

Carbon flows in a subtidal fine sand community from the western English Channel: a simulation analysis

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ABSTRACT: Organic carbon flows through the Pierre Noire fine sand community (Bay of Morlaix, France) are described with a trophodynamic point model. Data collected during several annual cycles are used to calibrate the seasonal variations of each benthic compartment. Mean annual values of state variables are correctly simulated. In a first approach, the seasonal variations were simulated using 2 forcing functions: input of energy and temperature influence. In a second run, spawning and recruitment effects were introduced as regulating factors for the macrobenthic compartments. The resulting annual carbon budget synthesizes the information we have on this common type of ecosystem. Phytoplankton production represents the major food supply to the benthic system and the importance of pelagic-benthic coupling in this area is confirmed. A large proportion of the carbon input is consumed by bacteria which is the main trophic source for meiofauna. Meiofauna is an important link between the bacteria + detritus and the carnivore level, and cannot be considered as an independent food web. The significance of regulation factors such as spawning and recruitment processes in the dynamics of the macrofauna is explored.

INTRODUCTION

Fine sand communities dominated by the bivalve *Abra alba* are very common in the Northwestern European seas. In the English Channel they are limited to the shallow waters of bays and estuaries, and are usually well separated from other bottom types (rocks, pebbles, gravel and coarse sand). The community of Pierre Noire is dominated by *Abra alba* and the polychaete *Hyalinoecia bilineata* and is located in the Bay of Morlaix (western English Channel).

Marine ecosystem modelling has traditionally been dominated by plankton dynamics. Many of the recent investigations in modelling the benthos were developed with generic ecosystem models such as GEMBASE (General Ecosystem Model for the Bristol Channel and the Severn Estuary; Radford 1979), the continental shelf food web simulation analysis (Pace et al. 1984), the Cumberland Basin model (Keizer et al. 1987), and the Ems Estuary model (Baretta & Ruardij

1988) which represents the most powerful contribution in dynamic modelling of benthic processes. These simulation analyses have provided useful insight into the functioning of the benthic subsystem and its relationships with the pelagic. However, development of benthic submodels is hindered by lack of adequate quantitative information on benthic organisms and on local properties of benthic communities (Silvert 1991). This applies particularly to the lack of continuous series of biomass data for each of the compartments of a benthic community, since such a data base requires substantial field work involving several specialists.

Application of the simulation modelling technique to estimating the carbon flows in the *Abra alba* community of Pierre Noire was motivated by the availability of a large body of data from field experiments. Qualitative and quantitative data are available from several studies on most of the benthic components: microphytobenthos, bacteria, meiofauna, macrofauna and predation by demersal fishes (Boucher et al. 1984,

Dauvin 1984, 1988, 1989, 1990, Boucher 1985, Dauvin & Ibanez 1986, Riaux-Gobin et al. 1989). Detailed observations have been made on seasonal changes of biomass, for dominant species or taxonomic groups which are of particular relevance to food chain dynamics.

These data have here been gathered and applied to a trophodynamic point model. Special attention is paid to the simulation of seasonal changes of the biotic compartment biomasses driven by food supply and temperature. The possible role of other regulator factors as spawning and recruitment in the general dynamics of the benthic system is examined.

The fluxes calculated by the model cannot be directly validated, and as such should be considered with some caution. Where possible, they are compared to literature data to ascertain whether their order of magnitude is consistent with reality. In the present work, the only possible way to assess the consistency of the model results is to determine the correspondence between simulated standing stocks and field values. The credibility of the simulation is estimated first on the average annual biomass, which is the primary type of information, and then on the seasonal variations of each biotic compartment.

MATERIAL AND METHODS

Study site. The Pierre Noire community covers a well-defined area of about 20 km² in the eastern part of the Bay of Morlaix, France, at about 20 m depth (Cabioc'h 1968) (Fig. 1). The main characteristics of the abiotic and biotic conditions at Pierre Noire have been described by Dauvin (1984). The sediment is fine sand with a median particle size between 140 and 180 μm (about 1 % of particles < 63 μm) and a low particulate organic carbon content comprising from 0.10 to 0.40 % of the dry sediment weight. The bottom water temperature varies ordinarily between 8.8 °C in winter and 15.3 °C in summer, and salinity between 34.50 ‰ in winter and 35.30 ‰ at the beginning of the autumn.

Model structure. The model is closely related in concept to the food web simulation model developed for the 'Normand-Breton' coarse sand gulf community (Chardy 1987), itself derived from the work of Pace et al. (1984). It is a trophodynamic 'point model' composed of 11 biotic and abiotic compartments. The simulation is restricted to the carbon flows related to benthic secondary production, and is similar to the model of Warwick et al. (1979) of the benthic community of the Lynher estuary (UK). Three pelagic

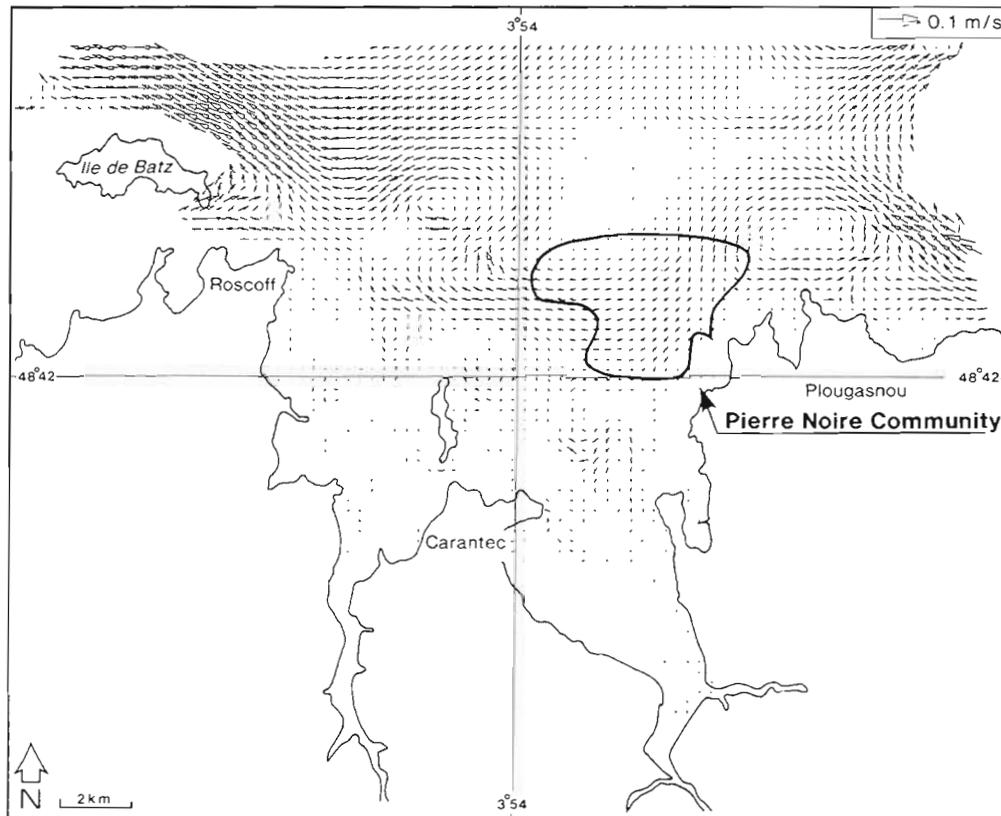


Fig. 1. Residual circulation of water masses in the Bay of Morlaix, from Salomon & Breton (1987)

compartments and the microphytobenthos are external variables considered as sources of carbon for the benthic organisms. The state variables are the biomasses of the 7 benthic compartments defined below. All variables are expressed in g C m^{-2} . For each state variable, as for the whole benthic system, the sum of inputs equals the sum of outputs, over a period of 1 yr and under steady state conditions.

The behaviour of the state variables is described by a set of differential equations of the form:

$$dx/dt = \text{rate of gain} - \text{rate of loss.}$$

Interactions between compartments are modelled using the general equation initiated by Wiegert (1975) and generalized by Pace et al. (1984) (see Appendix 1).

External variables: We used pelagic data obtained by Wafar (1981), Wafar et al. (1983) and Sournia et al. (1987) at Stations 'Bloscon' and 'Astan' located about 4 nautical miles from Pierre Noire in the western part of the Bay of Morlaix where the minimum depth is 25 m.

Y1. Phytoplankton. Monthly chlorophyll *a* measurements by fluorimetry and primary production estimates using the ^{14}C method were carried out during the period February 1979 to June 1980. Biomass of phytoplankton in carbon units was derived from the conversion $\text{C:chl } a = 40$ (Steele 1974).

Y2. Zooplankton. Standing stock of zooplankton was based on monthly dry weight measurements, converted to carbon using a conversion coefficient of 0.40. Zooplankton was collected by vertical hauls with a WP 2 net (200 μm mesh size).

Y3. Suspended particulate detritus is the allochthonous source of energy for the benthic layer and was estimated from monthly measurements of particulate organic matter (POC) in the water column (CHN auto-analyser). Dead organic matter was estimated by subtracting the amount of carbon in living phytoplankton from measured POC.

Y4. Microphytobenthos. Chloropigment (chl *a* and phaeopigments) concentrations were measured from sediment cores (5.72 cm^2) collected by divers (Boucher et al. 1984) or by a 21 cm^2 'Rouvillois' benthic corer (Riaux-Gobin et al. 1989). A conversion coefficient of $\text{C:pigments} = 40$ was used to express the standing stock of microphytobenthos in carbon units.

State variables: The biological state variables represent functional groups defined by feeding mode and size criteria.

Benthic field observations were made at the Pierre Noire locality. Nematode and copepod densities were estimated after sieving the sediment on a 40 μm mesh; three 5.72 cm^2 cores were taken by diver at each sampling (Boucher 1980, 1983, 1985). The densities of the temporary meiofauna (juveniles of macrobenthic

species) and of the polychaetes of the permanent meio-benthos were estimated after sieving the sediment on 180 μm mesh; five 160 cm^2 Reineck cores were taken at each sampling (Dauvin 1989). The densities of the macrobenthic species were estimated after sieving the sediment on a 1 mm circular mesh; ten 0.1 m^2 Smith MacIntyre grabs were taken at each sampling (Dauvin 1984, 1989).

X1. Benthic detritus. Detrital organic matter on/in the sediment layer is a passive, abiotic storage compartment.

X2. Bacteria associated with benthic detritus were estimated from sediment collected by Scuba divers (Boucher et al. 1984). Density was obtained by acridine orange direct count and converted to biomass with a conversion coefficient of $10^{-13} \text{ g C bacterium}^{-1}$ (Guidi 1981).

X3. Mixed macrobenthic invertebrate species (suspension and surface deposit feeders). The grouping of suspension feeders, deposit feeders and suspension/deposit feeders proposed by Arntz & Brunswig (1976) was adopted. These species feed on the organic matter at the sediment surface originating mainly from plankton production and, to a lesser degree, on microphytobenthos and benthic bacteria. This group forms about 25 % of the total biomass of the macrobenthic fauna. It consists of amphipods (e.g. *Ampelisca* spp.), bivalves (e.g. *Abra alba*) and numerous species of polychaetes (e.g. Paraonidae, Spionidae) (Table 1).

X4. Subsurface-deposit feeders. These species live in the sediment (e.g. *Euclymene oerstedii*, *Scoloplos armiger*; Table 1); their food consists of detritus and bacteria in the sediment. This group represents only 6 % of the total biomass of the macrobenthic species.

X5. Meiofauna. Nematodes, including *Richtersia kreisi*, *Microlaimus conspicuus*, *Chromaspirina renaudae*, *Cylindrotheristus divertens* and *Prochromadorella ditlevseni*, are the dominant group of the meiofauna (65 to 86 % of the biomass). Microgastropods (6 to 13 % of the biomass) and harpacticoid copepods (2.5 to 12 % of the biomass) are common. Other meiofauna, including gastrotrichs, halacarids, oligochaetes and turbellarians are rare (Boucher 1980). Polychaetes of the permanent meiofauna (Syllidae, Dorvilleidae) form an important part (about 40 % of the biomass) of the fauna between 0.18 and 1.0 mm. Juveniles of macrobenthic species (0.18 to 1.0 mm) are dominated by polychaetes, amphipods and bivalves which represent, respectively, 74 %, 15 % and 7 % of the total biomass of the temporary meiofauna (Dauvin 1989). Meiofauna and juveniles of macrobenthic invertebrates feed on detritus and bacteria.

X6. Carnivores I. This group consists of motile macrobenthic invertebrate predators, especially the polychaetes *Nephtys hombergii*, *Marphysa bellii*,

Table 1. Biomass of the main species (biomass >1 % of total macrobenthos in 1986) from the 4 macrobenthic compartments

% of total macrofaunal biomass	
X3. Mixed (suspension and surface-deposit feeders)	
<i>Ampelisca</i> spp.	7.5
<i>Polydora pulchra</i>	5.4
<i>Spio decoratus</i>	2.7
<i>Ampharete acutifrons</i>	1.8
<i>Spiophanes bombyx</i>	1.2
<i>Venus ovata</i>	1.1
Paraonidae	1.0
X4. Subsurface-deposit feeders	
<i>Euclymene oerstedii</i>	1.8
<i>Scoloplos armiger</i>	1.4
X6. Carnivores I	
<i>Nephtys hombergii</i>	28.1
Nemertians	6.1
<i>Marphysa bellii</i>	3.1
<i>Hyalinoecia bilineata</i>	1.0
X7. Carnivores II and omnivores	
<i>Nassarius reticulatus</i>	13.8
<i>Pagurus bernardus</i>	8.2
<i>Eulalia sanguinea</i>	1.0

Hyalinoecia bilineata, and nemerteans (Table 1). It forms more than 44 % of the total biomass of the macrobenthic fauna.

X7. Carnivores II. This group is formed by omnivorous (e.g. *Eulalia sanguinea*) and necrophagous (e.g. *Nassarius* spp., *Pagurus bernardus*) invertebrates (Table 1) and demersal fishes (e.g. *Trisopterus minutus*, *Callionymus lyra*, *Echiichthys vipera*). This group represents more than 24 % of the total biomass of the macrobenthic fauna. Stomach content analysis of the 13 main species of demersal fishes showed that they feed on macrobenthic fauna, especially crustacean amphipods; polychaetes and bivalves are only secondary prey (Dauvin 1988).

Limitations: The first theoretical limitation is that all compartments are confined within recognizable spatial boundaries. This is partly acceptable for a spatially well defined benthic unit, as the present *Abr alba* community, where migratory processes are low. However hydrodynamic transport of the surrounding water is ignored. The required assumption is that pelagic conditions at the boundaries are similar to those within the area, or that exchanges with neighbouring water are weak. These assumptions are not unrealistic if we consider the model of residual circulation established by Salomon & Breton (1987) in the area (Fig. 1), which exhibits maximum residual currents of 0.02 m s⁻¹ at low tide and 0.05 m s⁻¹ at high tide. In addition to this argument, the area studied is located within a large coastal zone without any remarkable hydrological discontinuity.

A second limitation (the greater one) is the assumption that biological compartments are homogeneous in terms of feeding mode and individual weight, which is of course far from reality. Despite these limitations, sufficient ecological data have been collected on the community under study to legitimise an attempt to represent carbon flows in the total system coherently.

Forcing functions. In a first run, the model was driven by the energy sources supporting benthic secondary production and temperature. Other regulating factors, such as spawning and recruitment of the macrofauna, were introduced later.

Autochthonous source of carbon: This source represents the fraction of primary pelagic production available to the benthos, and benthic primary production. The amount of phytoplankton production reaching the bottom is that portion which is not consumed in the water column. For each day, it was calculated as total primary production less production of exudates and grazing by zooplankton.

Extracellular products were assumed to be 20 % of daily production. Jones & Henderson (1987) and Newell et al. (1988) observed that 10 to 30 % of the carbon flow from primary production is channelled to the water column as soluble products.

Grazing of zooplankton on phytoplankton is a function of food concentration, temperature and standing stock of zooplankton. The basic formulation given in Kremer & Nixon (1978) was used:

$$Gr_i = Rmax_0 e^{(\alpha t_i)} - e^{(-k Phyt_i)}$$

where Gr_i = uptake of phytoplankton on Day i by zooplankton; $Rmax_0$ = Maximum ration of zooplankton at 0 °C [assumed to be 0.3 g C (g C)⁻¹ d⁻¹]; t_i = temperature on Day i ; α = temperature rate constant (assumed to be = 0.069); k = Ivlev constant (assumed to be = 15, for a phytoplankton concentration expressed in g C m⁻³); $Phyt_i$ = phytoplankton concentration on Day i .

Faeces production by zooplankton was assumed to be 30 % of food ingestion (Conover 1966), all of which reaches the benthic layer.

In situ primary production by phytobenthos was calculated using a daily production/biomass (P/B) ratio of 0.055 for the standing stock of the upper centimeter of sediment. This resulted in an annual production of 10 g C m⁻², which is comparable to the results reported from the Bay of Douarnenez, France (Bodin et al. 1985), where similar conditions exist.

Allochthonous source of carbon: A portion of the detritus suspended in the water column is transferred to the benthic layer. The daily sedimentation rate increases under calm weather conditions and decreases in windy periods. From the trap experiments conducted in the Bay of Morlaix (Dauvin 1984), the sedi-

mentation rate was assumed to be maximum with a wind of 5 knots and zero over 15 knots.

Temperature: The basic physiological rates used in the biological processes are temperature-dependent with a Q_{10} of 2. The temperature effect was described by the formulation:

$$Tcor_i = e^{0.069 \times (t_i - 12)}$$

where $Tcor_i$, the temperature correction factor on Day i , is equal to 1 at the annual mean temperature value (12 °C).

Biological processes.

General assumptions: Interactions between compartments are modelled using the general equations developed by Wiegert (1975), and applied by Pace et al. (1984) and Chardy (1987). For any biological compartment, input is ingestion or uptake, and output is the sum of egestion, respiration, physiological mortality and predation (see Appendix 1). The rate of uptake is controlled by 2 functions which implement the effects of resource limitation and intracompartamental competition (see Appendix 2). For compartments feeding on more than one resource, a feeding preference value was assigned.

Parametrization: Parameter values are presented in Appendix 1. The basic metabolic rates of the different macrofauna compartments were derived from detailed population studies over a period of several years in the Bay of Morlaix (Dauvin 1984, 1991). P/B ratios, which are the basis for the derivation of the physiological parameters, are presented for each macrofaunal compartment in Table 2. For meiofauna and bacteria, only biomass values are available.

For meiofauna, the annual P/B ratio was set at 15, which is intermediate between the value of 9 proposed by Gerlach (1971) and the more recent estimate of 20 by Vranken & Heip (1986).

For the macrofauna and meiofauna compartments, respiration rate was derived from the empirical relationship established by Schwinghamer et al. (1986):

$$\log_{10} R_a = 0.367 + 0.993 \log_{10} P_a$$

where R_a and P_a = annual respiration and production respectively.

Concerning benthic bacteria, annual respiration was assumed to equal annual production. This assumption was adopted by several authors (e.g. Williams 1984, Schwinghamer et al. 1986, Bratbak 1987, Thingstad 1987).

Assimilation efficiency is treated as a constant in the present model. An approximate average of assimilation efficiency was derived from reported values in the literature for the same or related species as those in each compartment. For the 'mixed' compartment, the assimilation efficiency can vary from 25 to

Table 2. Mean annual biomass (g C m^{-2}), production ($\text{g C m}^{-2} \text{yr}^{-1}$) and P/B ratio, derived from Dauvin (1984, 1991), Boucher et al. (1984) and Boucher (1985)

	Biomass	Production	P/B
Mixed	0.50	1.506	3.0
Subsurface deposit-feeders	0.118	0.354	3.0
Meiofauna	0.28	?	?
Carnivores I	0.877	1.052	1.2
Carnivores II	0.482	0.723	1.5
Bacteria	0.98	?	?

75 %, depending on the dominant feeding type, which may be suspension or deposit feeding (Widdows & Bayne 1971, Tenore & Dunstan 1973, Tenore & Gopalan 1974, Newell & Bayne 1980, Dame & Patten 1981, Navarro & Winter 1982). An overall assimilation efficiency of 50 % was taken for this group. For deposit-feeders, estimated assimilation values are usually lower. An average efficiency of 20 % for feeding on detritus was derived from the values obtained by Dame & Patten (1981) and Pace et al. (1984), and a value of 65 % for feeding on bacteria (Hargrave 1970, Tenore et al. 1982).

An estimate of ingestion rate was calculated from the general energy budget $C = P + R + F + U$ (where C = consumption, P = production, R = respiration, and F = faeces) (Crisp 1984). Excretion (U) is considered negligible here in terms of the total carbon flux of the compartments. Taking into account the results of Loo & Rosenberg (1989) on bivalve suspension-feeding dynamics in Laholm Bay (Kattegat), we consider that annual mean ingestion represents half of the maximum potential feeding capacity. The rate of maximum uptake was deduced from this assumption.

The maximum specific uptake rate of labile organic carbon by benthic bacteria was assumed to be 0.75 d^{-1} , in accordance with the Ems Dollard model assumption from Baretta & Ruardij (1988).

Non-predatory mortality determines the part of the production which is not assigned to predation, but returns to detritus. Few data are available from the literature on these parameters and they lie between 5 % (Silvestre 1990) and 40 % (Brylinsky 1972). We assumed a mean value of 20 % of annual production for each compartment.

The benthic detritus state variable represents a passive storage of organic carbon. This detrital pool is divided into a labile and a refractory part according to the sources of the detrital material. Only the labile component is utilized by fauna and heterotrophic bacteria. Very few data are available on the precise ratio of the labile to the refractory components of detrital material. The range of values obtained from experiments on bacterial degradation lies between

50 % for planktonic phytodetritus (Westrich & Berner 1984) and <1 % for marine sediment (Nedwell 1987). Organic carbon coming from the water column has 2 sources: local primary production (including faecal pellets of zooplankton) and allochthonous material. Observations by Iturriaga (1979) in the Baltic Sea indicate that the degradable organic fraction of the particulate organic matter that reaches the sediment is related not only to the production of the upper water layers, but also to transformations that take place during sedimentation. Following Lancelot & Billen (1985) we assume that the labile fraction of fresh phytoplankton accounts for 50 % of the original material. Assuming that the most labile fraction is consumed in the water column as extracellular products, earlier estimated at 20 % of phytoplankton production, we arrive at 30 % of the phytoplankton detritus reaching the bottom as labile organic carbon. The labile component of allochthonous sedimented material is taken to be 10 %, which appears to be high, considering the observations of Grant & Hargrave (1987) on labile organic carbon in the upper centimeter of coastal sediment from Halifax Harbour (Nova Scotia, Canada). Microphytobenthos production, considered as living material, is partitioned into 50 % labile and 50 % refractory organic carbon.

Control functions: A detailed discussion of these functions is available in Wiegert et al. (1981) (see Appendix 2). The ingestion rate can depend on either the standing stock of the donor or that of the recipient. For each 'donor-recipient' pair, 4 parameters must be included in the control functions which are the thresholds at which food limitation or food saturation occurs. Field and laboratory observations on the values of the thresholds are scarce. In the present study carrying capacity of the system (G_{jj}) for the recipient compartment is based on the maximum observed biomass in the field. The threshold below which no limitation occurs (A_{jj}) is derived from the relation $G_{jj} = 10 A_{jj}$ (Pace et al. 1984).

Assumptions on donor-density-dependent thresholds are even more artificial, as few data are available. The refuge level (G_{ij}) is the minimum concentration of donors below which no predation occurs. This value was assumed to be 10 times below the mean observed biomass. The satiation thresholds, under which the ingestion rate of the recipient is maximum, were determined by calibration, assuming that maximum specific predation is a characteristic not only of the predator, but also of the prey population (Legovic 1989).

Consumers usually feed on more than one food source, so a feeding preference parameter (P_{ij}) is included in the ingestion rate control according to the dominant feeding preference, or selection, of each compartment.

RESULTS

Annual carbon flows and budget

In the initial run of the model, seasonal forcing functions were (1) inputs of organic carbon from the water column plus microphytobenthic production, and (2) temperature effects on physiological processes. Mean values of biomass and annual fluxes, given in Fig. 2, were obtained after complete stabilization of the system which occurred after a number of runs depending on the initial values of the state variables. Agreement with average measured biomass was good (cf. Table 2 & Fig. 2). At this stage, the results of the simulation provide a rough outline of the community carbon flows.

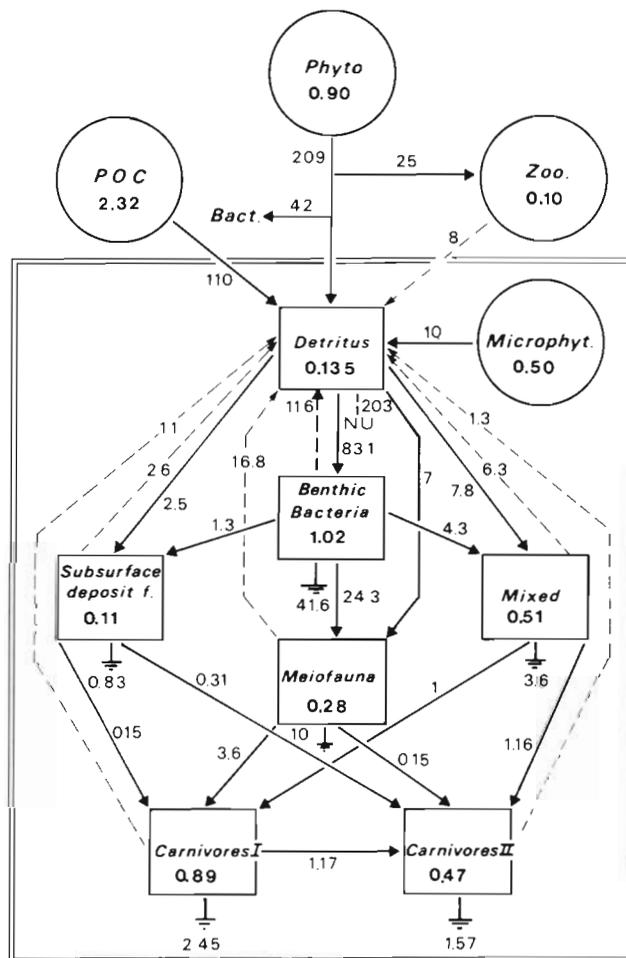


Fig. 2. Annual carbon flows for the *Abra alba* community: results from the model. Exogeneous variables are in circles; endogeneous variables are in squares. \longrightarrow : trophic fluxes; \dashrightarrow : faeces + non-predatory mortality; \perp : respiration; \square : boundary of the benthic system; POC: particulate organic carbon; Phyto.: phytoplankton; Zoo.: herbivorous zooplankton; Microphyt.: microphytobenthos; NU: not used (stored or exported). Biomasses in g C m^{-2} . Annual average flows in $\text{g C m}^{-2} \text{yr}^{-1}$.

Phytoplankton production and allochthonous sources of carbon are the 2 main inputs to the benthic system. The annual sedimented phytoplankton biomass is estimated at 53 % of total input, and represents 68 % of pelagic primary production. The simulation shows that much of the phytoplankton primary production is consumed by the benthos and demonstrates the importance of benthic-pelagic coupling. Sedimented allochthonous carbon contributes 41 % of the total supply of organic carbon for the benthos, but contributes only 18 % to the labile carbon pool, useful to benthic consumers. Other sources, such as faecal pellets, are negligible.

The annual respiration of benthic heterotrophs in the model is $61 \text{ g C m}^{-2} \text{ yr}^{-1}$, 70 % of which can be attributed to bacteria. Ecological efficiencies (production/ingestion ratio) for benthic fauna vary from 13 to 26 %. Annual P/B ratios calculated from the output of the model are quite near to those determined in field studies or estimated from the literature: 22.3 for 'bacteria', 14.5 for 'meiofauna', 4 for 'mixed', 4.2 for 'deposit-feeders' and 1.3 for 'carnivores I'.

In the model, the food supply entering the benthic system is mainly utilized by the microbiota (85 %), which itself is largely consumed by the meiofauna (80 %). The carbon flow diagram clearly shows the central route: [detritus] \rightarrow [microbiota] \rightarrow [meiofauna]

which constitutes the major pathway of energy transfer within the benthic system. Conversely, bacteria are not the principal source for macrofauna and contribute about one third of the diets of deposit-feeders and mixed feeders.

Seasonal cycle of state variables

The accuracy of the simulation results in relation to the data is not quantified. The quality of the simulation is judged by visual comparison of measured standing stocks and calculated curves.

Fig. 3 shows seasonal variations in the 6 biotic compartments. The seasonal cycle of bacteria is strongly related to the input of labile organic carbon (Fig. 4) which itself reflects, to a large degree, the pelagic primary production input. The magnitude of the annual variations is quite realistic, but the maximum peak in June appears too early and is overestimated. This discrepancy may be partly explained by the fact that, in the model, phytoplankton production is instantaneously channelled to the benthos, while in the sea, an approximate sedimentation time of 20 d would be necessary for this transfer.

The meiobenthos compartment follows the dynamics of the bacteria, but with a shift of the biomass peak to the end of the summer period. Field measurements of

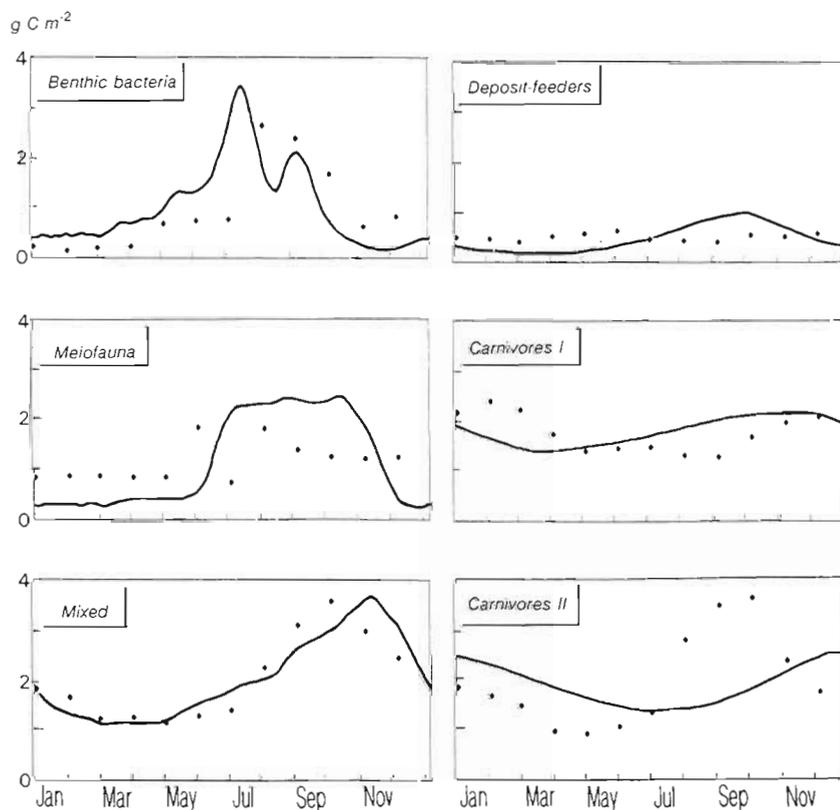


Fig. 3. Simulated biomasses (in g C m^{-2}) of the benthic compartments over an annual cycle. (•) Observations; (—) simulations

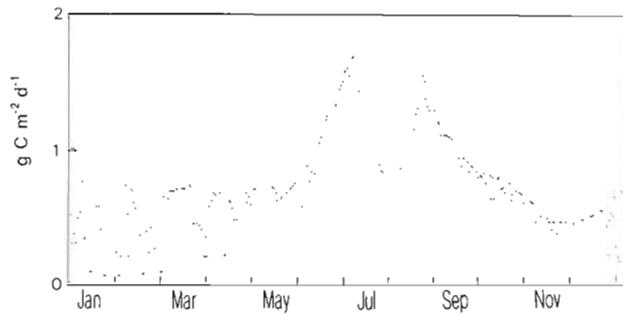


Fig. 4. Simulation of daily net sedimentation of organic carbon in the Bay of Morlaix

the meiofauna compartment exhibit a more complex pattern, with a decline in July, which is not reproduced by the model.

Seasonal changes of the 'mixed' state variables is well simulated, both in amplitude and phase, except for a discrepancy in timing of the maximum biomass. The shape of the seasonal curve is in good accordance with inputs of carbon from the water column and bacterial dynamics, with a slow response time, producing a delay of about 3 mo in the arrival of the maximum biomass.

Deposit-feeders show continuously low biomass and no marked seasonal variations. The simulated curve exhibits the same general trend as the 'mixed' compartment, the feeding sources being the same. Field measurements confirm the lack of a maximum biomass in September.

Carnivores I and II are not adequately simulated, seasonal variations being out of phase and with damped amplitude. Food availability and temperature factors are insufficient to simulate the dynamics of the higher trophic levels of the benthic food web which may be affected by other regulating factors such as spawning and recruitment.

Spawning and recruitment effects

Spawning and recruitment effects can be introduced in the simulation insofar as knowledge of the life cycle of the major populations of the macrofauna compartments is available. Periods of spawning and recruitment were derived from studies by Dauvin (1984, 1990). The spawning function drives the release of the amount of energy equivalent to the annual gonad production in daily portions over the spawning period (see function *SPAWN*; Appendix 3). Gonad production is estimated at 20 % of annual somatic production (Admiraal et al. 1988). The energy released is transferred to the pelagic system and is considered as an output.

Recruitment effects are more complex to simulate. Settlement of larvae makes a very small contribution to biomass (Admiraal et al. 1988), but significantly modifies the mean individual weight of the compartment. Basic metabolic rates, as exponential functions of individual weight, therefore are strongly affected. This is illustrated by examination of the size frequency distribution of the *Abra alba* population in 1980 (Dauvin 1984). The variation of the P/B ratio was approximated using the function defined by Schwinghamer et al. (1986): $P/B = 0.525 W_1^{-0.304}$ (Fig. 5), mean individual weight (W_1) being derived from a length-weight allometric relationship. The P/B ratio varies between 0.4 and 4 during an annual cycle. From these observations we can expect that the recruitment effect may be an important regulator mechanism of standing stock fluctuations.

Recruitment was simulated by increasing the basic ingestion and respiration rates of the macrofauna compartments by a factor of 2 when the mean individual weight is considered to be minimum (see function *RECRUITMENT*; Appendix 3). The other parameters, established for the first standard run, were not modified. Larval settlement is neglected in the model.

Introducing spawning and recruitment effects into the model does not affect the results for microbiota, meiofauna, and mixed and subsurface deposit-feeders (Fig. 6). There is good agreement between observed data and model results for carnivores I from April to December, the period during which spawning and recruitment occur (Fig. 6). But the model still does not correctly simulate standing stock variations during the first 4 mo of the year. A possible explanation is that some species within the compartment are, in reality, able to use detritus from the water column, and are not strictly carnivorous as modelled. A change of feeding habits can also occur between juveniles (detritivorous) and adults (strictly carnivorous), as in *Nephtys hombergii*.

Simulation of carnivores II is partly corrected in the second part of the year compared to the first analysis,

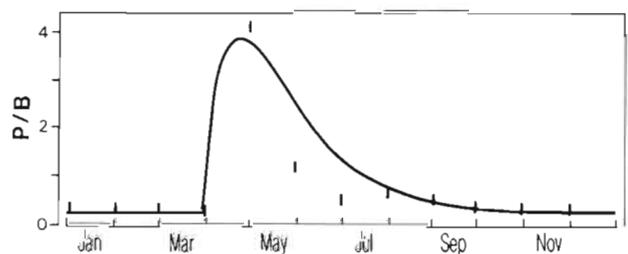


Fig. 5. Calculated production/biomass (P/B) ratio (points) over an annual cycle using the function of Schwinghamer et al. (1988), with adjusted line: $P/B = 0.525 W_1^{-0.304}$ (where W_1 = mean individual weight)

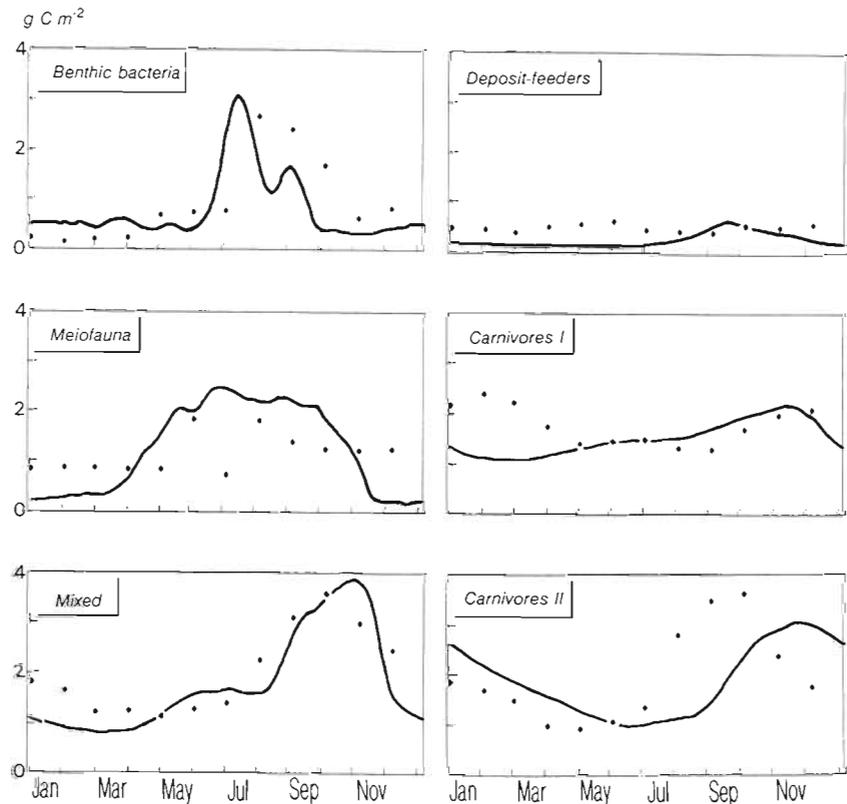


Fig. 6. Simulated biomasses (in g C m^{-2}) of the benthic compartments over an annual cycle after introduction of spawning and recruitment effects. (•) Observations; (—) simulations

but the simulated maximum of biomass is almost 2 mo later than in field observations. This reflects a strong 'predator-prey' link with carnivores I, which represents, in the model, the main trophic source for carnivores II. This link is probably much too rigid, and more diverse feeding by carnivores II would reduce the lag of the maximum biomass in the model.

Sensitivity analysis

In order to ascertain which physiological parameters have a large influence on the results, a sensitivity analysis was performed by running the model with different values of parameters. The results are illustrated in Table 3 which shows the relative sensitivity of each compartment to an increase of 10% of the value of each physiological rate. For example, an increase of 10% in I_2 , the maximum rate of consumption of bacteria, produces an increase of biomass of the compartments 'bacteria', 'deposit-feeders' and 'carnivores I' compartments, and a decrease of the compartments 'mixed', 'meiofauna' and 'carnivores II'. The sum of absolute values of the relative changes expresses the 'total change' (Brylinsky 1972) and defines the most sensitive parameters. In view of the wide variability of almost all reported parameter values in the literature, an increase of 10% is a minor change; nevertheless it

gives an idea of the relative influence of the physiological rate on the output state variable. Mortality is not a sensitive parameter. Highest total changes are caused by increasing maximum ingestion rate of the 'mixed' and 'meiofauna' compartments, carbon conversion efficiency of the 'bacteria' compartment, and egestion rate of the 'mixed' compartment. This analysis shows the highest relative sensitivities to the parameters driving the carbon flow through 'bacteria' and 'meiofauna' compartments, through which the transfer of energy is the greatest. These changes illustrate the trophic competitive relationships between the compartments, particularly between 'mixed', 'deposit-feeders' and 'meiofauna', at one level, and 'carnivores I' and 'carnivores II', at a second level.

DISCUSSION

A general view of the annual carbon budget of the *Abra alba* community of the Bay of Morlaix indicates that phytoplankton production is the largest organic carbon source for the benthos and that 68% of the primary production is consumed by the benthos. This estimate is similar to observations made in the *Abra alba* community of the western Baltic, where 61% of the pelagic production was found to reach the sea-floor (Arntz 1978). Previous studies in shallow water have

Table 3. Results of the sensitivity analysis. Relative sensitivity in percent change of biomass to an increase of 10 % of parameter values. Total change is the sum of the absolute values of the relative changes. For explanation of parameters, see Appendix 1

Parameter	X2 Bacteria	X3 Mixed	X4 Deposit	X5 Meiofauna	X6 Carnivores I	X7 Carnivores II	Total change
I ₂	9.25	-10.65	7.96	-5.96	0.79	-13.68	48.30
I ₃	-28.54	50.89	-40.71	16.84	-4.17	42.95	184.10
I ₄	-14.67	8.68	8.85	9.12	-1.24	12.18	54.73
I ₅	-28.15	8.68	-33.63	28.42	-0.34	20.73	116.94
I ₆	9.35	-5.72	7.08	-5.61	3.83	-8.76	40.35
I ₇	-15.75	-6.71	-23.01	15.79	-4.73	3.42	69.40
R ₂	-40.65	9.66	-46.02	14.74	-4.39	10.04	125.50
R ₃	15.55	-19.53	15.04	-6.67	2.93	-23.29	83.01
R ₄	1.28	0.59	-10.62	0.00	0.90	-7.05	20.44
R ₅	0.59	5.33	1.77	-7.02	-1.69	-7.69	24.08
R ₆	-2.17	4.54	0.88	0.35	-2.14	-6.62	16.70
R ₇	-7.58	17.16	0.88	2.46	2.70	-6.84	37.62
M ₂	-14.17	7.89	-9.73	7.37	-1.46	7.48	48.11
M ₃	1.18	-1.78	0.88	-0.35	0.23	-1.92	6.34
M ₄	0.20	-0.20	-0.88	0.00	0.00	-0.43	1.71
M ₅	0.49	0.00	0.00	-0.70	-0.23	-0.64	2.06
M ₆	0.00	0.00	0.00	0.00	-0.23	-0.21	0.44
M ₇	-0.30	0.59	0.00	0.35	0.11	-0.43	1.78
E ₃	24.61	-29.78	23.01	-9.12	4.05	-32.05	122.63
E ₄	5.51	-4.54	-14.16	-1.75	-0.11	-5.56	31.63
E _{4b}	-0.79	2.56	-5.31	0.70	0.90	-4.27	14.54
E ₅	15.94	0.99	11.50	-14.39	-5.29	-9.83	57.94
E ₆	-2.85	2.76	-1.77	1.75	-1.58	0.43	11.14
E ₇	-1.87	3.75	0.00	0.70	0.68	-1.92	8.92

shown that the part of primary production sinking to the bottom ranges from 25 to 60 % (Zeitzchel 1979). Thus, strong benthic-pelagic coupling could be an important feature of the carbon budget of the *Abra alba* community.

In terms of total organic carbon, allochthonous matter constitutes a significant input (41 % of the total) which is in agreement with most of the budgets established in coastal areas such as the Wadden Sea or Ems-Dollard estuary (Kuipers et al. 1981, De Wilde & Beukema 1984, Baretta & Ruardij 1988). But the contribution of this source as a food supply, which assumes a distinction, at least, between labile and refractory carbon, is rarely outlined in carbon flow studies.

The overall annual consumption of the benthic heterotrophic compartment (61 g C m⁻² yr⁻¹) is in good agreement with estimates for other subtidal areas such as the Fladen Ground of the North Sea (50 to 70 g C m⁻² yr⁻¹; De Wilde et al. 1986) and the continental shelf of New England, USA (48 g C m⁻² yr⁻¹; Rowe et al. 1988). It is considerably higher than the results of De Wilde et al. (1984) for the Oyster Ground, North Sea (28 g C m⁻² yr⁻¹) and lower than Baretta & Ruardij's (1988) estimate from the model of the western Wadden Sea (192 g C m⁻² yr⁻¹)

The total heterotrophic benthic biomass of the Pierre Noire fine sand community is 3.28 g C m⁻². This value is lower than the biomass of 8.1 g C m⁻² measured by Warwick et al. (1979) on a mud-flat in the Lynher estuary (Cornwall, UK) where *Nephtys hombergii* is dominant or the estimate of 6.6 g C m⁻² in an *Abra alba* community of the North Sea by Gerlach (1978), but similar to the biomass of 2 to 4 g C m⁻² measured by Rees (1983) at some stations of *Abra alba/Venus striatula* along the North Sea coast of Yorkshire, UK. The peculiarity of the Pierre Noire community trophic structure is that the top consumers of the food web, which are the carnivorous compartments, represent 42 % of the total heterotrophic biomass. This property has strong implications on the contribution of microbiota and meiofauna to the general features of carbon flow.

Regarding the role of particulate organic matter in benthic nutrition, Levinton et al. (1984) noted 'it is likely that a complex answer to the detritus-microbes-benthos nutrition problem will emerge'. The contribution of the bacteria to the fluxes in benthic food webs is still poorly known. Estimation of bacterial production in the sediment is a way to determine such a contribution (Van Duyl & Kop 1990). The mean production value estimated from the model (116 mg C m⁻² d⁻¹) is

of the same order of magnitude as field results from comparable subtidal ecosystems: 30 to 390 mg C m⁻² d⁻¹ in the Dutch Wadden Sea (Van Duyl & Kop 1990), 100 to 810 mg C m⁻² d⁻¹ in a coastal zone off Georgia, USA (Fallon et al. 1983) and 43 mg C m⁻² d⁻¹ in a coastal zone of Germany (Meyer-Reil et al. 1980). These values suggest that bacteria are a significant trophic link between detritus and benthic organisms. Data on the seasonal variation of bacterial biomass in temperate subtidal sediment are very scarce. However, the simulation gives a range between 0.2 and 4.8 g C m⁻² which is in good agreement with bacterial biomass variations measured in the top 5 cm in a shallow marine bay of the northern Adriatic Sea (Herndl et al. 1987). The link between the variation of organic carbon input and seasonal pattern of bacterial biomass supports the idea that benthic microbiota is limited by the supply of organic material, most of which comes from the water column via sedimentation (Meyer-Reil 1987, Billen & Lancelot 1988, Cole et al. 1988, Van Duyl & Kop 1990). The partitioning of the available detritus among benthic bacteria, meiofauna and macrofauna is dependent on the response time of each compartment to changes in food supply (Baretta & Ruardji 1988). The microbiota, having the shortest generation time and fastest response, consumes 84 % of the detritus. The role of meiobenthos as potential food for macrofauna is still a matter of research today. The concept of an 'independent food web with a low predation pressure' (Banse & Mosher 1980) has been supported by several authors. McIntyre et al. (1970) and Gerlach (1971) hold that meiobenthos represents a supplementary, but not essential, food source for the macrobenthos, mostly for subsurface deposit-feeders, in accordance with the lack of selectivity of their nutritional mode. The general picture of the carbon flows through the *Abra alba* community of the Bay of Morlaix, exhibited by the model, does not support this view. The existence of the 'upper part' of the food web is strongly linked to meiofauna production. In their review of the productivity of marine nematodes, Vranken & Heip (1986) outline examples of fish and crustacean diets in which the meiofauna component is well represented. The main argument in favour of the importance of meiofauna as an important link between bacteria/detritus and carnivores in our model is the low biomass of the deposit-feeders and suspension feeders, whose production is insufficient to support the energy demand of the top consumers.

Seasonal variations of the benthic compartment are satisfactorily simulated at low trophic levels, except for the meiobenthos which is probably contains most complex mix of feeding modes. Discrepancies between the simulation and field data are large in the 'upper part' of the benthic food web due to limitations in

the model. One limitation is that carnivorous diet is probably more flexible and opportunistic than in our theoretical representation of the food web. The Lynher model (Warwick et al. (1979) clearly illustrates that *Nephtys hombergii* is incapable of surviving as a strict predator. Their most realistic simulation has been achieved by allowing *Nephtys* to feed on phytobenthos as well as meiofauna and deposit feeders. Possible adaptive changes in the diet might occur according to the availability of the food source supplies. Another important limitation in our model is that the dynamics of carnivores, which are composed of long-lived species, cannot be described only by 'growth-related' processes formulated by a set of 'donor-recipient' functions. Even a rough simulation of the spawning and recruitment processes improves the results. Time of spawning may be partly driven by temperature, but at this state of our knowledge, we cannot derive a predictive function of recruitment from a simple formulation. The success of recruitment is dependent on a complex of factors (hydrodynamics, food, temperature, juvenile mortality, larval fixation, etc.) and is still a central problem of population dynamics (Dauvin 1989, 1990).

CONCLUSION

Any carbon flow investigations dealing with benthic ecosystems encounter the same major elements: sources of organic matter, significance of the bacteria as a trophic source, importance of the meiofauna to higher trophic levels, competition among macrofauna consumers, efficiencies of the energy transfers, etc.

In summary, carbon flow pathways within the *Abra alba* community of the Bay of Morlaix have the following main features:

- (1) Phytoplankton production represents the major food supply for the benthic system and confirms the importance of the pelagic-benthic coupling in such an area.

- (2) A large proportion of the carbon input is consumed by the bacteria (84 %), which itself constitutes the main trophic source (80 %) for the meiofauna. The microbiota is not the most important diet for mixed and deposit-feeders, which mainly consume sedimented detritus.

- (3) Meiofauna is an important trophic link between the basic food supply (bacteria + detritus) and the carnivore level, and cannot be considered as an independent food web.

- (4) Efficiencies of energy transfer range from 13 to 26 %, which is in accordance with the mean values encountered in similar ecosystems.

Dynamics of the benthic compartments formulated by growth-related processes are unrealistic in the

higher trophic levels of the food web. Two main reasons are: the lack of realism in the modelled diet of the carnivores, which might feed more opportunistically, and the lack of regulation factors such as spawning and recruitment.

Taking into consideration spawning and recruitment effects, as forcing functions in the model, improves the agreement with the observations for the carnivore compartments. Thus, spawning and recruitment may be considered important regulating factors. Modelling these processes, however, requires detailed population

studies and cannot be based on simple formulations because of the diversity and complexity of the factors involved.

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APPENDIX 1

General equation used for simulation of interactions between biotic compartments (from Pace et al. 1984):

$$\frac{dX_j}{dt} = \sum_{i=1}^m (P_{ij} \cdot I_j \cdot X_j \cdot F_{ij} \cdot F_{jj} \cdot (1 - E_j) - (M_j + R_j) \cdot X_j) - \sum_{k=1}^n (P_{jk} \cdot I_k \cdot X_k \cdot F_{jk} \cdot F_{kk})$$

where X_j = biomass of compartment j ; I_j = maximum specific rate of ingestion of j ; P_{ij} = feeding preference for a resource i by j ; F_{ij} = limitation on ingestion of j by the scarcity of the resource i (see Appendix 2, Control functions); F_{jj} = limitation on ingestion of j by intracompartamental competition (see Appendix 2, Control functions); E_j = proportion of ingestion which is egested; M_j = non-predatory mortality rate; R_j = respiration rate; i ($= 1 \dots m$) = available resources for j ; k ($= 1 \dots n$) = predators for j .

Differential equations for each of the 6 biotic compartments are written employing the general format of Eq. (1). Values of biotic compartment rates are given in Table A1.

Table A1. Values of biotic compartment rates used in the model. All values are d^{-1} except egestion which is dimensionless

Compartments		Ingestion I_i	Respiration R_i	Mortality M_i	Egestion E_i
Benthic bacteria	X_2	0.75		0.030	
Mixed	X_3	0.09	0.19	0.0014	
Deposit-feeders	X_4	0.12	0.019	0.0015	0.80–0.35 ^a
Meiofauna	X_5	0.54	0.095	0.010	0.50
Carnivores I	X_6	0.026	0.0075	0.0005	0.20
Carnivores II	X_7	0.034	0.0094	0.0040 ^b	0.20

^aDeposit-feeders egest 80 % of the detrital carbon ingested and 35 % of the bacterial carbon ingested
^bMortality rate of the top predators (Carnivores II) is assumed to be equal to P/B ratio

APPENDIX 2

Control functions (from Wiegert et al. 1981)

Control by scarcity of a resource, or donor:

$$F_{ij} = 1 - \frac{(A_{ij} - X_i)}{(A_{ij} - G_{ij})}$$

where X_i = biomass of the donor compartment i ; A_{ij} = satiation threshold of i : if $X_i > A_{ij}$ then $F_{ij} = 1$; G_{ij} = threshold biomass below which the specific ingestion rate of the recipient compartment j is zero (refuge level): if $X_i < G_{ij}$, then $F_{ij} = 0$.

Control by intracompartamental competition:

$$F_{ij} = 1 - 1 - \left(\frac{(R_j + M_j)}{I_j(1 - E_j)} \right) \left(\frac{(X_j - A_{jj})}{(G_j - A_{jj})} \right)$$

where X_j = biomass of the compartment j ; A_{jj} = threshold biomass below which the specific ingestion rate of j is maximal: if $X_j < A_{jj}$, then $F_{jj} = 1$; G_j = threshold biomass above which the specific ingestion rate of j is equal to maintenance:

$$\text{if } X_j > G_j, \text{ then } F_{jj} = \frac{(R_j + M_j)}{I_j(1 - E_j)}$$

Threshold values are given in Tables A2 & A3.

Table A2. Values of the resource thresholds (A_{ij} , G_{ij}) and feeding preferences (P_{ij}) of the trophic fluxes (F_{ij})

Flux (F_{ij})	A_{ij}	G_{ij}	P_{ij}
F_{12}	0.40	0.01	
F_{13}	0.20	0.02	0.60
F_{14}	0.20	0.02	0.70
F_{15}	0.20	0.02	0.30
F_{23}	1.20	0.10	0.40
F_{24}	1.00	0.10	0.30
F_{25}	0.50	0.01	0.70
F_{36}	0.40	0.32	0.20
F_{46}	0.40	0.12	0.20
F_{56}	0.10	0.03	0.60
F_{37}	0.80	0.05	0.30
F_{47}	0.35	0.01	0.30
F_{57}	0.80	0.03	0.10
F_{67}	1.40	0.09	0.30

Table A3. Values of the intracompartamental threshold (A_{ij} , G_{ij})

Compartment	A_{ij}	G_{ij}
X_2	0.50	5.00
X_3	0.40	4.00
X_4	0.05	0.50
X_5	0.07	0.70
X_6	0.15	1.50
X_7	0.13	1.13

APPENDIX 3

Function SPAWN:

$$y_j = a_1 - b_1 \cos(2(j - c_1)/365) \text{ (if } y_j < 0 \text{ then } y_j = 0)$$

where y_j = daily biomass released; a_1 = parameter controlling the spreading of the spawning period; b_1 = parameter controlling the quantity of biomass released; c_1 = parameter controlling the period of the maximum spawning peak; j = day of the year.

Function RECRUITMENT:

$$f_j = a_2 - b_2 \cos(2(j - c_2)/365) \text{ (if } f_j < 1 \text{ then } f_j = 1)$$

where f_j = corrective factor for the physiological rates; a_2 = parameter controlling the spreading of the recruitment period; b_2 = parameter controlling the intensity of f_j ; c_2 = parameter controlling the period of the maximum recruitment peak; j = day of the year.

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