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Oxygen profile in deep-sea calcareous sediment calculated on the basis of measured respiration rates of deep-sea meiobenthos and its relevance to manganese diagenesis*

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Abstract: The respiration rate of deep-sea meiobenthos collected using a submersible was measured using a gradient stoppered-diver technique, and the vertical profile of dissolved oxygen concentration in the sediment was calculated on the basis of the respiration rate using a steady-state model. At stations where the vertical profile of MnO_2 content showed a distinct peak in the subsurface 20 to 30 cm layer of the sediment, oxygen penetrated to significant depths in the sediment. However, at stations where an MnO_2 peak was seen in the top few centimeters of the sediment, oxygen was completely consumed by benthic organisms within the 0–1 cm layer. This result supports the idea that manganese diagenesis within calcareous sediment is mainly regulated by biological processes through the respiratory activities of benthic organisms.

1. Introduction

In vertical sections of deep-sea calcareous sediment collected using a box corer, three distinct layers of different coloration are usually clearly observed (BERGER *et al.*, 1979). The uppermost layer, named the monotonic layer (SWINBANKS and SHIRAYAMA, 1984), has no visible trace fossil, but soft X-ray radiographs reveal numerous infilled burrows, suggesting the presence of intense bioturbation. The next layer is called the mottled layer, in which many trace fossils are visible not only in radiographs but also to the naked eye. In the deepest layer, the faded layer, trace fossils are hard to see and the sediment is bleached in color, suggesting reduced condition.

SWINBANKS and SHIRAYAMA (1984) showed that there is a close relationship between the three layers and the vertical distribution of manganese oxide (MnO_2) in the sediment. At all seven stations they examined, a distinct peak was seen in the profile of the MnO_2 content. In the study of FROELICH *et al.* (1979), a model was proposed to explain the pattern of MnO_2 distribution in relation to the oxygen concentration in the interstitial water, and they suggested that the depth of MnO_2 peak corresponds to the deepest layer of the sediment into which free oxygen penetrates by diffusion or advection. In the study of SWINBANKS and SHIRAYAMA (1984), the depth of MnO_2 peak was found to agree well with the depth of the most darkly colored layer, which suggests that the coloration of the calcareous sediment was caused by the precipitation of MnO_2 within the sediment. In addition, the depth of the peak correlated significantly with the maximum depth index of the vertical distribution of meiobenthos, defined as the depth above which 95% of total meiobenthic individuals occur, which is also believed to be controlled by oxygen availability (SHIRAYAMA, 1984a).

According to SHIRAYAMA (1984a), the maximum depth index is related to the abundance of meiobenthos, and it in turn has a close correlation to the organic matter flux in deep-sea sediments (SHIRAYAMA, 1984b). Summarizing the above findings, SWINBANKS and SHIRAYAMA (1984) concluded that the depth of the MnO_2 peak is mainly regulated by the organic matter flux to the sediment surface through the mediation of biological process which controls oxygen distribution within the sediment.

In their study, subsurface MnO_2 peaks were found at depths of between 20 to 30 cm at five out of seven stations examined, while at the

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other two stations (Stations SC-14 and SC-16), the peak was in the surface layer of sediment at 2 and 4 cm depths respectively. At the latter two stations, the abundance of meiobenthos was very high for a deep-sea environment, and they suggested that due to the high density of benthic organisms, most oxygen is consumed within a thin layer of the sediment and, as a result, MnO_2 peak occurred near the sediment-water interface.

Although meiobenthic abundance at the stations with a surface MnO_2 peak was much higher than at other deep-sea stations (SHIRAYAMA, 1984b; THIEL, 1975), it was about the same as for shallow-water areas (MCINTYRE, 1969). The depth of oxygen penetration into the sediment is largely controlled by the respiration of benthos, and in shallow-water, free oxygen is known to penetrate only a few mm into the sediment (REVSBECH *et al.*, 1980a). In the deep sea, however, some kinds of organisms, e.g. demersal fishes, are known to reduce their metabolic activity by more than two orders of magnitude (SMITH and HESSLER, 1974). Therefore, if the respiration rate of benthic invertebrates also decreases drastically in the deep sea, it would become impossible for them to exploit all of the available dissolved oxygen within a few centimeters of the sediment.

Recently SHIRAYAMA (in prep.) succeeded in measuring the respiration rate of deep-sea meiobenthos using a modified cartesian diver technique. In the present study, on the basis of Shirayama's data, the vertical distribution of oxygen in the sediment was calculated using the equation of BOULDIN (1968) and the possibility of whether benthic organisms can consume oxygen completely within the very surface layer of the sediment is discussed.

2. Materials and methods

The calcareous deep-sea sediments were collected from seven stations in the western Pacific (SWINBANKS and SHIRAYAMA, 1984), using an USNEL box corer (HESSLER and JUMARS, 1974). Various subcores were taken from the box core samples, and the methods of processing these subcores were described in detail in our previous paper (SWINBANKS and SHIRAYAMA, 1984). The dissolved oxygen concentration of the near bottom water collected with a 0.5 l water sampler attached to the box corer, was determined using the Winkler method.

The measurement of the rate of meiobenthic respiration was carried out using a sediment sample collected at a depth of 1510 m at 39°17′N, 142°41′E using the submersible Shinkai 2000. The sediment sample was kept cool and conveyed to a cold laboratory (5°C) on land as quickly as possible. In the laboratory, meiobenthic organisms were sorted out under a dissecting microscope, and the respiration rate of these organisms was measured individually using a gradient stoppered-diver technique described by HAMBURGER (1981). After the measurements, each organism was fixed in 5% seawater formalin, extracted in glycerol, and their body volume was measured using a microscope and camera-lucida and their wet weight calculated after the method of WARWICK and PRICE (1979).

On the basis of the measured respiration rate of meiobenthos and their biomass in each layer of the sediment, the concentration of dissolved oxygen within the interstitial water was calculated using the equation of BOULDIN (1968) which was applied by REVSBECH *et al.* (1980a, b).

3. Results

a) The respiration rate of deep-sea meiobenthos

The respiration rate of thirteen nematodes, one polychaete and one harpacticoid copepod was measured in the present study. The rate of nematode respiration ranged from 1.2 to 9.6 (mean=4.7) $\mu l O_2$/individual/h, or 350 to 3300 (mean=1900) $\mu l O_2$/g wet weight/h. As a rule, the weight specific respiration rate tended to be larger as the weight of the individual became smaller. The weight specific respiration rates of the copepod and polychaete were close to those of the nematodes, the values being 520 and 350 $\mu l O_2$/g/h, respectively. These values are comparable to the respiration rates of shallow-water meiobenthos measured at comparable low temperatures (5°C) (PRICE and WARWICK, 1980; nematodes: 1600; polychaetes: 340; copepods: 550 $\mu l O_2$/g/h). This finding suggests that it is possible not only for shallow-water but also deep-sea benthic organisms to consume free oxygen completely within the surface few centimeters of sediment.

b) Calculation of the vertical profile of oxygen concentration within the sediment

According to BOULDIN (1968) the dissolved oxygen concentration in the sediment is a function of the respiration rate of benthic organisms, and the relationship at steady state can be expressed by the following equation.

$$Cx = R/2D \times (X^2 - 2X\sqrt{2DCo/R} + 2DCo/R), \quad (1)$$

where Cx is the concentration of dissolved oxygen at depth X in the sediment, Co the

Table 1. Dissolved oxygen concentration ($\mathrm{m}l\,O_2/l$) in calcareous sediment calculated using the steady-state model and measured respiration rate for deep-sea nematodes.

(A) Stations with a surface MnO_2 peak

Station	Depth in sediment (cm)	Oxygen concentration	Station	Depth in sediment (cm)	Oxygen concentration
SC-14	0.0	2.9	SC-16	0.0	3.5
	0.2	1.5		0.2	2.3
	0.4	0.56		0.4	1.4
	0.6	0.077		0.6	0.67
	0.8	0		0.8	0.22
				1.0	0.020
				1.2	0

(B) Stations with a subsurface MnO_2 peak

Station	Depth in sediment (cm)	Oxygen concentration	Station	Depth in sediment (cm)	Oxygen concentration
SC-8	0.0	3.3	SC-10	0.0	2.8
	0.2	2.7		0.2	2.0
	0.4	2.2		0.4	1.3
	0.6	1.7		0.6	0.79
	0.8	1.3		0.8	0.40
	1.0	0.92		1.0	0.14
	1.2	0.70		1.2	0.043
	1.4	0.51		1.4	0.0044
	1.6	0.35		1.6	0
	1.8	0.22			
	2.0	0.12	ST. 4	0.0	3.7
	2.2	0.073		0.2	2.8
	2.4	0.039		0.4	1.9
	2.6	0.016		0.6	1.3
	2.8	0.0034		0.8	0.74
	3.0	0.00021		1.0	0.36
	3.2	0		1.2	0.22
				1.4	0.11
SC-9	0.0	2.8		1.6	0.045
	0.2	1.7		1.8	0.010
	0.4	0.92		2.0	0.00040
	0.6	0.38		2.2	0
	0.8	0.086			
	1.0	0.0081	SC-15	0.0	3.4
	1.2	0		0.2	1.8
				0.4	0.78
				0.6	0.17
				0.8	0.0019
				1.0	0

concentration of dissolved oxygen at the sediment-water interface, R the total respiration of oxygen per unit volume of pore water and D the diffusion coefficient of oxygen within the sediment. The value of D was measured by REVSBECH *et al.* (1980b) in various cases. Since the type of the sediment in the present study is mostly foraminiferal ooze, the value of 8×10^{-6} cm²/sec will be used in the following calculation as in the calculation of REVSBECH *et al.* (1980a).

Although R includes both biological and chemical respiration, the latter is often negligible in the deep sea (SMITH, 1978). In order to estimate the total biological respiration, which includes the respiration of micro-, meio-, and macrobenthos, from the respiration rate of meiobenthos measured in the present study, the following equation was used.

$$R = Rn \times Bn / F / W, \qquad (2)$$

where Rn is the weight specific respiration rate of nematodes, Bn the biomass of nematodes, F the contribution of nematodes to the total biological respiration expressed as a fraction and W the water content of the sediment. Although the respiration rates of a deep-sea polychaete and copepod are also available, only the data of nematodes were used, since replicate measurements were not made for the former organisms in the present study.

According to GERLACH (1971), the ratio of macrofaunal to meiofaunal respiration is 1:5 and YINGST (1978) reported that the respiration rates of meiobenthos and microbenthos in the sediment are nearly the same. Within the meiobenthos, nematodes were reported to occupy around half of the total respiration (WARWICK *et al.*, 1979). Using these values, the contribution of nematodes to the total benthic respiration (F) was estimated to be around 23%. Since Rn was determined in the present study (1900 $\mu l O_2$/h/g) and the values of Bn and W are already known (SHIRAYAMA, 1984a), the value of R can be calculated using eq. (2).

On the basis of the obtained value of R, the oxygen concentration at every 0.2 cm depth in the sediment was calculated using eq. (1) (Table 1). At the stations which showed a surface MnO_2 peak, the concentration of oxygen decreased drastically and benthic organisms con-

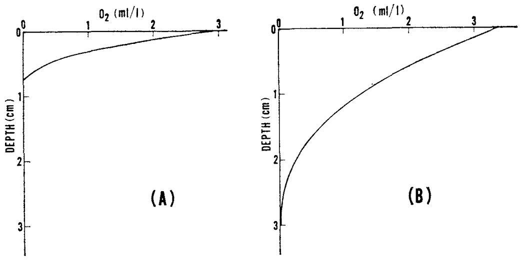

Fig. 1. Vertical profile of dissolved oxygen concentration within the sediment calculated using the steady-state model (BOULDIN, 1968) and measured respiration rates for deep-sea nematodes. (A) Station SC-14, where an MnO_2 peak was found at a depth of 2.0 cm. (B) Station SC-8, where a subsurface MnO_2 peak was found at a depth of 23.5 cm.

sumed all the oxygen within nearly one centimeter of sediment (Fig. 1A), due to their high biomass. In contrast, free oxygen could still be seen at depths greater than one centimeter at most of the stations with a subsurface MnO_2 peak (Fig. 1B).

4. Discussion

The decrease of biological activity with increase of the water depth due to the limited energy flow to the deep-sea floor has previously been considered to be a common phenomenon. However, at least in the case of meiobenthos, the respiratory activity of deep-sea species is not significantly reduced. It should be noticed that the present measurements were carried out under decompressed laboratory conditions. However, the effect of decompression is known to be minimal for organisms living at depths shallower than 2000 meters (SOMERO *et al.*, 1983). Thus, the activity of meiobenthos measured in the present study is considered also to be high *in situ*. This result supports the argument of SWINBANKS and SHIRAYAMA (1984) that through the oxygen consumption of benthic organisms, biological processes predominate over chemical processes in regulating manganese diagenesis within the sediment.

This argument seems particularly valid in the case of a surface MnO_2 peak. On the basis of eq. (1), the depth where $Cx = 0$ (h) is given as $h = 2DCo/R$ (REVSBECH *et al.*, 1980a, b). In a rough calculation, R must be larger than 5×

$10^{-5}\ \mu lO_2/cm^3/sec$ or $2\ mlO_2/m^2/h$, in order for the value of h to be less than 1 cm. This value of R is nearly the same as the highest value of sediment community respiration ever measured using the bell jar technique in the deep sea (SMITH, 1974). The values of R obtained in the present study for the stations with a surface MnO_2 peak were 1.8 and $3.2\ mlO_2/m^2/h$, which agree well with the required value. Therefore, if biological activity is not greatly affected by the increase in water pressure, it is quite possible for benthic organisms to utilize all the free oxygen within a few centimeters of the surface of the sediment, and, as a result, the MnO_2 peak would be expected to occur close to the surface of the sediment.

In the case of the stations with a subsurface MnO_2 peak, the calculated depth of oxygen penetration was always shallower than the depth of observed MnO_2 peak. The most probable reason for this discrepancy is bioturbation. Up until now measured rates of bioturbation in the deep sea have been based on the movement of sedimentary particles, and the values are too slow to explain the present discrepancy. However, for the distribution of oxygen in the sediment, movement of interstitial water should be considered. Macrofauna, especially polychaetes, have a considerable effect on the local distribution of many kinds of elements around their vertical burrows made within the sediment (ALLER and YINGST, 1978). In addition to this, however, the role of interstitial organisms is also important, if their high density (more than 10^6 individuals $/m^2$) is taken into consideration. Although it is very difficult for meiobenthos and nanobenthos of microscopic size (BURNETT, 1981; THIEL, 1983) to move the sandy particles, they can stir interstitial water very easily by their active movement through interstitial spaces. Since meiofaunal activity still seems to be high in the deep sea, as shown in the present study, their vertical mixing of interstitial water may be considerable, and oxygen will be conveyed into the depths of the sediment without the movement of sedimentary particles. In future studies of the diagenesis of pelagic sediments, therefore, keen attention should be paid to not only the mixing of sedimentary particles by macrobenthos, but also the mixing of interstitial water due to the activity of interstitial meiobenthos and nanobenthos.

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深海産メイオベントスの呼吸量の測定結果に基づいて計算された深海石灰質堆積物中の酸素分布とそのマンガンの続成との関係

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要旨: 深海潜水艇を用いて採集した深海産メイオベントスの呼吸量を，勾配フタ付浮きばかり法を用いて測定し，その結果に基づいて，平衡モデルを用いて堆積物中の溶存酸素濃度の鉛直断面を計算した。酸化マンガンの鉛直分布が堆積物の表層下20～30 cmの層に集中している地点では，酸素が堆積物のかなりの深度まで侵入していた。しかし酸化マンガンの集中が表層数cmに見られる地点では，酸素が底生生物によって表層0～1 cmの層で完全に消費されてしまった。この結果は，石灰質堆積物中でのマンガンの続成が，底生生物の呼吸活性を通して，生物学的過程に主に支配されているとする考えを支持している。