

A Simulation Model of a Deep Meiobenthic Compartment: A Preliminary Approach

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With 6 figures and 1 table

Key words: Simulation model, deep sea, *Nematoda*, meiofauna.

Abstract. On the basis of data obtained during the ECOMARGE programme and during an annual survey of a deep station (910 m), a first attempt at modelling the carbon flux through a simplified benthic system is presented. Three compartments are simulated: organic matter, bacteria, nematodes. Several hypotheses are proposed by the present simulation: constant or seasonal input of organic matter, intra-compartmental control or lack thereof. The pulses related to the seasonal input of organic matter and to the internal kinetics of the system are described. Nine to 11 mg C · m⁻² · d⁻¹ are necessary to equilibrate the carbon budget of this simplified deep-sea benthic system.

Problem

During the last few years, considerable interest has been focused on studying the dynamics of energy transfer to the deep sea and the utilization of food resources by the deep-sea benthos (ROWE, 1983, 1987). To this end, a multi-disciplinary programme was developed to investigate the ECOSystem of continental MARGins (ECOMARGE) in the north-western Mediterranean (DE BOVEE *et al.*, 1990). An attempt is made here to simulate the transfer of energy through a simplified deep-sea benthic chain: organic matter, bacteria, meiofauna. This last compartment is evaluated based on the nematodes, which are the dominant group of metazoan meiofauna (THIEL, 1983; HEIP *et al.*, 1985). The environment is characterized by a lack of organic material production and constant temperature (13°C).

Following CHARDY (1987), our simulation model is defined in terms of the management of resources. The purpose of the present simulation is to estimate the amount of energy transfers which could equilibrate the needs of a deep nematode community in the course of time. Two hypotheses, a temporal stability of supply and a seasonality in vertical flux, are tested.

Material and Methods

1. General framework of the model

The continental margin of the Gulf of Lions presents different morphological structures (Gor & ALOISI, 1990; STANLEY *et al.*, 1976). Biological research has been carried out in five canyons. Studies by DE BOVEE *et al.* (1990) have attempted to elucidate the distribution of the metazoan meiofauna on the continental slope. A decrease of meiofaunal densities, largely explained by the decrease of available resources (see THIEL, 1983), was observed after a multifactorial analysis of the results. The multivariate method also highlighted the relationship between faunal fluctuations and seasonal and organic matter variations. The limits for the biological values for the simulated station were obtained from the statistical limits imposed by a factorial analysis (LEBART *et al.*, 1984) of the results from the continental margin.

In addition, the simulation model is based on the results obtained from a reference station located at 910 m depth in the Lacaze Duthiers canyon. The parameters of the biological compartments (BUSCAIL *et al.*, 1990) and the flux of organic matter were sampled seasonally (MONACO *et al.*, 1990).

The simulated station is located in a canyon at 1000 m depth. The sediment consists of a terrigenous mud containing 86 % clay and 10 % sand. The hydrological conditions are specific to the north-western Mediterranean and are characterized by a constant bottom temperature above 13°C.

2. Model structure

In the mathematical formulation of a simulated ecosystem, it is first necessary to define the state variables and the flux functions for the variables (GRANT, 1986). Obviously, some of the control functions are supported by theoretical considerations. The goal in solving a simulation model is to

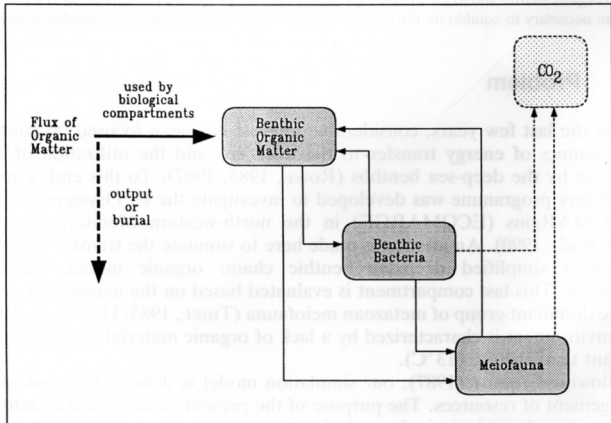


Fig. 1. Conceptual diagram of the simulation model showing the energy flow through the simplified deep-sea benthic system.

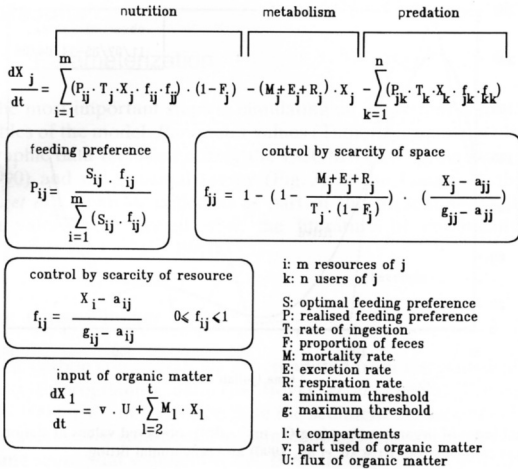


Fig. 2. Mathematical formulation of relations between the different compartments of the model and for the input of organic matter.

synthesize, in a few parameters, a great number of factors, some of which may be unknown (DEANGELIS, 1988). A part of the challenge is to find "the simplest model capable of generating an observed pattern" (CASWELL, 1988).

The process flow diagram on which the model is based is shown in Fig. 1. In the present study the state variables are the biomass of 3 compartments: organic matter, bacteria, meiofauna. The respired CO₂ is a sink compartment. Three different kinds of fluxes are formulated:

(1) a driving function which describes the input of organic matter to this compartment, (2) the flux among the compartments, and (3) the flux of physiological processes.

The general equations (Fig. 2) developed by WIEGERT *et al.* (1981), PACE *et al.* (1984), and CHARDY (1987) were used to simulate the biological processes and the interactions between compartments according to three fundamental relationships: (1) utilization of a resource or prey by a compartment; (2) utilization of a compartment by its predators; (3) loss due to physiological functions (mortality, respiration, excretion).

Control of the flux between compartments was accomplished by: ingestion rate, feeding preference, scarcity of resource, and scarcity of space. The rates of faecal production determined the amount of the flux not assimilated by a compartment.

3. Model functioning

Two different methods were employed to simulate the input of organic matter (U): (1) a mean constant flux; (2) a variable flux obtained from a polynomial fitting of the seasonally observed data (Fig. 3). The ingestion rate (T_j) is the maximal rate for a compartment under optimal conditions, when the amount of food is in excess and no intra-compartmental competition occurs. The feeding preference (S_{ij}) describes the importance of each kind of resource for a predator. From the (S_{ij}) ratio, new values (P_{ij}) are computed each time to account for the scarcity of resources (f_{ij}). For a user (j), the sum of P_{ij} is always equal to 1.

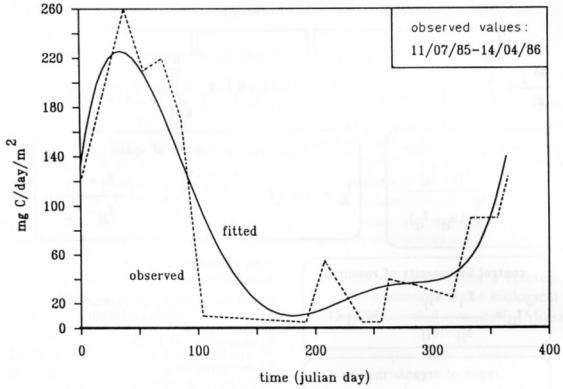


Fig. 3. Seasonal input of organic matter ($\text{mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$): observed values at station P 10 in the Lacaze Duthiers canyon (from BUSCAIL *et al.*, 1990) and polynomial fitting.

Control by scarcity of resource f_{ij} simulates the hypothesis that the use of resources is a function of abundance. Below the minimum threshold abundance a_{ij} the resource is not utilized. Above the maximum threshold (g_{ij}) the resource is utilized at the maximum rate. Between the two thresholds the rate of utilization changes linearly.

Similarly, control by scarcity of space (f_{ij}) simulates the hypothesis of intra-compartmental competition, as the increase of a compartment is a function of its own density. Below the minimum threshold biomass (a_{ij}) there is no competition between individuals. Above the maximum threshold (g_{ij}), the maximal biomass is reached and ingestion is equal to maintenance costs. Between these thresholds, values change linearly.

In coastal areas, control by scarcity of space can be ecologically consistent with field observations; in the deep sea, its importance should not be as marked. This control allows the simulation of the gradual impact on higher trophic levels which, however, is not directly part of the model. This hypothesis is tested by several model simulations including the optional use of the scarcity of space control function.

The metabolic functions are mortality, excretion, and respiration. Mortality is the biomass which returns to the organic matter compartment. Excretion is a soluble waste product. Respiration is a flux of carbon to the CO_2 compartment sink. M_j , E_j , and R_j are the rates of mortality, excretion, and respiration, respectively.

First-order differential equations provide a flexible format for ecological modelling. The fourth-order Runge-Kutta method with a time step of $1/10$ day was used to integrate the simultaneous equations.

4. Units

All the data are converted to organic carbon equivalents. The biomass is expressed in $\text{mg C} \cdot \text{m}^{-2}$ for a sedimentary layer 2 cm thick. The highest meiofauna concentrations are found in the surface and subsurface levels to a depth of 2 cm (DINET & VIVIER, 1979; THIEL, 1983; THISTLE & SHERMAN, 1985). Flux values are expressed in $\text{mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$. The rates of physiological functions (mortality, excretion, respiration) are expressed in $\text{mg C} \cdot \text{mg C (of biomass)}^{-1} \cdot \text{d}^{-1}$.

Results

1. Parameterization

One of the most important steps in simulating an ecosystem is to parameterize the variables of the model. Parameter values (Table 1) are mainly obtained from oceanographic data recorded during the ECOMARGE programme (DE BOVEE *et al.*, 1990) and the seasonal survey (Fig. 3) in the Lacaze Duthiers canyon (BUSCAIL *et al.*, 1990) or collected as part of the present study (Fig. 4). The unknown values are derived from the literature or empirically estimated (CHARDY, 1987; PACE *et al.*, 1984).

a. Organic matter

The organic carbon concentrations are computed from the statistically analyzed ECOMARGE programme data (DE BOVEE *et al.*, 1990). They range from 0.50 % (67,000 mg C · m⁻²) to 0.56 % of the sediment dry weight (75,000 mg C · m⁻²). The average for continental margin samples is thus: 0.53 % (71,000 mg C · m⁻²). Using sequential sediment traps, BUSCAIL *et al.* (1990) calculated a mean constant flux of 33 g C · m⁻² · y⁻¹ (Fig. 3). This figure is converted to 90 mg C · m⁻² · d⁻¹ for the present study.

Table 1. Parameter values used. See text and Fig. 2 for explanations of parameters.

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j	organ. mat.:	Xinit	T	M	E	R	F											
1	bacteria :	71000	30.0	6.26	0.050	0.173	0.600	0.00										
3	meiofauna :	37.0	0.50	0.020	0.000	0.039	0.40											

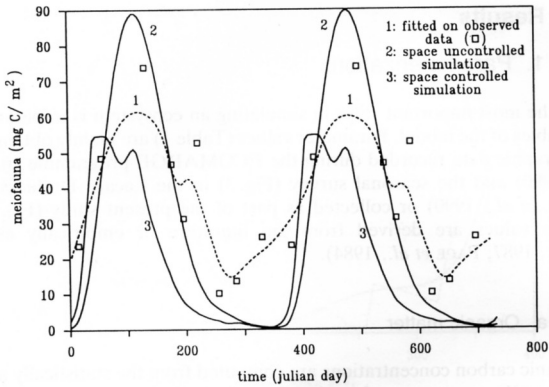


Fig. 4. Observed seasonal variations of the nematode biomass ($\text{mg C} \cdot \text{m}^{-2}$) at station P10 in the Lacaze Duthiers canyon; simulated nematode biomass with space control function and 11% organic matter flux; simulated nematode biomass without space control function and 9% organic matter flux.

b. Bacteria

The mean bacteria density is 10^8 bacteria $\cdot \text{ml}^{-1}$ sediment (direct counts; D. DELILLE, pers. comm.). On the basis of an average of $11.3 \cdot 10^{-12}$ $\text{mg C} \cdot \text{bacteria}^{-1}$ in a muddy sediment (MEYER-REIL *et al.*, 1987), the mean bacterial biomass is approximated to $30 \text{ mg C} \cdot \text{m}^{-2}$. When the bacterial biomass is equal to or lower than $1/10$ of its mean value ($3 \text{ mg C} \cdot \text{m}^{-2}$) this compartment is no longer utilized by the meiofauna. Respiration ($R = 0.6 \text{ mg C} \cdot \text{mg C (bact)}^{-1} \cdot \text{d}^{-1}$), excretion ($E = 0.173 \cdot \text{d}^{-1}$), and ingestion rates ($T = 6.26 \cdot \text{d}^{-1}$) are taken from PACE *et al.* (1984) and CHARDY (1987).

c. Meiofauna

Nematodes are suggested as a possible tool for simulating the metazoan meiofauna energetics as they possess important characteristics such as numerical dominance, high species diversity, and trophic diversity.

Nematodes are probably the most abundant metazoans in subtidal and deep sediments (HEIP *et al.*, 1985; JENSEN, 1988). In the western Mediterranean continental margin, they represent 92.4% of total meiofauna numbers. Biomass values are lower and range from 28% (HANSON *et al.*, 1981) to 82% (RACHOR, 1975). Values are generally close to 50%: 37% (WIGLEY & MCINTYRE, 1964); 48.7% (DE BOVEE, 1981); 46% (SHIRAYAMA, 1984). In the deep sea, however, they could gain in importance due to the lower energetic content of the harpacticoid copepods ($3090 \text{ cal} \cdot \text{mg}^{-1}$) found by DINET (1980).

Following PETERS (1983), we assume that the size structure is an efficient indicator of metabolic activity. The individual biomass values are obtained from biometrical analysis of the nematode community (DE BOVEE, 1987 a, b) using the following equation:

$$\text{Log (D.W. } \mu\text{g)} = 2.470848 \cdot \text{Log (L } \mu\text{m)} - 7.96632$$

A 51.03 % carbon equivalent facilitates the expression of individual biomass in terms of organic carbon (DE BOVEE, 1987 b).

The two linear regressions:

$$\text{Log (N } \cdot 10 \text{ cm}^{-2}) = -0.0006629 \cdot \text{Z (m)} + 3.2605$$

$$\text{Log (B } \mu\text{g C } \cdot 10 \text{ cm}^{-2}) = -0.0006260 \cdot \text{Z (m)} + 2.1955$$

express quantitatively the nematode distribution along the margin (DE BOVEE, 1988): numbers (N), biomass (B), bathymetry (Z).

The computed density value for a theoretical station located at 1000 m is 396 indiv. $\cdot 10 \text{ cm}^{-2}$, biomass is 37.03 mg C $\cdot \text{m}^{-2}$. The mean individual biomass is 0.0934 $\mu\text{g C} \cdot \text{indiv.}^{-1}$. The densities computed from the statistical analysis range from 16–592 indiv. $\cdot 10 \text{ cm}^{-2}$. The corresponding biomass values are 1.495 and 55 mg C $\cdot \text{m}^{-2}$.

A linear regression:

$$\text{Log (R } \mu\text{g C } \cdot \text{d}^{-1}) = 0.8544 \cdot \text{Log (D.W. } \mu\text{g C)} - 1.3477$$

relating the respiration (R) to the body weight (D.W.) was obtained from the multispecific values given by WIESER & KANWISHER (1960, 1961), TEAL & WIESER (1966), SCHIEMER & DUNCAN (1974), WIESER *et al.* (1974), WARWICK & PRICE (1979), TIETJEN (1980); see also OTT & SCHIEMER (1973), HEIP *et al.* (1982, 1985), and SCHIEMER (1987). The Respiratory Quotient = 0.85 (HARGRAVE, 1973; SMITH, 1978). The *in situ* respiration (0.039 mg C $\cdot \text{mg C}^{-1} \cdot \text{d}^{-1}$) is computed for a $Q_{10} = 2$ (PRICE & WARWICK, 1980); the related coefficient is 1.62 at 13°C.

The coefficient of mortality (0.022) is obtained from the data of DE BOVEE (1981) for the sublittoral nematode community from Banyuls-sur-Mer (North-west Mediterranean). This coefficient supports the hypothesis of a regular and constant mortality and a low predation.

From the values reviewed by HEIP *et al.* (1985) and SCHIEMER (1987), a maximum ingestion rate of 0.5 mg C $\cdot \text{mg C}^{-1} \cdot \text{d}^{-1}$ is adopted. The assimilation is 60 % of the ingestion. Excretion and faeces therefore account for 0.4 mg C $\cdot \text{mg C}^{-1}$ ingested (MARCHANT & NICHOLAS, 1974). From the data of MONTAGNA (1984), an estimate of the ingestion rate (bacteria plus diatoms) would range from 2.02 to 0.57 mg C $\cdot \text{mg C}$ (of nematode) $^{-1} \cdot \text{d}^{-1}$. The problems of ingestion rates in bacteria-feeding nematodes have been discussed by HERMAN & VRANKEN (1988); they calculated an ingestion rate exceeding 1.5 mg C $\cdot \text{mg C}^{-1} \cdot \text{d}^{-1}$ with an assimilation rate of 25 %.

Our chosen value (60 % assimilation rate, *i. e.*, 0.5 mg C $\cdot \text{mg C}^{-1} \cdot \text{d}^{-1}$) is justified by the lower quantities of trophic resources in the deep sea versus coastal areas or under supoptimal experimental conditions. The present simulation model makes the assumption – taking into account the range of data for the continental margin – that the ingestion rate is food-dependent. When little energy is available in the environment, only a small quantity of food can be ingested by the organisms and, consequently, the ingestion rate is small (SCHIEMER, 1987; ROMEYN & BOUWMAN, 1983). Under conditions of lower food

abundance, the assimilation efficiency would increase, thus producing a high assimilation rate (see the detailed analysis of SCHIEMER, 1987, for *Plectus palustris*).

The nematode community sampled at the P 10 station in the Lacaze Duthiers canyon is highly diversified (SHANNON index = 5.5). The species association is similar to that described by VITIELLO (1969; 1976) for the bathyal mud off Marseilles. Dominant species are mostly members of the *Comesomatidae* (*Sabatieria conicauda*, *S. hilarula*, *Hopperia massiliensis*), which can contain up to 40% of sampled individuals. In terms of the feeding types defined by WIESER (1953), the deposit feeders, ("1A" and "1B") contain 64.2% of the total individuals, (8.2 and 56%, respectively). The predatory and omnivorous nematodes ("2B"), with a wide and armed buccal cavity (20.3% of individuals), are dominated by the *Sphaerolaimidae*. The epistrate feeders ("2A") only occur in small numbers (8.4% of organisms). Of particular interest is the presence of a mouthless species containing up to 7.1% of all individuals. In the deep sea, JENSEN (1988) estimated that the bacteriophageous nematodes constituted 90% or more of the fauna. Our observations indicate slightly lower values. According to the feeding structure proposed by JENSEN (1987, 1988), our model assumes that 70% of the individuals (the deposit feeders and the epistrate feeders) are mainly bacteria-feeders. The remaining (30%) utilize the non-bacterial organic matter. Obviously, this latter group is extremely heterogeneous and contains predators, scavengers, omnivores, and gutless nematodes.

2. Simulation

Several trials were done with different proportions of the organic matter flux available to the organisms, with and without the scarcity of space function. Step by step, all the simulations were examined. We retained the runs for which the simulated mean meiofauna biomass was the nearest to the observed biomass.

The results of the retained simulations are illustrated by Figs. 5 and 6. Both a mean constant input of organic matter and a seasonal flux are simulated.

a) with the scarcity of space function, the needs of the benthic system are 10% of the organic matter input flux;

b) without this function the needs are 9% of the input flux.

The fluxes are expressed in $\text{mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, the biomasses of bacteria and nematodes in $\text{mg C} \cdot \text{m}^{-2}$.

a. With the scarcity of space control function

Constant flux (Fig. 5 A). When the rate of utilization of the input flux is lower than 8%, the results are inconsistent and the values of nematode biomass sharply decline. At 10% ($9 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$), the system is linear without any pulse. For this step, the maximum values reached by the bacteria ($9 \text{ mg C} \cdot \text{m}^{-2}$) and nematodes ($40 \text{ mg C} \cdot \text{m}^{-2}$) are lower than the control values. At 12% ($11 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$), some fluctuations begin to appear. Above a 15% rate of utilization ($13.5 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$), nematode biomass varies between the mean

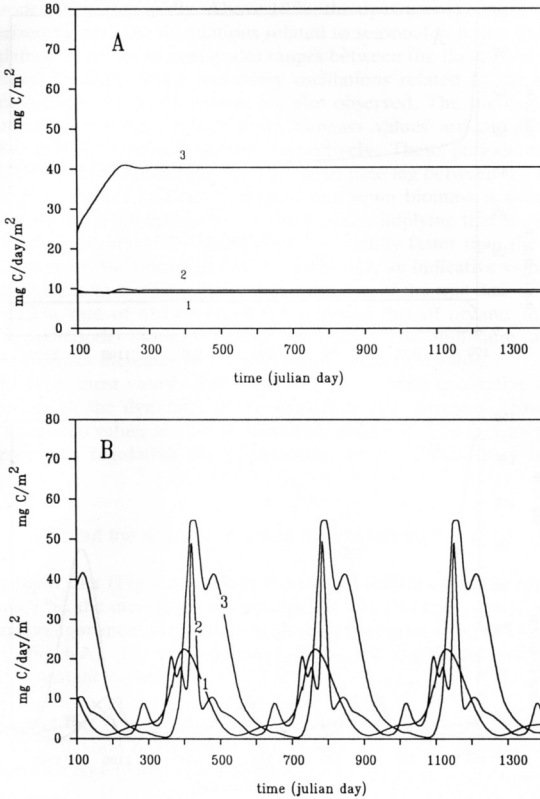


Fig. 5. Results of the simulations with space control.

A: 10% mean constant flux.

B: 10% seasonal flux.

1: influx of organic matter ($\text{mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$); 2: bacteria biomass ($\text{mg C} \cdot \text{m}^{-2}$); 3: nematode biomass ($\text{mg C} \cdot \text{m}^{-2}$).

and maximum values. For the higher rates, the magnitude of pulses decreases and the mean biomass approaches the theoretical maximum value ($55 \text{ mg C} \cdot \text{m}^{-2}$).

Examining the mean constant input of organic matter allows us to describe the functioning of the simulation model. When the trophic resources are at a low level ($< 8\%$), the bacteria compartment is maintained but the meiobenthic compartment disappears. The bacteria compartment is then only limited by the abundance of organic matter (scarcity of resource). When the flux increases, the

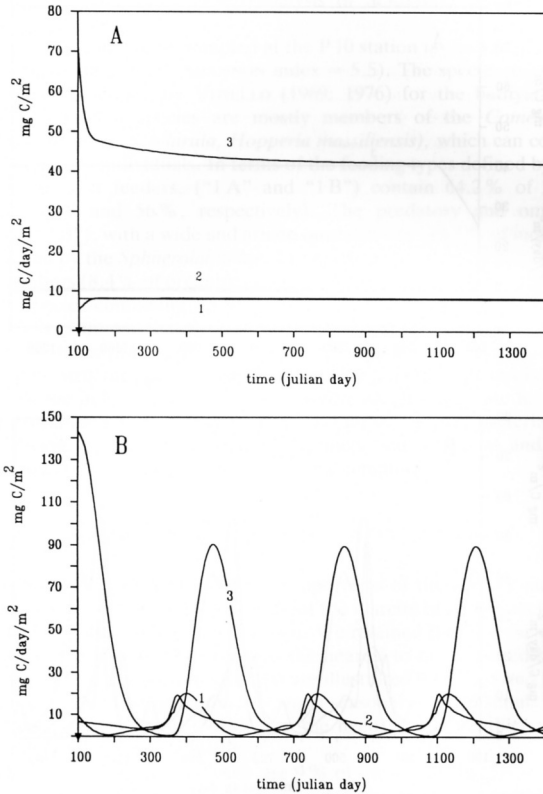


Fig. 6. Results of the simulations without space control.

A: 9% mean constant flux.

B: 9% seasonal flux.

(1: influx of organic matter ($\text{mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$); 2: bacteria biomass ($\text{mg C} \cdot \text{m}^{-2}$); 3: nematode biomass ($\text{mg C} \cdot \text{m}^{-2}$).

bacteria and meiofauna compartments are present. Bacteria abundance is then regulated by meiofauna predation. The nematode compartment is regulated by the scarcity of resource and by its own growth (scarcity of space). The fluctuations at fluxes greater than 10% result from the control functions of the model.

Seasonal flux (Fig. 5 B). When the rate of utilization of the input flux is lower than 8%, the results of the simulation are inconsistent and the low fluctuations

of nematodes decrease rapidly. Above 10%, the dynamics of compartments are characterized by periodic fluctuations related to seasonality in the food supply. The amplitude of pulses in nematodes ranges between the theoretical minimum and maximum values. Some secondary oscillations related to the inter- and intra-compartment control functions are also observed. The simulated periods of maximum and minimum nematode biomass values are obtained during April–May and September–October, respectively. These periods correspond well with the observed data (Fig. 4). The mean time lag between the maximum flux of organic matter and the simulated maximum biomass is 60 days. The observed time lag is slightly greater than 80 days, implying that the simulated kinetics of the utilization of organic matter is slightly faster than the observed kinetics. However, the observed time lag gives only an indicative value because the sampling strategy does not allow the estimation of the true date of the peak. Above a 12% rate of utilization of the seasonal flux of organic matter, the maximum nematode biomass values level out. The minimum and mean nematode biomass increases to the maximum theoretical value.

Our model is most valuable in suggesting the general qualitative and mean characteristics of the dynamics of the nematode compartment. However, the smallest simulated values are lower than those observed. This indicates that part of the processes regulating the populations, or the fluxes, may have been ignored.

b. Without the scarcity of space control function

Constant input flux (Fig. 6A). When the rate of utilization of the input flux is lower than 7%, the meiofauna disappears. At 9% ($8.1 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$), the meiofauna compartment is maintained close to the mean observed level ($42 \text{ mg C} \cdot \text{m}^{-2}$; Fig. 6A). Up to and above 10%, the simulated biomass shows unrealistic constant values.

Seasonal input flux (Fig. 6B). The most realistic mean value is obtained with a 9% rate of utilization of the input flux. Nevertheless, the meiofauna biomass values fluctuate widely and reach $88 \text{ mg C} \cdot \text{m}^{-2}$.

Discussion

According to several authors (see THIEL, 1983; PFANNKUCHE, 1985; ALONGI & PICHON, 1988; DE BOVEE *et al.*, 1990), food availability is very important in explaining the quantitative distribution of meiofauna along the continental margins. This specificity suggests an ecosystem in which the energetic transfers are food-limited. The present model simulates a three compartment system. The source compartment is the input of organic matter. The trophic resources are utilized by two other compartments. The first user is the bacteria compartment, which is mainly controlled by available resources and predation. The importance of the meiobenthic compartment in the ecosystem depends on its initial biomass and resource availability. Meiofauna mainly feed on the bacteria compartment, and low bacterial abundance may be a limiting factor.

In the deep sea, global metabolic experiments (SMITH & BALDWIN, 1984) as well as benthic animal observations (see TYLER, 1988) suggest a biological seasonality related to a seasonal influx of organic matter (ROWE, 1987). Similar conclusions are obtained in the Lacaze Duthiers canyon at 910 m from the comparative analysis of the particulate matter flux (Fig. 3) and quantitative meiofauna distribution (Fig. 4). According to the two concepts of temporal stability and predictable annual periodicity, the present model simulates four hypotheses: mean constant flux or seasonal influx of organic matter, controlled or uncontrolled by the scarcity of space.

For the constant flux model, regular pulses related to the control functions can be obtained under the scarcity of space control hypothesis.

A more realistic representation of the observed data is obtained from the seasonal simulation (Fig. 4), both with or without the scarcity of space hypothesis function. When this function is omitted, the simulated meiofauna variations are in phase with the observed fluctuations. For each hypothesis the simulated values of the mean level are close to the observed mean.

Our biological model is a simplification of a real ecosystem: only the bacterial compartment and roughly 50% of the biomass of the metazoan meiofauna are included. Consequently, the simulated amount ($9-11 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) of organic matter which appears to be necessary to equilibrate the energy requirements must be considered only as a minimum value. This result does not reach the high value ($31 \text{ g C} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$) obtained by DE BOVEE & LABAT (1989) from the Sediment Community Oxygen Consumption experiments. Their value may be an overestimate due to the technique used in shipboard experiments at sea bed temperature. The actual amount of organic matter used at the sediment-water interface remains difficult to determine. On the basis of the hypothesis of sedimentation developed by COURP & MONACO (1990), BUSCAIL *et al.* (1990) used two different methods to estimate the carbon budgets in the superficial layer. Using ^{14}C radiocarbon dating these authors considered the vertical flux at the bottom to be only $1 \text{ g C} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$, of which 40% would be buried and 60% consumed ($0.6 \text{ g C} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$); this latter value is only 2% of the flux measured with sediment traps. The ^{210}Pb dating would indicate a vertical input of $23.7 \text{ g C} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$; $12.2 \text{ g C} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ (51%) would be buried and $11.5 \text{ g C} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ would be consumed. This last result is comparable with the value computed with the proposed compartmental model.

SMITH (1987) concluded there is a deficiency in energy input to the sea bed if the vertical POC flux is the unique source. We suggest that the carbon budget of the meiofauna community could be equilibrated by additional horizontal advection of food supply (TYLER, 1988).

Summary

A simulation model is used to estimate the importance of energy transfers which could equilibrate the needs of a deep nematode community in the course of time.

The observed values for the compartments are obtained from the annual survey of a deep station (910 m) of the ECOMARGE programme. Surface

sediment organic matter concentrations ranged from 0.50% to 0.56% sediment dry weight (or $67,000 \text{ mg C} \cdot \text{m}^{-2}$ to $75,000 \text{ mg C} \cdot \text{m}^{-2}$, respectively), for a mean near-bottom flux input of $33 \text{ g C} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ ($90 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$). The mean organismal biomass approximated to $30 \text{ mg C} \cdot \text{m}^{-2}$ for the bacteria and $37 \text{ mg C} \cdot \text{m}^{-2}$ for the meiofauna.

In the simulations, when 9–11% of the input flux are used by the system ($9\text{--}10 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$), the meiofauna compartment is maintained close to the observed level, while bacterial biomass ($9 \text{ mg C} \cdot \text{m}^{-2}$) is lower than the observed value. At lower rates (<8%), the meiobenthic compartment disappears, at higher rates (>12%) the simulated biomasses show unrealistic values. With a seasonal input flux, the periods of the meiofauna biomass pulses correspond well with the observed data. The mean time lag between the maximum values of the organic matter input and the simulated maximum biomass is 60 days, slightly smaller than the observed value.

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