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Filter-feeders
Deposit-feeders
Pollutant
Bioturbation
Filtreur
Dépositivore
Polluant
Bioturbation

Interrelations in a microcosm with a suspension-feeder and a deposit-feeder. I : Experimental study

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ABSTRACT

A microcosm comprising a filter-feeding bivalve (*Venerupis decussata*), a deposit-feeding annelid (*Eupolymnia nebulosa*), and a monospecific suspension (bacteria or unicellular algae) was studied on the basis of compartmental analysis. The live suspension was labelled with ^{14}C. A series of experiments of varying duration permitted determination of the diffusion of radioactivity within the microcosm. We measured the consumption, the biodeposition of the monospecific live suspension by *Venerupis decussata*, and the subsequent use of the faeces by *Eupolymnia nebulosa*. A pollutant was introduced to test its influence on the distribution of ^{14}C in the system. This pollutant was found to be concentrated in the deposit-feeding annelids but not in the filter-feeding bivalves.

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RÉSUMÉ

Interrelations entre filtreurs et dépositivores en microcosme. I : Étude expérimentale

Un microcosme comprenant un bivalve filtreur (*Venerupis decussata*), un dépositivore (*Eupolymnia nebulosa*) et une suspension monospécifique (bactérie ou algue unicellulaire), a été étudié suivant une analyse de type compartimental. La suspension vivante est marquée au ^{14}C. Une série de plusieurs expériences de différentes durées permet de déterminer la diffusion de la radioactivité dans le système. Nous avons mesuré la consommation, la biodéposition de la suspension par *V. decussata*, et l'utilisation des fèces par *E. nebulosa*. L'influence d'un polluant sur la distribution du ^{14}C dans le système a été mesurée. Ce polluant est concentré dans l'annélide dépositivore mais pas dans le bivalve filtreur.

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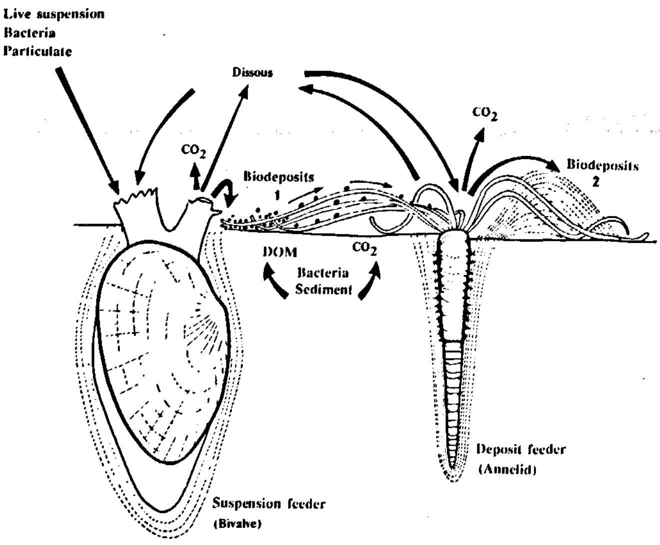
INTRODUCTION

Through defecation, filter-feeders constitute the most significant pathway for the biodeposition of particles from the water column to the sediment. On the bottom, biodeposits are mixed and consumed by deposit-feeders in a manner relative to their compaction, their bacterial decomposition and their organic content (Moriarty, 1982; Guidi and Tito de Morais, 1983). According to many authors, bacterial epiflora associated with sediment grains is the main food source of deposit-feeders (Hargrave, 1970; Kofoed, 1975; Yingst, 1976; Robertson and Newell, 1982). However, other scientists consider that detritus and microphytobenthic organisms may play a significant role in the nutrition of deposit-feeders (Tunicliffe and Risk, 1977; Cammen, 1980; Kemp, 1986).



Figure

Interrelations between the different compartments of the system.

Interrelations entre les différents compartiments du système.

Microphytobenthic organisms, as well as micro- and macroinvertebrates, contribute to the recycling of organic matter. Cahet and Gadel (1976) have measured the changes of the carbon to nitrogen ratio (C/N) in sediments and deposits. The short term kinetics of transfer have, however, largely been ignored. It was on such a microecosystem that one of us (J.-M.A.) measured the filtration, assimilation and biodeposition rates of the bivalve *Venus verrucosa* (Amouroux, 1982). In a semi-confined system, the complexity of the exchanges between water and animal necessitates a complete investigation of the particulate suspension and of the production and recycling of the dissolved substances. The aim of the present study is to measure the transfer kinetics between monospecific live suspensions and the sediment through the action of a filter-feeding bivalve and a deposit-feedind annelid (Fig.). The use of ^{14}C permits the not only of the particulate fraction consumed by the animals but also of the interaction between the different compartments which constitute the microcosm (Conover and Francis, 1973), although ^{14}C is recycled very rapidly and this study must be completed by the elaboration of an analog model of the system (Amouroux and Amouroux, 1988), which permits measurement and comparison of the transfer of organic matter between each of the different compartments (Part II: Modelling).

MATERIALS AND METHOD

Biological materials

Both *Venerupis decussata* and *Eupolymnia nebulosa* are very common in the shallow area of the harbour of Port-Vendres. They can also be found in the lagoons all along the Languedoc-Roussillon coast. *Venerupis decussata* is a filter-feeding bivalve; its siphons can reach 5 or 7 cm in length. *Eupolymnia nebulosa* is a tentaculate deposit-feeding polychaete (Grémare, 1988). The mucus produced by its tentacles ensures the capture of sand grains, which are then transported through the mouth through a large ciliary groove (Dales, 1955).

Both organisms were collected by scuba diving. In the laboratory they were kept in aquaria provided with running sea water. Epibionts were cleaned from the shells of the bivalves and the annelids were removed from their natural tubes, which they usually rebuilt quickly with the sediment used during the experiments. Before each experiment, 10 animals (5 bivalves and 5 annelids) were starved (3 days) in filtered sea water in a controlled temperature room (15°C), the water being changed daily.

The bivalves used for the experiments were some 36 mm in length, which corresponds to an ash-free dry tissue weight of 0.304 g. The average length of the annelids was some 7 cm, which corresponds to 0.182 g in ash-free dry tissue weight. For the annelids these length measurements are subject to error because of the constrictions exhibited by *Eupolymnia nebulosa*.

The bacteria, which belonged to the genus *Lactobacillus* sp., were isolated from Port-Vendres harbour. This species is motile and can be easily cultivated in the laboratory. Previous studies have permitted definition of the characteristics of its specific radioactivity variation with time (Amouroux, 1984; 1986 *a*).

Table 1

Diagram of the different experiments carried out. Figures at the top indicate the number of compartments in the system; those at the bottom indicate the numbers of the experiments.

Diagramme des différentes expériences réalisées. Les chiffres du haut indiquent le nombre de compartiments du système; ceux du bas le numéro de l'expérience.

ALGAE									BACTERIA							
7	7	6	5	6	5	4	3	N^{ber} of Compartments	3	4	5	6	5	6	6+1	6+1
▨	▨				▨			Bivalves			▨	▨			▨	▨
▨	▨					▨		Sediment		▨		▨		▨	▨	▨
▨	▨		▨					Annelids					▨	▨	▨	▨
▨								Pollutant								▨
7	6	5	4	3	2'	1	0		0	1	2	3	4	5	6	7

The algae was *Pavlova lutheri*, a chrysomonad whose mobility ensures homogeneous suspensions, and which measures between 4 and 6 µm in length. This species can be easily cultivated in the laboratory. A preliminary study has defined the characteristics of its specific radioactivity variation in time (Amouroux, 1984; 1986*b*).

Experimental arrangements

The experiments were carried out in 5 litres plexiglass cylinder chambers containing 2 litres of fine-grained sand and 2 litres of filtered sea water. This sand was collected in Port-Vendres harbour and placed in running sea water aquaria. The average size of the sediment grains was about 250 µm.

A gently bubbling air stream was passed through a lateral hole. This air was then collected on ethanolamine traps for measurement of $^{14}CO_2$.

The various durations of the experiments were 4, 10, 20 and 40 hours. Different experiments were carried out to measure the importance of the different exchanges (Tab. 1).

The sediment was placed in the mesocosm 48 hours before each experiment. The 5 annelids were introduced 24 h before measurements were started; because they burrow very rapidly the 5 bivalves were introduced at the beginning of each experiment. 20 mg of the ^{14}C labelled food was introduced immediately after the bivalves in each of the 4 chambers. The number of living cells introduced was determined directly by optic density (440 nm) and by Petri dish culture on Zobell solid medium. Counting of the algae was performed under the microscope with a Thoma scale-grid. For each duration 4 chambers were treated simultaneously: three contained animals and the fourth was used as a blank (no animals). For each experiment a balance of the radioactivity counted in the different compartments was established. All the measurements were carried out by liquid counting scintillation and corrected for background and machine efficiency. The results are expressed as percentage of the initial radioactivity (Amouroux, 1986*a*).

Table 2

Time-dependent variation of the initial radioactivity of the live suspension with sediment. Bacteria alone with sediment.

Évolution en fonction du temps de la radioactivité initiale de la suspension vivante avec sédiment.

			20 hours		40 hours	
	4 hours	10 hours	1	2	3	4
Particulate	–	–	40.6	40.6	35.6	37.8
DOM	–	–	31.5	38.4	21.8	27.5
CO_2	–	–	22.9	22.2	34.8	24.8
Sédiment	–	–	5.0	2.2	7.8	8.9
Live Bacteria	–	–	138.	128.	98.	140

The pollutant: Propyzamide. Introduction and analysis

The pollutant we used was Propyzamide (N-dimethyl-1,1 propynyl dichloro-3,5 benzamide), a product regularly used as presticide in agriculture and as a selective weed-killer for salad cultures. In spring and autumn, it is carried to the sea by heavy rains. It was introduced as a solution in sea water with a concentration of 1 mg per litre.

The animals were homogenized in a mortar with Fontainebleau sand in ethyl acetate. The mixture was further homogenized ultrasonically for 3 minutes and centrifuged for 5 minutes at 4 000 G. The supernatant was then filtered on phase-separating paper and the ethyl acetate fraction analysed by gas chromatography (Bastide and Coste, 1978).

RESULTS

Bacteria as food

Time-dependent variation of the bacteria alone

The time-dependent variation of the suspension alone in sea water has been quantified in a previous study (Amouroux, 1986*a*). After 4 hours, the suspension had lost 35 % of its radioactivity in CO_2 (1 %) and dissolved substances (34 %). After 10 hours, the dissolved substances were reabsorbed slowly but reached a steady state because of the emergence of non-recyclable substances. The CO_2 increased regularly as the radioactivity of the suspension declined slowly.

Time-dependent variation of the bacteria with sediment (Tab. 2)

Variation of the bacteria in time depends on the presence or absence of sediment. The number of live bacteria increased by 1/3 and at the same time the radioactivity decreased from 100 to 40 % (20 hours) and 36.5 % (40 hours). The $^{14}CO_2$ reached 30 % and the dissolved substances 25 % (40 hours). The sediment accounted for only 8.5 % of the initial radioactivity.

Time-dependent variation of the bacteria consumed by the bivalves without sediment (Tab. 3)

The bivalves filtered the suspension and collected more than 90 % of the suspended cells after 4 hours and

Table 3

Time-dependent variation of the radioactivity in the different compartments of the system "bivalves-bacteria without sediment". The results are expressed as a percentage of the initial radioactivity.

Évolution en fonction du temps de la radioactivité dans les différents compartiments du système bivalves-bactérie sans sédiment. Les résultats sont exprimés en pourcentage de la radioactivité initiale.

No.	4 hours			10 hours			15 hours			40 hours		
of experiment	1	2	3	4	5	6	7	8	9	10	11	12
Bivalves	70.5	76.1	80.9	57.7	57.3	57.6	–	–	–	35.7	28.3	15.0
Particulate	6.5	2.8	2.0	13.8	11.7	10.9	–	–	–	9.9	19.4	29.8
DOM	16.9	13.6	11.7	–	–	–	6.4	2.8	8.7	8.1	12.1	15.7
CO_2	6.1	7.5	5.4	–	–	–	20.1	26.7	24.3	46.2	40.2	39.5
Live Bacteria	–	–	–	1.8	0.7	1.5	2.1	1.8	0.6	4.8	25.0	53.0

Table 4

Time-dependent variation of the radioactivity in the different compartments of the system "bivalves-bacteria with sediment". The results are expressed as a percentage of the initial radioactivity.

Évolution en fonction du temps de la radioactivité dans les différents compartiments du système bivalves-bactéries avec sédiment. Les résultats sont exprimés en pourcentage de la radioactivité initiale.

No.	4 hours			10 hours			15 hours			40 hours		
of experiment	1	2	3	4	5	6	7	8	9	10	11	12
Annelids	2.3	3.6	3.2	8.5	6.8	8.6	–	–	–	23.6	16.3	20.0
Particulate	74.2	70.0	69.8	41.2	44.9	44.4	–	–	–	17.2	23.4	17.3
DOM	20.5	24.0	23.3	11.2	10.1	12.4	10.5	12.0	8.9	26.8	16.3	23.0
CO_2	3.0	2.4	3.7	39.1	38.2	33.6	42.2	43.9	35.2	32.4	44.0	39.7
Live Bacteria	–	–	–	–	–	–	39.3	25.0	21.4	23.1	36.5	25.0

about 80 % of the initial radioactivity. The radioactivity in the soft parts of the bivalves declined to 57 % after 10 hours and 26 % after 40 hours. The bacteria in suspension contained 4 % of the total radioactivity after 4 hours, 12 % after 10 hours and 20 % after 40 hours. This suggests either bacterial multiplication or resuspension of the non digested biodeposited bacteria. Dissolved substances accounted for 14.1 % of the initial radioactivity after 4 hours, 6.0 % after 15 hours and 12 % after 40 hours. The $^{14}CO_2$ reached 42 % after 40 hours.

Time-dependent variation of the bacteria consumed by the annelids without sediment (*Tab.* 4)

The radioactivity retained in the soft body of the annelids increased regularly from 3 % after 4 hours to 20 % after 40 hours. The radioactivity of the bacteria decreased from 71 % after 4 hours to 19 % after 40 hours. Dissolved substances increased quickly during the first 4 hours by 22 % and then decreased to 15 % after 10 hours. The CO_2 increased uniformly (39 % after 40 hours).

Time-dependent variation of the bacteria consumed by the bivalves with sediments (*Tab.* 5)

The radioactivity contained in the soft part of the bivalves with sediment was lower than that found without sediment: 25 % at 4 hours and 15 % after 40 hours. The suspended particulate organic matter changed from 100 % (To) to 5 % (4 hours). This level then remained fairly constant until 40 hours (1 to 1.5 %). The faeces of the bivalves were trapped on the sediment and the undigested viable cells could not be resuspended. The radioactivity of the dissolved substances slowly increased during the first 4 hours (27 %) and then declined slowly (7.5 % at 40 hours). The $^{14}CO_2$ increased regularly from 6.8 % (4 hours) to 34 % (40 hours). The radioactivity of the sediment increased rapidly during the first 4 hours (36.5 %) and slowly thereafter: 46 % (10 hours), 43.5 % (15 hours) and 42 % (40 hours).

Time-dependent variation of the bacteria consumed by the annelids with sediment (*Tab.* 6)

With sediment, the annelids did not feed actively, and their radioactivity remained very low (between 1 and 2 %). Much of the suspension was not consumed (37 % after 4 hours) and a part was trapped by the sediment; it was resuspended by the bioturbative action of the annelids (33 % after 10 hours, 48.5 % after 15 hours and 44 % after 40 hours). The CO_2 increased to 23 % after 4 hours and declined to 16 % after 40 hours: the live free diatoms of the sediment consumed the CO_2 by residual photosynthesis. This suggests the transfer by the sediment and the suspension (resuspended particulate matter). The radioactivity of the dissolved substances fluctuated from about 30 % after 4 hours to 14 % after 15 hours and 22 % after 40 hours.

Table 5

Time-dependent variation of the radioactivity in the different compartments of the system "annelids-bacteria without sediment". The results are expressed as a percentage of the initial radioactivity.

Évolution en fonction du temps de la radioactivité dans les différents compartiments du système annélides-bactéries sans sédiment. Les résultats sont exprimés en pourcentage de la radioactivité initiale.

No. of experiment	4 hours		10 hours		15 hours		40 hours	
	1	2	3	4	5	6	7	8
Bivalves	28.1	21.2	21.2	20.0	20.1	19.0	13.7	16.6
Particulate	6.2	3.8	1.4	1.0	1.2	2.2	1.3	1.5
DOM	28.7	25.2	22.0	18.9	11.5	13.2	8.5	7.1
CO_2	6.3	7.2	11.2	12.0	23.3	22.0	29.7	38.2
Sediment	30.7	42.6	44.2	48.1	43.9	43.6	46.8	36.6
Live Bacteria	4.2	4.8	0.9	0.6	0.3	1.3	1.9	2.7

Table 6

Time-dependent variation of the radioactivity in the different compartments of the system "annelids-bacteria with sediment". The results are expressed as a percentage of the initial radioactivity.

Évolution en fonction du temps de la radioactivité dans les différents compartiments du système annélides-bactéries avec sédiment. Les résultats sont exprimés en pourcentage de la radioactivité initiale.

No. of experiment	4 hours		10 hours		15 hours		40 hours	
	1	2	3	4	5	6	7	8
Annelids	1.0	0.9	1.0	1.2	1.5	1.5	2.0	1.6
Particulate	38.1	35.3	33.4	32.5	47.1	49.9	41.5	46.5
DOM	32.3	29.4	32.2	33.6	18.5	13.3	19.1	23.8
CO_2	21.4	25.2	23.3	21.5	18.2	21.4	17.8	13.8
Sediment	7.2	9.2	10.1	11.2	14.7	13.9	19.6	14.3
Live Bacteria	131	140	128	169	113	138	97	110

Time-dependent variation of the radioactivity in the different compartments of the system "bacteria-bivalves-annelids-sediment" (*Tab.* 7 *A and B*)

The radioactivity of the bacteria decreased very quickly during the 2 first hours and then remained constant (about 3 % of the initial radioactivity) until 40 hours. In the soft body of the bivalves, the radioactivity quickly increased: 58 % after 1 hour and then declined regularly (32 % after 4 hours, 19 % after 20 hours). It reached 18 % after 40 hours. The radioactivity of the sediment reached 32 % after 4 hours, 42 % after 10 hours and then slowly declined to 40 hours. This suggests a recycling of

Table 7

Time-dependent variation of the radioactivity in the different compartments of the entire system "lactobacillus sediment-annelids-bivalves". The results are expressed as a percentage of the initial radioactivity. Numbers indicate the different references of the experiments for different durations. A) Raw data; B) Mean raw data.

Évolution en fonction du temps de la radioactivité dans les différents compartiments du système complet bactéries-sédiment-annélides-bivalves. Les résultats sont exprimés en pourcentahe de la radioactivité initiale. Les chiffres indiquent les différentes expériences de durées différentes. A) Résultats bruts; B) moyennes.

No.	4 hours		10 hours		20 hours			40 hours		
of experiment	1	2	3	4	5	6	7	8	9	10
Bivalves	26.0	35.9	16.3	25.6	17.7	16.5	15.8	9.2	9.3	11.9
Annelids	0.2	0.3	1.0	0.5	0.8	0.4	0.4	1.6	0.6	0.7
Particulate	4.4	6.5	13.0	5.6	13.8	3.6	10.9	11.8	8.8	9.0
DOM	14.9	13.1	17.4	12.6	12.5	4.1	5.4	10.7	9.8	10.6
CO_2	18.0	18.2	21.5	18.3	28.7	30.4	28.0	24.1	25.9	28.5
Sediment	38.5	26.0	30.8	37.4	26.5	45.0	39.5	42.6	45.6	39.3
Live Bacteria	9.4	15.0	25.8	7.3	4.2	0.9	17.0	21.9	9.2	14.2

No. of experiment	4 hours	10 hours	20 hours	40 hours
Bivalves	31.0	21.0	16.6	10.1
Annelids	0.2	0.8	0.5	1.0
Annelids	5.5	9.3	9.3	9.8
DOM	14.0	15.0	11.0	10.4
CO_2	18.1	19.9	29.0	26.2
Sediment	29.3	34.1	37.0	42.5
Live Bacteria	12.2	16.5	7.4	15.1

Table 8

Time-dependent variation of the initial radioactivity of the livre suspension of algae with sediment.

Évolution en fonction du temps de la radioactivité de la suspension vivante d'algues avec sédiment.

	4 hours	20 hours
Particulate	52.5	34.5
DOM	9.5	12.5
CO_2	0.5	0.5
Sediment	37.5	52.5
Suspension (number)	54.5	45.0

the biodeposits. The $^{14}CO_2$ quickly increased during the first hours (20 % after 4 hours) and then very slowly to 40 hours (27 % after 40 hours). This implies the existence of a metabolic consumption by the living cells associated to the sediment.

Table 9

Time-dependent variation of the radioactivity in the different compartments of the system "bivalves-algae without sediment". The results are expressed as a percentage of the initial radioactivity. A) Raw data; B) Mean raw data.

Évolution en fonction du temps de la radioactivité dans les différents compartiments du système bivalves-algues sans sédiment. Les résultats sont exprimés en pourcentage de la radioactivité initiale. A) Résultats bruts; B) moyennes.

A	10 hours			15 hours			40 hours		
No. of experiment	1	2	3	4	5	6	7	8	9
Annelids	60.5	65.4	57.5	48.7	52.7	50.1	70.5	61.3	66.5
Particulate	28.5	24.8	30.9	28.5	26.3	24.6	8.1	10.1	11.3
DOM	6.0	4.7	6.8	12.7	12.5	16.5	10.7	17.4	13.1
CO_2	4.4	5.1	4.8	10.1	8.5	8.8	10.7	11.2	9.1
Number of Algae	0	0	0	0	0	0	0	0	0

B	10 hours	15 hours	40 hours
Bivalves	61.1	50.5	66.2
Particulate	28.1	26.5	9.8
DOM	6.0	13.9	13.7
CO_2	4.8	9.1	10.3

Dissolved substances increased quickly during the first 2 hours until 21 %, declined to 10 hours (15 %) and 40 hours (10 %).

The radioactivity within the body of the annelids remained fairly constant throughout the experiment (about 1 %).

Algae as food

Time-dependent variation of the algae alone

The time-dependent variation of the suspension alone in sea water has been quantified in a previous study (Amouroux, 1986 *b*). The algae lost 20 % of their radioactivity in 4 hours, 25 % in 10 hours and 26 % in 40 hours. The greater part was lost through excretory products in dissolved form (DOM; 19 % in 4 hours, 24.5 % in 10 hours and 22.8 % in 40 hours). The CO_2 was 0.5 % in 4 hours, 0.8 % in 10 and 7.6 % in 40 hours. After 10 hours the dissolved substances were reabsorbed slowly but reached a steady state by substitution of non-recyclable substances. The CO_2 increased regularly as the radioactivity of the suspension declined slowly.

Time-dependent variation of the algae with sediment (Tab. 8)

The time-dependent variation of the algae in the presence of the sediment was different from that of those without sediment. The number of live algae declined slowly and reached 54.5 % after 4 hours and 45 % after 10 hours. Their radioactivity decreased from 100 to 52.5 % after 4 hours and 34.5 % after 10 hours. The $^{14}CO_2$ was very low (0.5 % after 10 hours). The dissolved substances were 9.5 % after 4 hours and 12.5 % after 10 hours. The sediment accounted for 37.5 % of the initial radioactivity after 4 hours and 45.0 after 10 hours.

Time-dependent variation of the algae consumed by the bivalves without sediment (Tab. 9 A and B)

During the first 2 hours, the bivalves filtered the suspension steadily until it was totally clear of algae, which

Table 10

Time-dependent variation of the radioactivity in the different compartments of the system "annelids-algae without sediment". The results are expressed as a percentages of the initial radioactivity. A) Raw data ; B) Mean raw data.

Évolution en fonction du temps de la radioactivité dans les différents compartiments du système annélides-algues sans sédiment. Les résultats sont exprimés en pourcentage de la radioactivité initiale. A) Résultats bruts ; B) moyennes.

A	10 hours			15 hours			40 hours		
No. of experiment	1	2	3	4	5	6	7	8	9
Annelids	21.9	21.5	17.8	19.1	25.8	21.8	11.5	9.9	10.9
Particulate	61.1	66.7	68.0	64.4	51.6	58.2	67.3	65.4	70.0
DOM	15.9	9.4	11.9	11.8	18.4	16.4	12.2	17.2	13.1
CO_2	2.0	2.4	2.3	4.7	4.2	3.6	8.5	7.5	6.0
Number of Algae	0	0	0	0	0	0	0	0	0

B	10 hours	15 hours	40 hours
Annelids	20.4	22.2	10.8
Particulate	65.3	58.1	67.6
DOM	12.4	15.5	14.2
CO_2	2.2	4.2	7.3

were then in the gut or had been excreted. The radioactivity in the soft parts of the bivalves decreased from 61.1 % after 10 hours to 50.5 % after 15 hours and increased to 66.2 % after 40 hours. The particulate organic matter (POM) contained 28.1 % of the total radioactivity after 10 hours, 26.5 % after 15 hours and 9.8 % after 40 hours. This suggests a recycling of the biodeposits through bacterial activity. The dissolved substances accounted for 6.0 % of the initial radioactivity after 10 hours, 13.9 % after 15 hours and 13.7 % after 40 hours. The $^{14}CO_2$ reached 10.3 % after 40 hours.

Time-dependent variation of the algae consumed by the annelids without sediment (Tab. 10 A and B)

The radioactivity retained in the soft body of the annelids reached 22.2 % after 15 hours and declined to 10.8 % after 40 hours. The radioactivity of the POM rose to 65.3 % after 10 hours, declined to 58.1 % after 15 hours and rose to 67.6 after 40 hours. The dissolved substances rose to 15.5 % after 15 hours and then decreased to 14.3 % after 40 hours. The $^{14}CO_2$ increased slowly (7.3 % after 40 hours).

Table 11

Time-dependent variation of the radioactivity in the different compartments of the entire system "algae-sediment-annelids-bivalves". The results are expressed as a percentage of the initial radioactivity. A) Raw data ; B) Mean raw data.

Évolution en fonction du temps de la radioactivité dans les différents compartiments du système complet algues-sédiment-annélides-bivalves. Les résultats sont exprimés en pourcentage de la radioactivité initiale. A) résultats bruts ; B) moyennes.

No. of experiment	4 hours		10 hours		20 hours		40 hours	
	1	2	3	4	5	6	7	8
Bivalves	72.0	70.2	47.8	45.8	38.9	46.3	32.0	40.0
Annelids	0.7	2.6	10.0	4.0	9.0	7.4	4.8	3.8
Particulate	1.4	0.2	0.9	1.3	0.6	0.7	1.3	3.0
DOM	4.5	4.1	3.4	3.7	2.0	2.3	7.1	7.6
CO_2	0.9	0.6	2.2	2.1	8.7	7.6	7.5	9.1
Sediment	20.5	22.3	35.7	43.0	40.8	35.7	47.3	36.5

B	4 hours	10 hours	20 hours	40 hours
Bivalves	71.1	46.8	42.6	36.0
Annelids	1.6	7.0	8.2	4.3
Particulate	0.8	1.1	0.7	2.1
DOM	4.3	3.6	2.2	7.3
CO_2	0.8	2.2	8.1	8.4
Sediment	21.4	39.3	38.2	41.9

Time-dependent variation of the radioactivity in the different compartments of the system "algae-bivalves-annelids-sediment" (Tab. 11 A and B)

The radioactivity of the algae decreased very quickly during the 2 first hours and the radioactivity of the total POM was 0.8 % after 4 hours and varied slowly: 1.1 % after 10 hours, 0.7 % after 20 hours and 2.1 % after 40 hours. In the soft body of the bivalves the radioactivity increased quickly: 57.1 % after 4 hours and then declined regularly (46.8 % after 10 hours, 42.6 % after 20 hours, and 36.0 after 40 hours). The radioactivity within the body of the annelids varied from 1.6 % after 4 hours to 7.0 % after 10 hours, 8.2 % after 20 hours and 4.3 % after 40 hours. The radioactivity of the sediment reached 21.4 % after 4 hours, 39.3 % after 10 hours and 41.9 after 40 hours. The $^{14}CO_2$ increased slowly during the first 4 hours (0.8 %) and reached 8.1 after 20 hours and then was very stable until 40 hours (8.4 %). This implies some metabolic consumption by the living part of the sediment. The dissolved substances reached 4.3 % after 4 hours and decreased to 2.2 % (20 hours) and then increased again to 7.3 % after 40 hours.

Effects of the pollutant

Time-dependent variation of the radioactivity in the different compartments of the system "bacteria-bivalves-annelids-sediment and pollutant" (Tab. 12 A and B)

In the presence of the pollutant, the time-dependent variation of the complete system does not show any drastic change relative to the complete system without pollutant. The concentration of pollutant in the water (0.35 ppm) consequently remained constant with time. At the end of the experiment (40 hours), the body of the annelids contained 2.4 – 10 ppm, but the bivalves contained only 0.12 – 0.50 ppm. These findings are of interest because the two organisms have very different feeding modes (filter-feeding *versus* deposit-feeding). Relative to the volume of water processed by these two animals, the result is surprising: the differences between the concentration of pollutant in the body of the two species are in opposition. The bivalves filter all the water in the tank many times whilst the annelids do not filter but only scrape the bottom.

Time-dependent variation of the radioactivity in the different compartments of the system "algae-bivalves-annelids-sediment and pollutant" (Tab. 13 A, 13 B)

The time-dependent variation of the complete system and pollutant did not change in comparison with the

Table 12

Time-dependent variation of the radioactivity in the different compartments of the entire system "bacteria-sediment-annelids-bivalves with pollutant". The results are expressed as a percentage of the initial radioactvity. A) Raw data; B) Mean raw data.

Évolution en fonction du temps de la radioactivité dans les différents compartiments du système complet bactéries-sédiment-annélides-bivalves avec polluant. Les résultats sont exprimés en pourcentage de la radioactivité initiale. A) Résultats bruts; B) moyennes.

No.	4 hours		10 hours		20 hours			40 hours		
of experiment	1	2	3	4	5	6	7	8	9	10
Bivalves	–	–	12.5	14.3	19.3	20.2	17.3	17.8	17.3	20.8
Annelids	0.4	1.2	1.4	1.3	1.0	1.1	1.3	2.2	4.3	3.0
Particulate	7.6	21.1	3.6	3.0	8.9	2.1	15.8	7.4	3.0	6.5
DOM	12.7	14.1	14.1	19.0	6.0	17.2	6.8	7.6	7.8	9.0
CO_2	17.2	17.8	19.1	21.9	17.7	14.4	16.6	21.1	20.0	22.2
Sediment	–	–	49.3	40.5	47.1	45.0	42.2	43.9	47.6	38.5
Live Bacteria	26.7	47.0	6.7	12.1	12.0	3.5	23.5	0.06	1.0	6.3

	4 hours	10 hours	20 hours	40 hours
Bivalves	–	13.4	18.9	18.6
Annelids	0.8	1.3	1.1	3.2
Particulate	14.3	3.4	8.9	5.6
DOM	13.4	16.5	10.0	8.1
CO_2	17.5	20.5	16.3	21.1
Sediment	–	44.9	44.8	43.4
Live Bacteria	36.8	9.4	13.0	2.6

complete system without pollutant.

Consequently, the concentration of pollutant in the water (0.35 ppm) did not vary in time. The body of the annelids contained 2.40 ppm after 4 hours, 7.70 ppm after 20 hours and 2.73 ppm after 40 hours, whereas the bibalves contained only 0.23 – 0.55 ppm. These results are interesting in that the bivalves filter the sea water and consume the suspension, while the annelids do not filter the water but collect food on the bottom without feeding on biodeposits. The differences between the concentration of pollutant in the body of the two species are in opposition.

Table 13

Time-dependent variation of the radioactivity in the different compartments of the entire system "algae-sediment-annelids-bivalves with pollutant". The results are expressed as a percentage of the initial radioactivity. A) Raw data; B) Mean raw data.

Évolution en fonction du temps de la radioactivité dans les différents compartiments du système complet algues-sédiment-annélides-bivalves avec polluant. Les résultats sont exprimés en pourcentage de la radioactivité initiale. A) Résultats bruts; B) moyennes.

A No. of experiment	4 hours 1	 2	10 hours 3	20 hours 4	 5	40 hours 6	 7
Bivalves	47.8	68.3	41.9	37.8	43.4	38.3	33.1
Annelids	5.4	1.6	14.7	13.4	6.5	6.2	5.0
Particulate	0.1	1.2	0.7	2.8	2.0	2.5	4.5
DOM	3.7	6.0	4.0	3.0	2.4	3.2	5.2
CO_2	1.3	0.7	2.2	3.1	5.7	8.1	8.9
Sediment	41.7	22.2	36.5	39.9	40.0	41.7	43.3

B	4 hours	10 hours	20 hours	40 hours
Bivalves	58.0	41.9	40.6	35.7
Annelids	3.5	14.7	10.0	5.6
Particulate	0.7	0.7	2.4	3.5
DOM	4.8	4.0	2.7	4.2
CO_2	1.0	2.2	4.4	8.5
Sediment	32.0	36.5	40.0	42.5

DISCUSSION

The study of the different experiments described above reveals many different phenomena. In the first place, the bivalves filter the whole suspension in less than 4 hours and their faeces and pseudofaeces settle on the bottom during the next hours (after 4 to 40 hours). In the absence of sediment, the annelids are able to consume a part of the bacteria in suspension because their tentacles are stretched in all directions under the surface of the water and throughout the tank (Fauchald et Jumars, 1979; Taghon and Jumars, 1984; Daeur *et al.*, 1983; Frithsen and Doering, 1986). In the presence of sediment, the tentacles creep on the bottom and the annelids cannot collect efficiently any suspended bacteria but only those lying on the bottom. With sediment and bivalves, the annelids scrape the bottom with their tentacles, inducing the disaggregation of the soft faeces of the bivalves and the resuspension of associated bacteria. This phenomenon of bioturbation, which is not observed in the absence of annelids, is revealed by an increase in the number of suspended bacteria between 4 and 20 hours. The decline after 20 hours is due to the action of the bivalves which fed on this new suspension. This explains why the radioactivity of the suspension does not increase. It is due to the loss of labelling by the bacteria via exudation. The annelids cannot consume the monospecific biodeposits of the bivalves efficiently when they are only composed of bacteria. The radioactivity incorporated may thus have very different origins: 1) the decantation of the suspension; 2) the biodeposition of the bivalves and annelids; 3) the absorption of dissolved substances (Henrichs and Doyle, 1986).

It seems that the silt-clay particles contained in the biodeposits give them more cohesion (Migniot, 1968) and enhance their possible consumption by a deposit-feeder. If the annelids cannot profit from the bacterial suspension biodeposited by the bivalves, they manifest a very strong mechanical action which results in bioturbation (Hargrave, 1970). This phenomenon may stimulate the feeding of the bivalves, as described by other authors (Weinberg and Whitlach, 1983; Bricelj *et al.*, 1984; Murphy, 1985), and enhances bivalve production. The analysis shows that the pollutant is concentrated in the body of the annelids even if they are not directly consuming the suspension and are unable to consume the faeces of the bivalves. This might be explained by difference of chemical composition of the mucus of the bivalves and the annelids. This pollutant is hydrophobe and difficult to dissolve easily in water; the sediment, and especially the silt-clay particles therein, seem able to adsorb it. The bivalves filter several times the entire volume of the microcosm, but they do not concentrate Propyzamide in large quantities. We believe that this difference may be due to the mode of contact between the sediment and the feeding organs of *Eupolymnia nebulosa*. The pollutant seems to have an action on the respiratory metabolism of the annelids and the bivalves (Amouroux and Gremare, in prep.) but does not affect the short term transfer of organic matter between the different compartments of the system.

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