Interrelations in a microcosm with a suspension-feeder and a deposit-feeder. II: Modelling

Suspension-feeders
Deposit-feeders
Pollutant
Bioturbation
Modelization

Filtreurs
Dépositivores
Polluant
Bioturbation
Modélisation

Jean-Michel AMOUROUX [a], Jacques AMOUROUX [b], Jean BASTIDE [c], Guy CAHET [d], Antoine GRÉMARE [a]

[a] Centre National de la Recherche Scientifique, Laboratoire Arago 66650 Banyuls-sur-Mer, France.

[b] École Nationale Supérieure de Chimie de Paris (ENSCP), Université Pierre-et-Marie-Curie, 4, place Jussieu, 75252 Paris Cedex 05, France.

[c] Institut Universitaire de Technologie, Université de Perpignan, avenue de Villeneuve, 66000 Perpignan, France.

[d] Laboratoire Arago, 66650 Banyuls-sur-Mer, France.

Received 29/7/88, in revised form 24/4/89, accepted 28/4/89.

ABSTRACT

A microcosm comprising a filter-feeding bivalve (*Venerupis decussatus*), a deposit-feeding annelid (*Eupolymnia nebulosa*), a live monospecific suspension and sediment was studied on the basis of a compartmental analysis. The consumption and biodeposition of two different live suspensions of bacteria and algae by *Venerupis decussatus* were measured. Suspensions was labelled with ^{14}C. A series of experiments of varying duration made it possible to quantify the diffusion of ^{14}C from suspensions to animals and sediment. An analog model of radioactivity changes in the different compartments of the system was elaborated. Constants of exchanges of organic matter between compartments, and amounts of organic matter which transited through the different compartments were calculated. Annelids scraped the biodeposits of the bivalves and this bioturbation resulted in the resuspension of such particulate matter. The impact of a pollutant on the kinetics of exchanges was assessed by comparison of two models. Presence of the pollutant did not affect general exchanges between compartments.

Oceanologica Acta, 1990. **13**, 1, 69-78.

RÉSUMÉ

Interrelations entre filtreurs et dépositivores en microcosme. II : Modélisation

L'étude des interrelations entre un bivalve filtreur (*Venerupis decussata*), une annélide dépositivore (*Eupolymnia nebulosa*) et une suspension monospécifique vivante (algues unicellulaires ou bactéries) est réalisée en microcosme. L'analyse compartimentale du système permet de mesurer l'évolution des différents compartiments du système en fonction du temps. La modélisation analogique conduit à la quantification des flux de matière entre les compartiments et à la mesure des quantités consommées et assimilées. Il est possible de figurer l'évolution de compartiments non accessibles à l'expérimentation. L'impact d'un polluant sur les échanges mesurés ou calculs s'avère faible. Ce travail montre l'importance des phénomènes de bioturbation sur les recyclages de la matière organique déposée sur le sédiment.

Oceanologica Acta, 1990. **13**, 1, 69-78.

INTRODUCTION

In an earlier paper (Amouroux *et al.*, 1989), we studied experimentally: 1) the consumption; and 2) the transfer of two monospecific live suspensions (bacteria and algae) from the water column to the water-sediment interface through the action of a filter-feeding bivalve and a deposit-feeding annelid. The aim of the present study was: 1) to measure the transfer-kinetics between the live suspensions and the sediment; and 2) to quantify radioactivity changes that could not be determined by experimental procedures.

The use of ^{14}C permits the study of both: 1) the consumption of particulate matter by suspension- and deposit-feeders; and 2) the interactions between the different compartments of the microcosm (Conover and Francis, 1973). However, ^{14}C is a non conservative tracer which is very rapidly recycled inside closed experimental chambers. Such recycling complicates the interpretation of experimental data. Conover and Francis (1973), and then Dring and Jewson (1982) recommended compartmental analysis coupled with analog modelling for the studies of trophic transfers in marine food chains. In the present paper we have adopted this approach, and constructed a model describing the exchanges between compartments in a "suspension-suspension-feeder- deposit-feeder" system.

The influence and transfer of a pollutant dissolved in the water has already been studied as a disturbing factor of the kinetics of organic matter consumption in the system (Brockway *et al.*, 1984; Huckins *et al.*, 1984; Larsson, 1983; Spain *et al.*, 1980). In the present study we compared the two models "suspension- suspension-feeder-deposit-feeder" in the presence and in the absence of an organic pollutant, "Kerb". This new approach leads to quantification of the effect of the pollutant.

MODELLING

The experimental study of the "suspension- suspension-feeder-deposit-feeder" system was carried out using compartmental analysis and a radioactive tracer. The diffusion, as a function of time, of the tracer through the different compartments was measured experimentally. Such an analysis is especially appropriate for this kind of study (Goldstein and Elwood, 1971; Grégoire, 1972; Conover and Francis, 1973; Smith and Horner, 1981; Amouroux, 1984; *a*; *b*; Amouroux and Amouroux, 1988; Amouroux *et al.*, 1989) and leads to an analog modelling which permits quantification and comparison of exchanges between compartments.

The system was divided into several compartments following the method described in a previous paper (Amouroux and Amouroux, 1988). Measurements of the transfer of organic matter between the different compartments of the system were calculated on the basis of differential (rather than linear) equations. The complete system was composed of 6 compartments: suspension; bivalves; annelids; dissolved substances; sediment; and CO_2 (Fig. 1). Changes of radioactivity in the different compartments resulted from multiple exchanges between compartments. For example: 1) suspensions were filtered by bivalves which produced faeces, dissolved substances and CO_2, and consumed dissolved substances; 2) suspensions produced dissolved substances and CO_2, and consumed dissolved substances; 3) annelids consumed dissolved substances and faeces of the bivalves, and produced faeces, dissolved subtances and CO_2; 4) the sediment received faeces, and consumed and produced CO_2. Such complexity makes it difficult to study all the components of the system simultaneously. The "suspension-suspension-feeder-deposit-feeder-sediment" system was consequently divided into several subsystems composed of only 3 or 4 compartments: 1) "suspension" (alone in seawater); 2) "suspension-sediment"; 3) "suspension-suspension-feeder"; 4) "suspension-deposit-feeder"; 5) "suspension-suspension-feeder-sediment"; and 6) "suspension-deposit-feeder-sediment" (Vietinghoff, 1984). For each of these subsystems, an analog model was established and tested relative to experimental data. Kinetic constants of the submodels were integrated into the general model of the complete system. After fitting the models it was possible to quantify exchanges between compartments.

The computation of the consumed, ingested (in particulate form) and assimilated amounts of organic matter by the bivalves required computation of the cumulated amounts of radioactivity within the different compartments. This could only be achieved by modelling the system. The amount consumed was set as the total amount of radioactivity corresponding to bivalve soft parts plus excretory products (faeces, DOM, NRDOM, CO_2). The amount ingested was set as the difference between total consumption (see above) and DOM consumed by the bivalves. The amount assimilated was set

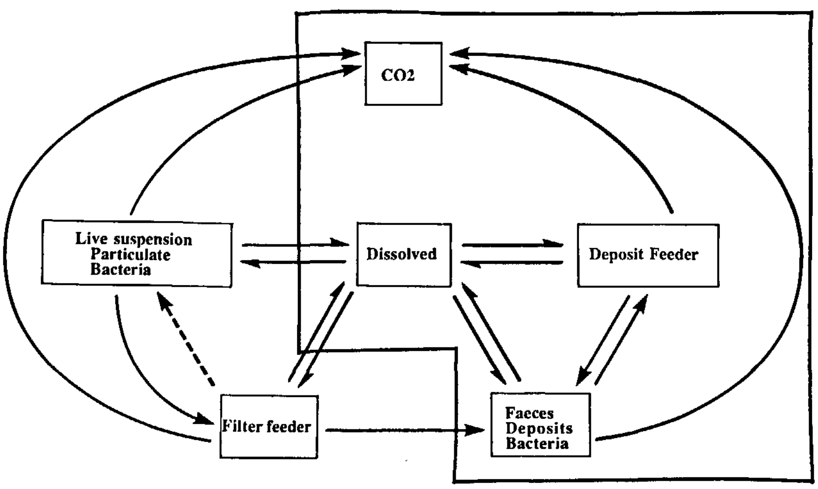

Figure 1
Presentation of the different compartments of the system and their relations.
Présentation des différents compartiments du système et de leurs relations.

Table 1

Comparison of results for bacteria and algae after fitting the model. The amount of cumulated radioactivity is listed for each compartment after 40 hours. 1) Faeces; 2) CO_2 produced by bivalves; 3) NRDOM produced by bivalves; 4) DOM produced by bivalves; 5) DOM consumed by bivalves. The amounts of radioactivity presents in each compartment are shown and the amounts consumed, ingested and assimilated are calculated. Values are expressed as percentages of initial radioactivity.

Comparaison des résultats pour les bactéries et les algues après ajustement du modèle. Les quantités cumulées sont indiquées pour chaque compartiment après 40 heures. 1) Fécés; 2) CO_2 produit par les bivalves; 3) NRDOM produit par les bivalves; 4) DOM produit par les bivalves; 5) DOM consommé par les bivalves. Les quantités de radioactivité présentes dans chaque compartiment sont exposées à la suite et les quantités consommées, ingérées et assimilées sont calculées. Les valeurs sont exprimées en pourcentage de la radioactivité initiale.

	Bacteria	Bacteria Kerb	Algae
40 hours cumulated			
(1) Faeces	146.1	165.4	221.0
(2) CO_2 prod. Biv.	47.7	54.1	4.6
(3) NRDOM	9.5	0.0	0.7
(4) DOM prod. Biv.	118.5	134.1	109.6
(5) DOM cons. Biv.	94.8	33.5	69.3
40 hours present			
Particulate	2.4	3.5	1.9
Bivalves	14.3	18.1	37.9
Faeces Sediment	40.3	48.2	–
Faeces	–	–	10.8
DOM	5.0	6.6	3.2
NRDOM	9.5	0.0	0.7
CO_2	28.6	23.5	5.2
Amount consumed	335.8	371.7	373.8
Amount ingested	241.0	338.2	304.5
Faeces produced	146.1	165.4	221.0
Faeces recycled	105.7	117.1	200.2
DOM consumed	94.8	33.5	69.3
Amount assimilated	189.7	206.3	152.8

as the difference between total consumption and faeces produced.

The different computations were carried out on an analog computer EAI and were completed using STELLA (R) software on a MacIntosh microcomputer.

"Bacteria-bivalves-annelids-sediment" system (Tab., Fig. 2, 3, 4, 5 and 6)

This system is composed of 6 compartments: bacteria (suspension); bivalves; annelids; dissolved substances; sediment; and CO_2 (Fig. 2).

Changes of radioactivity in the different compartments resulted from multiple exchanges between compartments. Bacteria were filtered by bivalves which produced faeces, dissolved substances and CO_2, and consumed dissolved substances. Bacteria produced dissolved substances and CO_2, and consumed dissolved substances. Annelids consumed dissolved substances, faeces of the bivalves, and produced faeces, dissolved substances and CO_2. Sediment received faeces of the

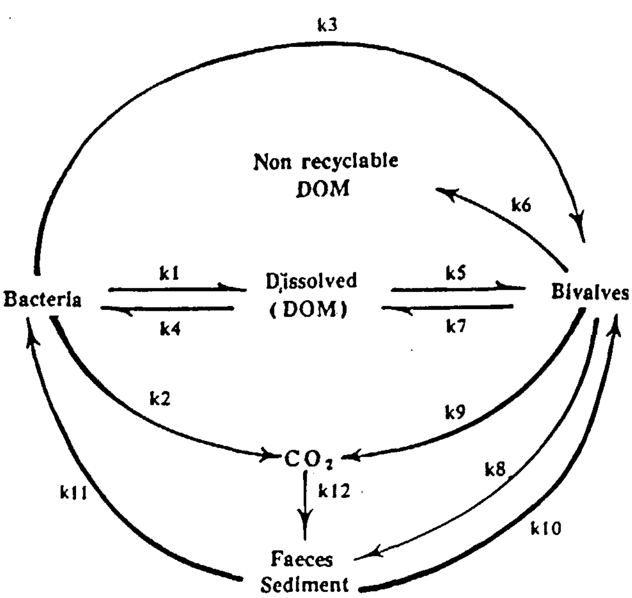

Figure 2

"Bacteria-bivalves" system. Six-compartment model showing exchanges studied and numbered kinetic constants of mass transfer (k 1 to k 12).

Système "bactéries-bivalves". Le modèle à six compartiments montre les échanges étudiés et les valeurs des constantes de transfert de masse (k 1 à k 12).

System "bacteria- bivalves-annelids- sediment".

Constant	Code	Values as h^{-1}
Bacteria	k_1	0.1400
	k_2	0.1700
	k_3	1.5000
DOM	k_4	0.3800
	k_5	0.1200
	k_6	0.0120
Bivalves	k_7	0.1500
	k_8	0.1850
	k_9	0.0600
Sediment	k_{10}	0.0400
	k_{11}	0.0600
CO_2	k_{12}	0.0450

System "bacteria- bivalve-annelids- sediment + Kerb".

Constant	Code	Values as h^{-1}
Bacteria	k_1	0.1450
	k_2	0.1600
	k_3	1.5300
DOM	k_4	0.3830
	k_5	0.1050
	k_6	0.0000
Bivalves	k_7	0.1500
	k_8	0.1850
	k_9	0.0600
Sediment	k_{10}	0.0234
	k_{11}	0.0806
CO_2	k_{12}	0.0708

System "algae- bivalves-annelids- sediment".

Constants	Code	Values as h^{-1}
Alage	k_1	0.0961
	k_2	0.0000
	k_3	1.8180
DOM	k_4	0.3216
	k_5	0.4603
	k_6	0.0004
Bivalves	k_7	0.0600
	k_8	0.1210
	k_9	0.0025
Sediment	k_{10}	0.0830
	k_{11}	0.0800
Faeces	k_{12}	0.1850
	k_{13}	0.2010
	k_{14}	0.0400
CO_2	k_{15}	0.1040
Annelids	k_{16}	0.7315

bivalves and annelids, consumed CO_2 (by benthic diatoms), and produced CO_2 and dissolved substances. These interrelations are presented in Figure 2.
The mass-transfer dynamics of the system "bacteria-suspension-feeder-deposit-feeder-sediment" were simulated by an interaction of "kinetic" equations reflecting rates of exchanges between compartments:

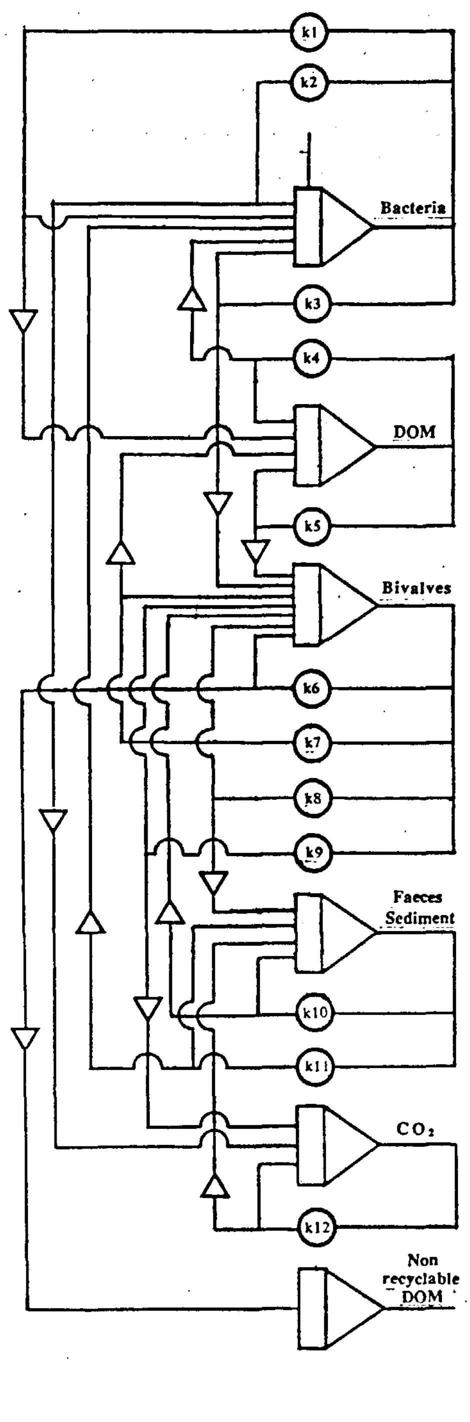

Figure 3

Modelling. Circuit diagram of the analog computer model. The annelids are not represented because of their low importance. They are considered as a bioturbating system at the sediment-sea water interface. The different exchanges are represented with the corresponding constants.
Modélisation. Schéma du circuit du modèle sur le calculateur analogique. Les annélides ne sont pas représentés en raison de leur faible importance. Ils sont considérés comme un système bioturbateur à l'interface eau-sédiment. Les différents échanges sont représentés avec les constantes correspondantes.

$$\frac{d[\text{Bact}]}{dt} = +k_4[\text{DOM}] + k_{11}[\text{Faeces Sed}] - k_1[\text{Bact}] - k_2[\text{bact}] - k_3[\text{Bact}]$$

$$\frac{d[\text{DOM}]}{dt} = +k_7[\text{Biv}] + k_1[\text{Bact}] - k_4[\text{DOM}] - k_5[\text{DOM}]$$

$$\frac{d[\text{Biv}]}{dt} = +k_5[\text{DOM}] + k_3[\text{Bact}] + k_{10}[\text{Faeces Sed}] - k_6[\text{Biv}] - k_7[\text{Biv}] - k_8[\text{Biv}] - k_9[\text{Biv}]$$

$$\frac{d[\text{Faeces Sed}]}{dt} = +k_8[\text{Biv}] + k_{12}[CO_2] - k_{10}[\text{Faeces Sed}] - k_{11}[\text{Faeces Sed}]$$

$$\frac{d[CO_2]}{dt} = +k_2[\text{Bact}] + k_9[\text{Biv}] - k_{12}[CO_2]$$

$$\frac{d[\text{NR DOM}]}{dt} = +k_6[\text{Biv}].$$

A diagram of the analog computer circuit simulating the foregoing equations with their constants and values is presented in Figure 3. The compartment "annelids" was not included into the model, because its radioactivity remained equal to zero throughout the experiments. A part of the DOM produced by the bivalves was not recycled either by bacterial suspension or bivalves: it constituted the compartment "non-recyclable DOM".

After fitting the model, the different curves representing the changes of radioactivity within compartments were drawn. It was then possible to deduce the exact shapes of the different curves (from T 0 to 40 hours; Fig. 4). $^{14}CO_2$ reached 29 % after 40 hours but was then reabsorbed by the sediment (probably by the benthic diatoms; Fig. 4). At 10 hours the model was not exactly fitted with the experimental data corresponding to the radioactivity of annelids. Annelids resuspended the biodeposits of the bivalves and sedimented bacteria; they could not, however, consume the sedimented bacteria. The sediment radioactivity was fairly constant after 10 hours (41 % of the initial radioactivity). The radioactivity in the soft body parts of the bivalves reached 56 % after 1 hour, then declined quickly until 10 hours before reaching 16 % after 40 hours. Bacteria radioactivity declined quickly during the first 2 hours and then remained fairly stable (2 %) between 2 and 40 hours. Dissolved substance radioactivity increased to 20 % after 2 hours and then declined to 11 % after 15 hours before increasing slowly to 13 % after 40 hours. This kind of variation suggested a production of dissolved substances which was reabsorbed by bivalves and sediment. After 20 hours these products were no longer recycled.

The values of the constants obtained in the model are presented in Figure 3. Use of the software "Stella (R) computation permitted calculation of the different amounts of cumulated organic matter through the different compartments. The highest value corresponded to the consumption of the bacterial suspension by the

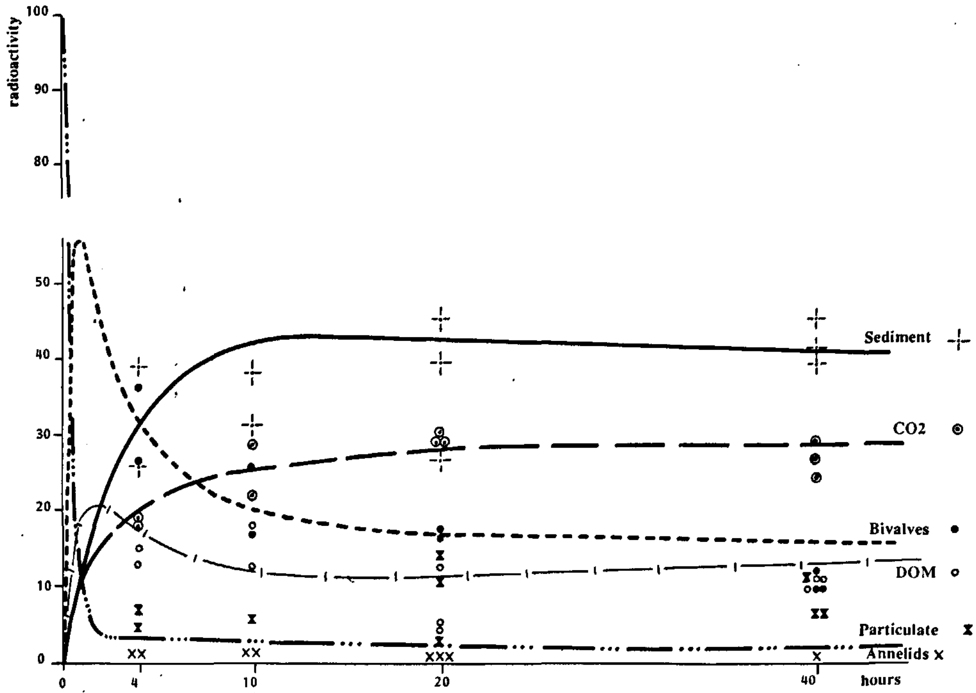

Figure 4
Modelling. Graphic representation of the time dependent variation of the radioactivity in the different compartments of the system "bacteria-sediment-annelids-bivalves" without pollutant.
Modélisation. Représentation graphique de la variation de la radioactivité en fonction du temps dans les différents compartiments du système "bactéries-sédiment-annélides-bivalves" sans polluant.

bivalves: 1.5 h^{-1}. After 40 hours, they received 3.3 times the total organic matter initially introduced into the system. The dissolved substances consumed by the bivalves had a kinetic constant of 0.12 h^{-1}. The dissolved substances produced by the bivalves had a kinetic constant of 0.15. h^{-1}. The DOM compartment received 150 % of cumulated organic matter, and 145 % were recycled after 40 hours (Fig. 5). The bivalves produced faeces (kinetic constant: 0.185 h^{-1}) and dissolved substances (kinetic constant: 0.15 h^{-1}): For the dissolved substances produced by the bacteria, the kinetic constant was 0.14. h^{-1}. For the CO_2 produced by the bacteria, the kinetic constant was 0.17. h^{-1}. All the cumulated CO_2 corresponded to 74.8 % of the initial radioactivity. Of this 74.8 and 46.2 % were recycled after 40 hours of experiment. After 40 hours the non-recyclable DOM corresponded to 9.5 % of initial radioactivity (Fig. 5).

The amount of organic matter consumed by the bivalves after 40 hours was set as the total of the amount in the soft parts of the bivalves plus the cumulated amount of faeces, CO_2 and DOM produced during this period: 14.3 + 146.1 + 47.4 + 128.0 = 335.8 % of the quantity initially introduced. The amount ingested was set as the amount consumed less the cumulated amount of consumed DOM: 335.8 − 94.8 = 241.0 % of the quantity initially introduced. The amount assimilated was set as the difference between the amount consumed less the cumulated amount of produced faeces: 335.8 − 146.1 = 189.7 % of the quantity initially introduced (Tab.).

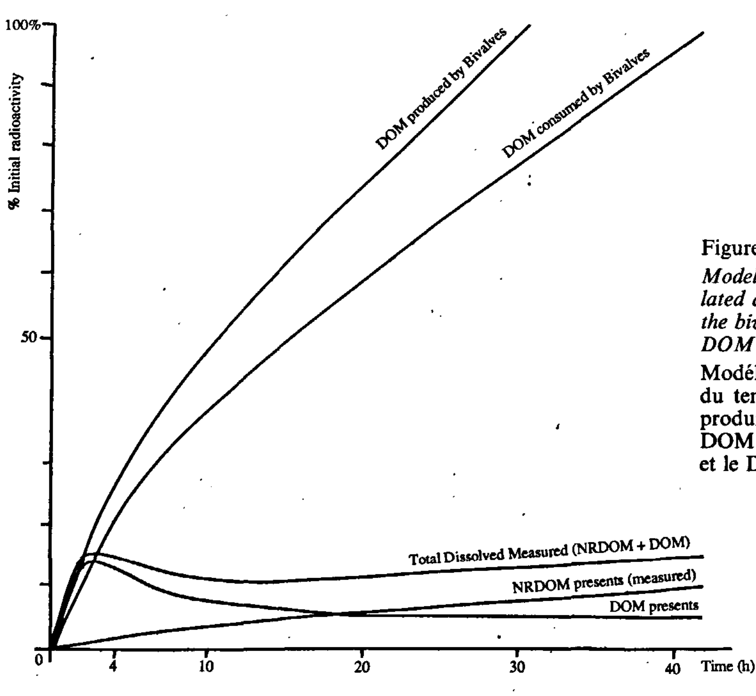

Figure 5
Modelling. Graphic representation of: the time variation of the cumulated amounts of dissolved organic matter produced and consumed by the bivalves; total DOM measured during experiment; non-recyclable DOM; and DOM calculated by computation.
Modélisation. Représentation graphique de la variation en fonction du temps des quantités cumulées de la matière organique dissoute produite et consommées par les bivalves, de la quantité totale de DOM mesurée durant l'expérience, ainsi que le dissous non recyclable et le DOM calculés par le calculateur.

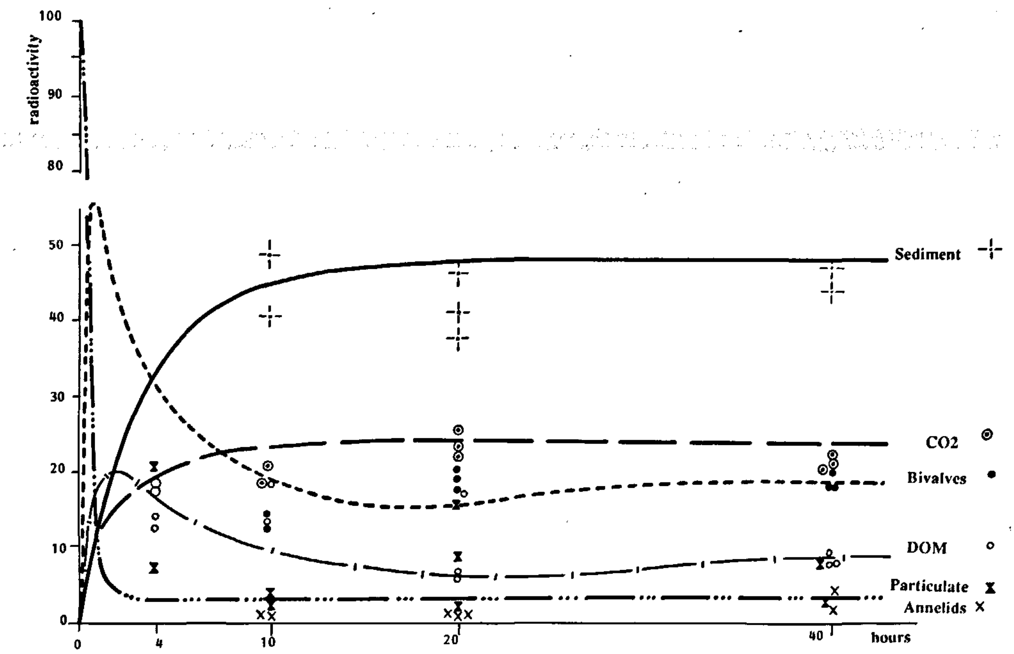

Figure 6
Modelling. Graphic representation of the time-dependent variation of the radioactivity in the different compartments of the system "bacteria- sediment- annelids- bivalves" with pollutant.
Modélisation. Représentation graphique de la variation en fonction du temps de la radioactivité dans les différents compartiments du système « bactéries- sédiment- annélides-bivalves » avec polluant.

The whole system was not significantly affected by the presence of the pollutant (Fig. 6). Kinetic constants of the two models were almost similar. This indicates that the pollutant did not affect the exchanges between the different compartments of the system "bacteria-suspension-feeder-deposit-feeder-sediment": the amounts consumed, ingested and assimilated were not very different from the amounts calculated without pollutant (Tab.).

"Algae-suspension-feeder-deposit-feeder-sediment" system (Tab., Fig. 7, 8, 9, 10, 11 and 12)

The diagram of the complete system is presented in Figure 7. The mass transfer dynamics of the system "algae - suspension-feeder - deposit-feeder - sediment" were represented by an interaction of "kinetic" equations reflecting the rates of exchanges between compartments:

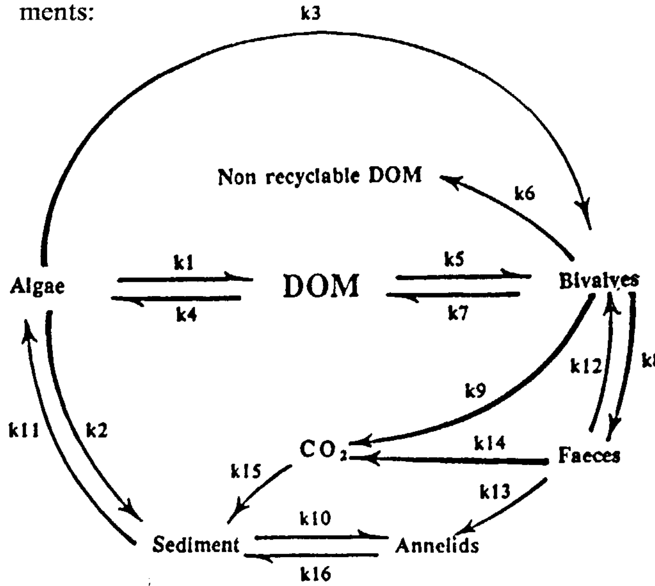

Figure 7
Présentation of the different compartments of the system "algae-bivalves- annelids-sediment" and their relations.
Présentation des différents compartiments du système algues-bivalves-annélides-sédiment et leurs relations.

$$\frac{d\,[\mathrm{Algae}]}{dt} = +k_4\,[\mathrm{Diss}] + k_{11}\,[\mathrm{Sed}] - k_1\,[\mathrm{Algae}] - k_2\,[\mathrm{Algae}] - k_3\,[\mathrm{Algae}]$$

$$\frac{d[\mathrm{DOM}]}{dt} = +k_1\,[\mathrm{Algae}] + k_7\,[\mathrm{Biv}] - k_4\,[\mathrm{DOM}] - k_5\,[\mathrm{DOM}]$$

$$\frac{d[\mathrm{Bivalves}]}{dt} = +k_3\,[\mathrm{Algae}] + k_5\,[\mathrm{DOM}] + k_{12}\,[\mathrm{Faeces}] - k_6[\mathrm{Biv}] - k_7\,[\mathrm{Biv}] - k_8\,[\mathrm{Biv}] - k_9\,[\mathrm{Biv}]$$

$$\frac{d[\mathrm{Sediment}]}{dt} = +k_2\,[\mathrm{Algae}] + k_{15}\,[\mathrm{CO_2}] - k_{10}\,[\mathrm{Sed}] - k_{11}\,[\mathrm{Sed}]$$

$$\frac{d[\mathrm{Faeces}]}{dt} = +k_8\,[\mathrm{Biv}] - k_{12}\,[\mathrm{Faeces}] - k_{13}\,[\mathrm{Faeces}] - k_{14}\,[\mathrm{Faeces}]$$

$$\frac{d[\mathrm{CO_2}]}{dt} = +k_9\,[\mathrm{Biv}] + k_{14}\,[\mathrm{Faeces}] - k_{15}\,[\mathrm{CO_2}]$$

$$\frac{d[\mathrm{NR\,DOM}]}{dt} = +k_6\,[\mathrm{Biv}]$$

$$\frac{d[\mathrm{Annelids}]}{dt} = +k_{13}\,[\mathrm{Faeces}] + k_{10}\,[\mathrm{Sed}] - k_{16}\,[\mathrm{Annelids}].$$

The diagram of the analog computer circuit simulating the foregoing equations with their constants and values is presented in Figure 9.

After fitting the model, the different curves representing the changes of radioactivity of the different compartments were drawn. It was then possible to interfer the total variation from T0 to 40 hours between experimental data (Fig. 9). $^{14}CO_2$ reached 8 % after 40 hours but was reabsorbed by the sediment (probably by benthic diatoms). Sediment radioactivity was fairly constant after 20 hours (42 % of initial radioactivity). The radioactivity in the soft body parts of the bivalves reached 79 % after 1 hour, then declined rapidly to 10 hours before reaching 38 % after 40 hours. The radioactivity of the algae remaining in the suspension (POM) declined quickly during the first 2 hours, then remained fairly stable (2 %) from 2 to 40 hours. The radioactivity of the dissolved substances increased to 6 % after 2 hours and then declined to 2 % between 15 to 40 hours. This change suggested a production of dissolved substances that were reabsorbed by bivalves and sediment.

The simulation also permitted calculation of changes of radioactivity in compartments where it could not be measured experimentally. Radioactivity corresponding to faeces produced by the bivalves (present at the water-sediment interface) was 16.6 % after 4 hours, 15.4 % after 10 hours and 10.8 % of the initial radioactivity after 40 hours (Fig. 10).

Radioactivity corresponding to faeces produced by the bivalves during 10 hours represented 74.4 % of the initial radioactivity and 221.0 % after 40 hours. The difference between the faeces on the bottom and the cumulated amounts (210.2 %) corresponded to the faeces resuspended and recycled by the bioturbation of the annelids.

The sediment received 80 % of the initial radioactivity after 20 hours (Fig. 10) and the annelids scraped and consumed 180 % of the initial radioactivity after 40 hours (Fig. 11). The quantities of dissolved organic matter (DOM; Fig. 12) produced by the bivalves was 63.5 % of the initial radioactivity after 20 hours, whereas the algae produced 7.6 % of the initial radioactivity after 20 hours. The $^{14}CO_2$ produced corresponded to 23.8 % of the initial radioactivity after 40 hours (Fig. 13).

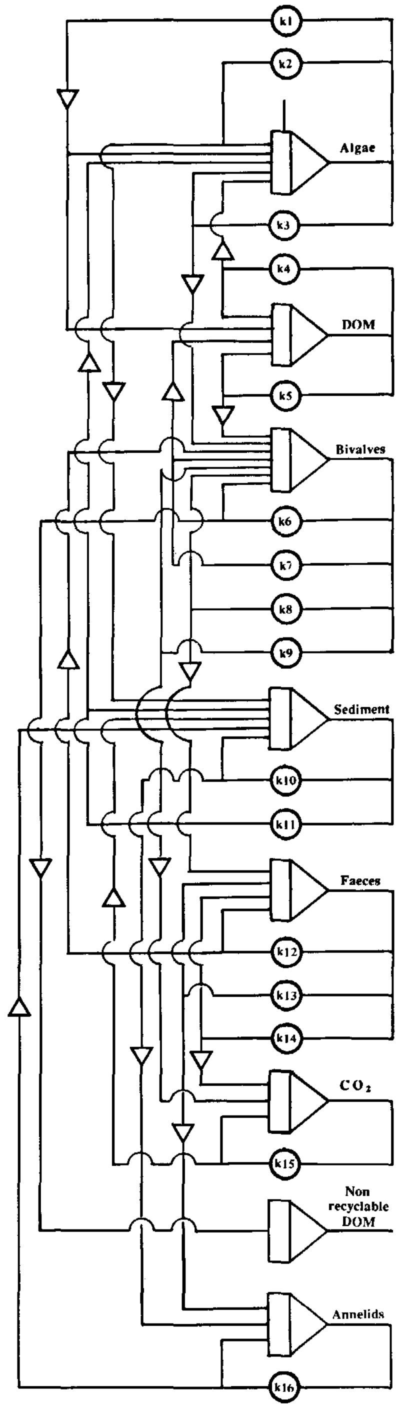

Figure 8

Modelling. Circuit diagram of the analog computer model. The different exchanges are represented with the corresponding constants.

Modélisation. Cablage du circuit du calculateur analogique. Les différents échanges sont représentés avec les constantes correspondantes.

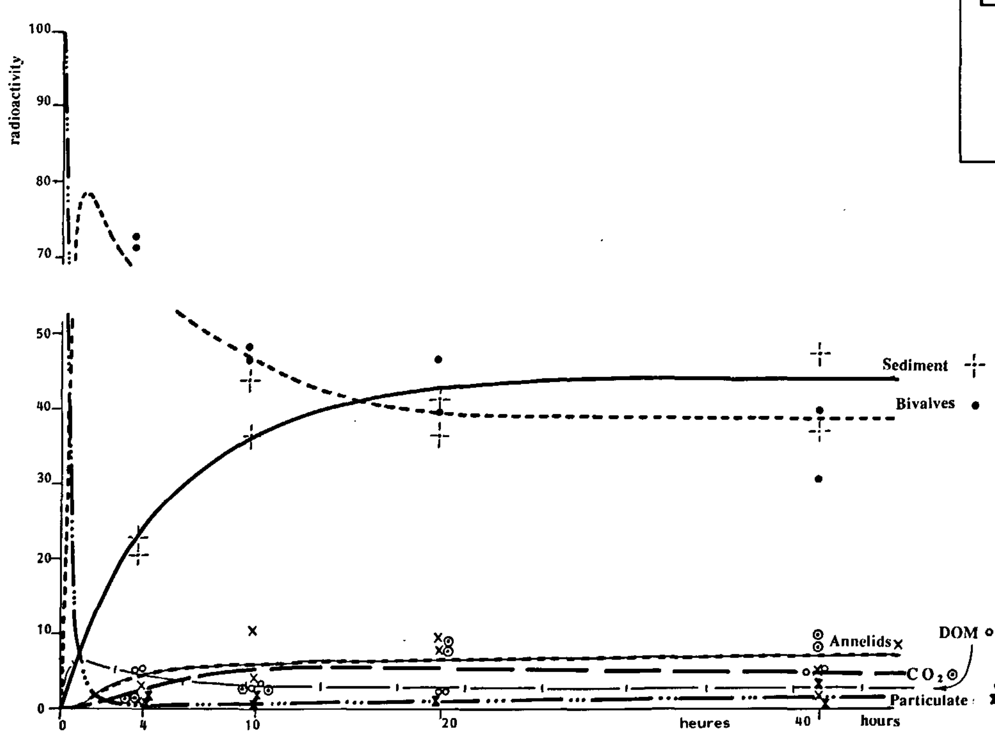

Figure 9

Modelling. Graphic representation of the time-dependent variation of the radioactivity in the different compartments of the system "algae- sediment-annelids - bivalves". No significative difference without or with pollutant explains only one representation.

Modélisation. Représentation graphique de la variation en fonction du temps de la radioactivité dans les différents compartiments du système « algues-sédiment-annélides-bivalves ». Le fait qu'aucune différence significative n'apparaisse avec et sans polluant, explique une unique représentation graphique.

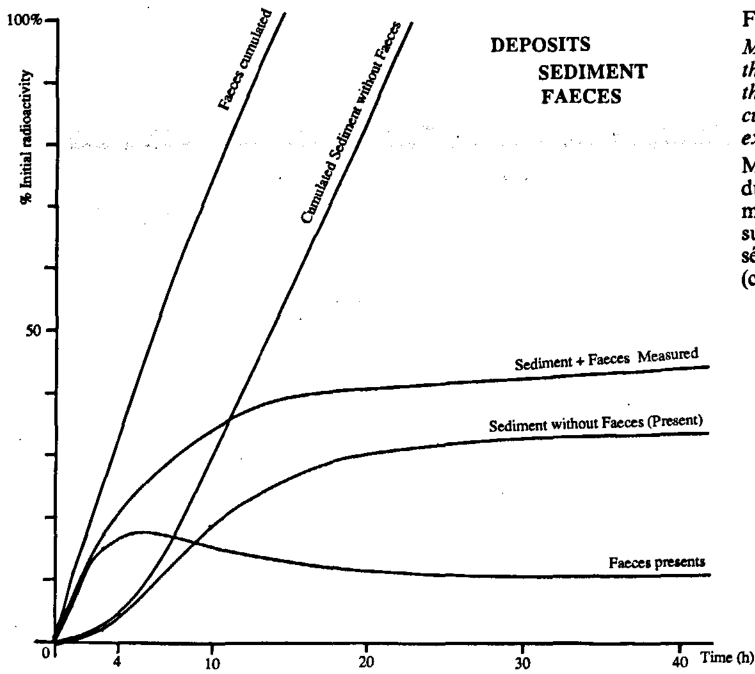

Figure 10

Modelling. Graphic representation of the time-dependent variation of the radioactivity cumulated in different compartments and the value of the radioactivity of the faeces of bivalves trapped on the bottom (non cumulated) (present), sediment without faeces, sediment with faeces experimentally measured, sediment (cumulated) and faeces (cumulated).

Modélisation. Representation graphique de la variation en fonction du temps de la radioactivité cumulée dans les différents compartiments et de la valeur de la radioactivité des fécès des bivalves piégés sur le fond (non cumulés) (présents), du sédiment sans les fécès, du sédiment avec les fécès mesurés expérimentalement, du sédiment (cumulé) et des fécès (cumulés).

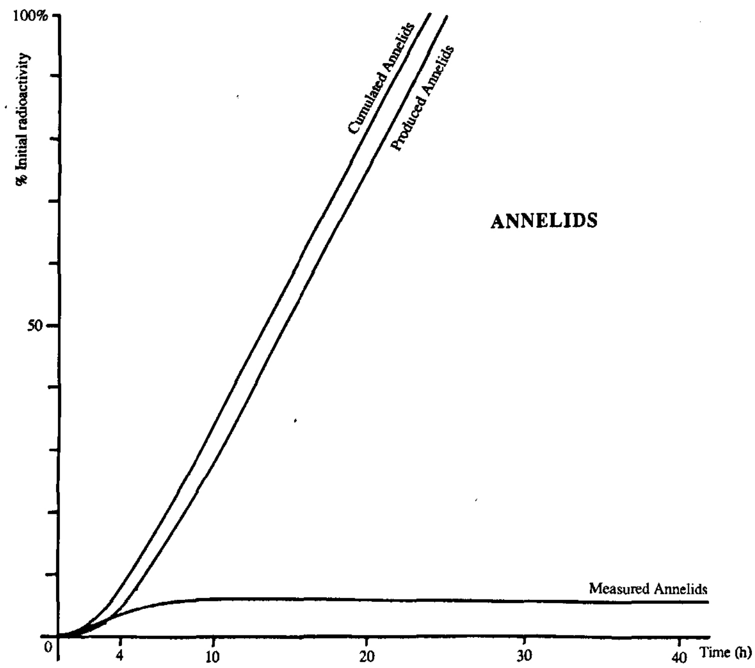

Figure 11

Modelling. Comparison between the radioactivity cumulated through the annelids and produced by the annelids, and the radioactivity measured in time.

Modélisation. Comparaison entre la radioactivité cumulée ayant transité au travers des annélides, produite par les annélides, et la radioactivité mesurée expérimentalement.

Kinetic constants of the model are presented in Figure 8. The highest value corresponded to the consumption of the algal suspension by the bivalves: 1.82. h^{-1}. For the dissolved substances consumed by the bivalves, the kinetic constant was 0.46. h^{-1}. For the faeces produced by the bivalves, the kinetic constant was 0.12. h^{-1}. For the dissolved substances produced by the bivalves, the kinetic constant was 0.06. h^{-1}. The kinetic constant corresponding to the production of dissolved substances by the algae was 0.09. h^{-1}. The kinetic constant corresponding to the CO_2 produced by the bivalves was 0.002 5. h^{-1}. For the faeces consumed by the bivalves, the kinetic constant was 0.18. h^{-1}. The amount of organic matter consumed by the bivalves after 40 hours was set as the total of the amount in the soft parts plus the cumulated amount of faeces, CO_2 and DOM produced during this period: 37.9+221.0+5.2+109.6 % = 373.7 % of the initially introduced quantity (Tab.). The amount ingested was set as the amount consumed less the cumulated amount of consumed DOM: 373.7−69.3 % = 304.4 % of the initially introduced quantity. The amount assimilated was set as the difference between the amount consumed less the cumulated amount of feaces produced: 373.7−221.0 % = 152.7 %.

The whole system was not affected by the presence of the pollutant. Kinetic constants obtained for the two models were fairly similar. Thus, the pollutant did not disturb exchanges between the different compartments.

DISCUSSION

The system "suspension-bivalves-annelids-sediment" comprises 6 compartments for the bacterial food and 8 compartments for the algae food. The compartmental study was carried out as a function of time. Following Lampert and Gabriel (1984), the diffusion of the radioactive tracer through the different compartments of the system was measured. The mathematical model of the system revealed the rates of organic matter transfer through the compartments. The model is a reasonable description of the kinetics of the tracer. For the recycling of organic matter, the experiments do not provide any information on the quantities of matter produced by each compartment. The analog simulation permitted the calculation of the exchange kinetics between the different compartments and the time variation of the compartments which are not accessible experimentally

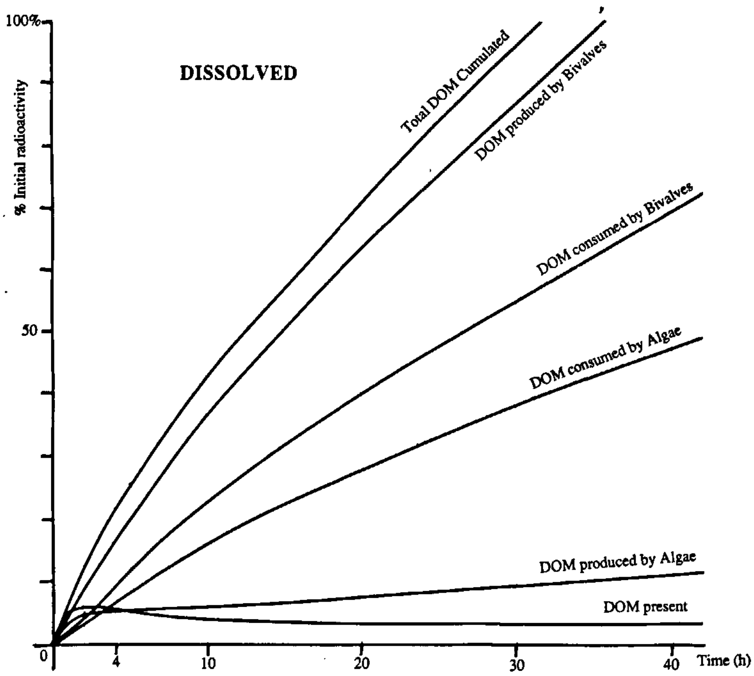

Figure 12

Modelling. Comparison of the radioactivity cumulated in the total DOM; DOM produced by the bivalves; DOM consumed by the bivalves; DOM consumed by the algae; DOM produced by the algae and DOM (non cumulated) present in solution during the experiment.

Modélisation. Comparaison de la radioactivité cumulée mesurée dans le DOM total, le DOM produit par les bivalves, le DOM consommé par les bivalves, le DOM consommé par les algues, le DOM produit par les algues et le DOM (non cumulé) présent en solution durant l'expérience.

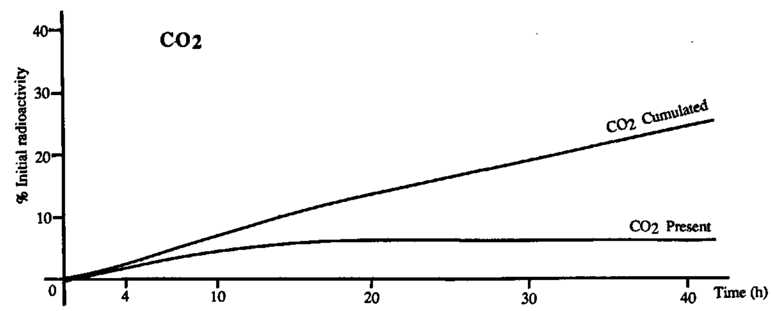

Figure 13

Modelling. Comparison between the radioactivity measured (present) and the radioactivity cumulated in $^{14}CO_2$.

Modélisation. Comparaison entre la radioactivité mesurée (présente) et la radioactivité cumulée dans le $^{14}CO_2$.

(Amouroux and Amouroux, 1988). It permits the mathematical determination of the amounts of DOM and faeces produced and recycled during the experiments.

The radioactivity of the bivalves increased rapidly during the two first hours and then declined. Perhaps the annelids were not active at the same time as the bivalves: it seems that they consume the deposits of the bivalves 3 hours after the start of the experiment. We do not take this phenomena for fitting our model and for this reason it is not exactly adjusted and fitted for annelids.

The radioactivity of the annelids remained fairly stable and very low: between 0.2 and 1 % for the bacterial food and 1.6 and 8.2 for the algal food. It was considered as zero for the bacterial food. This compartment "annelids" was mechanical compartment for bioturbative action but not a storage compartment. The annelids disaggregate biodeposits and mix the interface water-sediment (Rhoads, 1974; Aller and Yingst, 1978; Murphy, 1985). The annelids did not eat the deposits of the bivalves when they fed on bacteria but could eat a little of these biodeposits when the bivalves fed on algae. The sediment was a "cumulative" compartment: the suspension and faecal sedimentation increased slowly throughout the experiment (Doering and Oviatt, 1986). The diatoms living on the sand grains incorporated a part of the CO_2 produced.

The compartment "dissolved organic matter" was divided in two compartments: "DOM" and "non-recyclable dissolved". The "DOM" was a transit compartment acting as an interface between the bivalves and the suspensions. But a part of the dissolved substances excreted by the bivalves could not be metabolized by the live suspensions or the microflora associated with the sediment: it was a cumulative compartment. The amounts of organic matter transited through the different compartments were measured by computation.

The organic matter introduced at the start of the experiment was recycled 152 % for the bacterial food by the annelids after 40 hours. For algal food the annelids recycled 173 % of the organic matter as biodeposits (sedimented and faeces) after 40 hours. For the bacterial food, however, a very large amount of the organic matter transited through the dissolved organic matter: 136.1 % recycled for bacterial food after 20 hours than 117.7 % recycled for algal food after the same duration.

Numerous different models have been used to calculate the nutrition and assimilation in microcosms, mesocosms or ecosystems: Doering and Oviatt (1986) used predictive models for a mesocosm comprising filter- and deposit-feeding bivalves, Thingstad and Pengerud (1985) used a simple kinetic model, but Marra *et al.* (1988) have correctly explained that "the major limitation of this kind of model is that, because they are numerical, it can be difficult to identify crucial flows and transfers". Vietinghoff (1984) used an analog model for an ecological study on interelations in a natural ecosystem.

The importance of bioturbation has been demonstrated by different authors (Hines and Jones, 1985; Murphy, 1985; Doering *et al.*, 1986; Reichardt, 1988) but they do not calculate the transit of organic matter. Our work constitutes an approach to the solution for microecosystems or ecosystems quantification.

GENERAL CONCLUSIONS

In the system "suspension-suspension-feeder-deposit-feeder-sediment", bivalves were the propulsive element mixing the water and depositing the particulate matter as biodeposits (Doering *et al.*, 1986). On the bottom these biodeposits remained trapped until recycled by bacterial activity. The deposit-feeders activity modified this by disturbance and scraped the sediment interface. The biodeposits composed from bacterial suspensions were easily resuspended for they are soft and not dense. They contained a part of non-digested live bacteria that divided and were reconsumed by the bivalves and deposited again as faeces. When the biodeposits were derived from algal food, bioturbative action (Aller and Yingst, 1985; Branch and Pringle, 1987) could not resuspend living algae; particles alone were slowly deposited. The sediment accumulated the natural sedimentation and all the deposits from the bivalves. The filter-feeders recovered directly a part of the particulate organic matter resuspended by bioturbation and by the suspended bacteria and dissolved exudates enhanced by the resuspension (Branch and Pringle, 1987). The quantities of matter recycled can be very important, as shown by our computation: 70 % of the faeces are recycled during 10 hours and 85 % of the dissolved substances after 20 hours for the algal food. These values are still higher in the presence of bacteria.

The very rapid recycling of the organic matter explains why the low instantaneous values measured experimentally cannot provide the energy balance of the animal fed only with particulate organic suspension. It appears necessary to take in to consideration the dissolved organic matter as a trophic energy resource. Bioturbation can be good for some bivalves but as stressful for others, as shown by Murphy (1985) for *Mercenaria mercenaria.* The organic matter flux enhanced by the system "filter-feeders-deposit-feeders" may thus be considered to exert complex effects on the biology of benthic communities.

Acknowledgements

This research, which was supported by a grant from the *Ministère de l'Environnement* and with assistance from the Centre National de la Recherche Scientifique (CNRS), France, was carried out during 1985 at the Laboratoire Arago (LA No. 117).

We thank Dr R. C. Newell for helpful suggestions and constructive criticism of the manuscript in its English form.

REFERENCES

Aller R. C. and J. Y. Yingst (1978). Biochemistry of the tube-dwellings: a study of the sedentary polychaete *Amphitrite ornata* (Leidy). *J. mar. Res.*, **36**, 2, 201-254.

Amouroux J.-M. (1984). Preliminary study on the consumption of dissolved organic matter (exudates) of bacteria and phytoplankton by the marine bivalve *Venus verrucosa. Mar. Biol.*, **82**, 109-112.

Amouroux J.-M. (1986 *a*). Comparative study of the carbon cycle in *Venus verrucosa* fed on bacteria and phytoplankton. I: Consumption of bacteria (*Lactobacillus* sp.). *Mar. Biol.*, **90**, 237-241.

Amouroux J.-M. (1986 *b*). Comparative study of the carbon cycle in *Venus verrucosa* fed on bacteria and phytoplankton. II: Consumption of phytoplankton (*Pavlova lutheri*). *Mar. Biol.*, **92**, 349-354.

Amouroux J.-M. and J. Amouroux (1988). Comparative study of the carbon cycle in *Venus verrucosa* fed on bacteria and phytoplankton. III: Comparison of models. *Mar. Biol.*, **97**, 3, 339-347.

Amouroux J. M., A. Grémare and J. Amouroux (1989). Modelling of consumption and assimilation in Abra alba (Mollusca, Bivalvia). *Mar. Ecol.-Prog. Ser.*, **51**, 87-97.

Amouroux J.-M., J. Amouroux, J. Bastide and G. Cahet (1990). Interelations in a microcosm with a suspension feeder and a deposit feeder. I: Experimental study. *Oceanologica Acta*, **13**, 1, 61-68.

Branch G. M. and A. Pringle (1987). The impact of the sand prawn *Callianassa krausi* Stebling on sediment turnover and on bacteria, meiofauna and benthic microflora. *J. exp. mar. Biol. Ecol.*, **103**, 3, 219-235.

Brockway D. L., P. D. Smith and F. E. Stancil (1984). Fate and effects of pentachlorophenol in hard and soft water microcosms. *Chemosphere*, **13**, 12, 1363-1378.

Conover R. J. and V. Francis (1973). The use of radioactive isotopes to measure the transfer of material in aquatic food chains. *Mar. Biol.*, **18**, 272-283.

Doering P. H. and C. A. Oviatt (1986). Application of filtration rate models to field populations of bivalves: an assessment using experimental mesocosms. *Mar. Ecol.-Prog. Ser.*, **3**, 3, 265-275.

Doering P. H., C. A. Oviatt and J. R. Kelly (1986). The effects of the filter-feeding *Mercenaria mercenaria* on carbon cycling in experimental marine mesocosms. *J. mar. Res.*, **44**, 839-861.

Dring M. J. and D. H. Jewson (1982). What does ^{14}C upatke by phytoplankton really measure? A theoretical modelling approach. *Proc. R. Soc., Lond, ser. B*, **214**, 351-368.

Goldstein R. A. and J. W. Elwood (1971). A two compartment, three parameter model for the absorption and retention of ingested element by animals. *Ecology*, **52**, 5, 935-939.

Grégoire F. I. (1972). Pharmacocinétique et analyse compartimentale. *J. Pharm. Belg.*, **27**, 1, 98-111.

Hines M. E. and G. E. Jones (1985) Microbia biogeochemistry and bioturbation in the sediments of Great Bay, New Hampshire. *Estuar. coast. Shelf Sci.*, **20**, 729-742.

Huckins J. N., J. D. Petty and M. A. Heikamp (1984). Modular containers for microcosm and process model studies on the fate and effects of aquatic contaminants. *Chemosphere*, **13**, 12, 1329-1342.

Lampert W. and W. Gabriel (1984). Tracer kinetics in *Daphnia:* an improved two-compartment model and experimental test. *Arch. Hydrobiol.*, **100**, 1, 1-20.

Larsson P. (1983). Transport of ^{14}C.-labelled PCB compounds from sediment to water and from water to air in laboratory model system. *Wat. Res.*, **17**, 10, 1317-1326.

Marra J., L. W. Haas and K. R. Heinemann (1988). Time course of C assimilation and microbial food web. *J. expl. mar. Biol. Ecol.*, **115**, 263-280.

Murphy R. C. (1985). Factors affecting the distribution of the introduced bivalve, *Mercenaria mercenaria*, in a California lagoon. The importance of bioturbation. *J. mar. Res.*, **43**, 3, 673-692.

Reichardt W. (1988). Impact of bioturbation by *Arenicola marina* on microbiological parameters in intertidal sediments. *Mar. Ecol.-Prog. Ser.*, **44**, 149-158.

Rhoads D. C. (1974) Organism-sediment relations on the muddy sea floor. *Oceanogr. mar. Biol. a. Rev.*, **12**, 263-300.

Smith D. F. and S. M. J. Horner (1981). Tracer kinetic analysis applied to problems in marine biology. *Can. Bull. Fish. aquat. Sci.*, 210, 113-129.

Spain J. C., P. H. Pritchard and A. W. Bourquin (1980). Effects of adaptation on biodegradation rates in sediment/water cores from estuarine and freshwater environments. *Appl. environ. Microbiol.*, **40**, 4, 726-734.

Thingstad T. F. and B. Pengerud (1985). Fate and effect of allochthonous organic material in aquatic ecosystems. An analysis based on chemostat theory. *Mar. Ecol.-Prog. Ser.*, **21**, 53-69.

Vietinghoff U. (1984). Mathematical modelling of the ecosystem Barther Bodden. *Limnologica, Berl.*, **15**, 2, 253-262.