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A model of the effects of an infaunal xenophyophore on ^{210}Pb distribution in deep-sea sediment*

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Abstract: In an earlier paper we reported that the infaunal xenophyophore *Occultammina profunda*, collected from a box core of sediment from the Izu-Ogasawara Trench (sample depth 8260 m), contains high levels of the natural radionuclide ^{210}Pb (450-500 dpm/g dry) in both its protoplasmic body (granellare) and waste products (stercomes). We further suggested that, through the excretion of stercomes rich in ^{210}Pb, *O. profunda* may significantly affect the vertical distribution of ^{210}Pb in the sediment.

In the present paper we describe in detail the theory and assumptions behind the model of stercome excretion briefly described in our earlier paper and show that if *O. profunda* reproduces on a time-scale of months it will significantly influence the vertical distribution of ^{210}Pb in the sediment, resulting in a subsurface ^{210}Pb peak coincident with a peak in the vertical distribution of the xenophyophore. As stercome-producing rhizopods like *O. profunda* are abundant in many other regions of the deep sea, our model may have widespread applications.

1. Introduction

Knowledge of the depth and rate of bioturbation (sediment mixing by organisms) is essential for the modelling of early diagenesis and for interpretation of the stratigraphic record in deep-sea sediments. The radionuclide ^{210}Pb which has a half-life of 22 y is widely used for such studies (NOZAKI *et al.*, 1977; DEMASTER and COCHRAN, 1982; YAMADA *et al.*, 1983; SMITH and SCHAFER, 1984; COCHRAN, 1985). ^{210}Pb is derived from the radio-active decay of ^{226}Ra in the earth's crust and seawater, and unsupported ^{210}Pb (i.e., ^{210}Pb separated from ^{226}Ra) is transported to deep-sea sediments by sinking particulate matter which is rich in the radionuclide (SPENCER *et al.*, 1978; BACON *et al.*, 1985). In the absence of bioturbation or other mixing processes, unsupported ^{210}Pb would be confined to the top millimeter or so of deep-sea sediments because its half-life is short compared with the rate of sedimentation, but, as a result of mixing, unsupported ^{210}Pb can be found down to a depth of about 10 cm in deep-sea sediments.

In the standard mixing model used to estimate rates of bioturbation (e.g., NOZAKI *et al.*, 1977) it is assumed that mixing is a random diffusion-like process and that ^{210}Pb remains attached to refractory sedimentary minerals throughout mixing. As a result, unsupported ^{210}Pb should show an exponential decrease in concentration with depth in the sediment. Although deep-sea sediments do often show approximately exponential ^{210}Pb distributions (e.g., NOZAKI *et al.*, 1977), many exceptions exist (e.g., SMITH and SCHAFER, 1984).

One such exception was found by YAMADA *et al.* (1983) who described an "anomalous" ^{210}Pb distribution from a box core of sediment from the Izu-Ogasawara Trench in which the vertical distribution of ^{210}Pb showed a subsurface peak at 2-3 cm depth (Fig. 1). In a recent paper (SWINBANKS and SHIRAYAMA, 1986) we pointed out that this peak coincided with a peak in the vertical distribution of the infaunal xenophyophore *Occultammina profunda* (Fig. 1), the plasma body (granellare) and waste products (stercomes) of which were found to contain high levels of ^{210}Pb (450-500 dpm/g dry), and we suggested that this rhizopod may form the subsurface ^{210}Pb peak by feeding on ^{210}Pb-rich material at the sediment-water interface and then excreting the ^{210}Pb in stercomes at depth. Such a process of ^{210}Pb mixing differs substantially

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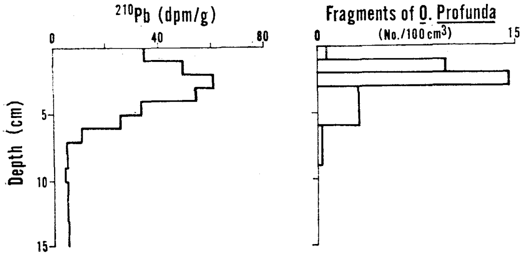

Fig. 1. The vertical distribution of ^{210}Pb (left) (after YAMADA *et al.*, 1983) and fragments of *O. profunda* (right) (after TENDAL *et al.*, 1982) in a box core of sediment from the Izu-Ogasawara Trench. The former distribution is based on one subcore of 100 cm^2 horizontal cross section, while the latter is the average distribution for four such subcores (not including that for ^{210}Pb).

from that envisaged in the standard mixing model as it involves highly selective redistribution of ^{210}Pb-rich material in a non-steady state fashion with little or no sediment mixing (*op. cit.*).

The case described by us for *O. profunda* may by no means be an isolated incident as other rhizopod protozoans producing masses of stercomes are abundant in oligotrophic regions of the deep sea (RIEMANN, 1983). Thus, ^{210}Pb distributions in deep-sea sediments may require substantial re-interpretation.

In the present paper, we describe in detail the theory behind the model of stercome excretion which was only briefly outlined in our earlier paper, and we then apply the model to the data collected from the Izu-Ogasawara Trench. Before describing the model, however, it is necessary to give a brief description of the important characteristics of infaunal xenophyophores in particular *O. profunda.*

2. Infaunal xenophyophores

Infaunal xenophyophores such as *O. profunda* construct a subsurface network of sediment tubes, the organism's test, in which they live below the sediment-water interface. Running through the centre of the tube is an unattached thread of protoplasm (granellare) surrounded by anastomosing strings of stercomare (Fig. 2). The stercomare consist of organic membrane tubes enclosing small black spherical pellets (stercomes) 10–20 μm in diameter which are thought to be waste and excretion products (TENDAL, 1972).

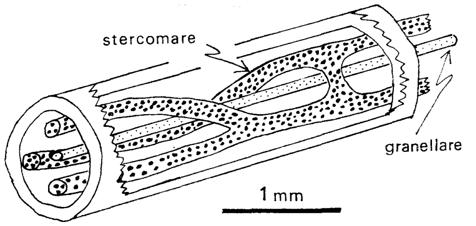

Fig. 2. Internal organization of an infaunal zenophyophore.

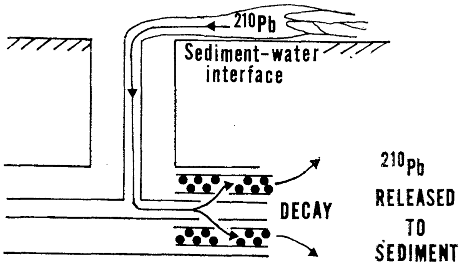

Fig. 3. Possible feeding mechanism in infaunal xenophyophores which results in ^{210}Pb transfer to the subsurface layers of the sediment. The xenophyophore extends its pseudopodia over the sediment-water interface and draws in particulate matter rich in ^{210}Pb. The ^{210}Pb is then stored in stercomes that subsequently decay releasing the ^{210}Pb to the immediately surrounding sediment.

Although little is known about the mode of feeding of infaunal xenophyophores, SWINBANKS (1982) has suggested on the basis of trace fossil evidence that these protozoans extend pseudopodia out through vertical outlets of their underground network and draw in food from the sediment-water interface (Fig. 3). The high levels of ^{210}Pb found in *O. profunda* support this view as the most likely source of the ^{210}Pb is particulate matter settling on the substrate (SWINBANKS and SHIRAYAMA, 1986).

With time, stercomes become lighter in colour and break down into grey flufflike material which appears to contain few if any refractory sedimentary minerals (SWINBANKS, 1982). During such decay ^{210}Pb in the stercomes is probably released to the immediately surrounding substrate (Fig. 3). Thus, ^{210}Pb is transfered from the sediment-water interface to the subsurface layers with little or no sediment mixing.

3. Model of stercome excretion

Our model consists of a 10-cm cube of sediment partitioned into 1-cm thick horizontal layers, the topmost of which forms the sediment-water interface (Fig. 4). The total inventory of unsupported ^{210}Pb in the cube is maintained at a constant value by a constant vertical flux of ^{210}Pb in the overlying water column. ^{210}Pb neither enters nor leaves through the vertical sides of the cube. For simplicity, porosity is held constant at the average value for all the layers and sedimentation is assumed to be negligible during the time intervals modelled (maximum 250 y).

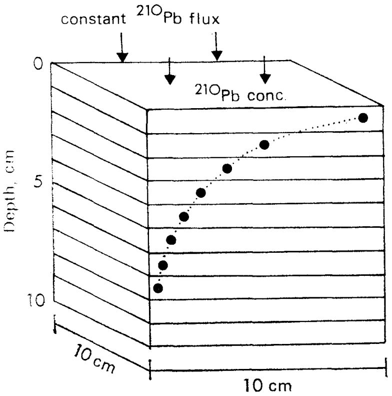

Fig. 4. Diagram of the model at time zero before the xenophyophore starts feeding.

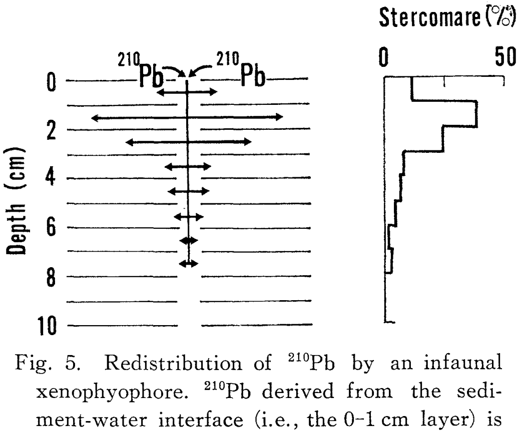

Fig. 5. Redistribution of ^{210}Pb by an infaunal xenophyophore. ^{210}Pb derived from the sediment-water interface (i.e., the 0–1 cm layer) is incorporated into stercomes in the subsurface layers in amounts proportional to the mass of stercomare in each layer (the diagram on the right gives the amount of stercomare in each layer as a percentage of the total amount of stercomare in the sediment).

Initially, ^{210}Pb decreases exponentially with depth in the sediment due to the mixing effects of organisms other than the xenophyophore (Fig. 4). Once the model starts to run, the xenophyophore takes in ^{210}Pb at the sediment-water interface (i.e., the 0–1 cm layer) and incorporates this ^{210}Pb into stercomes at a fixed concentration. The stercomes are then excreted into stercomare in the underlying subsurface layers in amounts proportional to the mass of stercomare observed in each layer (Fig. 5). At the same time, an equivalent amount of stercomes in the stercomare decays releasing ^{210}Pb to the immediately surrounding substrate (i.e., the mass of stercomare in each layer remains constant).

^{210}Pb mixing by other organisms is assumed to be a patchy process confined to the vast spaces between the xenophyophore network (even at its highest density *O. profunda* only occupies $\sim$0.1% of the volume of a 1-cm thick layer). As a result, stercome-derived ^{210}Pb is not immediately redispersed by other organisms but remains within the 1-cm thick layer to which it is assigned. This situation probably holds true for periods of time comparable to the half-

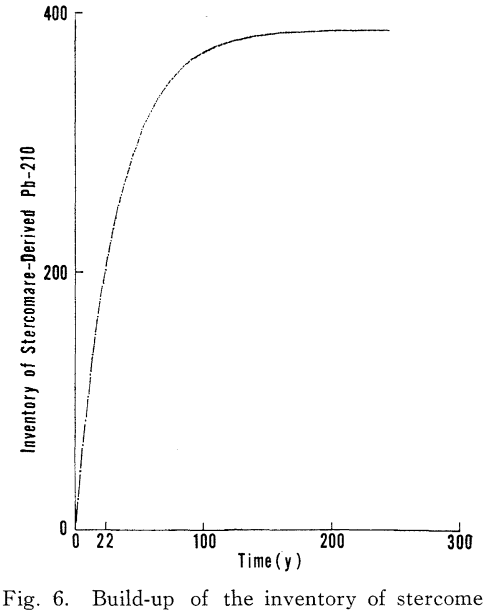

Fig. 6. Build-up of the inventory of stercome-derived ^{210}Pb, I_T, with time for a monthly input of ^{210}Pb to stercomes of 1 unit (arbitrary units).

life of ^{210}Pb (22 y), as shown by SMITH and SCHAFER's (1984) finding that ^{210}Pb distribution within 1-cm thick horizontal layers of surficial deep-sea sediments exhibits considerable lateral heterogeneity on a size scale of centimetres.

If the rate of input of ^{210}Pb to stercomes is k, then the total inventory of stercome-derived ^{210}Pb in all the layers after time T will be given by:

$$I_T = \int_0^T k\, e^{-\lambda t}\, dt = k\left(\frac{1}{\lambda} - \frac{1}{\lambda} e^{-\lambda t}\right),$$

where λ is the decay constant of ^{210}Pb. To obtain the resultant vertical distribution of ^{210}Pb at time T, this inventory is subtracted from the 0-1 cm layer and portions of the inventory are alloted to each layer according to the depth distribution of stercomare. As a result, the 0-1 cm layer is depleted in ^{210}Pb while ^{210}Pb is added to the subsurface layers.

As shown in Fig. 6, I_T rapidly builds up with time but eventually levels off to a constant value after about 250 years by which time the inventory has increased to almost 400 times the monthly input (to be exact the inventory reaches $1/\lambda$ or 386 times the monthly input). Fifty percent of the build-up occurs in 22 years.

The critical parameter to be determined in the model is k, the rate of input of ^{210}Pb, which depends on the rate of stercome formation. As stercomes are believed to be formed from material derived from particulate matter, the vertical flux of particulate matter at the sediment-water interface will constitute an absolute upper limit for the rate of stercome formation. We estimated that for the box core from the Izu-Ogasawara Trench the particulate matter flux is about 50-70 mg/100 cm^2/month, while for a dense patch of *O. profunda* the rate of stercomare formation was estimated to be well below this figure at between 2.5 to 30 mg/100 cm^2/month if the xenophyophore reproduces somewhere between once a month and once a year (SWINBANKS and SHIRAYAMA, 1986).

In the following section we present the results of modelling based on the box core data from the Izu-Ogasawara Trench (sources: TENDAL *et al.*, 1982; YAMADA *et al.*, 1983; SWINBANKS and SHIRAYAMA, 1986). Three rates of stercome formation within the above range are used in the model, namely, 5, 10 and 20 mg /100 cm^2/month, which yield values of k of 2.5, 5 and 10 dpm of ^{210}Pb/100 cm^2/month, respectively, for a ^{210}Pb content in stercomes of 500 dpm/g dry. These inputs of ^{210}Pb correspond to about 16, 31 and 62 %, respectively, of the total flux of ^{210}Pb to the sediment.

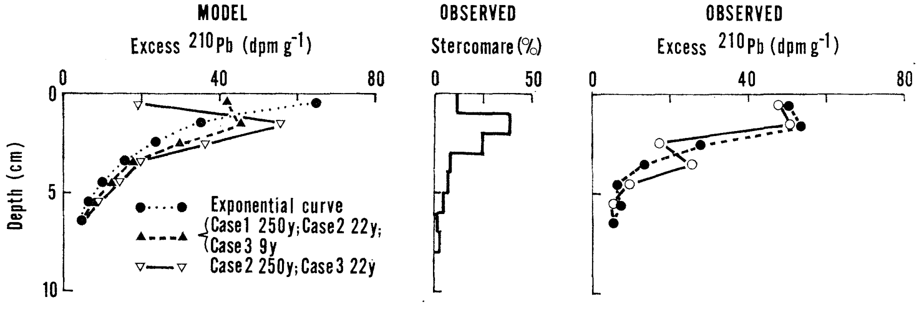

Fig. 7. Model results and observed distributions for the box core from the Izu-Ogasawara Trench. In the model on the left, three rates of stercome formation are considered: Case 1, 5 mg/100 cm^2/month; Case 2, 10 mg/100 cm^2/month; Case 3, 20 mg/100 cm^2/month. The dashed and solid curves in the model give the results after certain intervals of time, e.g., the dashed curve can be produced by a rate of 5 mg/100 cm^2/month (Case 1) acting for 250 years or by 10 mg/100 cm^2/month (Case 2) acting for 22 years or by 20 mg/100 cm^2/month (Case 3) acting for 9 years. The vertical distribution of stercomare of *O. profunda* shown in the middle diagram is as in Fig. 5 and is the average distribution for two subcores. The observed distributions of ^{210}Pb on the right are for the same two subcores used to determine stercomare distribution (different subcores from those in Fig. 1).

4. Results

Figure 7 presents the model results using data from the Izu-Ogasawara Trench. At a rate of stercome formation of 5 mg/100 cm^2/month, ^{210}Pb distribution begins to deviate significantly from the exponential curve after a few decades and when a steady-state is achieved after 250 years a small subsurface peak is formed at the depth of the peak in stercomare distribution. At a rate of 10 mg/100 cm^2/month, the same peak is formed in only 22 years and this develops into a pronounced peak by the time steady-state conditions prevail, while at a rate of 20 mg/100 cm^2 /month, the small subsurface peak is formed in only 9 years after 22 years it becomes pronounced and after 40 years the 0–1 cm layer is completely depleted in ^{210}Pb.

5. Discussion

As pointed out earlier, the assumption that stercome-derived ^{210}Pb remains within the layer within which it is emplaced probably only holds true for periods of time comparable to the half-life of ^{210}Pb (22 y). Thus, the peaks in the steady-state curves (i.e., those obtained after 250 y) would probably be less pronounced due to the mixing effects of other organisms. However, for shorter periods of time of the order of 22 years, the model is considered to yield realistic results.

The model shows that for stercome formation rates of about 10 to 20 mg/100 cm^2/month the observed ^{210}Pb distributions (Figs. 1 and 7) can be explained by the effects of *O. profunda*, and the marked subcore to subcore variation in the vertical distribution of ^{210}Pb can be attributed to the patchy distribution of the xenophyophore (TENDAL *et al.*, 1982). Looked at another way, the rates of stercome formation required by the model to explain the observed distributions suggest that *O. profunda* reproduces on a time-scale of months, a finding which supports other circumstantial evidence that xenophyophores grow quickly (SWINBANKS and SHIRAYAMA, 1986).

As stercome-producing rhizopods are abundant in oligotrophic regions of the deep sea (RIEMANN, 1983), our model may well be applicable to many other deep-sea areas. However, since benthic organisms including rhizopods typically attain their maximum densities in the surfacemost layer of sediment, the effects of rhizopods on ^{210}Pb distributions may not be immediately apparent. Nevertheless, they may downmix substantial amounts of ^{210}Pb, while causing little if any sediment mixing. Clearly the validity of the assumptions of the standard random diffusion mixing model need to be reassessed.

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内在性ゼノファイオフォアが深海堆積物中の鉛210の分布に及ぼす影響に関するモデル

D.D. SWINBANKS・白山義久

要旨: 前報において筆者らは，伊豆小笠原海溝（採集水深8260m）から得た柱状堆積物中より採集した内在性ゼノファイオフォアの一種である *Occultammina profunda* が，体細胞部（グラネラレ）と排泄物（ステルコマレ）のどちらにも，天然放射性核種である鉛210を高レベル（450〜500 dpm/g dry）に含んでいることを報告した。また，さらに筆者らは，鉛210に富んだステルコマレの排泄を通して，*O. profunda* が堆積物中の鉛210の鉛直分布に有意の影響を及ぼすであろうことを示唆した。

本報において筆者らは，前報の中で簡単に記載したステルコマレ排泄のモデルの背景にある理論並びに前提について詳細な記載を行ない，またもし *O. profunda* が数カ月ごとに再生産を行なうとすると，本種が鉛210の堆積物内における鉛直分布に対して有意の影響を及ぼし，ゼノファイオフォアの鉛直分布の極大と一致する表層下の鉛210の集中をもたらすことを示す。ステルコマレを生産する *O. profunda* のような根足類は他の多くの深海域においても豊富であり，筆者らのモデルは広範囲にわたる適応性を有するであろう。