, the annual  $P/B$  for nematodes would be 10.1 if production efficiency were 40 % and 35.3 if production efficiency were 70 %. The value (9) proposed by Gerlach (1971) was actually estimated for *Monhystera disjuncta* (feeding type 1B) and *Chromadora tenuis* (feeding type 2A). Feeding types 1A, 2A and 1B are predicted to have lower production efficiency than feeding type 2B (Table 3). A nematode community includes all feeding groups and often has high species diversity. As a result,  $P/B_{\text{generation}}$  and annual  $P/B$  of the nematode community in the Westerschelde Estuary are expected to be higher than three and nine, respectively. These may be the reasons why the production estimate proposed in the present article is twice that reported by Van Damme *et al.* (1980).

#### DECOMPOSITION OF ORGANIC MATTER

Daily defecation of nematodes with a  $249 \text{ mg C m}^{-2}$  standing stock (about 2000 ind.  $10 \text{ cm}^{-2}$ ) is  $73 \text{ mg C m}^{-2} \text{ d}^{-1}$ , or 74 % of their consumption. The present assimilation efficiencies (24-26 %) are low in comparison with values of 6 % to 52 % obtained in previous

**Table 4.** The ranges of female body size for dominant nematode species calculated by the observed length and width (Andrássy, 1956).

Dominant nematodes	Individual wet weight ( $\mu\text{g}$ )
<i>Daptonema setosum</i> (1B)	1-15
<i>Anoplostoma viviparum</i> (1B)	1-10
<i>Tripyloides gracilis</i> (1B)	0.5-2
<i>Viscosia viscosa</i> (2B)	1-2
<i>Thalassoalaimus septentrionalis</i> (1A)	1.5-2.6
<i>Dichromadora geophila</i> (2A)	0.5-5
<i>Dichromadora cephalata</i> (2A)	0.4-1.5
<i>Chromadora macrolaima</i> (2A)	0.3-2

**Table 5.** Example that annual  $P/B$  of nematode species are larger than nine.

Nematodes	Annual $P/B$	References
<i>Monhystera disjuncta</i> (1B)	69	Vranken & Heip, 1986
<i>Sabatieria punctata</i> (1B)	14.1-16.9	Vincx, 1989
<i>Daptonema tenuispiculum</i> (1B)	28.5-31.9	Vincx, 1989
<i>Ascolaimus</i> sp. (1B)	11.5- 14.8	Vincx, 1989

studies (Table 3). This may be explained by the high POC composition of the food sources in the detritus food chain system (Hummel *et al.*, 1988). We suggest that the average assimilation efficiency depends on the food source. We estimated a POC of up to 98% for the total nematode food sources in the present study site. This may be due to the fact that the most dominant species, *Viscosia viscosa*, is a scavenger rather than a predator, as defined later (Jensen, 1987). It feeds on large particles. Nematodes such as *V. viscosa* are significant players in the decomposition of organic detritus, thus promoting remineralization by bacteria. Findlay and Tenore (1982) found that the maximum mineralization rate can be doubled by adding only ten nematodes per  $10 \text{ cm}^2$ .

The standing stock of organic matter in the Westerschelde Estuary is  $106 \text{ mg C m}^{-2}$ , which dwarfs the decomposition rate of nematodes, estimated at  $73 \text{ mg C m}^{-2} \text{ d}^{-1}$ . Although the decomposition of POC by nematodes is important in promoting its mineralization by bacteria, it may have no effects on the overall carbon dynamics. However, nematodes have a high potential for decomposing POC and they may be more important than shown by this study, because nematode abundance often is far larger than the 2000 ind./ $10 \text{ cm}^2$  we observed.

#### ECOLOGICAL EFFICIENCY

A 23 % ecological efficiency (production per consumption) was estimated in the detritus food chain system of the brackish zone in the Westerschelde. This value is similar to the 22 % efficiency estimated by Warwick *et al.* (1979) for the producers' food chain system in the Lynher Estuary. A simulation of the meiofauna in the western English Channel gave a much lower (11 %) ecological efficiency (Chardy & Dauvin, 1992). Considering that nematodes compose 65-86 % of the biomass in the meiofauna compartment studied by these authors, the other components of the meiofauna must have a much lower ecological efficiency than that of nematodes. Marchant and Nicholas (1974) found an ecological efficiency of

22.4 % for a freshwater species of the genus *Pelodera* feeding on the bacteria *Escherichia coli*. A 59.8 % assimilation efficiency was reported for bacteria feeders by Marchant and Nicholas (1974), which is consistent with our prediction (54.8 % as a best fit value in Table 2). An ecological efficiency equal to 22-23 % may be characteristic of nematodes in most ecosystems.

#### FURTHER DEVELOPMENT OF THE MODEL

Chardy and Dauvin (1992) predicted a 30 % respiration to consumption ratio ( $10 \text{ g C m}^{-2} \text{ y}^{-1}$  respiration for a consumption of  $33.3 \text{ g C m}^{-2} \text{ y}^{-1}$ ), of which daily respiration rate to meiofauna biomass is 10 %. The respiration rate they predicted was ten times higher than our own prediction for nematodes. However, the meiofauna compartment defined by Chardy and Dauvin (1992) included 15-35 % of other components of the meiofauna, *i.e.*, microgastropods, copepods, gastrotrichs, halacarids, turbellarians, oligochaetes, polychaetes, amphipods, and bivalves. It is possible that nematodes have much lower respiration rates than other components of the meiofauna such as fast-moving copepods. The respiration of components of the marine meiofauna is generally considered to be very high; on the other side nematodes are known to excrete ammonium and amino acids and to produce mucus trails. The 3 % carbon loss for nematodes that is predicted by present study seems to be an underestimate. However, it is consistent with the 2.8-7.4 % respiratory energy losses calculated using Woombs and Laybourn-Parry's (1985) data. The lipid metabolism of free-living nematodes is much more important than their carbohydrate metabolism because of their lipids content is higher than their glycogen content in comparison with nematodes having different habit (Lee & Atkinson, 1977). The current model is based on carbon flows. In future studies, it will be interesting to combine this model with a model based on nitrogen flows to recalibrate the nematode respiration rate.

This modeling study was based on the hypothesis of a detritus food chain system for the study site (Hummel *et al.*, 1988), where the deposit-feeders compose more than 85 % of the biomass at the study site. However, setting POC as the main food source for all four feeding types of nematodes may cause some errors in simulation, especially for the diatom feeders that do not feed on POC at all. Further modeling at the species level may be required to correct those errors.

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