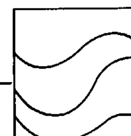

Quantitative estimation of biodiffusive and bioadvective sediment mixing: *In situ* experimental approach

Bioturbation
Bioadvection
Modelling
In situ experiment
Shallow sediment

Bioturbation
Bioadvection
Modélisation
Expérimentation *in situ*
Sédiment littoral

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ABSTRACT

An *in situ* experiment was conducted over a short period of time to quantify bioturbation with a pulse input of particulate and conservative tracers, the luminophores. Application of a biodiffusive and bioadvective model gives estimations of the mean biodiffusive mixing rate ($D = 4.3 \pm 2.8$ $cm^2.y^{-1}$) and the mean vertical transport rate ($V = 27.5 \pm 15.1$ $cm.y^{-1}$). The heterogeneity of the results from every core is attributed to the different composition of the benthic community in each of them, and provides evidence of the horizontal variability of the bioturbation measurements on the same site. Only experiments of brief duration permit assessment of the bioadvective and non-local mixing events that superimpose biodiffusion effects in most of the cores. The inclusion of the bioadvective term in the model decreases the biodiffusive mixing rate previously estimated from a simple biodiffusive model.

RÉSUMÉ

Quantification du mélange du sédiment par biodiffusion et bioadvection : une expérience *in situ*.

Une expérience a été réalisée dans les conditions *in situ* pour quantifier la bioturbation sur une courte période de temps. Des traceurs particulaires et conservatifs, les luminophores, sont déposés au début de l'expérience à la surface du sédiment dans une série de carottiers. L'application d'un modèle de mélange biodiffusif et bioadvectif sur les profils de traceurs permet d'estimer un mélange moyen biodiffusif ($D = 4,3 \pm 2,8$ $cm^2.a^{-1}$) et une vitesse moyenne de transport vertical ($V = 27,5 \pm 15,1$ $cm.a^{-1}$). L'hétérogénéité des résultats est attribuée à la différence de composition de la communauté benthique à l'intérieur de chaque carottier. Ces résultats démontrent la variabilité horizontale de la bioturbation mesurée sur un même site. Seule la mesure de la bioturbation sur une courte durée permet l'estimation des processus biologiques de transport vertical du sédiment, la biorégénération et la bioadvection, qui se superposent au mélange biodiffusif dans la plupart des carottiers. L'inclusion d'un terme pour la bioadvection dans le modèle diminue les estimations du mélange biodiffusif calculées antérieurement avec un modèle simplement biodiffusif.

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INTRODUCTION

Macrobenthic activity at the sediment-water interface generates various perturbations in the biogeochemical properties of the benthic boundary layer. One of the major modifications created by biological activity is sediment mixing.

In the benthic community each species generates a specific mixing mode depending on its ethology, especially on its feeding mode. The biological sediment mixing has been widely identified to an eddy diffusion process (Goldberg and Koide, 1962; Guinasso and Schink, 1975). This so-called biodiffusive mixing rate assumes that superimposition of whole community effects is similar to omnidirectional transports of adjacent parcels of sediment. Bioturbation studies performed with monospecific populations have indicated other types of mixing that produce vertical transport over a larger scale than biodiffusion. These mixing types have been described as non-local mixing (Boudreau, 1986; Smith *et al.*, 1986) or regeneration (Gardner *et al.*, 1987; Sharma *et al.*, 1987; Benninger *et al.*, 1979) and as bioadvective mixing (Robbins *et al.*, 1979; Fisher *et al.*, 1980; Rice, 1986). Bioadvection is produced by organisms that feed at depths in the sediment and egest upon the surface of the sediment. Large populations of these so-called conveyor-belt feeders (Rhoads, 1974) have the inherent capacity to accumulate sufficient sediment at the surface so that their effects on a tracer profile are similar to a high sedimentation rate. Regeneration, one form of non-local mixing, results in the subsequent filling of burrows with surface sediment which generates supplies of fresh material in deep sediment or subsurface egestion by inverse conveyor-belt feeding at the surface of the sediment.

Researchers have used several types of tracers to quantify the sediment mixing rate, but the most widely investigated are artificial or natural radionuclides (Guinasso and Schink, 1975; Aller, 1977; Turekian *et al.*, 1978; Benninger *et al.*, 1979; Cochran and Aller, 1979; De Master and Cochran, 1982; Imboden and Stiller, 1982; Aller and De Master, 1984; Cochran, 1985; De Master *et al.*, 1985; Kershaw, 1985; Stordal *et al.*, 1985; Yokoyama *et al.*, 1985; Smith *et al.*, 1986; Rice, 1986; Gardner *et al.*, 1987; Sharma *et al.*, 1987; Anderson *et al.*, 1988; Brand and Shimmield, 1991; Clifton, 1991; Zuo *et al.*, 1991). The use of radionuclides to quantify bioturbation gives assessments of macrobenthic influence on both interstitial pore water and particle migrations. As molecular diffusion interacts with bioturbation to transport solutes contained in interstitial water, the estimation of biological mixing often depends on the accuracy of estimating molecular diffusion in sediment (Li and Gregory, 1974). Only solid and conservative tracers yield direct quantification of sediment mixing. This idea was first applied by Glass (1969) who used microtektite distributions in deep-sea cores. Recently glass beads or sand grains marked with fluorescent paint have appeared in bioturbation studies (Mahaut and Graf, 1987; Gerino, 1990; Gerino and Stora, 1991; Teucher, 1991; Van Noort and Kraay, 1992). The present paper concerns an experiment monitored with natural sediment particles dyed with luminescent paint, known as luminophores.

Most radionuclides scavenge continuously to the sea floor. Studies of their steady-state profiles in sediment provide average mixing rates over a large period of time. If this information is useful to compare the average bioturbation from different sites, it remains necessary to measure mixing events at a precise time of the year. Furthermore, the major objective of bioturbation studies is to be able to include biological mixing in studies of organic matter in early diagenesis. As the half-life of organic matter is relatively short, it is also necessary to obtain precise information on the mixing rate and rapid mixing events. Our experiment was designed to examine these latter points. A pulse input of luminophore was deposited at the surface of the *in situ* sediment and the experiment was conducted over a short time period. These conditions produce non-steady state distributions of tracers that may give evidence for rapid mixing events.

This study relates to a shallow environment close to the Rhône river mouth in the Mediterranean Sea. In this estuary zone, the macrobenthic community is well developed and all the different mixing processes may interact at the same time. The preliminary results of this experiment have been discussed in a previous paper (Gerino, 1990) which only considers biodiffusive mixing. In this paper the entire experiment is presented, not only demonstrating the different mixing processes but also providing information on ways and means of improving bioturbation measurements.

MATERIAL AND METHODS

The experimental site was located 4°52'75 East and 43°22'92 North in the Gulf of Fos at a water depth of 5 m (Fig. 1). This site, a sheltered and shallow area on the northeastern Mediterranean coast, is very close to the Rhône river mouth and the salinity is low. The present benthic community is referred to "Muddy sand in sheltered area assemblage" (Pérès, 1982).

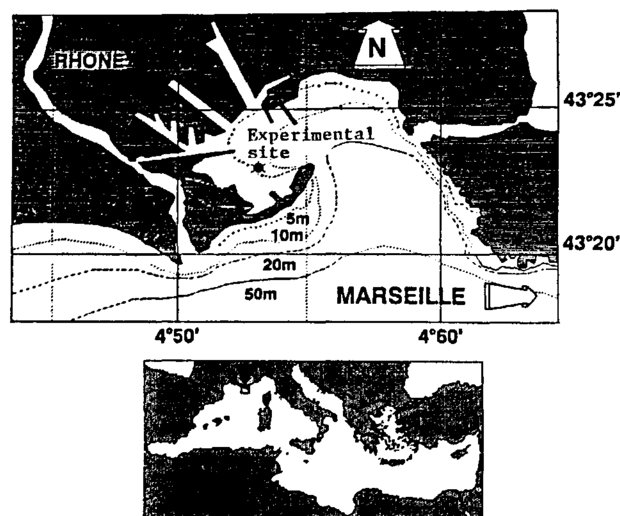


Figure 1

Experimental site in the Gulf of Fos, northeastern Mediterranean Sea.

Site expérimental dans le Golfe de Fos, Nord-Est de la Méditerrannée.

The tracers are natural sediment particles dyed in fluorescent paint, termed luminophores (Mahaut and Graf, 1987). Particle sizes ranging from 10 to 200 µm were selected to cover the most abundant fractions of the sediment at the experimental site. Different-coloured particles were used in order to count separately each size fraction of luminophores and render the tracer weight estimation more precise. The experiment began in December 1988 and lasted 58 days. At the beginning of the experiment, nine PVC cores (diameter = 11 cm and length 30 cm) were introduced over 25 cm in *in situ* sediment by scuba divers. Three similar cores were previously filled up with defaunated sediment from the same site and contaminated with tetraethyl lead to prevent colonization by macrofauna during the experiment (Arnoux *et al.*, 1988). These three control cores were introduced in the sediment next to the other cores. A mixture of 1 g of pink luminophores (particle diameters ranging from 10 to 100 µm) and 1 g of yellow luminophores (particle diameters from 100 to 200 µm) was added at the surface of the sediment in all the cores.In the knowledge that biological mixing was relatively rapid in this semi-estuarine sediment (Gerino, 1990; Gerino and Stora, 1991), the three first cores with macrofauna (E100, E200, E300) and one control core were collected after 22 days in *in situ* conditions. This short experimental duration also reflected an attempt to prevent the absence of tracers at the sediment surface. In order to analyse the effect of the experimental duration, two other series of cores remained for longer periods of time under the same conditions. The second series of cores (E400, E500, E600 and a control core) were collected after 43 days. The last series (E700, E800, E900, and a control core) were left for 57 days in the same conditions. Details of analyses were given in Gerino (1990). Basically, macrofauna and luminophore concentrations were determined in each section (thickness: 1 cm) of all the cores. In this paper, macrobenthic abundance is calculated integrating the top 2.5 dm of sediment.

RESULTS

The luminophore data are expressed in weight of tracer (g) per volume of dried sediment (cm^3). The vertical distributions of luminophores in the sediment of each core are presented in Figure 2. The total abundance of macrofauna in these cores is given in Figure 3 with the proportions of the different feeding groups, estimated by using the macrofaunistic composition and the feeding mode of each family (Coull, 1977; Fauchald and Jumars, 1979; George and George, 1980). Some of the organisms are classified into undetermined mode because their feeding mode has not yet been described in any literature.

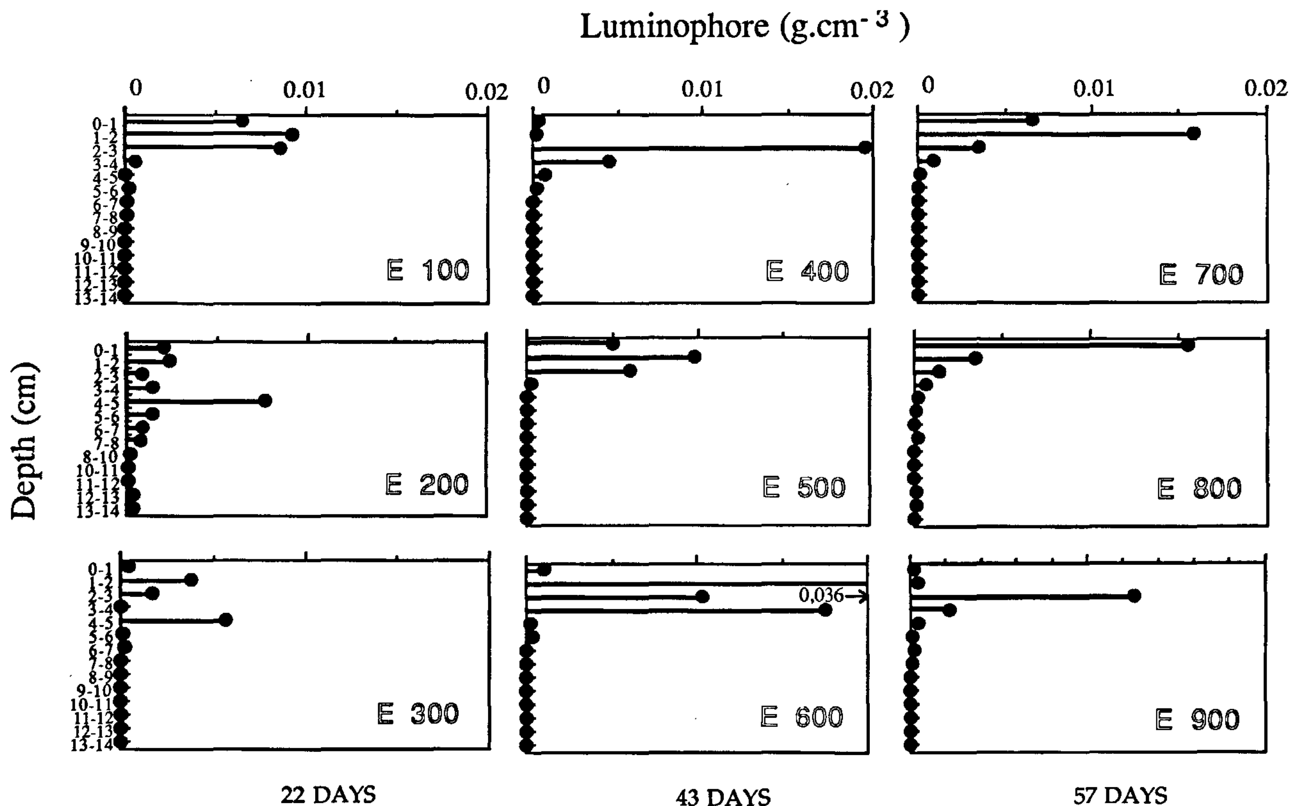


Figure 2

Luminophore distributions as a function of depth in each core of the time series experiment. After deposition of the tracers in the surface sediment, cores E100, E200, and E300 remained in situ *for 22 days; cores E400, E500 and E600 for 43 days; and cores E700, E800 and E900 for 57 days.*

Distribution des luminophores en fonction de la profondeur dans chaque carottier de l'expérience. Après déposition des traceurs à la surface du sédiment, les carottiers E100, E200 et E300 sont restés 22 jours dans les condition *in situ*, 43 jours pour les carottiers E400, E500 et E600, et 57 jours pour les carottiers E700, E800 et E900.

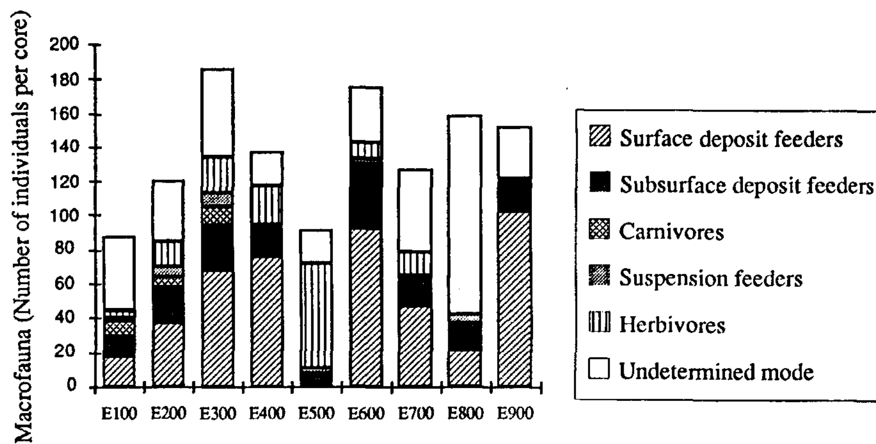


Figure 3

Macrobenthic abundances and proportions of the different feeding groups in each core.

Abondances du macrobenthos et proportions des différents groupes trophiques dans chaque carottier.

Core series 1 after 22 days *in situ* :

In the control core all the luminophores were still at the surface of the sediment when the core was collected. In the three cores with macrofauna, the luminophores were present in the sediment over a depth ranging from 6 to 14 cm. In core E100, the luminophore concentration was maximal in subsurface sediment between 1 and 2 cm. In core E200, most of the tracers were grouped between 4 and 5 cm in depth and a small accumulation of luminophores were found between 1 and 2 cm. The third core E300 also showed two peaks in subsurface sediment, between 1 and 2 cm and between 4 and 5 cm.

The mean abundance of the macrofauna in these three cores was equal to 54.8 (36.6-80.0) individual.dm^{-3} (mean, n=3 (min-max)). The benthos colonized the sediment down to 16 ± 2 cm. In these cores, deposit feeders were dominant and accounted for more than 50 % of the total organisms. In the control core a few organisms were found at the top of the sediment with a total abundance of 4.7 individuals dm^{-3}.

Core series 2 after 43 days *in situ* :

In the control core of this series, traces of luminophores were found to have penetrated 3 cm into the sediment. In cores with macrofauna, tracers were distributed around maximum concentrations located in subsurface sediment between 2 and 3 cm and between 1 and 2 cm in E400 and E500 respectively. In core E600, the luminophore distribution showed two peaks, between 1 and 2 cm and between 3 and 4 cm.

The mean abundance of macrofauna was equal to 56.1 (38.7-73.6) individuals.dm^{-3} (n = 3). The maximum depth of colonization varied between 11 and 17 cm in these cores. Deposit feeders were still dominant in these cores, except in E500 where herbivores, mainly epifauna, accounted for 66% of the community, and subsurface deposit feeders were absent. In the control core, the macrobenthos with an abundance equal to 12.5 ind.dm^{-3} was distributed in the three first centimetres of the sediment.

Core series 3 after 57 days *in situ* :

The amount of luminophores decreased regularly from the surface to 5 cm depth in the core E800. In other cores with macrofauna, luminophores were present to a depth of 13 cm and distributed around a level of high concentration located between 1 and 2 cm in E700 and between 2 and 3 cm in E900. In the control core of this series, luminophores were found down to 3 cm, where the concentration was very weak.

The mean abundance of the total macrofauna was estimated at 51.8 (36.6-66.9) individuals.dm^{-3} (n = 3). These organisms colonized the sediment down to 22 cm in E700 and to 9 and 10 cm in E900 and E800 respectively. Deposit feeders were dominant except in core E800, which presented a large proportion of undetermined mode. In the control core only 5 individual.dm^{-3} were encountered in the first centimetre of sediment.

DISCUSSION

Heterogeneity in the luminophore profiles:

The presence of the maximum tracer concentration at the sediment surface in every control core indicates that biological activity is responsible for the migration of the tracers in the other cores with macrofauna. This point also demonstrates that the core walls do not act as sediment traps.

The tracer profiles in each core with macrofauna are quite heterogeneous. The differences observed in the profiles of cores belonging to the same series may simply be explained by the dissimilar macrobenthic composition inside each core. This is an argument for the presence of distinct sediment mixing modes depending on the responsible feeding types. Combination of these different mixing modes with intensities directly related to the abundance of the responsible key species (Aller, 1977) produces a distinct reworking in each core.

Even if the total macrobenthic abundance remains relatively unchanged in the experimental cores, ranging from 87 to 190 individual per core, each core contains a sample of the community with a distinct specific composition. The variance of the macrobenthic abundance calculated with the whole cores (α^2=1476) is higher than the mean abundance of the macrobenthos (Am = 130.2 ind.per core). This indicates that the horizontal distribution of the macrobenthos at the studied site is not homogeneous on the decimetric scale (Elliot, 1977). The macrobenthic community at the studied site has a horizontal distribution with an aggregate pattern which increases the variance of macrobenthos

abundance between cores. Taking account of this fact, we considered and analysed each core separately instead of working on the average bioturbation in the three cores of the same series.

Different mixing modes

The distribution pattern of tracers as a function of sediment depth presents some distinct features. The gradient of concentration *versus* depth is never constant. The highest concentration is not located at the surface except in core E800. In this core, concentration decreases exponentially with sediment depth, a type of profile characteristic of a simple biodiffusive sediment mixing. In the remaining cores, the presence of tracer accumulations in the subsurface with a low concentration in the upper level can only be explained by different mixing modes. These mixing modes must quickly transport sediment in vertical directions over a larger scale than biodiffusion. Sediment reworking of two types produces these peaks of tracers in the subsurface. The first type consists of non-local mixing (Boudreau, 1986) or regeneration (Gardner *et al.*, 1987; Sharma *et al.*, 1987; Benninger *et al.*, 1979) and results from the presence of burrows, which may be built by surface or subsurface deposit feeders as well as carnivores and suspensivores. The other type comprises bioadvective mixing (Robbins *et al.*, 1979; Fisher *et al.*, 1980; Rice, 1986) and is produced by conveyor-belt organisms which are subsurface deposit feeders. Five cores (E200, E400, E500, E700, E900) had only one peak in the subsurface. Three other cores (E200, E300, E600) exhibited two subsurface peaks. The depth and the number of these accumulations is different for the three cores of the same series. Considering all the experimental cores, peaks are located between 0 and 5 cm. These subsurface accumulations of tracers provide evidence of vertical transport of sediment by the macrofauna.

Bioturbation parameters

Up to now, the biological reworking of sediment has been quantified by applying models which take into account either only biodiffusive mixing or only non-local mixing. The basic equation describing a conservative tracer distribution as a function of time and depth in sediment with biodiffusive mixing is given by Crank (1976) :

$$\frac{\partial C}{\partial t} = D\frac{\partial^2 C}{\partial z^2} \quad (1)$$

with C the concentration of tracers, t the time (y), D the biodiffusive mixing rate ($cm^2.y^{-1}$), and z the depth (cm) into the sediment from an origin fixed at the sediment-water interface. Among the different variables that may influence tracer distribution in sediment, the accumulation rate stands out as an important parameter, and is introduced in models to describe *in situ* measurements of sedimentological tracers. Numerous authors, including Goldberg and Koide (1962), Guinasso and Schink (1975), Benninger *et al.* (1979), Mauviel *et al.* (1982), Officer and Lynch (1982), Aller and De Master (1984), Stordal *et al.* (1985), and Yokoyama *et al.* (1985), have used a biodiffusive model whose mathematical formulation contains a supplementary term, W (expressed in $cm.y^{-1}$) to quantify the advection resulting from sedimentation rate (see Berner, 1980). The common equation is :

$$\frac{\partial C}{\partial t} = D\frac{\partial^2 C}{\partial z^2} - W\frac{\partial C}{\partial z} \quad (2)$$

Modelling of bioadvection mixing began with Fisher *et al.* (1980), who studied the bioturbation created by a population of conveyor-belt oligochetes. They described vertical advection of tracers during the period limited by the time when the tracers arrive in the zone of sediment ingestion. During this period, the input of tracers, initially at the surface of the sediment, is transported downward in the sediment with a rate V and without any biodiffusive mixing. The differential equation describing this type of advective mixing, V expressed in cm.y-1, and given by Fisher *et al.* (1980) is :

$$\frac{\partial C}{\partial t} = -V\frac{\partial C}{\partial z} \quad (3)$$

Deposit feeders, burrowing organisms and typical conveyor-belt organisms like *capitellidae* and *sipunculidae* are numerous in the experimental cores. All the different mixing processes (biodiffusion, bioadvection and non-local transports) may occur simultaneously in the experimental cores. In cores with well preserved subsurface peaks, vertical transport appears to be the dominant reworking mode. In these cores, notably E200, E300, E400, E600 and E900, the vertical transport is great enough to transit the pulse input through the mixing layer before much diffusive mixing takes place. In all the cores, biodiffusive mixing occurs with greater or less intensity depending on the core, and is superimposed on the vertical transports. The intensity of the biodiffusive mixing controls the spreading of the tracers around the maximal concentration. In order accurately to describe the mixing processes recorded in our cores, we used a model with one term for biodiffusive mixing and a second term for bioadvective mixing (Gerino, 1992) :

In these conditions the biological transport of a pulse input of tracers submitted to a global mixing is described under non-steady state conditions by to the differential equation :

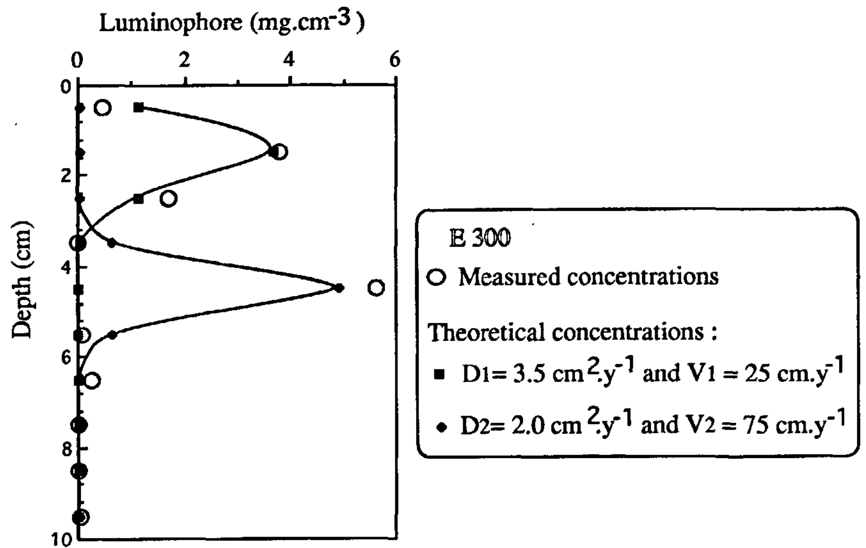
$$\frac{\partial C}{\partial t} = D\frac{\partial^2 C}{\partial z^2} - V\frac{\partial C}{\partial z} \quad (4)$$

Considering that the experiment was conducted over a very short period of time and that the maximal concentrations were still at the top of the sediment in the control cores, the sedimentation rate is not taken into account in the model. This equation is similar to equation (2), but the vertical transport rate characterizing accumulation effect in (2) is used to describe the biological advection in (4)

Figure 4

Theoretical and measured concentrations in core E300.

Concentrations théoriques et mesurées dans le carottier E300.



(Fisher *et al.*, 1980; Robbins *et al.*, 1979; Boudreau, 1986; Smith *et al.*, 1986).

The spatial boundary conditions are :

$$-D\frac{\partial C}{\partial z} + VC = 0 \quad \text{at } z = 0 \text{ and at } z = L$$

and the temporal boundary condition :

$$C = f(z) \quad \text{at } t = 0$$

with L the depth of the mixed layer (cm), and f(z) the initial tracer concentration in the interval z = [0,L]. These spatial boundary conditions state that the total flux across the upper surface of the sediment, as at the bottom of the mixed layer, is equal to zero. Under steady-state conditions, the solution for an instantaneous source at z = 0 and t = 0 is (Crank 1976) :

$$C(z^*,t) = \frac{M}{2\sqrt{\pi Dt}} \exp\left(\frac{-(z^*)^2}{4Dt}\right) \qquad (5)$$

Table 1

Estimated sediment biodiffusive mixing rates, D, and vertical transport rates, V, in each experimental core (In the case of a profile with two peaks of luminophores, D1 and V1 are mixing parameters determined from the upper peak, D2 and V2 are determined from the lower peak).

Coefficients de mélange biodiffusif et vitesses de transport vertical estimés dans chaque carottier. (Dans le cas de profil avec 2 pics de luminophores, D_1 et V_1 sont déterminés à partir du pic superieur, D_2 et V_2 sont déterminés à partir du pic inférieur.)

Core	E100	E200	E300	E400	E500	E600	E700	E800	E900
Time (y)	0.06	0.06	0.06	0.12	0.12	0.12	0.16	0.16	0.16
D_1 ($cm^2.y^{-1}$)	6.5	6	3.5	1	3.5	0.5	1	1.5	1
V_1 ($cm.y^{-1}$)	33.3	16.6	25	21.2	12.7	12.7	9.6	3.2	16
D_2 ($cm^2.y^{-1}$)		3.5	2			2.0			
V_2 ($cm.y^{-1}$)		75	75			29.7			

with $z^* = z - Vt$

and M is the tracers inventory in the interval from 0 to L cm.

The mean maximal depth of tracer penetration is equal to 9.1 ± 2.7 cm (mean ± $t_{0.05}$SE, n = 9). This layer of sediment, containing more than 90 % of the total macrofauna, is the mixed layer. In each core the biodiffusive mixing is quantified by the mixing rate D, and the vertical transport by the rate V (Tab. 1). For cores with one peak of tracers in the subsurface, vertical transport may result from bioadvection or bioregeneration, with the exception of core E500 where the absence of conveyor-belt organisms indicates that this accumulation is generated by bioregeneration. For all the cores with two subsurface peaks, the tracer profile is decomposed into two sub-profiles, each representing the results of one type of vertical transport. The sum of these two sub-profiles is strictly equal to the original profile. The biodiffusive - bioadvective model is applied separately on these sub-profiles. Values of D and V determined by best fit with a least square procedure between theoretical and measured profiles for each core of this experiment are grouped in Table 1. Comparison of theoretical and measured profiles in core E300 are given as examples in Figure 4. In the case of cores E200, E300 and E600 the two bioadvective rates V_1 and V_2 characterize two different vertical transport processes. The upper accumulation is generated by bioadvective transport. The lower peak may be generated by the same process or by bioregeneration. In the latter case, luminophores have sunk into open burrows at the beginning of the experiment, during tracer deposition. In these cores, intensity variations between D_1 and D_2 can be interpreted as fluctuations of mixing rate as a function of sediment depth. Agreement between the observed data and the theoretical values is excellent, indicating that the assumptions of the model are reasonable and represent a basically adequate description of the processes affecting sediment transport in this area.

From the nine studied cores the average biodiffusive mixing rate is estimated to 2.7 ± 1.3 $cm^2.y^{-1}$ (mean ± $t_{0.05}$SE). The average vertical transport rate is equal to 27.5 ± 15.1 $cm.y^{-1}$ (mean ± $t_{0.05}$SE).

Even if it is difficult to compare results from each core because of the heterogeneous macrobenthic composition, it appears that there is a tendency in fluctuations of bioturbation parameters with duration spent in *in situ* conditions. Both parameters D and V are maximal in the first series of cores and are much smaller in the last series, collected after 57 days.

We do notice that D values are particularly weaker in cores E400, E600, E700 and E900. In these cores, tracer concentrations at the sediment-water interface were very low at the end of the experiment and the amount of tracers initially deposited at the surface of the core has been incorporated in the deeper sediment. In these cores the low recorded sediment mixing rate does not indicate a low bioturbation activity, but rather an underestimation due to the lack of tracer at the sediment surface at the end of the experiment. In consequence, the average mixing rate has been calculated again, taking into account only cores where tracers were still present at the surface of the sediment at the end of the experiment. The corrected biodiffusive mixing rate is estimated equal to 4.3 ± 2.8 $cm^2.y^{-1}$. With calculations under non-steady state conditions the choice of the experiment duration is critical. In studies in zones of relatively high bioturbation, such as sheltered areas, shorter experiments yield better results.

The vertical transport rate cannot be influenced by the lack of tracers at the top of the sediment. Conveyor-belt organisms continuously supply material at the surface of the sediment and produce a vertical transport of the tracer profile independent of the distribution of the tracers. In the case of non-local events, the ingestion of tracers at the surface or the sinking of tracers into burrows at the beginning of the experiment must be great enough to create a peak at a depth in the sediment. The value of the vertical transport is not dependent on the amplitude of the peak.

The experiment design is not the only factor that may interfere with bioturbation parameter estimations. The decrease in the bioadvective term with time is normal if we consider more closely the transport mode of the conveyor-belt organisms. The bioadvection rate is similar to the velocity expressed as the ratio between the depth of migration and the time between tracer deposition and sampling, V=L/t.

(1) When the pulse input of tracers migrates downward because of effects of feeding, there exists a limit depth to the migration, F, located at the depth where the organisms ingest food and sediment (Fisher *et al.*, 1980). The tracer accumulation that reaches this point stops its transit, but the period of time taken into account still increases if the experimental duration is larger than the time equal to F/V.

(2) Then, tracers as well as the bulk of sediment are transported up to the surface, transiting through the guts of organisms. This phenomenon generates a second and smaller peak of tracers that migrates down into the sediment after a delay roughly equal to the time t = F/V. Both these effects lead to an apparent decrease of the estimated vertical velocity calculated with the duration of the experiment. This phenomenon is even more active in the case of non-local mixing events where surface sediment is transported down at a constant depth in the sediment. Results obtained with a shorter experimental period must give the best estimation of the velocity of vertical mixing. In the case of bioturbation parameter studies under steady-state conditions that integrate a much longer period of time, the vertical terms become negligible. This effect could explain why non-local and bioadvective terms scarcely appear in deterministic models to describe bioturbation. Only very short-term experiments are able to point them out.

From the luminophore distribution of the first series (Gerino, 1990), the previous estimation of the sediment mixing rate with a simple biodiffusive model was much greater, with an order of magnitude of 30 $cm^2.y^{-1}$. The difference with the actual estimation is attributed to the intervention of the bioadvective term in the present model that permits the best fitness of the theoretical profile and a more accurate measurement of the biodiffusion. Although the last estimation of the biodiffusion was in agreement with most previous measurements of the bioturbation in shallow environments (Matissof, 1982), this difference further shows the heterogeneity in the biodiffusive mixing intensity, depending on the model applied.

Because the macrobenthos is at the source of the bioturbation, the variability of the mixing parameters also depends on the horizontal variation of macrobenthic abundance. In the case of a shallow community with an aggregate pattern, the variance of the sediment mixing rate is also superior to the average mixing rate. The fluctuations of the calculated bioturbation parameters indicate that horizontal variation in bioturbation rates may occur in a single site.

REFERENCES

Aller R. (1977). The influence of macrobenthos on chemical diagenesis of marine sediments. PhD of Yale University, 600 p.

Aller R.C., D.J. De Master (1984). Estimates of particle flux and reworking at the deep-sea floor using $^{234}Th/^{238}U$ desequilibrium. *Earth Planet. Sc. Lett.*, **67**, 308-318.

Anderson R.F., R.F. Bopp, K.O. Buesseler, P.E. Biscaye (1988). Mixing of particles and organic constituents in sediments from the continental shelf and slope off Cape Cod : SEEP. -I results. *Cont. Shelf Res.*, **8**, 5-7, 925-946.

Arnoux A., G. Stora, E. Vacelet, P. Vitiello (1988). Étude expérimentale dans le milieu naturel de sédiment artificiellement contaminé par différentes formes chimiques d'un métal : Plomb. Évolution chimique et biologique du sédiment. *PIREN-ATP ECOTOXICOLOGIE* - Contrat n° **1294** - Rapport de fin de contrat, 22 p.

Benninger L.K., R.C. Aller, J.K. Cochran, K.K. Turekian (1979). Effects of biological sediment mixing on the ^{210}Pb chronology and trace metal distribution in a Long Island Sound sediment core. *Earth Planet. Sc. Lett.*, **43**, 241-259.

Berner R.A. (1980). *Early diagenesis. A theoretical approach.* Princeton University press, Princeton N.J., 241p.

Boudreau B.P. (1986). Mathematics of tracer mixing in sediment. I-Spatially-dependent, diffusive mixing. II: Non local mixing and biological conveyor-belt phenomena. *Am. J. Sc.*, **286**, 161-238.

Brand T., G. Shimmield (1991). The use of ^{210}Pb as an indicator of biological process affecting the flux and sediment geochemistry of organic carbon in the NE Atlantic. In : *Radionuclides in the study of marine processes.* P.J. Kershaw and D.S. Woodhead, Editors, London Elsevier Applied Science: 222-233.

Clifton R.J. (1991). The use of radionuclides (unsupported ^{210}Pb, ^{7}Be and ^{137}Cs) in describing the mixing characteristics of estuarine sediments. In : *Radionuclides in the study of marine processes.* P.J. Kershaw and D.S. Woodhead, Editors, London Elsevier Applied Science: 255-264.

Cochran J.K. (1985). Particle mixing rates in sediments of the eastern equatorial Pacific. Evidence from ^{210}Pb, $^{239,240}Pu$ and ^{137}Cs distribution at MANOP sites. *Geochim. Cosmochim. Acta*, **49**, 1195-1210.

Cochran J.K., R. Aller (1979). Particle reworking in sediments from the New York Bight apex : Evidence from $^{234}Th/^{238}U$ disequilibrium. *Estuar. Coast. Mar. Sc.* **9**, 739-747.

Coull B.C. (1977). *Ecology of marine benthos.* University of South Carolina Press, 467 p.

Crank J. (1976). *The mathematics of diffusion 1- Diffusion-mathematical models.* Oxford University Press, 2nd ed., England, 414 p.

De Master D.J., J.K. Cochran (1982). Particle mixing rates in deep-sea sediments determined from ^{210}Pb and ^{32}Si profiles. *Earth Planet Sc. Lett.*, **61**, 257-271.

De Master D.J., B.A. McKee, C.A. Nittrouer, D.C Brewster., P.E. Biscaye (1985). Rates of sediment reworking at the Hebble site based on measurements of ^{234}Th, ^{137}Cs and ^{210}Pb. *Mar. Geol.*, **66**, 133-148.

Elliot J.M. (1977). *Some methods for the statistical analysis of sample of benthic envertebrates.* Freshwater Biological Association, Scientific publication **25**, 157 p.

Fauchald K., P.A. Jumars (1979). The diet of worms : a study of Polycheate feeding guilds. *Oceanogr. Mar. Biol. Ann. Rev.*, **17**, 193-284.

Fisher J.B., W.L. Lick, P.L McCall., J.A. Robbins (1980). Vertical mixing of lake sediments by tubificid oligochaetes. *J. Geophys. Res.*, **85**, 3997-4006.

Gardner L.R., P. Sharma, W.S. Moore (1987). A regeneration model for the effect of bioturbation by fiddler crabs on ^{210}Pb profiles in salt marsh sediments. *J. Environ. Radioact.*, **5**, 25-36.

Gérino M. (1990). The effects of bioturbation on particle redistribution in Mediterranean coastal sediment. Preliminary result. *Hydrobiologia*, **207**, 251-258.

Gérino M. (1992). Etude expérimentale de la bioturbation en milieu littoral et profond. Quantification des structures de bioturbation et modélisation du remaniement biologique du sédiment. Thèse de Doctorat, Université Aix-Marseille II, 208 p.

Gérino M., G. Stora (1991). Analyse quantitative *in vitro* de la bioturbation induite par le polychète Nereis diversicolor. *C. R. Acad. Sci. Paris*, **313**, III, 489-494.

George J.D., J.J. George (1980). *La vie marine.* L. Leventhal Ltd, London, 173 p.

Glass B.P. (1969). Reworking of deep-sea sediments as indicated by the vertical dispersion of the Australasian and Ivory Coast microtektites horizons, *Earth Planet. Sci. Lett.*, **6**, 409-415.

Goldberg E.D., M. Koide (1962). Geochronological studies of deep-sea sediments by the ionium/thorium method. *Geochim. Cosmochim. Acta*, **26**, 417-450.

Guinasso N.L., D.R. Schink (1975). Quantitative estimates of biological mixing rates in abyssal sediments. *J. Geophys. Res.*, **80**, 21, 3032-3043.

Imboden D.M., M. Stiller (1982). The influence of radon diffusion on the ^{210}Pb distribution in sediments. *J. Geophys. Res.*, **87**, 557 - 580.

Kershaw P.J. (1985). ^{14}C and ^{210}Pb in NE Atlantic sediments : Evidence of biological reworking in the context of radioactive waste disposal. *J. Environ. Rad.*, **2**, 115-134.

Li Y., S. Gregory (1974). Diffusion of ions in sea water and in deep-sea sediments. *Geochim. Cosmochim. Acta*, **38**, 703-714.

Mahaut M.L., G. Graf (1987). A luminophores tracer technique for bioturbation studies. *Oceanologica Acta*, **10**, 3, 323-328.

Matissof R. (1982). Mathematical models of bioturbation. In : *Animal-sediment relations.* Mc Call P.L. and M.J.S. Tevest Editors, Plenum Press London N.Y., 289-330.

Mauviel A., H.Y. Nguyen, R. Chesselet, M. Sibuet, Y. Yokoyama, G. Auffret (1982). Etudes des variations des taux de bioturbation par la spectrométrie gamma non destructive (GeHP) dans 3 zones sédimentaires de l'Atlantique Nord à 2000 m et à plus de 4000 m de profondeur. *Bull. Inst. Géol. Bassin d'Aquitaine*, **31**, 257-274.

Officer C.B., D.R. Lynch (1982). Interpretation procedures for the determination of sediment parameters from time-dependent flux inputs. *Earth Planet Sci. Let.*, **61**, 1, 55-62.

Pérès J.M. (1982). Major benthic assemblages. *Marine Ecology*, **5**, 1, p 373-522.

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

Rice D.L. (1986). Early diagenesis in bioadventive sediments : relationships between the diagenesis of beryllium-7, sediment reworking rates and the abundance of conveyor-belt deposit-feeders. *J. mar. Res.*, **44**, 1, 149-184.

Robbins J.A., P.L. Mc Call, J.B. Fisher., J.R. Kreszoski (1979). Effects of deposit feeders on migration of ^{137}Cs in lake sediments. *Earth Planet. Sc. Lett.*, **42**, 277-287.

Sharma P., L.R. Gardner, W.S. Moore, M.S. Bollinger (1987). Sedimentation and bioturbation in a salt march as revealed by ^{210}Pb, ^{137}Cs an ^{7}Be studies. *Limnol. Oceanogr.*, **32**, 2, 313-326.

Stordal M.C., J.W. Johnson, N.L. Guinasso, D.R. Schink (1985). Quantitative evaluation of bioturbation rates in deep ocean sediments. II. Comparison of rates determined by ^{210}Pb and $^{239/240}Pu$. *Mar. Chem.*, 17, 99-114.

Smith J.N., B.P. Boudreau, V. Noshkin (1986). Plutonium and ^{210}Pb distributions in Northeast Atlantic sediments subsurface anomalies caused by non local mixing. *Earth Planet. Sc. Lett.*, **28**, 1, 15-28.

Teucher M. W. (1991). Luminophores and a new scanning system for demonstration of the bioturbation particle transport in marine sediments. 212 - Institut für Meereskunde- Christian-Albrechts-Universität. Kiel. p 71.

Turekian K.K., J.K. Cochran, D.J. De Masters (1978). Bioturbation in deep sea deposit rates and consequences. *Oceanus*, **21**, 1, 34-41.

Van Noort G. J. and G. W. Kraay (1992). Measurement of bioturbation in the mesocosm experiment using a new method. In: *Benthic response to eutrophication in manipulated marine sandy sediment - Meso/boxcosm Research 1990.* NIOZ - Rapport 1992-4, 39-42.

Yokoyama Y., H.V. Nguyen, C.E. Lambert, R. Chesselet (1985). Etude de la bioturbation dans les sédiments superficiels de la Méditerranée occidentale par le traceur ^{210}Pb. *Oceanologica Acta*, **8**, 3, 285-291.

Zuo Z., D.Eisma, G.W. Berger (1991). Determination of sediment accumulation and mixing rates in the Gulf of Lions (Mediterranean sea). *Oceanologica Acta*, **14**, 3, 253-262.