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**EXPERIMENTAL STUDY OF THE EFFECT OF
KAOLINITE ON THE INGESTION AND THE
ABSORPTION OF MONOSPECIFIC SUSPENSIONS
OF PAVLOVA LUTHERI BY THE FILTER-FEEDING
BIVALVE VENUS VERRUCOSA**

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EXPERIMENTAL STUDY OF THE EFFECT OF KAOLINITE ON THE INGESTION AND THE ABSORPTION OF MONOSPECIFIC SUSPENSIONS OF *PAVLOVA LUTHERI* BY THE FILTER-FEEDING BIVALVE *VENUS VERRUCOSA*

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INGESTION
ABSORPTION
PHYTOPLANKTON
FILTER-FEEDERS
BIVALVES
KAOLINITE

ABSTRACT. – We investigated the ingestion and the absorption of the filter-feeding bivalve *Venus verrucosa* Linné fed on *Pavlova lutheri* Droop in the presence of different concentrations of kaolinite (i.e., between 0 and 50 mg.l⁻¹). We used ¹⁴C-sodium bicarbonate to label the algae. In the presence of bivalves, the exchanges of radioactivity between compartments were always dominated by the transfer between POM and bivalves. However, there were significant differences in radioactivity partitioning among compartments depending on the concentration of kaolinite. The observed transfers resulted from the interactions between ingestion, absorption, biodeposition, and recycling of biodeposits. The coexistence of these processes did not allow to determine directly ingestion rates and absorption efficiencies, which required the use of mathematical modelling. The model used during the present study is identical to the one previously designed to describe the utilisation of a suspension of *Escherichia coli* by *Venus verrucosa*. It simulates the exchanges of radioactivity between compartments and allows the quantification of ingestion and absorption. It is complicated by the occurrence of pseudofaeces production at the highest kaolinite concentration. Our results show no significant differences in both ingestion rates (10 mgDW.h⁻¹ at 0 and 5 mg.l⁻¹ of kaolinite) and absorption efficiencies (about 57 % at 0 and 5 mg.l⁻¹ of kaolinite) below the threshold of pseudofaeces production. Filtration and thus ingestion rates were significantly reduced for a kaolinite concentrations of 50 mg.l⁻¹. Apparent absorption efficiency was also much lower (about 34 %) during the 50 mg.l⁻¹ experiment. In addition, the highest concentration of kaolinite induced higher biodeposition and recycling rates of labelled material. These results are discussed in view of the existing literature.

INGESTION
ABSORPTION
PHYTOPLANKTON
FILTREURS
BIVALVES
KAOLINITE

RÉSUMÉ. – Nous avons étudié l'effet de différentes concentrations de kaolinite (entre 0 et 50 mg.l⁻¹) sur l'ingestion et l'absorption du Bivalve filtreur *Venus verrucosa* Linné nourri avec *Pavlova lutheri* Droop. Les algues ont été marquées avec du ¹⁴C bicarbonate de sodium. Dans les enceintes expérimentales contenant des Bivalves, les échanges de radioactivité les plus importants interviennent toujours entre les compartiments MOP et Bivalves. La répartition de la radioactivité entre compartiments est cependant significativement affectée par la concentration de kaolinite. Les transferts de radioactivité observés résultent de l'interaction entre les processus d'ingestion, d'absorption, de biodéposition, et de recyclage des biodépôts. La coexistence de ces processus ne permet pas la détermination directe des taux d'ingestion et des efficacités d'absorption qui requiert l'élaboration d'un modèle mathématique. Le modèle utilisé est semblable à celui ayant été développé pour décrire l'utilisation d'une suspension d'*Escherichia coli* par *Venus verrucosa*. Il simule les échanges de radioactivité entre compartiments et permet le calcul de l'ingestion et de l'absorption. Ce modèle est compliqué par la production de pseudofaeces à la concentration de kaolinite la plus élevée. En dessous du seuil de production des pseudofaeces, nos résultats ne montrent pas de différences significatives tant pour ce qui concerne les taux d'ingestion (10 mgPS.h⁻¹ à 0 et 5 mg.l⁻¹ de kaolinite) et les efficacités d'absorption (environ 57 % à 0 et 5 mg.l⁻¹

de kaolinite). Les taux de filtration et donc d'ingestion sont par contre significativement réduits à une concentration de kaolinite de 50 mg.l^{-1} . L'efficacité d'absorption apparente est également beaucoup plus faible (environ 34 %) à cette concentration. De plus, la concentration de kaolinite la plus élevée induit une augmentation de la biodéposition et du recyclage du matériel radioactif. Ces résultats sont discutés au vu de la littérature existante.

INTRODUCTION

The quality of the particulate organic matter (POM) available to coastal benthic invertebrates shows important temporal changes (Berg and Newell 1986, Fegley *et al.* 1992). Part of this variability is seasonal and mostly reflects changes in the relative importance of the different components of the POM pool (Tenore 1988). However, modifications in POM quality may also result from impulsional events and especially meteorological processes controlling sediment resuspension. In a recent study (Charles *et al.* 1995), we investigated temporal changes in the quality of sediment-trap collected materials by using a bioassay approach based on the measurement of ingestion rates and absorption efficiencies by the bivalve *Abra ovata*. Our results strongly suggest the existence of a negative effect of bottom sediment resuspension on absorption efficiency. They are further supported by similar data concerning growth rates (Baudart 1994, Grémare *et al.* 1997). The existence of a negative relationship between sediment resuspension and absorption efficiency of sediment trap material may result from 2 different mechanisms: (1) a simple dilution of a relatively rich food source (i.e., originating from the water column) by a more refractory material originating from the sediment, or (2) a direct effect of the particulate inorganic matter (PIM) load on absorption.

This second hypothesis is apparently supported by the results of several studies assessing the effect of resuspended bottom sediment on growth in suspension-feeding bivalves (Winter 1976, Kiorboe *et al.* 1980, 1981, Langdon and Siegfried 1984, Urban and Langdon 1984). These authors indeed reported an enhancement of suspension-feeding bivalves' growth rates in the presence of low concentrations of PIM. One of the invoked explanation being an increase in absorption rates either due to a "grinding effect" (Murken 1976 cited by Urban and Langdon 1984) or to a modification in gut residence time (Bayne *et al.* 1987). However, most of the experimental studies carried out since then have failed to detect any significant increase in ingestion rates and absorption efficiencies associated to the augmentation of the PIM load (Bricelj and Malouf 1984, Robinson *et al.* 1984, Hawkins *et al.* 1986, Bayne *et al.* 1987, Iglesias *et al.* 1992).

Such a discrepancy may be due to the fact that most of these scientists (Kiorboe *et al.* 1981, Mohlenberg and Kiorboe 1981, Iglesias *et al.* 1992, Navarro *et al.* 1992) have used natural sediment which act both as an "inert turbidity producing agent and a food supplement" (Bricelj and Malouf 1984). Along the same lines, Bayne *et al.* (1987) stated that changes in absorption efficiencies of the blue mussel *Mytilus edulis* may result from an interaction between average particle size and organic content resulting from the introduction of PIM. In order to unravel such interactions, it seems thus more appropriate to use: (1) radio-labelled food sources (Bricelj and Malouf 1984), and (2) artificial substrates such as kaolinite for manipulating the concentration of PIM (Robinson *et al.* 1984, Bayne *et al.* 1987, Cranford & Gordon Jr 1992, Urban & Kirchnan 1992).

The aim of the present study was to assess changes in ingestion rates and absorption efficiencies of the filter-feeding bivalve *Venus verrucosa* fed on a monospecific suspension of *Pavlova lutheri* and submitted to increasing concentrations of kaolinite.

MATERIALS AND METHODS

Biological material: Monospecific cultures of *Pavlova lutheri* (INSERM, Villefranche-sur-Mer) were grown on a F/2 medium (Guillard and Ryther 1963) at 18 °C under constant illumination (1700 lux). After 8 days, the algae were labelled for 48 hours with ^{14}C sodium bicarbonate (ISOTOPCHIM, specific activity; $2109 \text{ MBq.mmol}^{-1}$). The excess of label was then subsequently removed by 2 centrifugations (3000 rpm for 10 min).

The clam *Venus verrucosa* is abundant all along the coasts of France and more specifically on the Atlantic and the Channel where it is submitted to an intensive exploitation. Although it is not heavily harvested on the French Mediterranean coast, *V. verrucosa* is also present in most of the infralittoral biota of the Mediterranean (Amouroux 1982). The clams used during the present study have been collected from shallow water (about 1.5 m depth) in Port-Vendres harbour, France, during April 1994. To prevent any significant contamination with other biota, they were carefully scrubbed and were allowed to clear their guts for 24 h before use. Clams were adapted to the experimental temperature 48 hours prior to each experiment.

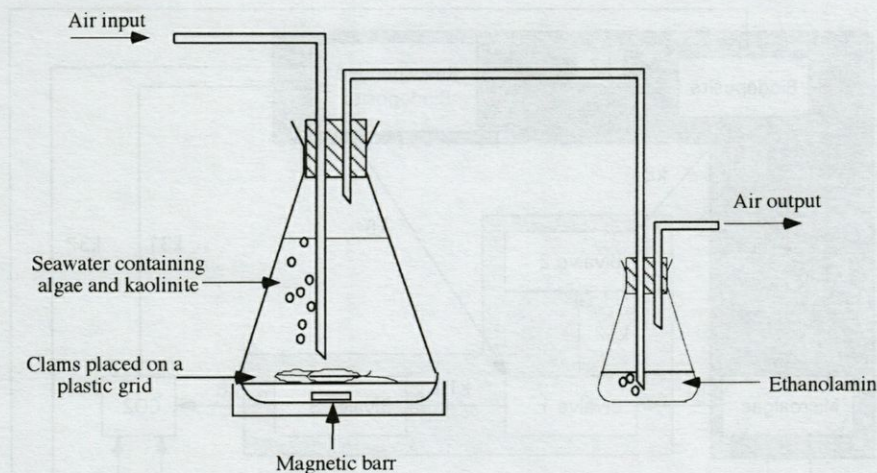


Fig. 1. – Experimental set-up used during the feeding experiments

Generality on the experimental approach: The experimental approach used during the present study combines compartmental analysis and analog modelling (Grémare *et al.* 1991). Compartmental analysis consisted in measuring temporal changes of the partitioning of radioactivity between the different compartments (i.e., Particulate Organic Matter, Bivalves, Dissolved Organic Matter, and CO_2) of a closed system. Modelling then allows the transfers of radioactivity between compartments to be computed.

Compartmental analysis: Five bivalves corresponding to a total flesh dry weight of 5 g were introduced into each experimental chamber, which was filled with 1 litre of filtered ($1.2 \mu\text{m}$) seawater and 10 mg dry weight of labelled *Pavlova lutheri*. The dry weights of the clams were calculated from the length-weight relationships proposed by Amouroux (1982). The seawater was mixed by bubbling air. At the outlet, air was passed through ethanolamin traps to capture the labelled gaseous CO_2 (Fig. 1, Amouroux 1982).

Experiments were carried out at 15°C in total darkness. Three chambers were used for incubation in the presence of bivalves and three further chambers as controls (i.e., incubation of *P. lutheri* alone in seawater containing either 0 or $50 \text{ mg}\cdot\text{l}^{-1}$ of kaolinite). Five incubation periods (1, 4, 10, 20 and 50 h) and 4 concentrations of kaolinite (0, 5, 10 and $50 \text{ mg}\cdot\text{l}^{-1}$) were tested. These concentrations have been retained after preliminary trials showing that *V. verrucosa* was producing pseudofaeces for kaolinite concentrations superior to $10 \text{ mg}\cdot\text{l}^{-1}$ (Chaabeni 1994).

The changes in the partitioning of the radioactivity within experimental chambers containing microalgae, seawater, plus eventually bivalves and kaolinite were monitored according to Charles *et al.* (1992a).

At the end of each experiment, the bivalves were recovered, rinsed with tap water, dissected and individually hydrolysed in 10 ml 1N NaOH at 60°C for 24 h. Their radioactivity was assessed by liquid scintillation counting of two 1 ml subsamples each. The total radioactivity of the "bivalves" compartment was taken to be the sum of the radioactivity of all 5 bivalves.

The seawater was filtered through a $0.2 \mu\text{m}$ Nucleopore membrane to separate dissolved from particulate

organic matter (POM). Membranes were hydrolysed in 20 ml 1N NaOH at 60°C for 24 h. Two 1 ml subsamples were counted by liquid scintillation to evaluate the radioactivity of the POM compartment.

Two 1 ml subsamples of the ethanolamin traps were counted by liquid scintillation to determine the radioactivity of gaseous CO_2 . 200 ml of the filtered seawater was then placed in a stoppered bottle and acidified (2 ml of 95% H_2SO_4). The resulting CO_2 (which corresponds to dissolved CO_2) was captured on an ethanolamin trap. The radioactivity of the CO_2 compartment was considered to be the sum of the radioactivity of gaseous and dissolved CO_2 .

Two 5 ml subsamples of filtered seawater were taken after acidification and counted by liquid scintillation to determine radioactivity of dissolved organic matter (DOM).

All radioactivity measurements were carried out on a Beckman LS5000 CE liquid scintillator. Dynagel (Baker) was always used as scintillation cocktail except for CO_2 where 5% of PPO and 0.5% of bis MSB (Packard) was used. All counts were checked for chemiluminescence, corrected for quenching, and then expressed as % of the total radioactivity within each experimental chamber. Counting efficiencies were always $> 90\%$.

Modelling: Our model is similar to the one used by Charles *et al.* (1992b). Its structure is presented in Fig. 2. The system was closed, and initially considered to be composed of six compartments: microalgae, bivalves, DOM, CO_2 , biodeposits, and resuspended biodeposits. We introduced, three second-order time-delays to account for the time lags between ingestion and (1) production of faeces, (2) production of DOM, and (3) production of CO_2 by bivalves. In the model this resulted in the subdivision of the bivalve compartment into three subcompartments: Bivalves 1 (radioactivity in the anterior part of the digestive tract), Bivalves 2 (radioactivity which has not been absorbed by the bivalves), and Bivalves 3 (radioactivity which has been absorbed by the bivalves). This procedure introduced an intermediary step in the transfers from the bivalve compartment to biodeposits, DOM and CO_2 compartments.

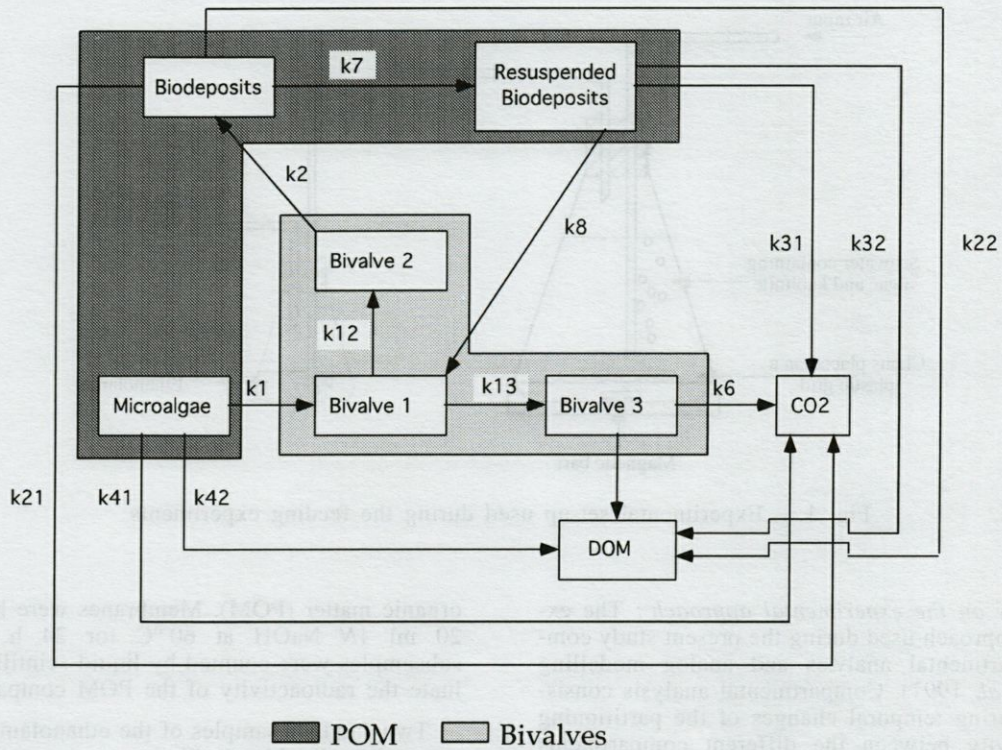


Fig. 2. - Modelling. Diagram of the "Microalgae-Bivalve" system showing exchanges studied and numbered kinetic coefficients of mass transfer.

Therefore, in its final form, the model was composed of eight compartments :

Mass transfer dynamics of the system "bivalves-microalgae-seawater" were represented by an interaction of "kinetic" equations reflecting the rate of exchanges between the compartments :

$$\begin{aligned}
 d [\text{Micr}]/dt &= - (k_1 + k_{41} + k_{42}) [\text{Micr}] \\
 d [\text{Biv 1}]/dt &= k_1 [\text{Micr}] + k_8 [\text{Resbio}] - (k_{12} + k_{13}) [\text{Biv 1}] \\
 d [\text{Biv 2}]/dt &= k_{12} [\text{Biv 1}] - k_2 [\text{Biv 2}] \\
 d [\text{Biv 3}]/dt &= k_{13} [\text{Biv 1}] - (k_6 + k_5) [\text{Biv 3}] \\
 d [\text{DOM}]/dt &= k_5 [\text{Biv 3}] + k_{42} [\text{Micr}] + k_{32} [\text{Res bio}] + k_{22} [\text{Biodep}] \\
 d [\text{Biodep}]/dt &= k_2 [\text{Biv 2}] - (k_7 + k_{22} + k_{21}) [\text{Biodep}] \\
 d [\text{CO}_2]/dt &= k_6 [\text{Biv 3}] + k_{41} [\text{Micr}] + k_{21} [\text{Biodep}] + k_{31} [\text{Res bio}] \\
 d [\text{Res bio}]/dt &= k_7 [\text{Biodep}] - (k_8 + k_{31} + k_{32}) [\text{Res bio}] \\
 d [\text{POM}]/dt &= d [\text{Micr}]/dt + d [\text{biodep}]/dt + d [\text{Res bio}]/dt \\
 d [\text{Biv}]/dt &= d [\text{Biv 1}]/dt + d [\text{Biv 2}]/dt + d [\text{Biv 3}]/dt
 \end{aligned}$$

where k_i = kinetic coefficients of mass transfer (h^{-1}),

k_1 = filtration of microalgae by bivalves, k_2 = biodeposition by bivalves, k_5 = production of DOM by bivalves, k_6 = production of CO_2 by bivalves, k_7 = resuspension from biodeposits, k_8 = filtration of resuspended biodeposits by bivalves, k_{12} = transit along the digestive tract of bivalves, k_{13} = absorption by bivalves, k_{21} = production of CO_2 by biodeposits, k_{22} = production of DOM by biodeposits, k_{31} = production of CO_2 by resuspended biodeposits, k_{32} = production of DOM by the resuspended biodeposits, k_{41} = production of CO_2 by microalgae, k_{42} = production of DOM by microalgae and [X] corresponds to radioactive content of

compartment X (expressed as percentage of total radioactivity initially introduced into system).

Modelling was carried out on a Macintosh micro-computer using the software Stella®. POM (i.e., the sum of microalgae, biodeposits, and resuspended biodeposits) was used together with DOM, CO_2 , and bivalves (i.e., the sum of bivalves 1, bivalves 2, and bivalves 3) when fitting the model to the experimental data. The values of k_{41} and k_{42} (0.0035, and 0.0032, respectively) were deduced from the fitting of a sub-model to the changes in partitioning of the radioactivity in the control chambers. It was assumed that biodeposits and resuspended biodeposits were producing DOM and CO_2 at the same rate as the microalgae compartment (i.e., $k_{21} = k_{22} = k_{31} = k_{32} = 0.0006$). Due to the low amounts of radioactive DOM and CO_2 recorded during the study, this assumption was not essential when fitting the model to the experimental data (see also Charles *et al.* 1992b).

Calculation of ingestion rates and absorption efficiencies : Ingestion rates and absorption efficiencies were computed from the values of the kinetic coefficients of the fitted models as proposed by Charles *et al.* (1992b). Initial ingestion rates were computed using the following formula :

$$I = k_1 \cdot [\text{Micr}]$$

where I is the ingestion rate ($\text{mgDW} \cdot \text{h}^{-1}$), k_1 is the kinetic coefficient corresponding to the filtration of microalgae (h^{-1}), and $[\text{Micr}]$ is the quantity of microalgae initially introduced in the system (mgDW). Absorption efficiency was defined as the ratio between the quantity of absorbed and ingested organic matter. The

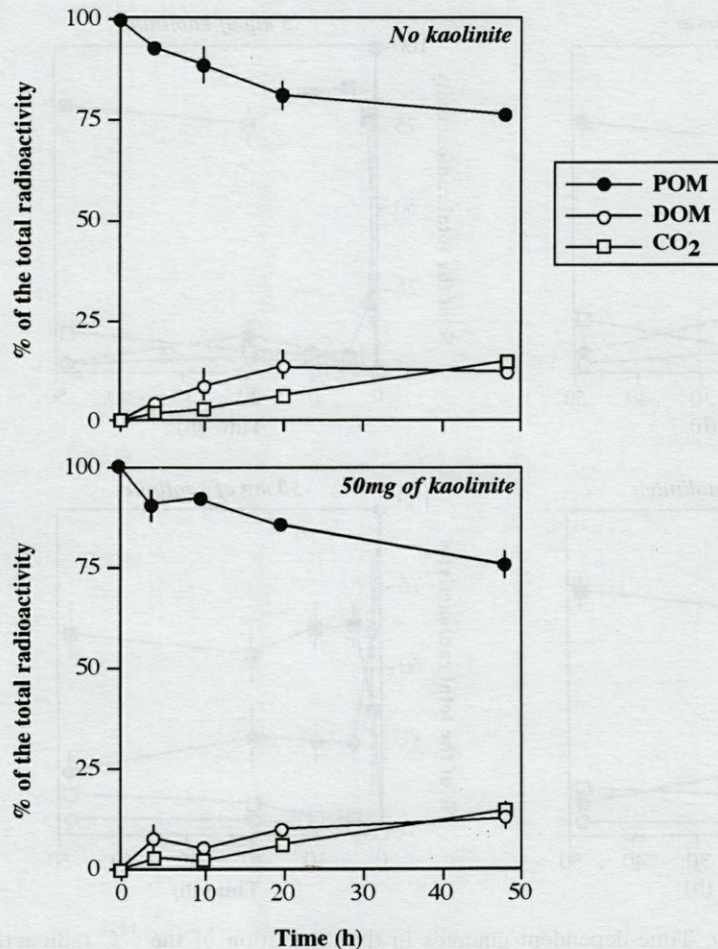


Fig. 3. – Controls. Time-dependent changes in the repartition of the ^{14}C radioactivity.

amount of ingested organic matter was taken as the cumulative amount of radioactivity resulting from the transfer from microalgae to bivalves. The amount of absorbed organic matter was computed by two different methods: either as the difference between the quantity of ingested organic matter and the amount of radioactivity transiting between the compartments bivalves 1 and bivalves 2, or as the cumulative amount of radioactivity transiting between the compartments bivalves 1 and bivalves 3. The first of these two procedures leads to an overestimation of absorption, whereas the second one leads to an underestimation of absorption (Grémare *et al.* 1991; Charles *et al.* 1992b; Charles 1993).

RESULTS

Compartmental analysis

Controls

Figure 3 shows the changes in the partitioning of radioactivity within the control chambers for

two concentrations of kaolinite (i.e., 0 and 50 $\text{mg}\cdot\text{l}^{-1}$). The effect of kaolinite concentration and time (i.e., experiment duration) on the amounts of radioactivity corresponding to POM, DOM and CO_2 were assessed by using two-way ANOVAs. For all these compartments, there was a significant effect of experiment duration ($p = 0.0001$, $p = 0.011$ and $p = 0.0001$, respectively). On the contrary, kaolinite concentration did not have any significant effect ($p = 0.30$, $p = 0.42$, $p = 0.30$, respectively). It was thus possible to use the average radioactivity (i.e., between the 0 and the 50 $\text{mg}\cdot\text{l}^{-1}$ experiments) to describe changes in the repartition of radioactivity within the controls. Radioactivity of POM declined over time to represent 74.9% of the total radioactivity after 48 hours. Meanwhile, radioactivity corresponding to DOM increased from 0 to 11.7% of the total radioactivity. Radioactivity of CO_2 also increased significantly with incubation duration. This compartment accounted for 13.4% of the total radioactivity after 48 hours of incubation.

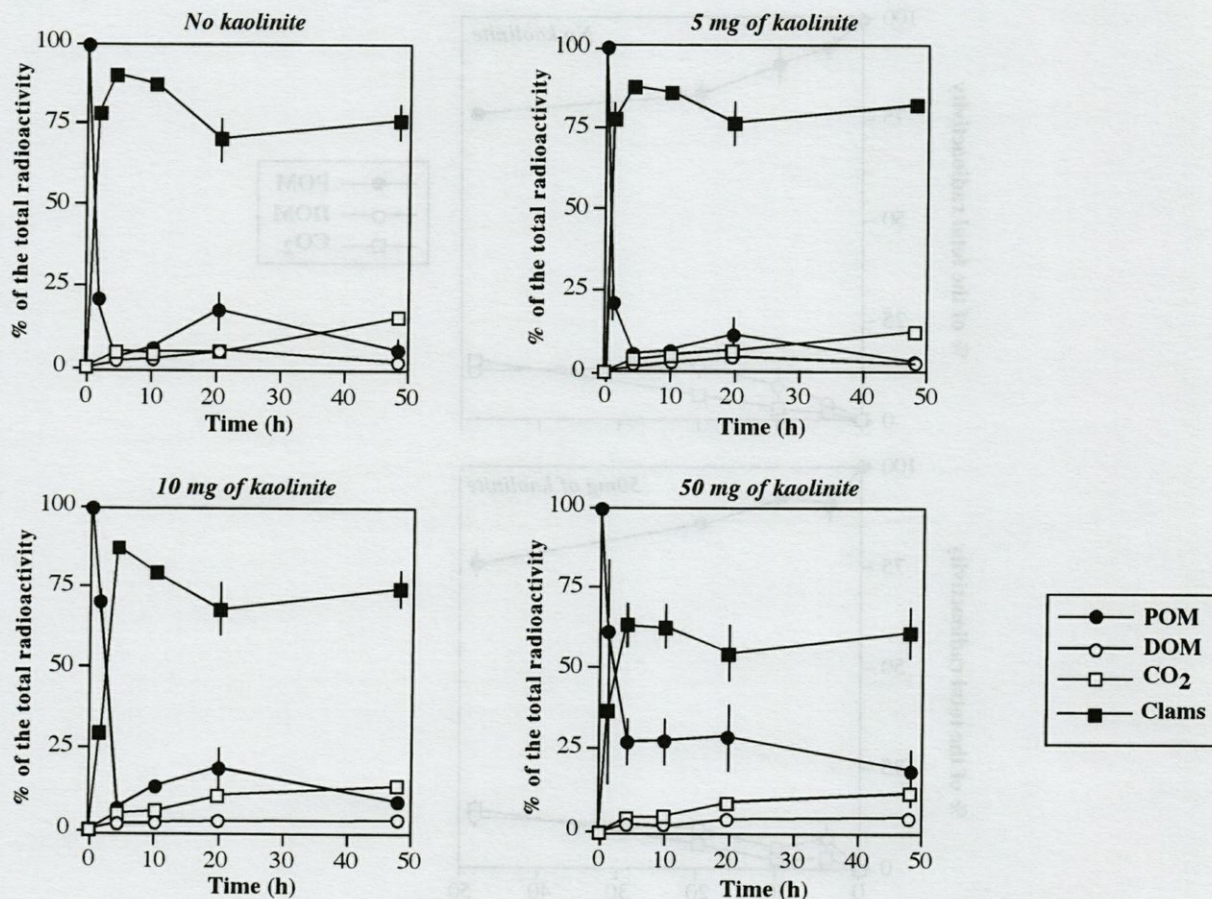


Fig. 4. - *Venus verrucosa*. Time-dependent changes in the repartition of the ¹⁴C radioactivity within experimental chambers containing bivalves.

Clams

Figure 4 shows changes in the partitioning of radioactivity within the experimental chambers containing *Venus verrucosa*. For all the tested compartments (i.e., POM, bivalves, DOM and CO₂), there was a significant effect of incubation duration two-way ANOVAs, $p = 0.0001$ in all cases). For POM, bivalves and DOM, there was also a significant effect of kaolinite concentration (two-way ANOVAs, $p = 0.0001$ in all cases). There was no significant effect of kaolinite concentration on the amount of radioactivity corresponding to CO₂ (two-way ANOVA, $p = 0.23$).

The radioactivity within the clams themselves drastically increased during the first hour of the experiments. After 1 hour, radioactivity corresponding to the bivalves represented 78.7 and 78.6% of the total radioactivity in the experimental chambers containing 0 and 5 mg.l⁻¹ of kaolinite, respectively. This proportion was much lower for the chambers containing higher concentrations of kaolinite (29.6 and 37.6% of the total radioactivity for the 10 mg.l⁻¹ and 50 mg.l⁻¹ experiments, respectively). For all tested concentra-

tions, the radioactivity corresponding to the clams was maximal after 4 hours of experiment. These maxima were close to 90% except for the chambers containing 50 mg.l⁻¹ of kaolinite where bivalves accounted for only 64.5% of the total radioactivity after 4 hours. The period between 4 and 20 hours was then characterised by a slight decrease of the radioactivity corresponding to the bivalves preceding a stabilisation at 48 hours.

Temporal changes of the radioactivity corresponding to POM were inverted relative to those concerning bivalves thereby suggesting that the major exchanges of radioactivity occurred between these two compartments. The first 4 hours of the experiments corresponded to an important decline due to the filtration of the labelled microalgae by the clams. The period between 4 and 20 hours usually corresponded to a slight increase in the radioactivity corresponding to POM thus probably reflecting biodeposition by the clams. The final proportion of the total radioactivity corresponding to POM was much higher for the chambers containing 50 mg.l⁻¹ of kaolinite than for the other 3 tested concentrations (19.8 versus only about 5.5% of the total radioactivity).

Table I. – Kinetic coefficients of mass transfers corresponding to the fitted models.

k_i	Concentration of kaolinite (mg.l ⁻¹)			
	0	5	10	50
k_1	1.0000	1.0000	0.9000	0.2600
k_2	0.0750	0.0750	0.0900	0.2000
k_5	0.0000	0.0000	0.0000	0.0002
k_6	0.0058	0.0045	0.0046	0.0046
k_7	0.0700	0.1100	0.1000	0.1000
k_8	1.000	1.0000	0.2600	0.2600
k_{12}	0.0750	0.0750	0.0900	0.2000
k_{13}	0.1000	0.1000	0.1000	0.1000
k_{21}	0.0035	0.0035	0.0035	0.0035
k_{22}	0.0032	0.0032	0.0032	0.0032
k_{31}	0.0035	0.0035	0.0035	0.0035
k_{32}	0.0032	0.0032	0.0032	0.0032
k_{41}	0.0035	0.0035	0.0035	0.0035
k_{42}	0.0032	0.0032	0.0032	0.0032

Radioactivity of DOM always remained very low (i.e., less than 5.3 % of the total radioactivity).

CO₂ radioactivity was not significantly affected by the concentration of kaolinite. It increased slowly but significantly during the incubation period to represent about 14.5 % of the total radioactivity after 48 hours.

Modelling

Table I shows the kinetic coefficients of the fitted models. The fittings of the models to the experimental data concerning the 4 tested concentrations of kaolinite are presented in Figure 5. The cumulative quantities of ingested microalgae and recycled biodeposits in the presence of the 4 tested concentrations of kaolinite are shown in Figure 6. The corresponding quantities of radioactive biodeposits and CO₂ produced by the bivalves are presented in Figure 7. The computation of these quantities provides more specific information on the different processes occurring between microalgae and bivalves.

During the first 4 h of incubation, the predominant process was the filtration of the algal sus-

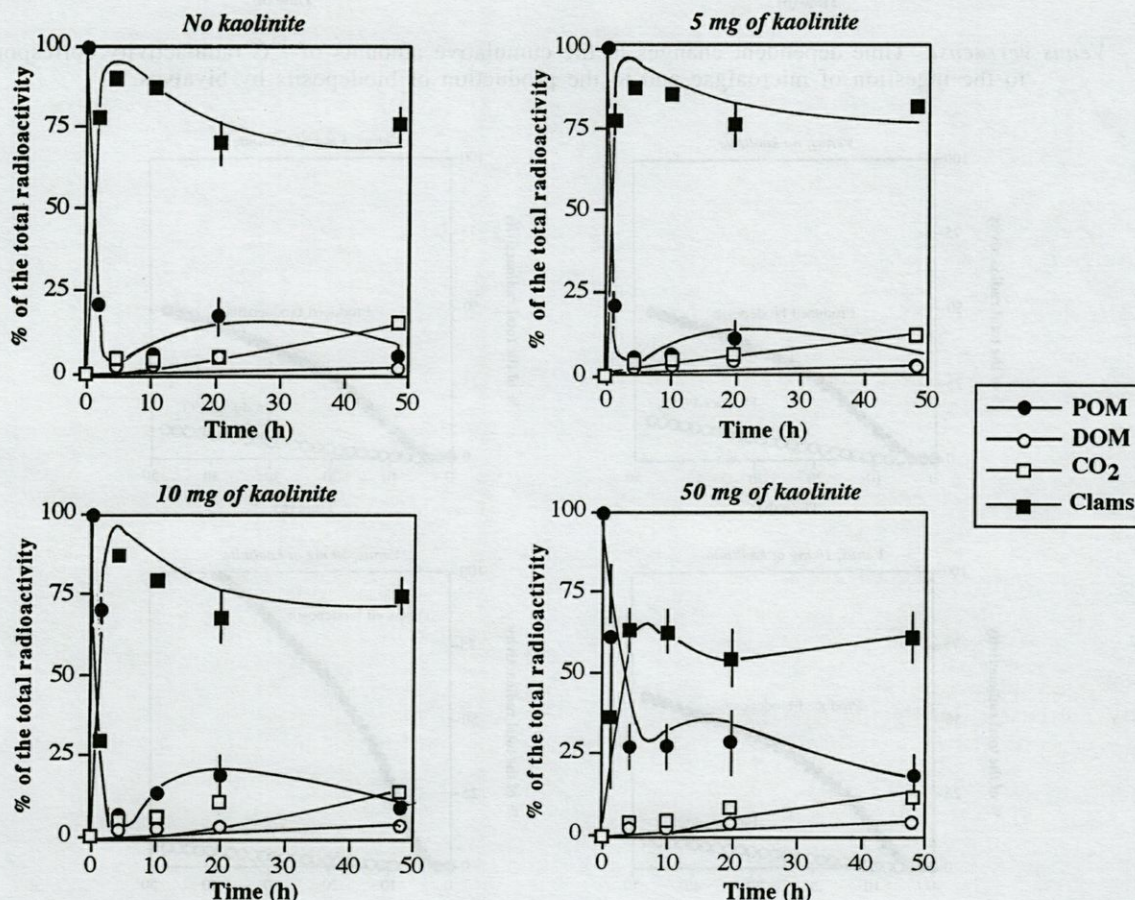


Fig. 5. – Modelling. Fitting of the “microalgae-Bivalve” models to the experimental data corresponding to the 4 tested concentrations of kaolinite.

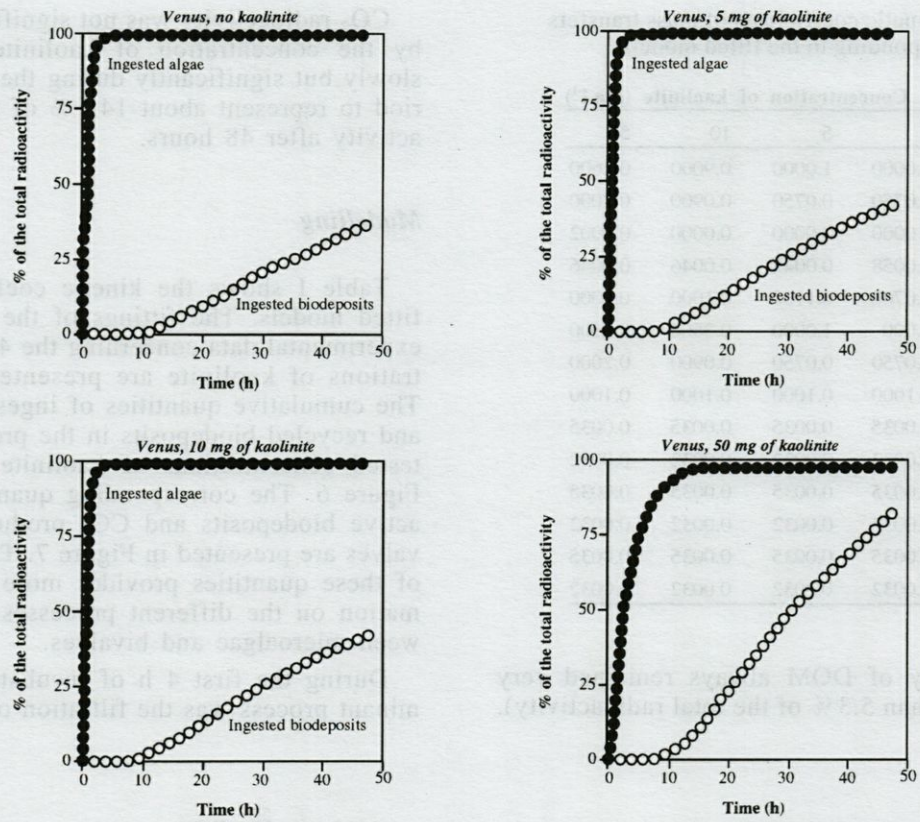


Fig. 6. – *Venus verrucosa*. Time-dependent changes in the cumulative amounts of ¹⁴C radioactivity corresponding to the ingestion of microalgae and to the production of biodeposits by bivalves.

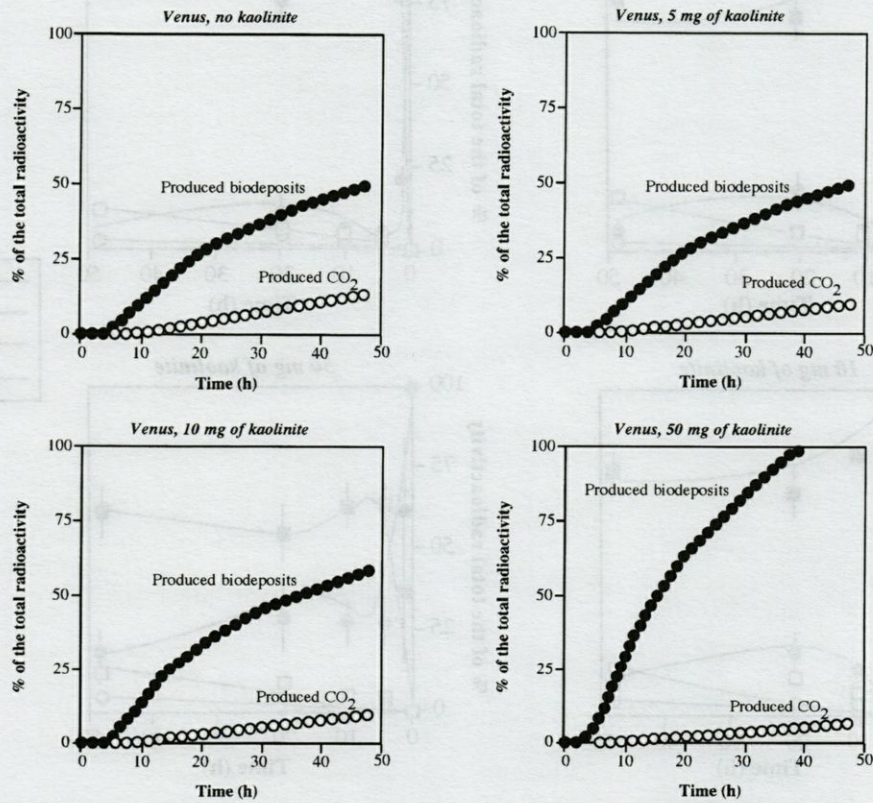


Fig. 7. – *Venus verrucosa*. Time-dependent changes in the cumulative amounts of ¹⁴C radioactivity corresponding to the production of CO₂ and biodeposits by bivalves.

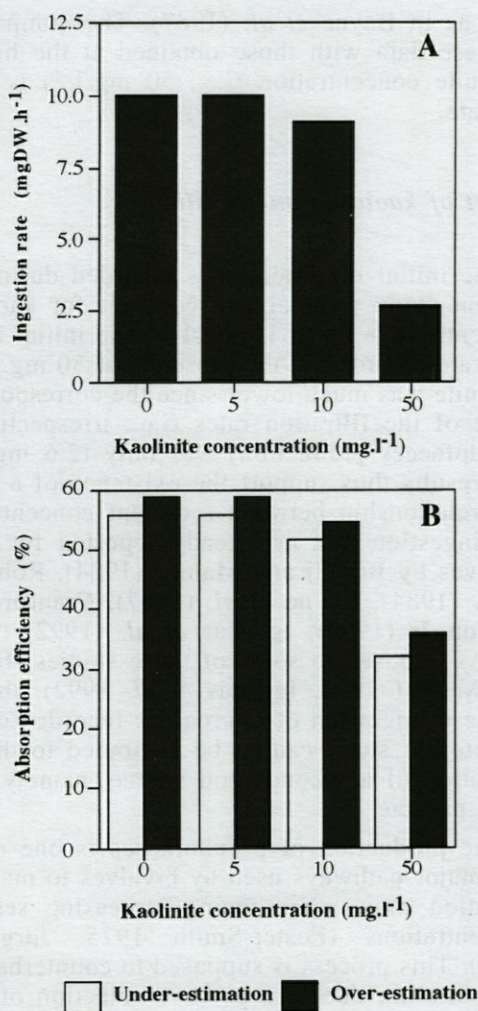


Fig. 8. - *Venus verrucosa*. Relationship linking kaolinite concentration and: (A) initial ingestion rate, and (B) the two estimations of absorption efficiency. Please note that the ingestion estimate provided for the 50 mg.l⁻¹ experiment corresponds to a "filtration" rate, and that the absorption estimates provided for the 50 mg.l⁻¹ experiment corresponds to "apparent" absorption efficiencies.

pension by the bivalves, which resulted in a decrease in POM radioactivity and in an increase in bivalve's radioactivity. After that, production of biodeposits predominated until 20 h of incubation, resulting in increased POM radioactivity and in decreased bivalve's radioactivity. The recycling of these biodeposits then allowed to reach an equilibrium between POM and Bivalves.

In the presence of low concentrations of kaolinite (i.e., 0, 5 and 10 mg.l⁻¹), radioactivity ingested as microalgae reached almost 99% of the initial radioactivity after only 4 h incubation. This proportion was only 66.5% in the experimental chambers containing 50 mg.l⁻¹ of kaolinite. For all tested concentrations, consumption of resuspended biodeposits began to be significant after

8 hours of incubation. The recycling of biodeposits was positively correlated with kaolinite concentration. At the end of the experiments, it represented between 35.2 (no kaolinite) and 81.6% of the total radioactivity (50 mg.l⁻¹).

The cumulative amount of radioactivity corresponding to the production of biodeposits by the bivalves began to be significant after 4 hours of incubation. It increased with kaolinite concentration. After 48 hours of incubation, it represented between 49.0 (no kaolinite) and 109.8% of the total radioactivity (50 mg.l⁻¹).

The cumulative amount of radioactivity corresponding to the production of CO₂ by the bivalves correlated negatively with kaolinite concentration. At the end of the experiments, it represented between 7.6 (50 mg.l⁻¹) and 13.7% of the total radioactivity (no kaolinite).

Ingestion and absorption

The ingestion rates determined for the 4 concentrations of kaolinite ranged between 2.6 and 10 mgDW.h⁻¹ corresponding to specific ingestion rates ranging between 0.52 and 2 mgDW.gDW⁻¹.h⁻¹ (cf. Fig. 8A). Ingestion rates seemed to correlate negatively with kaolinite concentrations. Ingestion rates (10 mgDW.h⁻¹, specific ingestion rate of 2 mgDW.gDW⁻¹.h⁻¹) were strictly identical in the absence or in the presence of low concentration (i.e., 5 mg.l⁻¹) of kaolinite. They were only slightly lower (9 mgDW.h⁻¹, specific ingestion rate of 1.8 mgDW.gDW⁻¹.h⁻¹) for the intermediate concentration (10 mg.l⁻¹). At last, ingestion rates were much lower (2.6 mgDW.h⁻¹) for the high kaolinite concentration (50 mg.l⁻¹, specific ingestion rate of 0.52 mgDW.gDW⁻¹.h⁻¹).

The absorption efficiencies for the 4 tested concentrations of kaolinite are presented in Fig. 8B. Absorption efficiencies were also affected by the concentration of kaolinite. The two estimations of absorption (between 55.3 and 58.6%) were identical in the absence and in the presence of low concentration (i.e., 5 mg.l⁻¹) of kaolinite. Absorption was only slightly lower (between 50.9 and 54.2%) for the intermediate concentration (10 mg.l⁻¹ of kaolinite). As observed for ingestion, absorption was much lower (between 32.3 and 35.3%) for the high kaolinite concentration (50 mg.l⁻¹).

DISCUSSION AND CONCLUSION

Structure of the model

The model is designed to simulate the exchanges of radioactivity within the experimental cham-

bers containing bivalves. Since the radioactivity is exclusively associated to the microalgae, the kinetic coefficients and thus the ecophysiological parameters derived from the fitting of the model to experimental data thus refers to the consumption of microalgae. The major problem in the modelling process was the simulation of pseudofaeces production. In fact, the application of analog modelling to the analysis of the transfer in aquatic food chains assumes that we are dealing with continuous phenomena (Amouroux and Amouroux 1988, Amouroux *et al.* 1989, Grémare *et al.* 1989, 1991). In closed experimental systems, this is probably not the case for pseudofaeces production since this process is cued by total sestonic concentration which rapidly declines during the time-course of the experiment (see the results of the compartmental analysis). During the present study we have chosen to simulate the pseudofaeces production by a transit through the compartments bivalves 1 and bivalves 2 (i.e., the same pathway as for faeces production) due to the impossibility to experimentally separate faeces from pseudofaeces. Moreover, the creation of a direct link between microalgae and biodeposits (i.e., corresponding to the production of pseudofaeces) would have presented the drawbacks of: (1) using two different types of models depending on kaolinite concentrations, and (2) introducing another kinetic coefficient allowing to adjust the balance between POM and bivalve radioactivity at high silt concentrations.

Nevertheless, this choice has important consequences. Indeed, below the threshold of pseudofaeces production, the constant k_1 strictly corresponds to ingestion whereas below this concentration it corresponds to filtration (i.e., total retention of the material, which will either be rejected as pseudofaeces or as faeces).

The same precaution should be observed when comparing absorption efficiencies recorded for kaolinite concentrations below and above the threshold of pseudofaeces production. Below this threshold the kinetic coefficient of mass transfer k_2 corresponds to defecation whereas above this threshold it accounts both to the production of faeces and pseudofaeces. Thus the absorption efficiencies computed below the threshold of pseudofaeces production are real (i.e., true absorption efficiencies) whereas those computed above the threshold are only "apparent" (for a similar problem see Iglesias *et al.* 1992).

During our experiments pseudofaeces production only occurs during the experiments carried out with a kaolinite concentration of 50 mg.l⁻¹ (see discussion below). Results of the modelling approach thus allow for a direct comparison of both ingestion rates and absorption efficiencies recorded at low sediment concentration (i.e., below the threshold of pseudofaeces production)

such as in Bayne *et al.* (1987). The comparison of these data with those obtained at the highest kaolinite concentration (i.e., 50 mg.l⁻¹) is more delicate.

Effect of kaolinite on ingestion

The initial ingestion rates recorded during the present study were almost constant for kaolinite concentrations up to 10 mg.l⁻¹. The initial ingestion rate recorded in the presence of 50 mg.l⁻¹ of kaolinite was much lower since the corresponding value of the filtration rates (i.e., irrespective of pseudofaeces production) was only (2.6 mg.l⁻¹). Our results thus support the existence of a negative relationship between sediment concentration and ingestion rate as already reported for other bivalves by Bricelj and Malouf (1984), Robinson *et al.* (1984), Bayne *et al.* (1987), Cranford and Gordon Jr (1992), Iglesias *et al.* (1992) (Table II). As opposed to some of these studies (Bricelj and Malouf 1984, Iglesias *et al.* 1992), the decrease in ingestion of microalgae recorded during the present study cannot be attributed to the exploitation of a second food source, namely sediment particle.

The production of pseudofaeces is one of the two major pathways used by bivalves to maintain ingestion rates when facing increasing sestonic concentrations (Foster-Smith 1975, Jørgensen 1990). This process is supposed to counterbalance food dilution due to a positive selection of food particle relative to silt (Jørgensen 1990, Urban and Kirchnan 1992). It is therefore interesting to assess the relationship between the threshold of pseudofaeces production and changes in ingestion rates. In *Venus verrucosa*, there is no production of pseudofaeces for kaolinite concentrations inferior or equal to 10 mg.l⁻¹ (Chaabeni 1994). This result is supported by the analysis of the rates of biodeposition occurring within the experimental chambers. Biodeposition rates were almost constant for kaolinite concentration up to 10 mg.l⁻¹. They were then much higher for the 50 mg.l⁻¹ experiment. Since in our model there is no differentiation between biodeposits produced as faeces and pseudofaeces (see above), we believe that this increase reflects the onset of production of radioactive pseudofaeces (i.e., containing microalgae). Thus, during the present study, there was only a slight decrease (i.e., 10%) in ingestion rates in the absence of pseudofaeces production. This result is different from what has been reported (i.e., an average decrease of 53%) for *Mytilus edulis* fed on *Phaeodactylum tricoratum* in the presence of low silt concentration (Bayne *et al.* 1987).

The effect of sediment concentration on ingestion selectivity in bivalves has already been stu-

Table II. – Review of the literature data regarding the effect of sediment concentration on the nutrition of filter-feeding bivalves. SFG : Scope for growth, a : apparent absorption efficiency, l : at low concentration, h : at high concentration.

Species	Food	Sediment type	Selectivity	Ingestion	Absorption	SFG	Growth	References
<i>C. edule</i>	<i>T. suecica</i>	Natural	Positive ^l	Negative	Negative	-	-	Iglesias <i>et al.</i> 1992
<i>C. virginica</i>	<i>I. galbana</i>	Kaolinite + starch	Negative	Not significant	-	-	-	Urban & Kirchnan 1992
<i>C. virginica</i>	Artificial diets	Kaolinite	-	-	-	-	Positive ^l	Langdon & Siegfried 1984
<i>C. virginica</i>	<i>I. galbana</i> <i>T. pseudonana</i>	Kaolinite	-	-	-	-	Positive	Urban & Langdon 1984
<i>M. mercenaria</i>	<i>P. paradoxa</i>	Natural	Negative	Negative	Negative	-	-	Bricelj & Malouf 1984
<i>M. edulis</i>	<i>D. marina</i>	Natural (H ₂ O ₂)	Not significant	Positive	-	-	Positive	Winter 1977
<i>M. edulis</i>	<i>P. tricornutum</i>	Natural	Not significant	Maximal ^l	Negative ^h	-	-	Kiorboe <i>et al.</i> 1980
<i>M. edulis</i>	<i>P. tricornutum</i>	Natural	-	-	-	-	Positive ^l	Kiorboe <i>et al.</i> 1981
<i>M. edulis</i>	<i>P. tricornutum</i>	Natural (ashed)	-	-	Negative	-	-	Hawkins <i>et al.</i> 1986
<i>M. edulis</i>	<i>P. tricornutum</i>	Natural (ashed in most cases)	-	Negative	Negative	Negative (Not significant)	-	Bayne <i>et al.</i> 1987
<i>P. magellanicus</i>	<i>T. suecica</i>	Bentonite	-	Negative	-	-	Negative	Cranford & Gordon 1992
<i>S. soldissima</i>	<i>I. galbana</i>	Attapulgit	-	Negative	Negative	-	-	Robinson <i>et al.</i> 1984
<i>S. subtruncata</i>	<i>P. tricornutum</i>	Natural	-	-	-	-	Positive ^l	Mohlenberg & Kiorboe 1981
<i>V. verrucosa</i>	<i>P. lutheri</i>	Kaolinite	-	Negative ^h Not significant ^l	Negative ^{h,h} Not significant ^{h,l}	-	-	Present study

died in several species (Kiorboe *et al.* 1980, Iglesias *et al.* 1992; Bricelj and Malouf 1984, Urban and Kirchnan 1992) (Table II). The results are somehow contradictory. Employing a dual tracer technique, Urban and Kirchnan (1992) reported that an increase in kaolinite concentration significantly reduces the ability of the American oyster *Crassostrea virginica* to preferentially ingest rice starch rather than the microalgae *Isochrysis galbana*. The existence of a negative correlation between silt concentration and selection efficiency has also been reported for *Mercenaria mercenaria* fed on a mixture of *Pseudoisochrysis paradoxa* and natural sediment (Bricelj and Malouf 1984). Based on the comparison of chlorophyll *a* contents in the suspension and in the pseudofaeces, Kiorboe *et al.* (1980) concluded that selection efficiency of *M. edulis* was independent of silt concentration. To our knowledge, the only published result suggesting the existence of a positive effect of silt concentration on selection efficiency has been obtained for the cockle *Cerastoderma edule* in the presence of low concentrations of silt (Iglesias *et al.* 1992). It is however important to point out that during these two last studies elevated silt concentration also induced a reduction in ingestion rates. In other word, in most cases selection efficiency does not totally compensate food dilution. This observation is supported by the diminution of retention efficiency of several bivalves submitted to high sestonic concentrations (Palmer and Williams 1980, Wilson 1983, Barillé *et al.* 1993). Besides this, there are some indirect lines of evidence suggesting that the sorting of particles is probably not very efficient in *Venus verrucosa*. Indeed, the ratio of the ingestion rates between the 5 and the 50 mg.l⁻¹ experiment was greater than 3.8, which is very comparable to the corresponding dilution of microalgae (ratio from 1 to 4). Thus, the production of pseudofaeces by *V. verrucosa* apparently does not induce a significant increase in the concentration of microalgae

within the ingested material as observed by Kiorboe *et al.* (1980) for the selective filter-feeding bivalve *M. edulis*. The major cause of the decrease in ingestion rates of *V. verrucosa* when submitted to increasing concentrations of kaolinite is thus probably the rejection of (labelled) microalgae in the pseudofaeces, which is also consistent with the increased bio-deposition rates recorded during the 50 mg.l⁻¹ experiment (see above).

Effect of kaolinite on absorption

The existing data strongly suggest a negative effect of silt concentrations on ingestion rates of filter-feeding bivalves (Table II). However, the literature data regarding the effect of silt concentration on the nutrition of filter-feeding bivalves are less clear for absorption efficiencies than for ingestion rates. This is partly due to the range of variation in measured absorption efficiencies and to methodological problems. During the present study, we found that absorption efficiencies of *Pavlova lutheri* by *V. verrucosa* were almost constant below the threshold of pseudofaeces production. This result can be compared with those of Bayne *et al.* (1987) regarding the blue mussel *M. edulis* submitted to a mixture of algae and silt at low concentrations. These authors reported a significant decrease in net absorption efficiencies (as measured by the ash ratio method). However these authors also observed negative absorption efficiencies for the low quality diets suggesting that there might have been some problems with the experimental procedure. Thus, gross absorption efficiencies (measured based on the use of ¹⁴C labelled food) and digestion efficiencies (based on chlorophyll *a* measurements) were assessed during a second set of experiment. In this last case, there was no clear relationship between diet quality and either digestion or gross absorption

efficiency, which is in good agreement with the data recorded during the present study.

As stated in the first section of the discussion, absorption efficiency recorded for the 50 mg.l⁻¹ experiment is only "apparent" which complicates the comparison with data recorded below the threshold of pseudofaeces production. Iglesias *et al.* (1992) recorded both true and apparent absorption efficiencies of the cockle *Cerastoderma edule* fed on a mixture comprising different proportions of *Tetraselmis suecica* and silt. They reported that the difference between true and apparent absorption efficiencies was positively correlated with the total sestonic concentration and the proportion of silt in the diet. The difference between true and relative absorption efficiencies reached 13.1% for a mixture of silt and algae and as much as 23.1% for silt. These values are of the same order of magnitude than the difference between the absorption efficiency of *V. verrucosa* during the 10 mg.l⁻¹ (50.9-54.2%) and the 50 mg.l⁻¹ experiment (32.3-35.3%). It is thus not possible to reach a definitive conclusion on the effect of silt on true absorption of *V. verrucosa* based on the sole results of this set of experiments.

Impact of resuspension on the utilisation of POM by benthic invertebrates

The results of the present study show that the impact of the presence of kaolinite in suspension mainly occurs above the threshold concentration of pseudofaeces production. This suggests that below this threshold, the presence of mineral particles originating from the bottom sediment would have only little effect on the utilisation of phytoplankton by *Venus verrucosa*. Above this threshold, the situation is slightly different since there is an important decrease of ingestion rates. It is difficult to reach a definitive conclusion relative to absorption efficiencies since the values computed below and above the threshold of pseudofaeces production are not directly comparable (see the first and the third section of the discussion).

These results are in relatively good agreement with the existing literature assessing the effect of silt concentration on filtration by suspending bivalves which supports the existence of a decline in both ingestion rates and absorption efficiencies at high silt concentrations. However, the analysis of this literature also suggests that the response to silt concentration is species (Palmer and Williams 1980) or even population specific (Bayne *et al.* 1987). The exact assessment of the effect of sediment resuspension on the bioenergetics of suspension-feeding bivalves will thus necessitate an increase in the number of the biological models tested.

Moreover, suspension-feeders are not the only organisms present at the water-sediment interface. The nutrition of surface and sub-surface deposit-feeders is also likely to be affected by resuspension events (Charles *et al.* 1995). Deposit-feeders are adapted to exploit a very poor food source (Lopez and Levinton 1987), they are thus often able to sort particles with a very high efficiency depending on an array of parameters including size, density, and organic coating (Jumars *et al.* 1982). However, in these organisms, the sorting process is not depending on any critical concentration of silt. Therefore, it would be very interesting to assess the effect of kaolinite concentration on the rates at which benthic deposit-feeders exploit a given food source in order to better understand the exact effect of sediment resuspension on the functioning of benthic trophic network.

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