Experimental study of the interactions between a natural ^{14}C radiolabelled sediment and a deposit-feeding bivalve: *Abra alba*

Deposit-feeder
Modelling
Methodology
Nutrition
Carbon 14

Dépositivores
Modèlisation
Méthodologie
Nutrition
Carbone 14

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ABSTRACT

Changes of radioactivity in a natural ^{14}C labelled sediment were monitored over a 120-hour period in the presence and in the absence of the deposit-feeding bivalve *Abra alba*. In both cases, the sediment showed great instability during the first ten hours of the experiment. The consequences of this result on the experimental protocol used for the study of the interactions between natural sediments and deposit-feeders are discussed. In controls, the instability is produced by an initial decrease of radioactivity in the sediment, whereas in the presence of *Abra alba*, it corresponds to an initial increase of radioactivity. Analysis of previously published data suggests that such responses may result from the inhibition or the stimulation of the bacterial component of the sediment. Two analog models describing the exchanges of radioactivity in the absence and in the presence of *Abra alba* are proposed.

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RÉSUMÉ

Étude expérimentale des interactions entre un sédiment naturel marqué au carbone 14 et un bivalve dépositivore: *Abra alba*

L'évolution temporelle de la radioactivité contenue dans un sédiment vivant marqué au ^{14}C a été mesurée pendant 120 heures en présence et en l'absence du bivalve dépositivore *Abra alba*. Dans ces deux cas, le marquage du sédiment montre une très grande instabilité durant les 10 premières heures d'incubation. Les conséquences de ce phénomène sur les protocoles expérimentaux des études concernant les interactions entre sédiment et dépositivores benthiques sont discutées. Dans les témoins, l'instabilité se traduit par une baisse significative du pourcentage de radioactivité contenu dans le sédiment. En présence d'*Abra alba*, au contraire, l'instabilité correspond à une forte augmentation de la radioactivité contenue dans le sédiment. L'analyse de travaux antérieurs suggère que ces réponses peuvent être causées par l'inhibition ou la stimulation de la fraction bactérienne associée aux grains de sédiment. Deux modèles analogiques simulant les échanges de radioactivité en présence et en l'absence de *Abra alba* sont proposés.

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INTRODUCTION

The particulate organic matter (POM) deposited at the water/sediment interface is highly heterogenous with respect to its origin and level of degradation. This results in very complex interactions between POM and benthic deposit-feeders, since these interactions appear to depend on the origin and on the level of degradation of the available POM (Tenore *et al.*, 1982). In order to unravel such interactions, two approaches have been used:

1) identification of the origin of the organic matter ingested by deposit-feeders by tracing specific indices such as carotenoid pigments, fatty acid profiles, and carbon stable isotope ratio;

2) use of radiolabelling methods to study the interaction between homogenous components of sedimented POM and deposit-feeders.

This second approach has been carried out on artificial substrates such as monospecific cultures of diatoms (Calow, 1975; Decho, 1986; Amouroux *et al.*, 1989; Grémare *et al.*, 1989), monospecific culture of bacteria (Grémare and Amouroux, 1988) and detritus artificially prepared from a given macrophyte (Tenore, 1975; Tenore *et al.*, 1977; Tenore and Hanson, 1980; Kemp, 1986), as well as on natural sediments in which only a given component has been radiolabelled (Montagna, 1983 and 1984, Lopez and Cheng, 1983; Montagna and Bauer, 1988; Forbes and Lopez, 1989; Blanchard, 1991). Moreover, the use of radioisotopes in the study of benthic food chains is complicated by the occurrence of short-term recycling within the experimental chambers (Conover and Francis, 1973; Grémare, 1990) and by the interaction with epibiotic bacteria (Carman, 1990).

Two solutions have been proposed to overcome this difficulty:

1) use of a pulse-chase design which minimizes recycling by reducing incubation periods (Lopez and Cheng, 1983);

2) coupling the experimental analysis of the diffusion kinetics of the radiotracer with (analog) modelling (Conover and Francis, 1973; Amouroux *et al.*, 1989; Grémare *et al.*, 1989; Amouroux *et al.*, 1990 *a* and *b*; Grémare *et al.*, 1991). Advantages and drawbacks of these two methods are discussed in detail in Grémare *et al.* (1991), but it is important to point out that the main advantage of the modelling approach is its possible extension to *in situ* measurements as shown by Montagna (1984).

In the case of natural sediments, the utilization of a radiotracer is complicated by the fact that the administration technique of the label may greatly affect its uptake by microbes (Dobbs *et al.*, 1989) and by meiofaunal deposit-feeders (Carman *et al.*, 1989). This effect is due to recovery from physical disturbance (Wainwright, 1987; Findlay *et al.*, 1990). Therefore, when limited to short-term incubation periods, experimental study of the interactions between natural radiolabelled sediment and deposit-feeders may result in misleading conclusions (Carman, 1990). Moreover, although it is well known that benthic macrofauna may affect the structure (Connor, 1982) and the metabolism of microbial populations associated with sediment (Connor, 1982; Reichardt, 1988), the effect of macrobenthic deposit-feeders on such recovery processes has been largely ignored. Therefore, the aims of the present study were:

1) to study the kinetics of the exchanges of radioactivity within the compartments consisting of CO_2, dissolved organic matter (DOM), and different sediment fractions) of a closed experimental system (natural radiolabelled sediment + seawater); and

2) to assess the impact of the deposit-feeding bivalve *Abra alba* on these exchanges over periods of several days.

MATERIALS AND METHODS

Animals

Abra alba (Wood) is a deposit-feeding bivalve which is common in all the lagoons along the Languedoc-Roussillon coast of France. It burrows 3 to 5 cm deep in the sediment and feeds at the surface of the sediment layer by means of a 4 to 5 cm long inhalant siphon; the exhalant siphon generates a regular current of water through its burrow where its faeces are deposited. In Mediterranean lagoons, this species appears to constitute an important component of the food regime of juvenile flatfish via sublethal predation (*i. e.*, siphon nipping). The clams used during these experiments were collected during spring 1989 at a shallow station (< 1 m) in the Canet lagoon (Western Mediterranean), and were then maintained in the laboratory for several weeks in tanks provided with running ambient seawater and natural (*i. e.*, sampling site) muddy sediment. Before each experiment, clams were allowed to clear their gut for 24 h in filtered seawater.

Sediment preparation

The mud used during this study was collected by decantation from laboratory tanks which had been provided with ambient running seawater for several months. The sediment was sieved through a 450 µm mesh and then labelled with ^{14}C glutamic acid (Commissariat à l'Énergie Atomique) for five days. The organic content amounted to 90 mg/gDW of sediment, and the algal content (as calculated by the content of chloropigments assuming that 1 µg of pigment correspond to 30 µgC: Neveux, pers. comm.) to 1.7 mg of carbon /g of sediment, mostly corresponding to live diatoms.

Experimental procedure

For each duration, the labelled sediment (8 g dry weight) and 300 ml of filtered seawater were placed in four 350 ml chambers. Thirty clams of known size, corresponding to a total of 185 mg dry flesh weight were introduced into three of the four chambers immediately after mud sedimentation. The last chamber was used as a control (incubation without

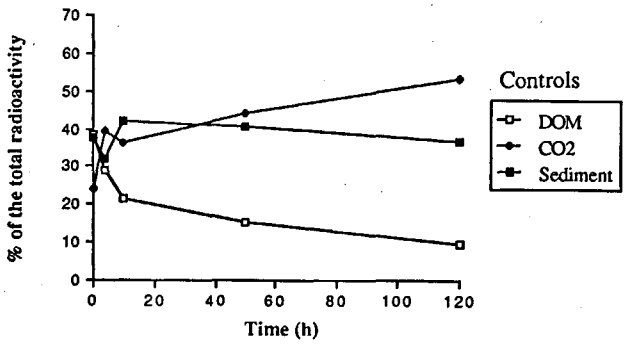


Figure 1

Controls, changes of radioactivity within the different compartments of the system studied. Standard deviations are included within points.

Témoins, changement de la radioactivité contenue dans les différents compartiments du système étudié. Les écart-types sont compris dans les points.

clams). Four experiments corresponding to four different time exposures (4, 10, 50, and 120 h) were carried out to assess the uptake of label by *Abra alba.*

^{14}C determination

At the end of each experiment, the radioactivities of the four compartments, sediment, DOM, CO_2, and animals were measured by liquid scintillation on a Beckman LS 5 000 CE liquid scintillator (Amouroux, 1986 *a*, *b*).

In order to determine the partitioning of the radioactivity within the sediment, and to identify which fractions of this sediment were indeed consumed by *Abra alba*, the radioactivity of the sediment was subdivided into several fractions (Cahet and Sibuet, 1986), corresponding to different steps in the chemical extraction procedure, as follows: the fraction soluble in dichloromethane + ethanol (fraction A which mostly corresponds to lipidic material; the fraction soluble in 2N HCl (fraction B which mostly corresponds to small peptides); the fraction soluble in 1N NaOH or 6N HCl (fraction C which mostly corresponds to alkalino and acido soluble macromolecules). Radioactivity of DOM was determined after filtration on a 0.2 µm membrane. The liquid medium was mixed by gentle air-bubbling sufficient for oxygenation, but which did not disturb the sedimentation process. At the outlet, air was passed through ethanolamin traps to capture labelled gaseous CO_2. For the determination of dissolved $^{14}CO_2$ production, 100 ml of filtered (0.2 µm) seawater were acidified in a bottle with a stopper fitted with a cup containing a filter paper saturated with ethanolamin. For the determination of sediment CO_2, sediment was acidified in the same way. Radioactivities corresponding to clams were determined after solubilization in hot NaOH (60°C, 12 h).

Calculations

All calculations are expressed as percentage of the total activity in the chamber or in the sediment. For incubations in the presence of animals, each point is the mean of three determinations. For controls (*i. e.* incubations without clams) each point corresponds to a single determination. Comparisons of the distribution of radioactivity within the different compartments between controls and chambers containing *Abra alba* were assessed using a χ^2 test (Sokal and Rohlf, 1981). Comparisons of the distribution of radioactivity within the different fractions of the sediment between controls and chambers containing *Abra alba* were achieved using G test for goodness of fit (Sokal and Rohlf, 1981).

RESULTS

Controls

The changes in the partitioning of radioactivity between the different compartments of the experimental system are shown in Figure 1. During the first 4 hours, the radioactivity in the sediment declined from 37.5 (t = 0) to 31.8 % (t = 4 h). It then reached 41.8 % (t = 10 h) before declining to 36.7 % by t = 120 h. Concurrently, radioactivity of DOM declined steadily from 38.5 (t = 0) to 9.5 % (t = 120 h). Radioactivity corresponding to dissolved, gaseous, and sediment CO2 increased from 24.0 at t = 0 to 38.2 % during the first four hours of the experiment. It then declined to 34.4 % (t = 10 h) before reaching 52.0 % by t = 120 h.

The changes in the partitioning of radioactivity between the different fractions of the sediment are shown in Figure 2. The radioactivity within fraction A declined from 6.2 % at t = 0 to 1.5 % at t = 50 h before increasing to 5.0 % at t = 120 h. In fraction B, radioactivity decreased from 37.7 to 30.0 % during the first 4 hours of the experiments, and then increased to 40.2 % by t = 10 h before decreasing again to 20.6 % by t = 50 h and increasing again (29.8 % by t = 120 h). In fraction C, radioactivity remained fairly constant during the first ten hours of the experiment (56.1 % at t = 0 h *vs* 55.8 % at t = 10 h) t before increasing to 77.8 % at t = 50 h .

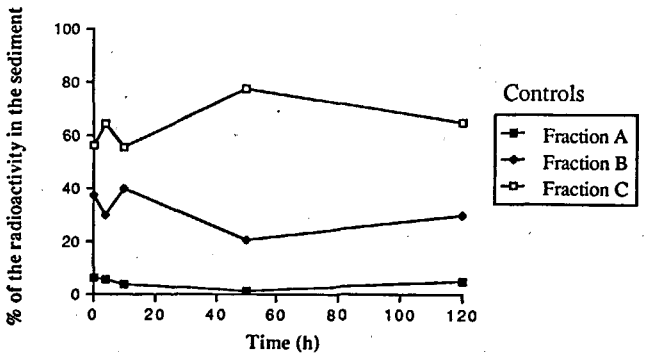


Figure 2

Controls, changes of radioactivity within the different fractions of the sediment. Standard deviations are included within points.

Témoins, changement de la radioactivité contenue dans les différentes fractions du sédiment. Les écart-types sont compris dans les points.

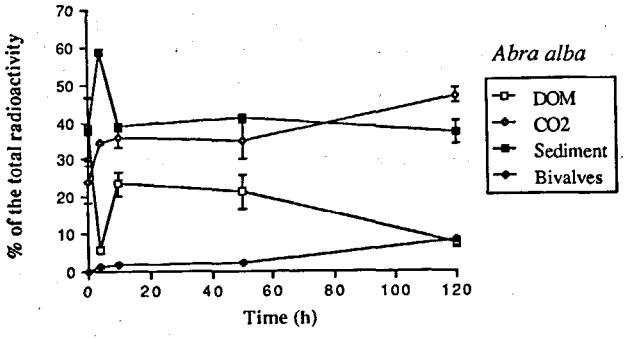


Figure 3

Abra alba, *changes of radioactivity within the different compartments of the system studied. Vertical bars are standard deviations.*

Abra alba, changement de la radioactivité contenue dans les différents compartiments du système étudié. Les barres verticales correspondent aux écart-types.

Abra alba

The changes in the partitioning of radioactivity between the different compartments of the experimental system in the presence of *Abra alba* are shown in Figure 3.

During the first four hours of the experiments, the radioactivity in the sediment increased from 37.5 to 58.7 % and then decreased to 37.3 % by t = 120 h ($p = 0.0043$, one-way ANOVA and *a posteriori* LSD tests; Sokal and Rohlf, 1981). The radioactivity of DOM declined from 38.5 (at t = 0) to 5.8 % (at t = 5 h) and then increased to 23.6 % at t = 10 h before declining to 7.5 % by t = 120 h ($p = 0.0001$, one-way ANOVA and *a posteriori* LSD tests). Radioactivity of dissolved, gaseous, and sediment CO_2 increased from 24.0 to 47.0 % at t = 50 h ($p = 0.0001$, one-way ANOVA and *a posteriori* LSD tests). Radioactivity within bivalves increased from 0 (at t = 0) to 8.2 % (at t = 120 h). Results of the χ^2 tests showed significant differences between controls and chambers containing *Abra alba* at t = 4 and 120 h, and no significant difference at t = 10 and 50 h ($\chi^2 = 57.165$, $p < 0.005$; $\chi^2 = 2.317$, $0.25 < p < 0.50$; $\chi^2 = 6.423$, $0.05 < p < 0.10$; $\chi^2 = 9.813$, $0.025 < p < 0.050$, for t = 4, 10, 50, and 120 h, respectively).

The changes in the partitioning of radioactivity between the different fractions of the sediment incubated in the presence of *Abra alba* are given in Figure 4. The radioactivity of fraction A showed no significant changes during the length of the experiment ($p = 0.1072$, one-way ANOVA), and ranged between 0.5 (at t = 50 h) and 7.9 % (at t = 4 h). Radioactivity of fraction B remained fairly constant during the first ten hours of the experiments (37.7 % at t = 0 vs 37.7 % at t = 10 h), and then declined to 18.5 % by t = 50 h ($p = 0.0016$, one-way ANOVA and *a posteriori* LSD tests). The radioactivity of fraction C remained fairly constant during the first ten hours of the experiments (56.1 % at t = 0 vs 57.8 % at t = 10 h) before increasing to 81.0 by t = 50 h ($p = 0.0015$, one-way ANOVA and corresponding *a posteriori* LSD tests). Results of G tests for goodness of fit showed that the distribution of the label within the different fractions of the sediment was not significantly affected by the presence of *Abra alba* ($G = 0.982$, $G = 0.479$, $G = 1.454$, $G = 4.679$; $p > 0.05$, for t = 4 h, t = 10 h, t = 50 h, and t = 120 h, respectively).

DISCUSSION

Methodological problems

Experimental studies assessing the utilization of sediment by macrobenthic deposit-feeders often involve a preliminary stage which corresponds to the labelling of the food (Lopez and Crenshaw, 1982; Crosby, 1985; Grémare *et al.*, 1991). Labelling is usually carried out via the "slurry"method (*i. e.*, mixing of the sediment with the radioisotope, *see* Lopez and Crenshaw, 1982; Lopez and Cheng, 1983; Forbes and Lopez, 1989). This stage seems to have important consequences since disturbances of the sediment may induce either microbial stimulation (Findlay and White, 1983) or inhibition (Findlay *et al.*, 1990) which may result in significant differences in radiolabel uptake by micro- (Dobbs *et al.*, 1989) and meiofauna (Carman *et al.*, 1989).

Results of the present study reveal the high instability in the radioactivity contained in a natural sediment radiolabelled using the slurry method. Such instability lasts for approximately ten hours both in controls and in experimental chambers containing *Abra alba*. More interestingly, in controls, the initial instability corresponds to a decrease (during the first four hours of the experiment) of the radioactivity within the sediment, whereas in chambers containing *Abra alba*, the initial instability corresponds to an increase of radioactivity within the sediment. These data can be compared with what is already known about microbial responses to disturbance. Physical perturbations are known to result in bacterial inhibition (Findlay *et al.*, 1990), which is comparable to what is observed in controls, *i. e.*, initial decrease of the radioactivity in sediment, probably corresponding to the decrease of radioactivity in the bacterial component of this sediment. Conversely, using

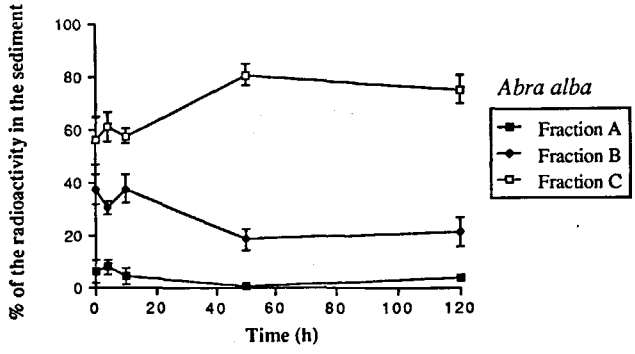


Figure 4

Abra alba, *changes of radioactivity within the different fractions of the sediment. Vertical bars are standard deviations.*

Abra alba, changement de la radioactivité contenue dans les différentes fractions du sédiment. Les barres verticales correspondent aux écart-types.

polymeric beta hydroxyalkalanoates as an indices of metabolic status, Findlay and White (1983) reported a stimulation of the bacterial community due to the presence of the deposit-feeding polychaete *Clymenella* sp. This, again is compatible with our data, *i. e.*, initial increase of radioactivity in sediment, and probably corresponds to an increase of the radioactivity in the bacterial component of this sediment).

This instability has important methodological implications for the study of the interactions between sediment and deposit-feeders. In fact, since in the marine environment, utilizations of radiolabelled food sources are often complicated by short-term recycling phenomena (Conover and Francis, 1973), there has been a trend to shorten the length of incubation period involved in the experimental study of benthic food chains (*i. e.*, use of pulse-chase design, Lopez and Cheng, 1983), the aim of this decrease being to ensure that the label of the tested food was stable over the length of the incubation. However, it should be stressed that because of:

1) the high instability of disturbed natural sediments; and

2) possible interferences with tested macrobenthic deposit-feeders, preliminary experiments must be carried out in order to determine the timing of the incubations relative to the recovering process of the sediment. Results of the present study would suggest a ten-hour time lag following the introduction of sediment and bivalves into the experimental chamber. It is unfortunate that no information has been provided on this crucial point in previous studies assessing the interactions between natural sediment and deposit-feeders (Lopez and Cheng, 1983; Forbes and Lopez, 1989).

An alternative to pulse chase design for the study "sediment-deposit-feeders" system is the coupling of compartmental analysis and analog modelling (Grémare , 1991), which allows for the *a posteriori* computation of fluxes between compartments. However, in the case of natural sediments, this approach is complicated by the lack of data relative to the distribution of radioactivity between the different components of the sediment. The use of different chemical extractions was an attempt to infer such information; however, in the present case this did not result in significant changes and it was impossible to relate with the different functional fractions of the sediment (*i. e.*, detritus, bacteria, diatoms). Nevertheless, the aim of the second part of the discussion is to propose mathematical models for the two studied systems (*i. e.*, controls and experimental chambers containing *Abra alba*).

Modelling

Experimental data showed that, during the first hours of incubation at least, the two systems (*i. e.*, controls and experimental chambers containing *Abra alba*) behaved in a different manner. This is likely to be due to differences in the response of the bacterial component associated to the sediment (Findlay and White, 1983; Findlay *et al.*, 1990). The sediment compartment was therefore considered as being composed of three subcompartments: namely bacteria (*i. e.*, microheterotrophs), diatoms (*i. e.*, microautotrophs) and detritus (dead particulate organic matter). Thus the models were composed of the following compartments: Dissolved Organic Matter (DOM), CO_2, bacteria, diatoms, detritus (+ bivalves for the experimental chambers containing *Abra alba*) exchanging radioactivity between each other (Fig. 5).

Changes of the distribution of radioactivity within the system result from two processes (*i. e.*, initial pertubation and long-term exchanges) corresponding to two different time scales (*i. e.*, 10 and 120 h). Long-term changes were first simulated using the models presented with continuous lines in Figures 5 and 6 for controls and experimental chambers containing *Abra alba*. The simulation of the initial changes of the radioactivity within the studied systems (*i. e.*, pertubation) was then carried out using a mathematical procedure recommended by Luyben (1973). This procedure, commonly used in chemistry, involves the creation of a fictive compartment (*i. e.*, FlashBact). The fictive compartment fuels the compartments which are initially stimulated (*i. e.*, CO_2 in controls, and bacteria and CO_2 in experimental chambers containing *Abra alba*). In order to balance radioactivity budgets, the instantaneous transfers of radioactivity from the fictive compartments were subtracted to the inhibited compartment (*i. e.*, bacteria and DOM for controls and experimental chambers containing *Abra alba*,

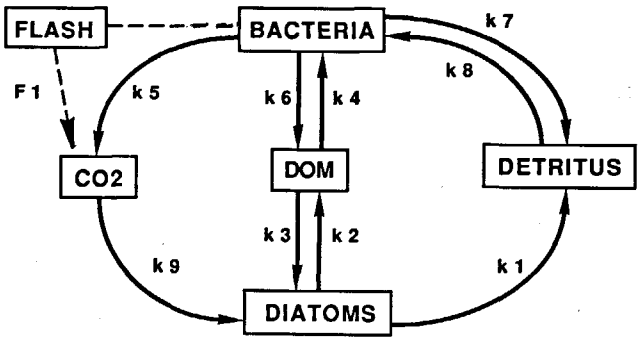


Figure 5

Controls, model simulating the exchanges of radioactivity.

Témoins, modèles simulant les échanges de radioactivité.

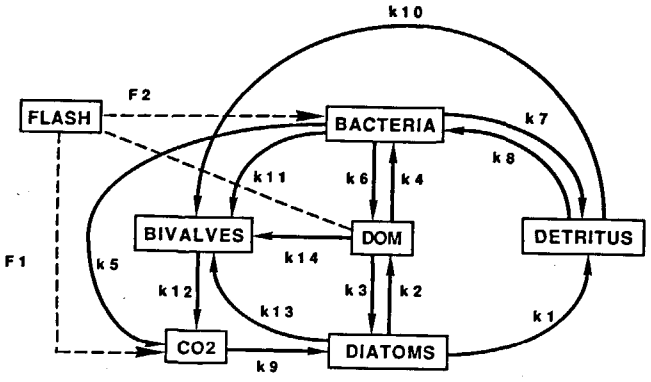


Figure 6

Abra alba, *model simulating the exchanges of radioactivity.*

Abra alba, modèle simulant les échanges de radioactivité.

Figure 7

Controls, fitting of the model to the experimental data.

Témoins, ajustement du modèle aux mesures expérimentales.

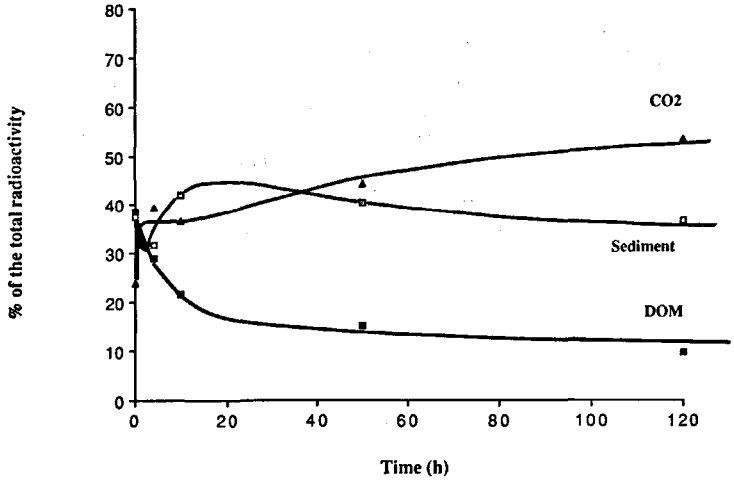
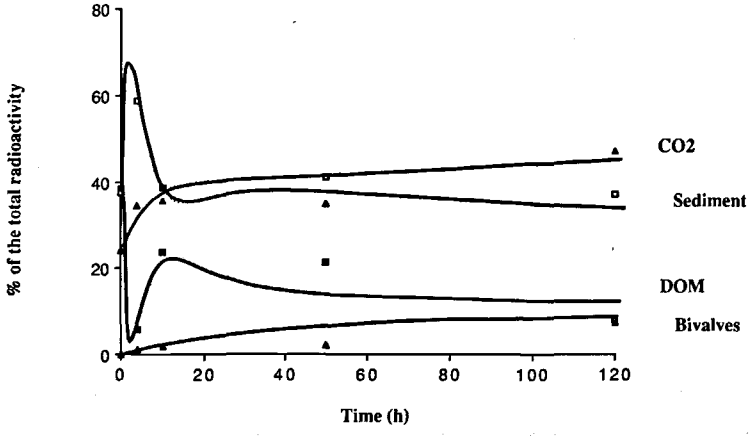


Figure 8

Abra alba, *fitting of the model to the experimental data.*

Abra alba, ajustement du modèle aux mesures expérimentales.



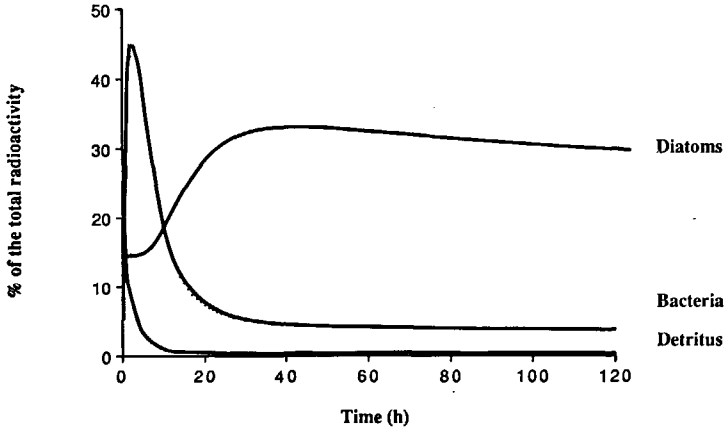


Figure 9

Controls, changes of radioactivity in the three subcompartments of the sediment.

Témoins, évolution de la radioactivité dans les trois sous compartiments constituant le sédiment.

Figure 10

Abra alba, *changes of radioactivity in the three subcompartments of the sediment.*

Abra alba, évolution de la radioactivité dans les trois sous compartiments constituant le sédiment.

respectively). The simulation of the initial pertubation is represented in dashed lines in Figures 6 and 7 for controls and chambers containing *Abra alba*, respectively. In both controls, and experimental chambers containing *Abra alba*, the radioactivity corresponding to the fictive compartment is almost equal to zero after only four hours of incubation.

Sets of differential equations representing the exchanges of radioactivity between compartments are given in Table 1. Assimilation of DOM by diatoms was introduced in the models since there is increasing experimental evidence that diatoms in general, and benthic diatoms in particular, are able efficiently to metabolize organic compounds (Bonin and Maestrini, 1981; Syrett, 1981; Admiraal *et al.*, 1984; Shah and Syrett, 1984; Admiraal *et al.*, 1986). The percentages of radioactivity contained in the different compart-

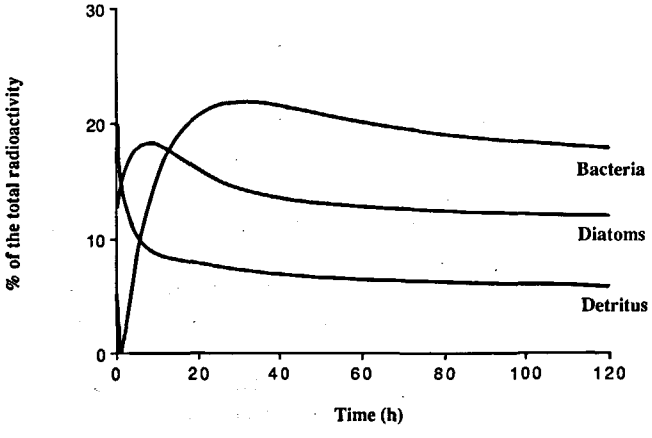


Table 1

Sets of differential equations simulating the exchanges of radioactivity within the two studied systems. k_i's are the kinetic coefficients of mass transfer, Fi's are the kinetic coefficients corresponding to the simulation of the initial pertubation of the system, [Xi]'s are the radioactive content of compartment X as a percentage of the total radioactivity in the system studied, and t is time.

Jeux d'équations différentielles simulant les échanges de radioactivité dans les deux systèmes étudiés. Les k_i sont les coefficients cinétiques de transfert de masse, les Fi sont les coefficients cinétiques correspondant à la simulation de la pertubation initiale du système, les [Xi] représentent le contenu radioactif du compartiment X exprimé en pourcentage de la radioactivité totale dans le système étudié, et t est le temps.

Controls

$$\frac{d[Sedt]}{dt} = \frac{d[Bact]}{dt} + \frac{d[Diat]}{dt} + \frac{d[Detr]}{dt}$$

$$\frac{d[Bact]}{dt} = +k_4[DOM] + k_8[Detr] - k_5[Bact] - k_6[Bact] - k_7[Bact] - F_1[Flash]$$

$$\frac{d[Diat]}{dt} = +k_3[DOM] + k_9[CO2]] - k_1[Diat] - k_2[Diat]$$

$$\frac{d[Detr]}{dt} = +k_7[Bact] + k_1[Diat] - k_8[Detr]$$

$$\frac{d[DOM]}{dt} = +k_2[Diat] + k_6[Bact] - k_3[DOM] - k_4[DOM]$$

$$\frac{d[CO2]}{dt} = +k_5[Bact] - k_9[CO2] + F_1[Flash]$$

$$\frac{d[Flash]}{dt} = -F_1[Flash]$$

Abra alba

$$\frac{d[Part]}{dt} = \frac{d[Bact]}{dt} + \frac{d[Diat]}{dt} + \frac{d[Detr]}{dt}$$

$$\frac{d[Bact]}{dt} = +k_4[DOM] + k_8[Detr] - (k_5 + k_6 + k_7 + k_{11})[Bact] + F_2[Flash]$$

$$\frac{d[Diat]}{dt} = +k_3[DOM] + k_9[CO_2] - (k_1 + k_2 + k_{13})[Diat]$$

$$\frac{d[Detr]}{dt} = +k_1[Diat] + k_7[Bact] - (k_8 + k_{10})[Detr]$$

$$\frac{d[DOM]}{dt} = +k_2[Diat] + k_6[Bact] - (k_3 + k_4 + k_{14})[DOM] - (F_1 + F_2)[Flash]$$

$$\frac{d[CO2]}{dt} = +k_5[Bact] + k_{12}[Biv] - k_9[CO_2] + F_1[Flash]$$

$$\frac{d[Biv]}{dt} = +k_{10}[Detr] + k_{11}[Bact] + k_{13}[Diat] + k_{14}[DOM] - k_{12}[CO_2]$$

$$\frac{d[Flash]}{dt} = -(F_1 + F_2)[Flash]$$

ments at t = 0 are presented in Table 2. Initial values of DOM, sediment, bivalves, and CO_2 were measured, whereas initial proportions of bacteria, diatoms and detritus were fixed to permit the simulation of the two systems studied.

The fitting of the model to the experimental data is presented in Figures 6 and 7, for experimental chambers containing *Abra alba* and controls, respectively. The corresponding kinetic constants (expressed in h^{-1}) are presented in Table 3. In the presence of *Abra alba* the stimulation of bacteria (k_{14}=0.2250) is about five times greater than the stimulation of CO_2 (k_{15} = 0.0431). This may be explained by the lack of correlation between bacterial production and

Table 2

Initial distribution of the radioactivity.

Répartition initiale de la radioactivité.

Percentages of the total radioactivity		
DOM	38.5	
CO_2	24.0	
Bivalves	0.0	
Sediment	37.5	
Bacteria		*5.0*
Diatoms		*12.5*
Detritus		*20.0*
Flash (controls)	13.5	
Flash (*Abra*)	110	

respiration (Cahet, personal observations). Radioactivity within the compartment sediment results from changes in the three compartments: bacteria, diatoms and detritus. In controls (Fig. 9), radioactivity corresponding to bacteria decreases rapidly during the first two hours of the experiment before increasing steadily 20 % by t = 35 h. Radioactivity corresponding to diatoms increases steadily during the first ten hours of the experiment (until 40 h) before declining and then remaining stable. Radioactivity corresponding to detritus decreases steadily (until t = 10 h) before remaining stable.

In experimental chambers containing *Abra alba* (Fig. 10), radioactivity corresponding to bacteria increases very rapidly during the first ten hours of the experiment (+ 30 %), then decreases until 50 h before remaining constant (5 % by t = 120 h). Radioactivity corresponding to diatoms increases steadily between 0 and 50 h before remaining stable. Radioactivity corresponding to detritus decreases steadily between 0 and 20 h and then remains stable and close to 0.

Table 3

Values of the kinetic constants used in the two fitted models.

Valeurs des constantes cinétiques utilisés dans les deux modèles ajustés.

Controls	*Abra alba*
$k_1 = 0.0850$	$k_1 = 0.0043$
$k_2 = 0.0324$	$k_2 = 0.0324$
$k_3 = 0.0800$	$k_3 = 0.0800$
$k_4 = 0.0112$	$k_4 = 0.1000$
$k_5 = 0.0275$	$k_5 = 0.0275$
$k_6 = 0.0381$	$k_6 = 0.3272$
$k_7 = 0.0180$	$k_7 = 0.0077$
$k_8 = 0.2271$	$k_8 = 0.3760$
$k_9 = 0.0099$	$k_9 = 0.0050$
	$k_{10} = 0.0045$
$F_1 = 0.9050$	$k_{11} = 0.0045$
	$k_{12} = 0.0200$
	$k_{13} = 0.0045$
	$k_{14} = 0.0020$
	$F_1 = 0.0150$
	$F_2 = 0.2250$

GENERAL CONCLUSIONS

Results of the present study revealed the high sensitivity of radiolabelled natural sediments to biotic disturbance. This instability is dependent on the presence, and probably on the identity of the deposit-feeder tested. In fact unpublished preliminary experiments carried out with the deposit-feeding polychaete *Eupolymnia nebulosa* suggest an initial increase of radioactivity in CO_2 and an initial decrease of radioactivity in sediment (*i. e.*, an amplification of what has been observed in controls during the present study).

Initial sediment instability has major implications for the experimental procedures that should be used for the study of the interactions between natural sediments and deposit-feeders. Two approaches may be proposed:

1) introduction of a time lag to permit the sediment to recover from the disturbance (*i. e.*, 10 h in the present case);

2) use of modelling to simulate the exchanges of radioactivity between compartments of the studied systems. Both of these approaches present drawbacks. The introduction of a time lag may result in unwanted contamination by the radioisotope. This is especially important when studying the utilization of a given component (such as diatoms or bacteria) of the sediment by deposit-feeders. The main weakness of the modelling approach is the lack of information concerning the distribution of the radioactivity within the different components of the sediment. It is important to point out that due to this lack of information, the model presented here is only a hypothesis accounting for the observed changes of radioactivity between compartments.

Nevertheless, the present study has shown that it is possible to simulate the exchanges of radioactivity in a complex system where two different kinetics (initial short-term pertubation and long-term changes) are occurring. The use of the model stresses the need for a quantification of the radioactivity corresponding to the different component of the sediment.

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