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

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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 14C. A series of experiments of varying duration made it possible to quantify the diffusion of 14C 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.


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.


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 substances 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” (Vitinghoff, 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...
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) CO2 produced by bivalves; 3) NRDOM
produced by bivalves; 4) DOM produced by bivalves; 5) DOM consumed
by bivalves. The amounts of radioactivity present in each compartment
are shown and the amounts consumed, ingested and assimilated
are calculated. Values are expressed as percentages of initial radioactivity.

<table>
<thead>
<tr>
<th>Compartment</th>
<th>Bacteria</th>
<th>Bacteria</th>
<th>Algae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Faeces</td>
<td>146.1</td>
<td>165.4</td>
<td>221.0</td>
</tr>
<tr>
<td>CO2 prod. Biv.</td>
<td>47.7</td>
<td>54.1</td>
<td>4.6</td>
</tr>
<tr>
<td>NRDOM</td>
<td>9.5</td>
<td>0.0</td>
<td>0.7</td>
</tr>
<tr>
<td>DOM prod. Biv.</td>
<td>118.5</td>
<td>134.1</td>
<td>109.6</td>
</tr>
<tr>
<td>DOM cons. Biv.</td>
<td>94.8</td>
<td>33.5</td>
<td>69.3</td>
</tr>
</tbody>
</table>

Comparaison des résultats pour les bactéries et les algues après
ajustement du modèle. Les quantités cumulées sont indiquées pour
each compartiment après 40 heures. 1) Fécés; 2) CO2 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.

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 CO2 (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 CO2, and
consumed dissolved substances. Bacteria produced dissolved
substances and CO2, and consumed dissolved substances.
Annelids consumed dissolved substances, faeces of the bivalves,
and produced faeces, dissolved substances and CO2. Sediment received faeces of the

Figure 2
“Bacteria-bivalves” system. Six-compartment model showing exchanges studied and numbered kinetic constants of mass transfer (k1 to
k12).

System “bacteria-bivalves-annelids-sediment”.

<table>
<thead>
<tr>
<th>Constant</th>
<th>Code</th>
<th>Values as h⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bacteria</td>
<td>k₁</td>
<td>0.1400</td>
</tr>
<tr>
<td></td>
<td>k₂</td>
<td>0.1700</td>
</tr>
<tr>
<td></td>
<td>k₃</td>
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<td></td>
<td>k₄</td>
<td>0.3800</td>
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<tr>
<td></td>
<td>k₅</td>
<td>0.1200</td>
</tr>
<tr>
<td></td>
<td>k₆</td>
<td>0.0120</td>
</tr>
<tr>
<td></td>
<td>k₇</td>
<td>0.1500</td>
</tr>
<tr>
<td></td>
<td>k₈</td>
<td>0.1850</td>
</tr>
<tr>
<td></td>
<td>k₉</td>
<td>0.0600</td>
</tr>
<tr>
<td></td>
<td>k₁₀</td>
<td>0.0400</td>
</tr>
<tr>
<td></td>
<td>k₁₁</td>
<td>0.0600</td>
</tr>
<tr>
<td></td>
<td>k₁₂</td>
<td>0.0450</td>
</tr>
</tbody>
</table>

System “bacteria-bivalves-annelids-sediment + Kerb”.

<table>
<thead>
<tr>
<th>Constant</th>
<th>Code</th>
<th>Values as h⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bacteria</td>
<td>k₁</td>
<td>0.1450</td>
</tr>
<tr>
<td></td>
<td>k₂</td>
<td>0.1600</td>
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<tr>
<td></td>
<td>k₃</td>
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<td></td>
<td>k₄</td>
<td>0.3830</td>
</tr>
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<td></td>
<td>k₅</td>
<td>0.1050</td>
</tr>
<tr>
<td></td>
<td>k₆</td>
<td>0.0000</td>
</tr>
<tr>
<td></td>
<td>k₇</td>
<td>0.1500</td>
</tr>
<tr>
<td></td>
<td>k₈</td>
<td>0.1850</td>
</tr>
<tr>
<td></td>
<td>k₉</td>
<td>0.0600</td>
</tr>
<tr>
<td></td>
<td>k₁₀</td>
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<td></td>
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<td>0.0600</td>
</tr>
<tr>
<td></td>
<td>k₁₂</td>
<td>0.0450</td>
</tr>
</tbody>
</table>

System “algae-bivalves-annelids-sediment”.

<table>
<thead>
<tr>
<th>Constants</th>
<th>Code</th>
<th>Values as h⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alage</td>
<td>k₁</td>
<td>0.0961</td>
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<tr>
<td></td>
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<tr>
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<td>k₈</td>
<td>0.1210</td>
</tr>
<tr>
<td></td>
<td>k₉</td>
<td>0.0600</td>
</tr>
<tr>
<td></td>
<td>k₁₀</td>
<td>0.0850</td>
</tr>
<tr>
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<td></td>
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<td>0.0708</td>
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<td>0.0400</td>
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<td></td>
<td>k₁₅</td>
<td>0.1040</td>
</tr>
<tr>
<td></td>
<td>k₁₆</td>
<td>0.7315</td>
</tr>
</tbody>
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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:

\[
\begin{align*}
\frac{d[Bact]}{dt} &= +k_4[DOM]+k_{11}[Faeces\ Sed] \\
-k_1[Bact]-k_2[bact]-k_3[Bact] \\
\frac{d[DOM]}{dt} &= +k_7[Biv]+k_1[Bact] \\
-k_4[DOM]-k_5[DOM] \\
\frac{d[Biv]}{dt} &= +k_5[DOM]+k_3[Bact]+k_{10}[Faeces\ Sed] \\
-k_6[Biv]-k_7[Biv]-k_8[Biv]-k_9[Biv] \\
\frac{d[Faeces\ Sed]}{dt} &= +k_8[Biv]+k_{12}[CO_2] \\
-k_2[Faeces\ Sed]-k_{11}[Faeces\ Sed] \\
\frac{d[CO_2]}{dt} &= +k_2[Bact]+k_9[Biv]-k_12[CO_2] \\
\frac{d[NR\ DOM]}{dt} &= +k_6[Biv].
\end{align*}
\]

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 T0 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” 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
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 consommée 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.
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-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-sediment" were represented by an interaction of "kinetic" equations reflecting the rates of exchanges between compartments:

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

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

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

\[
\frac{d[\text{Sediment}]}{dt} = +k_2[\text{Algae}]+k_{15}[\text{CO}_2]
\]
\[
-k_{10}[\text{Sed}]-k_{11}[\text{Sed}]
\]

\[
\frac{d[\text{Faeces}]}{dt} = +k_4[\text{Biv}]-k_{12}[\text{Faeces}]
\]
\[
-k_{13}[\text{Faeces}]-k_{14}[\text{Faeces}]
\]

\[
\frac{d[\text{CO}_2]}{dt} = +k_9[\text{Biv}]+k_{14}[\text{Faeces}]
\]
\[
-k_{15}[\text{CO}_2]
\]

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

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

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 interfere the total variation from T0 to 40 hours between experimental data (Fig. 9). $^{14}\text{CO}_2$ 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).
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 0.0025. 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 faeces 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.
INTERRELATIONS SUSPENSION/DEPOSIT-FEEDERS II: MODELLING

(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 CO2 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.

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