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A model of nematode dynamics in the Westerschelde Estuary

Jian Li [a,*], Magda Vincx [a], Peter M.J. Herman [b]

[a] Marine Biology Section, Zoology Institute, University of Gent, Ledeganckstraat 35, 9000 Gent, Belgium
[b] Center for Estuarine and Coastal Ecology, Netherlands Institute of Ecology, Vierstraat 28, NL-4401 EA, Yerseke, Netherlands

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Abstract

We developed a time dynamic model to investigate the temporal dynamics of nematode community in the brackish zone of the Westerschelde Estuary. The biomass of four nematode feeding groups observed from March 1991 to February 1992 is used to calibrate the model. Using environmental data as the input, the model predicts the temporal modification and interrelation of four nematode feeding groups. Nematodes achieve a dominant position in the community because of their lower loss rate (in respiration, excretion and natural death). Predators which are deposit-feeding macrobenthos control the variations of dominant nematodes, such as omnivores and non-selective deposit feeders. Food availability causes modification only for rare nematodes such as epigrowth feeders and selective deposit feeders. Temperature is a factor affecting both predation death and a loss including respiration, excretion and natural death. Overall, the modification of nematode community by food availability is much lower than by predator. The macrobenthos in the Westerschelde Estuary decrease from upstream to the estuarine mouth. The stability and standing stock of nematode population follow the opposite gradient of their predators. They increase from upstream to the estuarine mouth.

Keywords: Estuary ecosystems; Nematodes; Population dynamics

1. Introduction

The populations of marine free-living nematodes are the most abundant meiobenthos in estuaries (Heip et al., 1985). They show complex short- and long-term variations that may be seasonal (Coull, 1985a) or non-seasonal (Li and Vincx, 1993). Abundance peaks of dominant species can be present in any season (Wieser, 1977; Vincx, 1989; Li and Vincx, 1993). Simple multivariate statistical methods could not explain the temporal variability of nematode populations (Li and Vincx, 1993). Modeling could be used to assess the mechanisms that may control temporal variability of nematode populations.

The nematode community in the brackish zone of the Westerschelde Estuary has a lower biomass and higher temporal variation than in the marine zones (Li and Vincx, 1993). Van Damme et al. (1980) have restricted the ecological study of local meiobenthos to the general spatial distribution, in which the abundance of nematodes decreases from the sea to the inner part of the estuary. The brackish zone of the Westerschelde Estuary has a detritus food chain system while the marine zone has a coastal food chain system (Hummel et al., 1988). The different food chain system may cause a difference in nematode

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[*] Corresponding author. Present address: Marine Science Institute, University of Texas at Austin, P.O. Box 1267, Austin, TX 78373, USA. Fax: (+1-512) 749 6777.

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biomass level. However, a higher temporal variation of biomass in the brackish zone than in the marine zone may not be due to its detritus food chain system. The deposit feeders are the most common nematodes in the Westerschelde Estuary, comprising 45-47% of total nematode abundance (Li and Vincx, 1993). As the main food source for the deposit feeder group such as POC (particulate organic carbon) is 10^6 times higher than nematode biomass, food must rarely control the temporal variation of nematode biomass. Analysis of a long-term data set has suggested that predators could be as controlling factor for meiofauna (Coull, 1985b). Many faunae in the Westerschelde Estuary are recognized as predators for meiobenthos, e.g., ciliates (Hockin, 1982), Protohydra (Heip and Smol, 1975), Turbellaria (Elmgren, 1976; Reise, 1985), large nematodes (Wieser, 1953), shrimps (Bell and Coull, 1978), crabs (Scherer and Reise, 1981), mysids (Mauchlin, 1971) and fish (Gee, 1989; Scholz et al., 1991; Hamerlynck and Vanreusel, 1993). It would be interesting to assess through a modeling study the relative importance of predators and food in influencing the nematode population in the Westerschelde Estuary.

The temporal modification of nematode community in the brackish zone of the Westerschelde Estuary will be investigated by examining a time dynamic model. It includes the relationship between biomass of four nematode feeding groups and environmental parameters. The model will based on both daily and monthly intervals of data that include variations in two time scales. The four nematode feeding groups classified by Wieser (1953) are four state variables to be simulated to present the interrelationships of an ecosystem to understand the nematode dynamics in the Westerschelde Estuary. Sensitivity analysis may determine the importance of environmental factors to the system.

2. Methods and materials

We developed a time dynamic model to simulate the biomass of nematodes at a tidal coastal site in the brackish zone of the Westerschelde Estuary (Fig. 1). Nematode populations were sampled at 3-day intervals from 14 March 1991 to 10 May 1991 for a daily scale data and at monthly intervals from May 1991 to February 1992 for a monthly scale data. The sampling methods are described by Li and Vincx (1993). Average nematode feeding type biomass of replicates was used to calibrate the model. Co-observed data include total meiobenthic biomass, macrobenthos abundance and biomass, bacterial density, TOC (total organic carbons) content and chlorophyll-*a* concentration (Li, 1993).

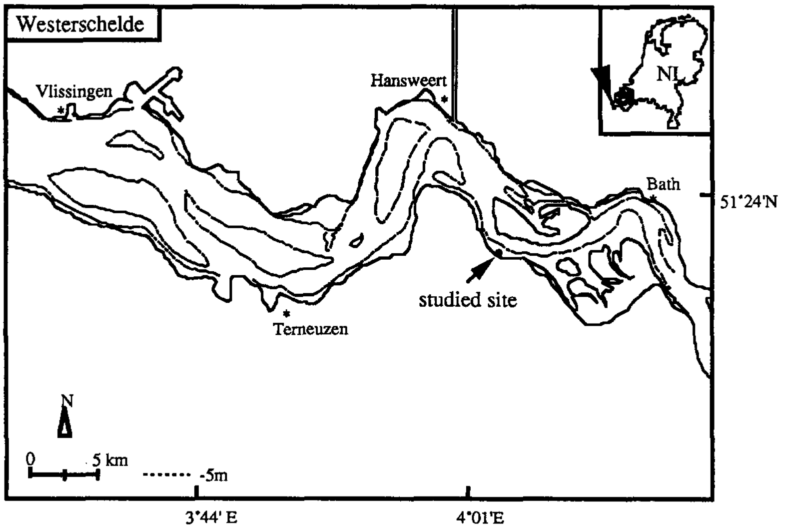

Fig. 1. The study site at the intertidal brackish zone of the Westerschelde (NL = Netherlands).

A time dynamic model represented a nematode system within a benthic compartment (Fig. 2). The model itself consists of many mathematical equations that calculate the variations of nematode biomass in response to variation of environmental data. The inputs of the model are the observed environmental data and the output of the model is the simulated nematode biomass. The model is made using FORTRAN77 language and facilitated by the PC software SENECA (*S*imulate *EN*vironment *EC*ology *A*nalysis) (De Hoop et al., 1992). The SENECA is designed to work with and develop simulation models of time-dependent processes and especially ecosystem models; it simplifies the model setup and supports the techniques of calibrations (e.g., estimating the best fit parameter values according to the goodness fit test).

The change rate of nematode biomass includes carbon conservation of a population (Crisp, 1971) and a loss by predation death:

$$\frac{\mathrm{d(NEM)}}{\mathrm{d}(t)} = C \cdot \mathrm{MAE} - \mathrm{LOSS} - \mathrm{PD} \qquad (1)$$

where NEM is nematode biomass for a feeding type, C is consumption, MAE is average assimilation efficiency, LOSS is the losses include respiration, excretion and natural death and PD is predatory death. The equations for the calculation of each term in Eq. 1 are listed in Table 1.

Table 1
The formula used in the model

(2)	$C = \dfrac{\mathrm{NEM} \cdot \mathrm{CIR} \cdot F \cdot Q_{10}^{(T-20)/10}}{F + \mathrm{HCIRF}}$
(3)	$\mathrm{MAE} = \Sigma \dfrac{\mathrm{FAE} \cdot F}{\mathrm{SF}}$
(4)	$\mathrm{LOSS} = \mathrm{NEM} \cdot \mathrm{LR} \cdot Q_{10}^{(T-20)/10}$
(5)	$\mathrm{PD} = \mathrm{PRED} \cdot \mathrm{GR} \cdot \exp\left(-\dfrac{\mathrm{PEXP}}{\mathrm{NEM}}\right) \cdot Q_{10}^{(T-20)/10}$

Variables: C = consumption; NEM = nematode biomass; F = single food source; T = temperature; SF = total food source; MAE = average assimilation efficiency; LOSS = loss in respiration excretion and natural death; PD = predation death; PRED = predators.

Parameters: CIR = maximal consuming rate of nematode; HCIRF = food concentration that nematode reach half CIR; Q_{10} = temperature effects; FAE = assimilation efficiency for a single food source; LR = loss rates of nematodes include respiration, excretion and natural death; GR = grazing rates with which predators consuming nematode; PEXP = effect of aggregating distribution of nematode for their predation death.

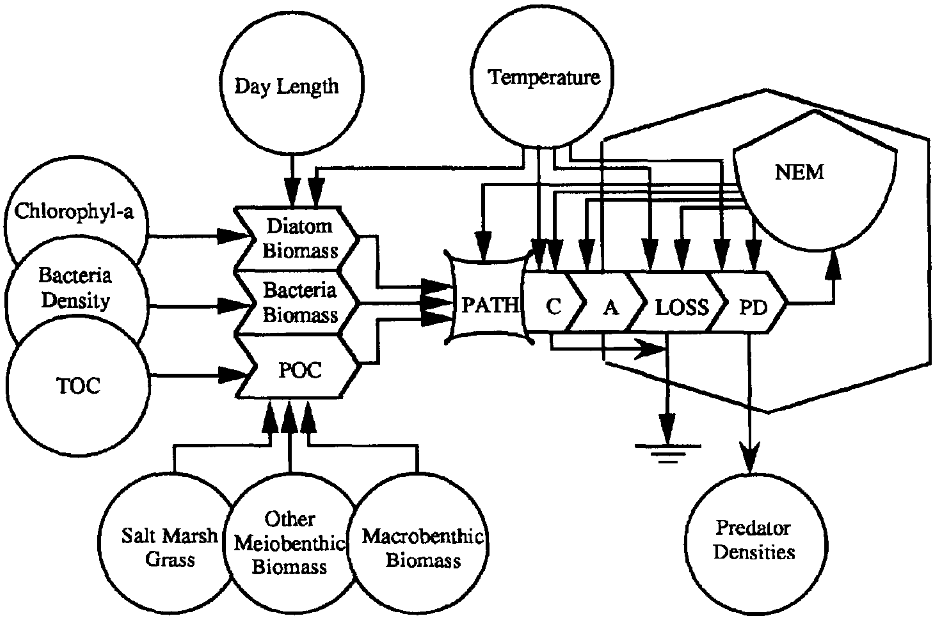

Fig. 2. The model structure of the nematode community in energy-circuit language (Odum, 1972) (NEM = biomass of a nematode feeding type; C = consumption; A = assimilation; LOSS = the loss in respiration, excretion and natural death; PD = predation death).

The model includes the simulation of four nematode feeding types (Wieser, 1953): selective deposit feeders (1A), non-selective deposit feeders (1B), epigrowth feeders (2A) and omnivores/predators (2B). They are four state variables and they are four single food sources for the predator nematode too. To simplify the complex feeding interactions, a path is used for each single food source to each nematode feeding type. The path equals "0" for not feeding while "1" for feeding. Most paths are fixed (zero or one), except a few are set as parameters for the model to calibrate (between zero and one to see how the weight of the path should be). These include: (1) all 1A, 2A and 1B nematodes do not consume themselves; (2) 2B consume certain part of nematodes (using a parameter); (3) all nematodes con-

Table 2
The best fit parameters, parameter ranges before and after 12000 runs of calibration for the model

Parameters	Best fit values	Calibrated ranges	Initial ranges	Relative references
BACDTB	$5.07 \cdot 10^{-11}$	$1.04 \cdot 10^{-11}$, $6 \cdot 10^{-11}$	$1 \cdot 10^{-11}$, $9 \cdot 10^{-11}$	Meyer-Reil, 1977
MPR	12.06726	10.6372, 13.3325	10, 16	Admiraal, 1977
PMAR	0.761111	0.625331, 0.895759	0.001, 0.9	not
CIR	0.858037	0.7511, 1.126131	0.5, 2	Admiraal et al., 1983
HCIRF	282.6446	62.02356, 320.8734	1, 500	not
$Q_{10}(1)$ [a]	2.297279	2.146182, 2.696751	2, 3	review of Heip et al., 1985
LR(1)	0.09717	0.076681, 0.099575	0.01, 0.1	as above
LR(2)	0.030047	0.021967, 0.037398	0.01, 0.1	as above
LR(3)	0.051105	0.045538, 0.086193	0.01, 0.1	as above
LR(4)	0.011697	0.010402, 0.0569	0.01, 0.1	as above
FAE(1)	0.728046	0.546734, 0.796783	0.1, 0.8	Herman and Vranken, 1988
FAE(2)	0.227021	0.184065, 0.356099	0.1, 0.8	as above
FAE(3)	0.547837	0.237591, 0.639539	0.1, 0.8	as above
FAE(4)	0.716039	0.634206, 0.775096	0.1, 0.8	as above
GR(1) [a]	0.000000267	$3.79 \cdot 10^{-8}$, $5.11 \cdot 10^{-6}$	$1 \cdot 10^{-10}$, $8 \cdot 10^{-6}$	Heip and Smol, 1975
GR(2) [a]	0.00000195	$7.5 \cdot 10^{-7}$, $2.62 \cdot 10^{-6}$	0, $8 \cdot 10^{-6}$	not
GR(3) [a]	0.000000432	$3.63 \cdot 10^{-8}$, $3.04 \cdot 10^{-6}$	0, $8 \cdot 10^{-6}$	not
GR(4) [a]	0.06909	0.051435, 0.082404	0, 0.1	not
$Q_{10}(2)$ [a]	1.126114	1.009053, 1.726845	1, 3	not
$Q_{10}(3)$ [a]	2.003998	1.610523, 2.336522	1, 3	not
$Q_{10}(4)$ [a]	2.643547	2.50079, 2.838494	1, 3	not
PEXP(1)	8.942347	2.671569, 10.29917	0, 20	not
PEXP(2)	10.20318	1.712969, 12.13589	0, 20	not
PEXP(3)	4.516908	1.888912, 8.491923	0, 20	not
PEXP(4)	7.292774	5.547743, 12.6904	0, 20	not
PATH(1) [a]	0.46283	0.029584, 0.501918	0, 0.9	not
PATH(2) [a]	0.224228	0.114696, 0.895786	0, 0.9	not
PATH(3) [a]	0.252958	0.096205, 0.348306	0, 0.9	not
PATH(4) [a]	0.2456	0.143113, 0.811913	0, 0.9	not
PATH(5)	0.062058	0.004965, 0.239286	0, 1	not
PATH(6)	0.159128	0.013086, 0.357297	0, 1	not
PATH(7)	0.310824	0.004446, 0.415335	0, 1	not
PATH(8)	0.847816	0.737086, 0.995077	0, 1	not

BACDTB = mg C per bacteria cell; MPR = maximal production of mg C by diatom per mg chlorophyll-*a* per hour; PMAR = daily diffusion rate of sea grass; CIR = daily maximal consuming rate of nematode; HCIRF = half CIR food concentration; Q_{10} (1–4) = temperature effect on nematode, protohydra, turbellarian, polychaete and epibenthos; LR (1–4) = daily loss rate of 1A, 1B, 2A and 2B; FAE (1–4) = assimilation efficiency for consuming prey nematode, POC, bacteria and diatom; GR (1–4) = grazing rate of protohydra, turbellarian, polycheate and epibenthos; PEXP (1–4) = aggregating effect for predatory mortality of 1A, 1B, 2A and 2B; PATH (1–4) = the possibility of feeding path that POC consumed by 1A, 1B, 2A and 2B; PATH (5–8) = the possibility of feeding path that 1A, 1B, 2A and 2B consumed by 2B.

[a] Calibrated ranges were applied in sensitivity analysis.

sume certain part of particle organic matter; (4) all nematode consume bacteria; (5) all nematodes consume diatom except of 1A.

The production of salt marsh grass *Spartina townsendii* (MARPRO) is based on literature data (Wolff et al., 1979), which is a sinus function:

$$\mathrm{MARPRO}(T) = 26 + 25.9\sin\left(2\pi\left(\frac{T}{365} - 0.4712329\right)\right) \quad (6)$$

The production of the diatom is based on a chlorophyll-*a* production rate (Admiraal, 1977; Admiraal and Peletier, 1980) estimated with a sinus function of day length (DL) (Soetaert et al., 1992):

$$\mathrm{DL}(T) = 12.49 + 4.45\sin\left(2\pi\left(\frac{T}{365} - 0.2237718\right)\right) \quad (7)$$

The calibration of the model was conducted by randomly selecting parameter values from the initial ranges. The initial ranges of parameters come from references. Those parameters without information from literature were set as large as possible to cover all possibilities (Table 2): the grazing rates of predators (GR) are ranged as low as not grazing (zero) and as high as grazing all nematodes. The feeding path (PATH) from "0" to "1" includes no feeding and feeding. The aggregating effects (PEXP) include zero for no exponential relation between nematode abundance and grazing rate. The stable model for nematodes was reached after 4000 calibrating runs. We stopped the calibration after 12 000 runs, because the improvement in the goodness of fit was negligible. The best fit parameters were used to simulate the nematode dynamics. The sensitivity of a parameter to the system was presented in the output ranges of the simulation. The output ranges of the simulation are according to the best fit range of tested parameters while untested parameters were fixed at the best fit value. The sensitivity of a certain group of param-

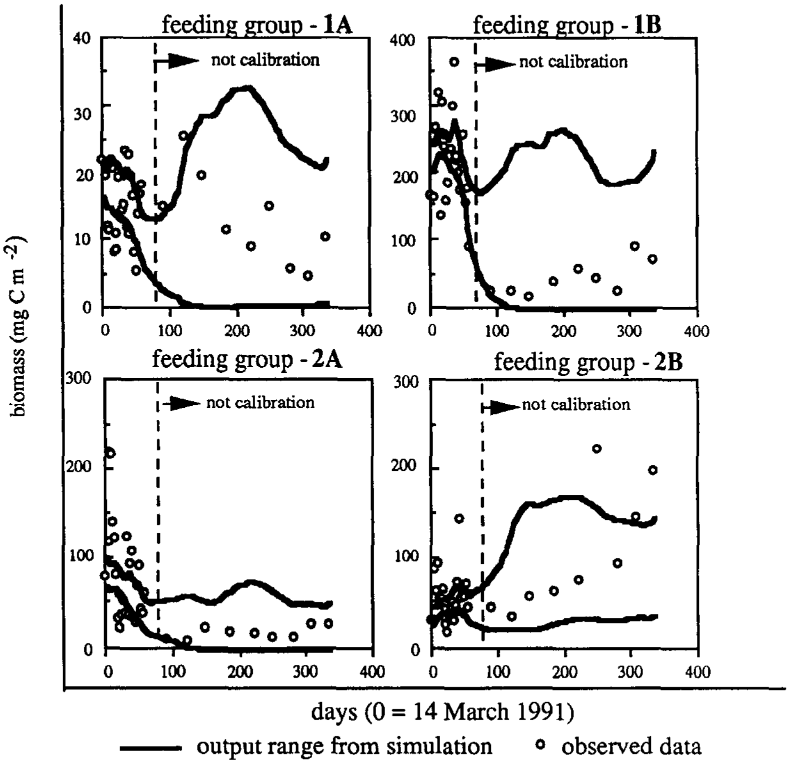

Fig. 3. The output ranges (maximum–minimum) of the simulation from sensitivity analysis (200 runs) according to the parameter ranges that calibrated (6000 runs) by only part of data.

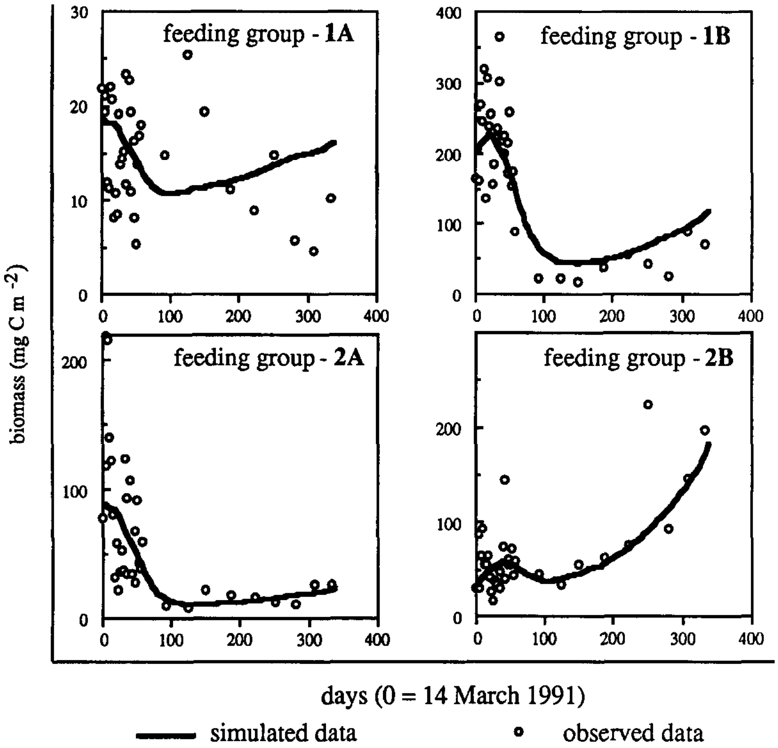

Fig. 4. The output of the model for the four feeding groups from the best fit parameters (after 12000 runs of calibration with both daily and monthly intervals of data).

eters was examined to find the importance of a certain environmental factor (Table 3).

To test the validation of the model, the simulation of the model based on part of the data set should validate against the other, unused part of the data set. The simulation based on daily scale data (from 14 March 1991 to 10 May 1991) is compared with the monthly scale data (13 June 1991 to 11 February 1992) (Fig. 3). The simulation shows that 2B has a similar stock level as 1B. The level of stocks for 1B

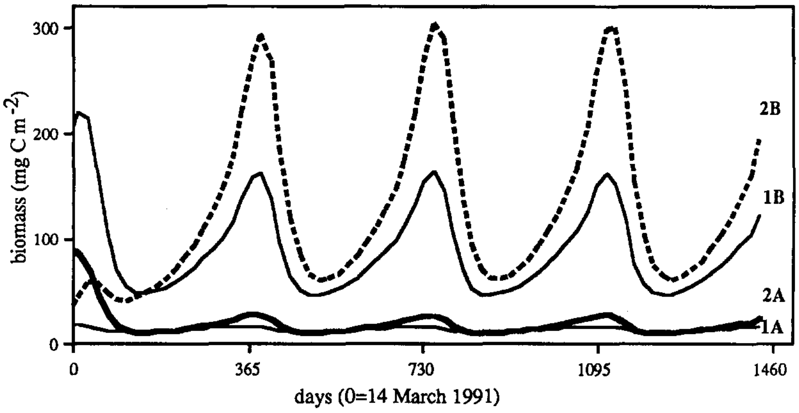

Fig. 5. The simulation of biomass (mg C · m^{-2}) for four nematode feeding groups for 1991–1995. The input is environmental data from 1991 to 1992 (1A = selective deposit-feeder; 1B = non-selective deposit-feeder; 2A = epigrowth-feeder; 2B = predator or omnivore).

Table 3
The parameters used in the sensitivity analysis to relate environmental factors and processes

Analyzed parameter groups	Related environmental factors	Related processes in model
four ratios of POC as the food for nematodes	food (both quantity and quality)	consumption, assimilation
four grazing rates for four predators	predator	predation
four Q_{10} for nematode and predators	temperature	consumption, 'loss' and predation

and 2B is higher than the ones for 1A and 2A, which is the same as the result from the calibration with both parts of the data (Fig. 4). The simulation based on both daily scale and monthly scale data is compared with a long-term data set (Li and Vincx, 1993). The model predicts that group 2B has the highest stock followed by 1B, 2A, and 1A (Fig. 5). This is the same as a 7-year observation at a nearby station (Li and Vincx, 1993). The model is valid for the brackish zone of the Westerschelde Estuary.

Estimated loss rates (including respiration, excretion and natural death) function by model for four feeding groups follow: 1A (0.097) > 2A (0.051) > 1B (0.03) > 2B (0.012) ("LR" in Table 1). Comparing the body size of the most dominant species among each feeding group from the station WO22, we found that *Daptonema setosum* (1B) or *Viscosia viscosa* (2B) is bigger than *Chromadora macrolaima* (2A), and *Halalaimus gracilis* (1A) is the smallest. The body size of an animal is positively correlated with respiration $R = aV^b$ (Banse, 1982) and negatively correlated with the respiration rate, $(aV^b)/V$, because of $b < 1$ ($b \approx 0.75$, see a review of Heip et al., 1985). The estimated values of parameters by the model follow biological rule.

We should like to point out that the simulation of this model is limited. The local primary production is mainly due to diatoms and calculated by total chloro-

Table 4
The mean values and the modification ranges (minimal–maximal) of a 4-year simulation of the nematode community (1991–1995)

Parameters	1A	1B	2A	2B	Total nematodes
Biomass (mg C · m^{-2})	13.8 (11.0–18.8)	90.9 (45.8–219.8)	21.5 (12.0–90.3)	125.9 (35.3–303.5)	252.1 (115.9–511.5)
Consumption (mg C · m^{-2} · d^{-1})	5.9 (2.8–10.2)	35.9 (15.4–89.5)	8.7 (3.7–39.1)	48.7 (15.3–115.3)	99.1 (43.4–195.4)
Consumption rate (% · d^{-1})	44.8 (19.4–87.4)	44.7 (19.4–87.4)	44.8 (19.4–87.3)	44.7 (19.4–87.4)	44.7 (19.4–87.4)
Assimilation (mg C · m^{-2} · d^{-1})	1.4 (0.7–2.4)	9.3 (3.9–24.4)	2.2 (0.9–10.5)	12.6 (4.1–29.6)	25.5 (10.9–50.9)
Defecation (mg C · m^{-2} · d^{-1})	4.5 (2.1–7.8)	26.5 (11.5–65.1)	6.5 (2.8–28.6)	36.1 (11.2–85.6)	73.6 (32.6–145.2)
Assimilation rate (% · d^{-1})	10.9 (4.7–20.9)	11.5 (4.9–21.9)	11.4 (4.9–21.6)	11.4 (4.9–21.7)	11.4 (4.9–21.7)
Assimilation efficiency (% · d^{-1})	24.3 (23.7–25.2)	25.8 (24.7–27.4)	25.5 (24.5–26.9)	25.6 (24.6.27.1)	25.6 (24.6–27.1)
Loss (mg C · m^{-2} · d^{-1})	0.7 (0.3–1.2)	1.3 (0.5–3.1)	0.5 (0.2–0.3)	0.7 (0.2–1.6)	3.1 (1.4–6.6)
Loss rate (% · d^{-1})	5.1 (2.2–9.9)	1.6 (0.7–3.1)	2.7 (1.2–5.2)	0.6 (0.3–1.2)	1.5 (0.6–3.1)
Production efficiency (% · d^{-1})	53.4 (52.3–55.0)	86.4 (85.8–87.2)	76.6 (75.7–77.9)	94.7 (94.5–95.0)	87.5 (83.9–90.2)
Predation death (mg C · m^{-2} · d^{-1})	0.8 (0.3–1.3)	8.1 (2.9–20.4)	1.8 (0.6–8.9)	11.7 (3.0–28.0)	22.4 (8.2–45.8)
Predation mortality (% · d^{-1})	5.8 (2.2–10.9)	10.0 (3.6–19.3)	8.8 (3.3–16.8)	10.6 (3.9–21.6)	9.9 (3.6–19.4)

phyll-*a*. Production of salt marsh grass is simply simulated with a forcing function. The effects of ciliates (Hockin, 1982) and other Protozoa are not considered in the model. The carbon flow path from food sources to nematode stock is partly fixed. The decrease in the number of parameters can decrease the uncertainty in the model, but this also simplifies the ecosystem. The simplified model system is limited in simulating the detail of the real system, e.g. the detailed variation of nematode biomass in the spring has not been simulated well. Modeling is uncompleted work since further development of the model is always possible according to new information and new idea. We will leave these deficiencies for further study. Synthesizing above points, we suggest that our model has a certain level of validation for a study in interrelation and discussing the results of the modeling is significant.

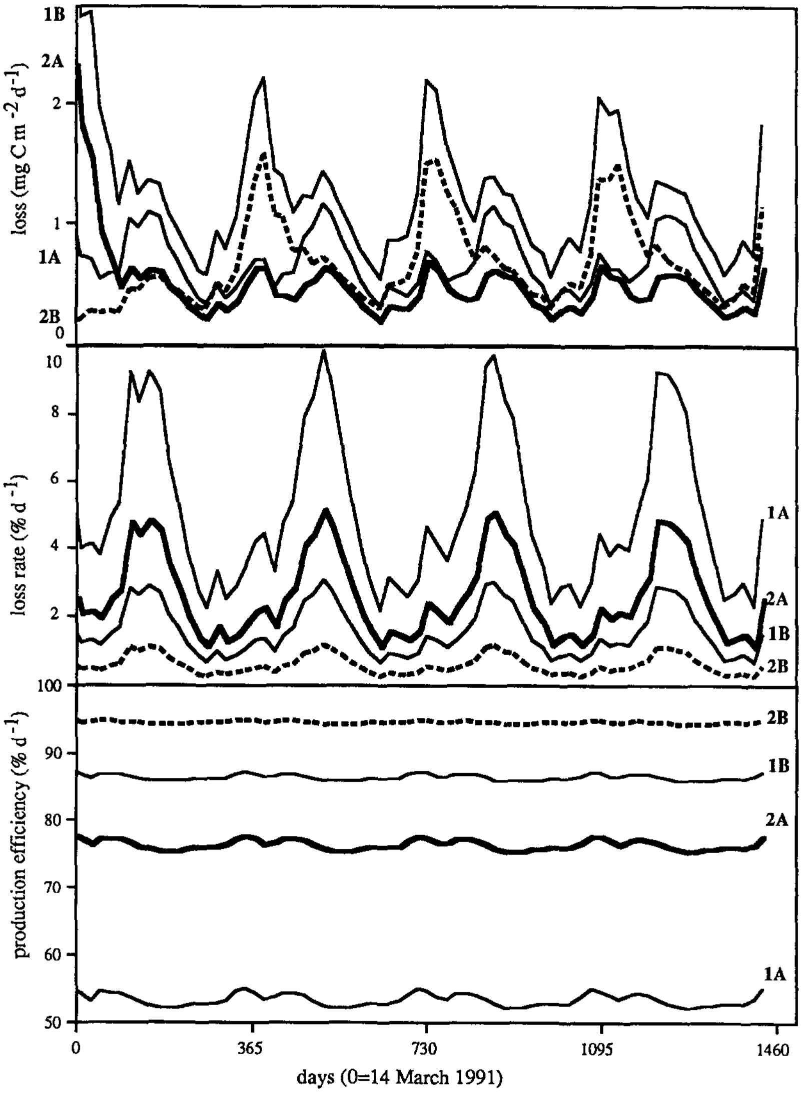

Fig. 6. The predicted daily loss (mg C • m^{-2} • d^{-1}) and daily loss rate (loss/biomass) in respiration, excretion and natural death, and daily production efficiency (production/(production + respiration)) for four nematode feeding groups.

3. Results

3.1. The prediction of nematode dynamics

Long-term variation (more than five years) of nematode biomass was simulated using the model with environmental data (14 March 1991 to 11 February 1992). The simulation showed that the omnivores (2B) and non-selective deposit feeders (1B) are the dominant nematodes in biomass while epigrowth feeders (2A) and selective deposit feeders (1A) are rare nematodes. The omnivores and non-selective deposit feeders composed 51% and 36% of total nematode standing stock while epigrowth feeders and selective deposit feeders composed only 9% and 4% (Table 4, Fig. 5). Dominant nematodes have a high level of consumption (36-49 mg C · m^{-2} d^{-1}), assimilation (9-13 mg C · m^{-2} · d^{-1}) and defecation (27-36 mg C · m^{-2} · d^{-1}) while rare nematodes have low levels of consumption (6-9 mg C · m^{-2} · d^{-1}), assimilation (1-2 mg C · m^{-2} · d^{-1}) and defecation (5-7 mg C · m^{-2} · d^{-1}) (Table 4). However, there are no differences among feeding groups for consumption rates (45% · d^{-1}), assimilation rates (11% · d^{-1}) or assimilation efficiencies (24-26% · d^{-1}) (Table 4). Food quantity and food quality are therefore not important for the difference among four feeding groups. Dominant nematodes have a higher level of predation mortality (10-11% · d^{-1}) than rare nematodes (6-9% · d^{-1}). The predation pressure does not cause a low standing stock and it is not important for the differences in stock among the four feeding groups. The "loss" distributions are complex (Fig. 6). However, dominant nematodes have a lower "loss" rate (1-2% · d^{-1}) than rare nematodes (3-5% · d^{-1}). The daily production efficiency (production/(production + loss)) is distinctly different among the four feeding groups being 53% for 1A, 77% for 2A, 86% for 1B to 95% for 2B (Fig. 6, Table 4). The "loss" rate is the main factor regulating different standing stock levels of nematodes within the community.

The biomass of a dominant nematode varies within a wide range from 35 to 303 mg C · m^{-2} for the 2B group, and from 46 to 220 mg C · m^{-2} for 1B. The rare nematodes vary within a narrow range from 11 to 19 mg C · m^{-2} for 1A and from 12 to 90 mg C · m^{-2} for 2A (Table 4, Fig. 5). There are two consumption rate peaks per year during spring and summer (Fig. 7). Neither peak correlated with the food biomass. So, the modification of nematode biomass is not influenced by the food quantity. The modification of assimilation efficiency for each feeding group ranges from 23.5% to 27.5%, and has a modification range as low as ±3% (Table 4). The variations of assimilation are proportional to the

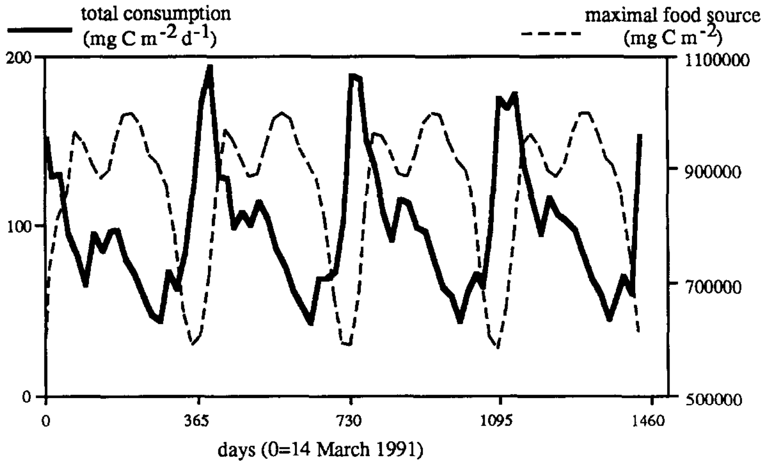

Fig. 7. The comparison between total food source (mg C · m^{-2}) for nematode and total daily consumption rate (mg C · m^{-2} · d^{-1}) of nematode according to the simulation.

variation of consumption. The food quality has less influenced the modification of nematode biomass as shown by the assimilation process. The production efficiency was stable with time for all groups (Fig. 6). The variation for total production efficiency is only from 83.9% to 90.2% (±3.2%). This means that the variation of nematode biomass is controlled by outside effects from the environment rather than by inside effects such as "loss" including expiration and natural death. Finally, predators of nematodes consume 9.9% of the total nematode biomass daily (Table 4). The modification of daily mortality is related to the dominance of nematode biomass. Dominant nematodes range from 3.6% to 19.3% for 1B (±7.9%), and from 3.9% to 21.6% for 2B (±8.9%). Rare nematodes range from 2.2% to 10.9% for 1A

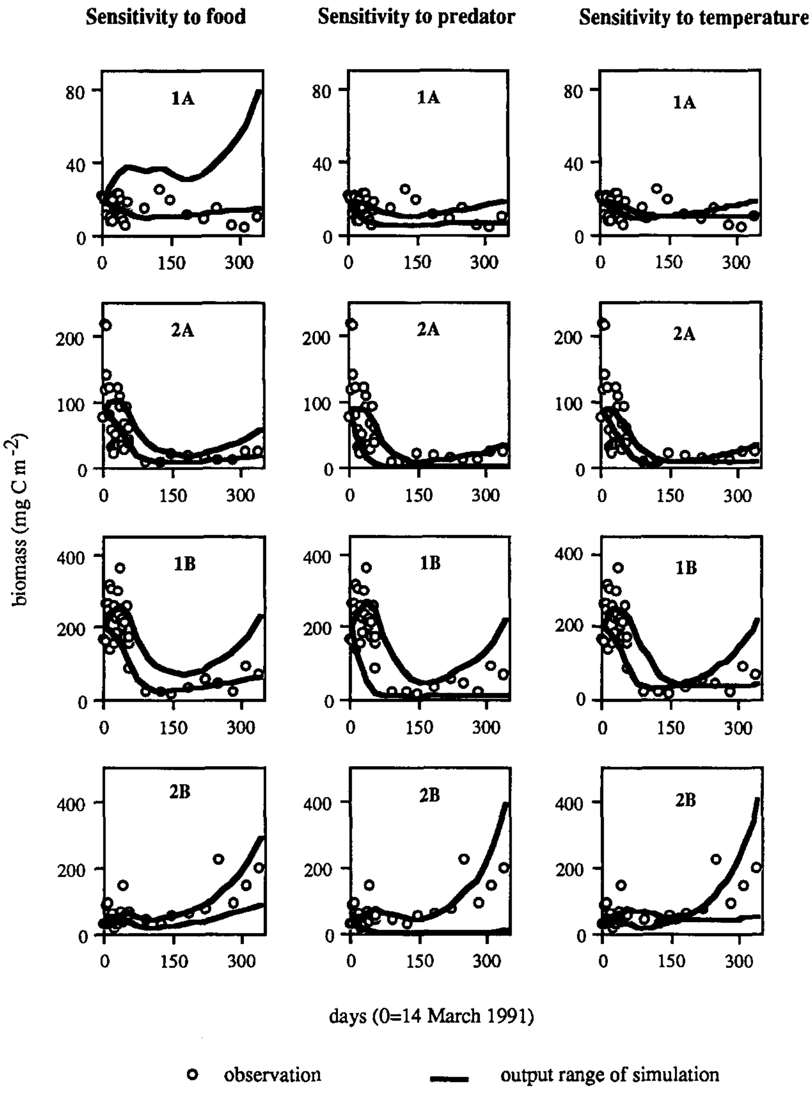

Fig. 8. The sensitivity analysis on three groups of parameters (Table 3): food availability, predation and temperature. The input are the ranges of each calibrated parameter in a group and the output are the simulation ranges (minimum–maximum) of biomass for four nematode feeding groups.

(±4.4%), and from 3.3% to 16.8% for 2A (±6.8%). It appears that predation is the main factor controlling the variation of nematode biomass through time.

3.2. Sensitivity to environmental factors

The sensitivity test shows that the dominant nematodes, omnivore nematodes (2B) and non-selective deposit feeders (1B) have higher sensitivity to predators and temperature than to food, of which the predator and temperature affect larger output ranges of nematode biomass than food (Fig. 8). The model is more sensitive to the predator and temperature factor than to the food factor for dominant nematodes. The largest output range of nematode biomass affected by food is found for selective deposit feeders (1A). The food availability may control only the rare nematodes. This may be due to the different food sources required. Dominant nematodes (1B and 2B) required deposit organic matter that is not limited in the Westerschelde Estuary. Rare nematodes (1A and 2A) required primary production such as the diatom and bacteria that may be limited in the Westerschelde Estuary. Over all, the predator and temperature factors are more important than the food for the temporal variability of nematodes in the Westerschelde Estuary.

4. Discussion

4.1. Predator control for nematode dynamics

Why does the nematode community have a higher standing stock level (higher 1B and 2B) and lower time variation in the marine zone of the Westerschelde Estuary than in the brackish zone (Li and Vincx, 1993)? We can explain this phenomenon with a "predator control" hypothesis. There is a higher proportion of deposit-feeding macrobenthos in the brackish zone than in the marine zone (Meire et al., 1991). This can cause a higher predation rate. So the brackish zone has a higher predation death and lower standing stock of nematodes than the marine zone. Temperature influences predation rate via an exponential relation. So a higher predation rate is associated with a higher modification in the brackish zone than in the marine zone. "Predator control" can also explain the estuarine gradient in the biomass of nematodes, which decreases from the mouth to the upstream in the Westerschelde estuary (Van Damme et al., 1980). The reason is that the deposit-feeding macrobenthos decrease from the upstream to the mouth (Meire et al., 1991).

"Predator control" might be valid for the total meiobenthos in the Westerschelde Estuary because nematodes are the dominant group of meiobenthos in both abundance and biomass (Van Damme et al., 1980). The annual P/B for the second dominant group, copepod, is not lower than for nematode, which is 9-10 (Gerlach, 1971) to 69 (Vranken and Heip, 1986) and 32 for local nematodes (Li, 1993). For example, P/B is 34.3 for *Tachidius discipes* (Herman et al., 1984) and 24.45 for *Paronychocamptus nanus* (Herman and Heip, 1985). Without a strong limitation, copepods should have higher standing stocks than nematodes. Therefore, their predators must consume them with high efficiency. The epibenthos is considered as the main predator for copepods (Gee, 1989). The "predator control" may be valid for copepods as well. However, copepods have a lower production efficiency than nematodes, for example, 37% for copepods (Herman and Heip, 1985), in comparison with 60-75% for nematodes (Herman and Vranken, 1988) and 50-95% in this study (Table 4). Copepod should have a higher assimilation efficiency than nematode has, because the P/B (P/B = assimilation efficiency · production efficiency) is similar between nematode and copepod. On this point, the food quality is more important for copepod than for nematodes because the assimilation efficiency depends on the food quality.

Predator control for nematode communities may be found in other ecosystems as well. In a long-term study (11 years) on both muddy and sandy meiobenthos in the North Inlet estuary, Coull (1985a) found that the abundance peak of meiobenthos is present in late winter or early spring in mud or in mid-summer in sand. The variability in abundance at the muddy site was approximately twice that of the sandy site. The sandy site has fewer deposit-feeding macrobenthos than the muddy site. Predator control may explain these interactions since the lower abundance of meiobenthos co-occurred with the higher polychaete abundance in the muddy site. The high temperature is intensifying those leading to predation pressure in summer. The lowest abundance of nematodes (or total meiobenthos) is present in summer. In the sandy site, a lower level of polychaete abundance is present. This positively correlated with meiobenthos. High temperature causes high production of meiobenthos as a function of Q_{10}. A high temperature can cause a high primary production and therefore high food quality for meiobenthos. So the abundance peak of meiobenthos is present in midsummer in sand. Predation control causes a lower level of fluctuation in the nematode or meiobenthic community of the sandy site than in the muddy site. Predator control should be considered in every study of meiobenthos dynamics.

Predator control is more sensitive on the dominant nematode rather than all nematodes. That means that there is no selective consumption of the predator on the nematode. The deposit-feeding polychaete *Heteromastus filiformis* comprises more than 95% of total macrobenthic abundance in the Westerschelde Estuary. They may be the main consumers of nematodes. Deposit-feeding macrobenthos focus on organic detritus-enriched areas on which the non-selective deposit feeder (1B) and omnivores (2B) are aggregating. For instance, the dominant species in the studied site is *Viscosia viscosa* (2B), a scavenger nematode (Jensen, 1987). The epigrowth feeders (2A) aggregate on the surface where there is enriched diatom abundance. The selective deposit feeders (1A), which feed on POC or bacteria (Heip et al., 1985), do not have the same distribution as organic detritus-enriched areas. The predation mortality for 1A and 2A nematodes is lower than for 1B and 2B nematodes (Table 4). The deposit-feeding macrobenthos feed on sediment and consume the nematodes incidentally. So, the higher the nematode biomass is, the more predators consume from this. 2B nematodes have a higher predation mortality than 1B nematodes have (Table 4). Deposit-feeding macrobenthos has mainly consumed the dominant nematodes, which causes the temporal modification of nematode community.

4.2. Community dynamics

What causes the different standing stock levels for different feeding groups within the same community? According to the results of model, the difference among the feeding groups is organized by their different "loss" rate. As the order is 1A (5.1%) > 2A (2.7%) > 1B (1.6%) > 2B (0.6%) (Table 3), the production efficiency is different among the four feeding groups. It is from 53% for 1A and 77% for 2A to 86% for 1B and 95% for 2B (Table 4, Fig. 6). The "loss" rate here is including the respiration rate, the excretion rate and the natural mortality. In carbon flow, respiration of the nematode seems the most important item (Heip et al., 1985). The fact of that 1A and 2A nematodes have a higher respiration rate than 1B and 2B nematodes may be due to the different feeding function. Jensen (1982) mentions that 2A nematodes feed on diatoms by sucking substrate rather than simply swallowing whole cells as 1B nematodes. Sucking costs more energy than swallowing. So the different respiration rates come from the different feeding mechanisms used by nematodes.

This modeling study predicts that the predators and temperature factors control the temporal variability of the nematode community in the Westerschelde Estuary. When environmental conditions (e.g., predators) are the same for different feeding groups in a nematode community, the different standing stock level among feeding groups is dependent on the different biological characteristics (respiration rate, natural mortality and feeding habit). The main predators for nematodes in the Westerschelde Estuary are the deposit-feeding macrobenthos that affect the dominant nematode species more than rare nematode species. The stress of predator control decreases from the upstream to the estuarine mouth following the decreasing gradient of deposit-feeding macrobenthos. The temporal modification of nematode biomass decreases from the upstream to the estuarine mouth, forming a gradient of stability and standing stock of nematode population along the estuary.

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