Vertical distribution of meiobenthos in the sediment profile in bathyal, abyssal and hadal deep sea systems of the Western Pacific

Vertical distribution
Sediment profile
Meiobenthos
Deep sea
Multivariate analysis
Distribution verticale
Profil sédimentaire
Méiobenthos
Haute mer
Analyse multivariée

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ABSTRACT

Vertical distribution of meiobenthos in the sediment profile was studied using 12 box corer samples collected in bathyal- to hadal-depths deep-sea systems of the Western Pacific. Organisms were obviously concentrated in the surface 0-1 cm layer of the sediment, and decreased exponentially in number with increase of depth in the sediment. At seven stations, organisms could not be found at depths greater than 12 cm, while at one station, nematodes and rhizopods could be found in the layer between 25 and 30 cm. To carry out analytical studies, two characteristics of vertical distribution, maximum depth and degree of concentration to the surface, were expressed using numerical indices, and to discriminate important environmental factors from factors of negligible effect, a stepwise method of multiple regression analysis was carried out between these numerical indices and twelve environmental factors. The results of analysis revealed that factors related to food-availability were effective in explaining the variance of the index denoting the degree of concentration, while oxygen availability was suggested to be a limiting factor for the maximum depth of distribution of meiobenthos in the sediment. This was especially clear when four biotic factors, density and biomass of macro- and meiobenthos, were added to the group of independent variables in the multiple regression analysis.

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RÉSUMÉ

Distribution verticale du méiobenthos dans le sédiment des étages bathyal, abyssal et hadal du Pacifique occidental

La distribution verticale du méiobenthos dans le sédiment a été étudiée sur 12 échantillons prélevés entre les étages bathyal et hadal du Pacifique occidental. Les organismes sont évidemment concentrés dans le premier centimètre de la couche de sédiment superficiel, et leur nombre diminue exponentiellement lorsqu'on s'enfonce dans le sédiment. En 7 stations, on ne trouve plus d'organismes dès que la profondeur dépasse 12 cm, tandis qu'à une station, nématodes et rhizopodes sont présents dans la couche comprise entre 25 et 30 cm. L'étude analytique a été conduite à l'aide de 2 caractéristiques de la distribution verticale, la profondeur maximale et la concentration superficielle, exprimées par des indices numériques. Pour mettre en évidence les paramètres importants de l'environnement, une méthode d'analyse par multirégression pas à pas a été appliquée à ces indices et à 12 paramètres de l'environnement.

Les résultats de l'analyse révèlent que les facteurs liés à la nourriture disponible expliquent la variance de la concentration, tandis que l'oxygène pourrait être un facteur limitant pour la profondeur maximale du méiobenthos dans le sédiment. C'est particulièrement évident lorsque 4 facteurs biotiques, densité et biomasse de macro- et méiobenthos, sont ajoutés aux variables indépendantes dans l'analyse par multirégression.

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INTRODUCTION

Among marine biologists, it is a commonly held view that benthic organisms are concentrated in the surface layer of the sediment. For deep-sea meiobenthos, their actual distribution has been described by several workers, *e.g.* Thiel (1972), Coull *et al.* (1977), Dinet and Vivier (1977) and Vivier (1978). However, the depths of sediment analysed in these studies were only 4 to 7 cm and did not cover the complete range of depth within which meiobenthos live. In the present study, using an USNEL box corer (Hessler, Jumars, 1974), sufficiently deep and undisturbed sediment samples were obtained, and organisms were sorted on land to a depth at which no specimen could be found. During the course of this study, it became possible to describe fully and precisely and to analyse the vertical distribution of deep-sea meiobenthos in the sediment profile.

Accumulated knowledge on the vertical distribution of shallow-water meiobenthos in the sediment profile suggests that food and oxygen availabilities are the main factors limiting the depth of invasion of meiobenthos into the sediment (Ansari *et al.*, 1980). Food supply, however, seems to be enough even at depths within the sediment in most cases, and many studies, *e.g.* Brafield (1964), Fenchel and Jansson (1966), Jansson (1967), Giere (1973) and Elmgren (1975), have shown a close relationship between the vertical distribution of meiobenthos and oxygen availability measured on the basis of redox potential or dissolved oxygen concentration in the interstitial water. In the deep sea, however, the problem as to which environmental factors regulate the vertical distribution of meiobenthos in the sediment profile has never been studied. In the present study, the relationships between the vertical distribution of meiobenthos and twelve environmental factors, including not only oxygen availability but also nutrient conditions and granulometric properties of the sediment, were analysed.

Two main properties of the vertical distribution of benthos in the sediment were recognized in the present study, namely the maximum depth of benthos and their degree of concentration to the surface layer of the sediment. To carry out analytical studies, these properties should be expressed by numerical indices. The index denoting the maximum depth has already been defined by Shirayama and Horikoshi (1982) in a study of vertical distribution of deep-sea macrobenthos, and this index is applied to meiobenthos in the present study. In addition, another index, expressing the degree of concentration, is newly defined. Stepwise multiple regression analysis was carried out between these indices and twelve environmental factors in order to determine the factors which significantly regulate the vertical distribution of meiobenthos.

A recent study by Reise and Ax (1979) on the distribution of so-called "thiobios" (*i.e.* organisms which are considered to prefer anaerobic, hydrogen sulfide-rich environments) has revealed that such organisms still tend to live in scattered, small patches of aerobic space thought to be created by the activities of macrobenthos within the anaerobic layer of the sediment. Such an effect of macrobenthic bioturbation seems to be considerable in regulating oxygen distribution in the sediment. The organisms not only actively pump oxygenated water but also create burrows which connect both sediment particles (Nichols, 1974; Chakrabarti, 1980) and interstitial waters (Kamp-Nielsen, 1974; Henricksen *et al.*, 1980; Gust, Harrison, 1981) at various depths with the seafloor surface of the sediment. In addition, meio- and microbenthos are reported to consume considerable quantities of dissolved oxygen in the interstitial water, and thus regulate oxygen distribution (Revsbech *et al.*, 1980). In the present study, therefore, biomass and numerical density of macro- and meiobenthos were added to the group of independent variables as biotic factors in a second run of the multiple regression analysis to determine whether biological factors regulate the vertical distribution of meiobenthos within the sediment.

MATERIALS AND METHODS

The sampling stations and the methods of sample treatment were described by Shirayama (1982; 1984; in press). In order to study the vertical distribution of meiobenthos, three subcores ($\Phi = 3.6$ cm, *i.e.* 10.2 cm^2) for the study of meiobenthos were sliced in the laboratory on board at intervals of 0-1, 1-2, 2-3, 3-6, 6-9, 9-12, 12-15, 15-20, 20-25 and 25-30 cm. The interval of slicing was increased with depth to ensure recognition of the disappearance of meiobenthos.

To discriminate effective variables from variables which have negligible effect on the vertical distribution of meiobenthos in the sediment profile, a stepwise method of multiple regression analysis (Wonnacott, Wonnacott, 1981) was carried out in the present study. To do this, the vertical distribution of meiobenthos was expressed numerically using two indices, the indices of maximum depth (*MD*) and degree of concentration to the surface

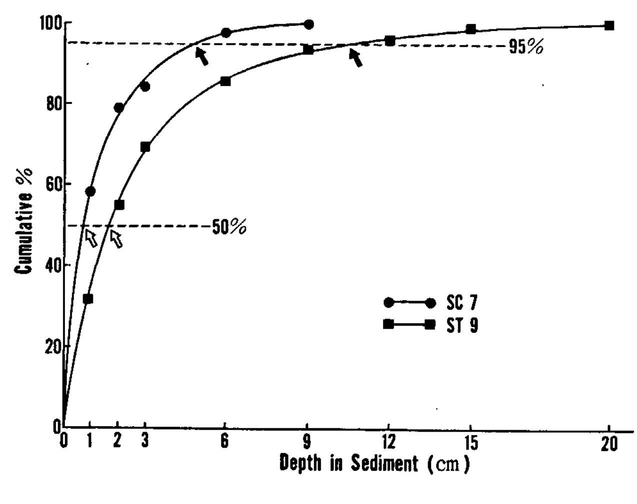

Figure 1

Examples of the cumulative percentage curve of the number of individuals drawn with respect to depth in the sediment. Using depths corresponding to intercepts of 50 and 95%, indicated by open and filled arrows respectively, the indices denoting two characteristics of vertical distribution of meiobenthos were calculated.

layer of the sediment (*DC*), as mentioned before. These indices were defined using two values, the depths of the 50 and 95% cumulatives, which were derived from the cumulative % curve of the number of individuals drawn with respect to the depth in the sediment (Fig. 1). The index of maximum depth (*MD*) was defined as the 95% value. This value indicates the habitat range of most but not all meiobenthos. The accuracy in determining the depth of an individual living in the deepest layer of the sediment cannot be better than the interval of slicing, since it was not possible to determine the position of a specific individual within the sliced sediment. In the present study, the accuracy was, therefore, 3 to 5 cm, and was considered to be too rough. In contrast, the depth corresponding to the 95% cumulative can be determined more accurately using interpolation. Therefore 100% was rejected and 95% was used as a measure of the maximum depth of distribution in the present study. The index of degree of concentration (*DC*) was defined as the value corresponding to 95/50%, *i.e.* the reciprocal of 50/95%. The ratio of 50 to 95% means percent of depth used by half of the organisms out of the total habitat range. Therefore, the value becomes large if the degree of concentration is low. The value *DC* was defined as the reciprocal of the ratio and will thus be large if organisms are strongly concentrated in the surface layer of the sediment. In the definition of these indices, the unit of numerical density was used. On this basis, it was considered better to exclude rhizopods (*e.g.* foraminifers and xenophyophores) from consideration, because during sample processing this kind of organism tends to be broken, with the result that only the number of fragments could be counted and not the number of individuals. If biomass was used as a unit, rhizopods could be included in the analysis. Nevertheless, numerical density is considered to be a more appropriate unit than biomass for defining the indices of vertical distribution of meiobenthos, since if the latter unit is used, the value of the index tends to be too strongly affected and badly biased by the occasional appearance of larger-sized specimens.

RESULTS

A data set of sixteen environmental factors was obtained in the present study (values are listed in Shirayama, 1982; 1984), consisting of twelve abiotic factors, *i.e.*, percentage of sand, silt and clay, median diameter, graphic mean diameter, sorting coefficient, skewness, water content, calcium carbonate content, organic carbon and nitrogen contents of the sediment, and dissolved oxygen concentration of the bottom water, and four biotic factors, *i.e.* biomass and density of macro- and meiobenthos. On the basis of the results of calcium carbonate content, the sediment at twelve sampling stations of the present study were divisible into two types. At those stations where water depth was greater than calcite compensation depth (CCD) (stations SC-5∼7, ST.5 and ST.9), the type of sediment was so-called "red clay", while at the other stations shallower than CCD (stations SC-8∼10, ST.4 and SC-14∼16), the sediment contained considerable quantities of biogenic calcite particles and was identical with "calcareous ooze". The vertical change of some sediment properties, *e.g.* organic nitrogen content, within a subcore was considerable, and thus in some cases, the range of values for two markedly different sediment types mentioned above, red clay and calcareous ooze, overlapped (Fig. 2). Therefore the mean value throughout the depth range where meiobenthos were living was chosen as the representative value for each station.

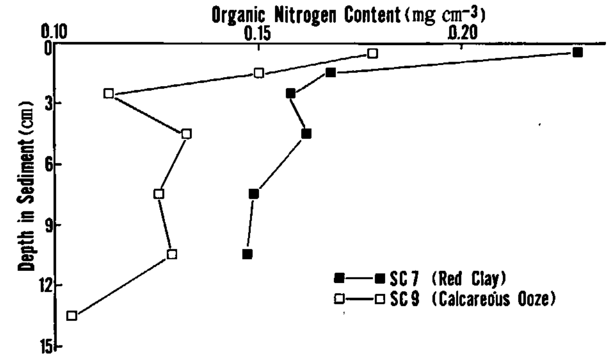

Figure 2

Vertical profile of organic nitrogen content at two stations with markedly different sediment types, i.e., *red clay* (■) *and calcareous ooze* (□). *Note that the range of values at each station is considerably large and thus the ranges of the two stations overlap.*

The meiobenthos collected at twelve stations in the deep-sea system of the Western Pacific were clearly concentrated in the surface layer of the sediment at both calcareous ooze and red clay stations in terms of both biomass (Fig. 3) and numerical density (Fig. 4). However, the degree of concentration differed from station to station in terms of biomass (Fig. 3) even if the range of vertical distribution was the same. For example, within three stations on Shatzky Rise (stations SC-14∼16), organisms decreased exponentially in biomass at stations SC-15 and 16, while at station SC-14, biomass in the subsurface layer (1-3 cm) was considerable. In terms of density, in contrast, the pattern of vertical distribution did not differ distinctly between stations (Fig. 4), and at all stations, meiobenthos decreased exponentially in number. However, the numerical index representing the degree of concentration (*DC*) was not constant, and its variance was explained significantly using the regression equation obtained by stepwise multiple regression analysis between *DC* and the twelve abiotic environmental factors listed above.

$$DC = -24 \times ON - 0.035 \times CC + 12.1, \quad r^2 = 0.46, \quad F = 14.27 > 5.32\,(DF: 2,33;\ p = 0.01), \qquad (1)$$

where *ON* is organic nitrogen content (mg cm^{-3}) and *CC* calcium carbonate content (%). The above equation indicates that within twelve abiotic environmental factors, only *ON* and *CC* significantly ($p < 0.05$) increase the proportion of variance of *DC* explained by the multiple regression equation. The above equation explains 46% of the total variance of *DC* (indicated by

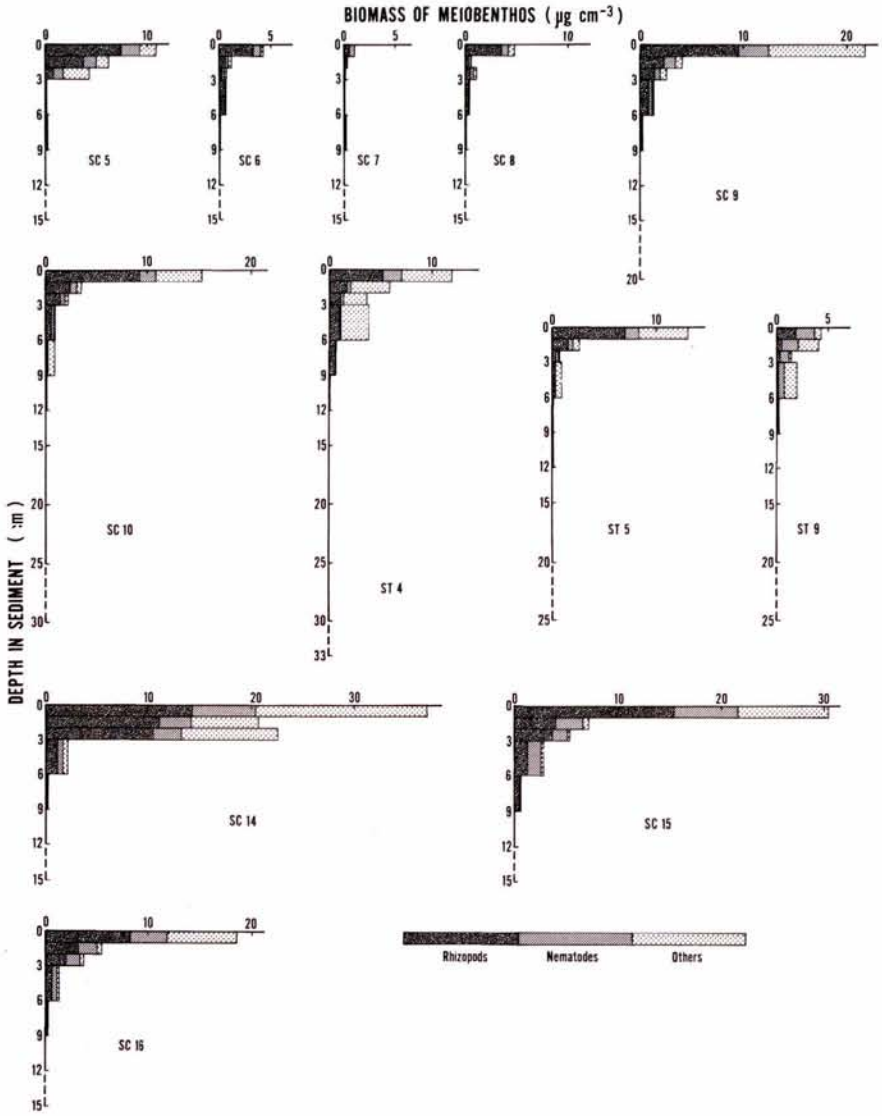

Figure 3

Vertical distribution of deep-sea meiobenthos in the sediment profile. Values are expressed in terms of biomass (ash-free dry weight). A broken line indicates the sediment layer in which organisms could not be found.

r^2). The meaning of F value is the same as that usually used in the analysis of variance, while in the case of multiple regression, degrees of freedom (DF) are given as (P, n-P-1), where P is the number of independent variables appeared in the regression equation, n the number of observations (*e.g.* in equation 1, $P = 2$ and $n = 36$). When all variables were standardized (*i.e.*, were transformed so as their mean and standard deviation become 0 and 1, respectively), the effect of each independent variable on the dependent variable could be compared using the absolute value (*i.e.*, the value regardless of sign) of the standard partial regression coefficient. the regression equation using standardized variables (indicated by asterisks) is:

$$DC^* = -0.73 \times ON^* - 0.55 \times CC^*. \qquad (2)$$

The above equation suggests that the influence of ON on DC is larger than that of CC.

The combination of two factors in equation (1), ON (organic nitrogen content) and CC (calcium carbonate content), is considered to be related to the organic matter flux, since the flux can be expressed by a combination of organic matter content of the sediment (*e.g.* ON) and sedimentation rate, and the latter parameter is closely correlated ($r = 0.93$) to the calcium carbonate content (CC) (Shirayama, 1984). In the regression equation (1), the partial regression coefficient of both ON and CC was negative, and thus the equation suggests that the degree of concentration of meiobenthos in the surface layer of the sediment is high at stations where organic matter flux is low. The regression equation did not change even when four biotic factors, *i.e.* density and biomass of macro- and meiobenthos, were added to the group of independent variables.

The depth of invasion of meiobenthos into the sediment differed from station to station. It was greatest at station ST.4, where four nematodes and two foraminifers were found in the layer between 25 to 30 cm. At seven stations (stations SC-5∼8 and SC-14∼16), meiobenthos could not be found deeper than the layer between 9 and 12 cm. In addition, at two of the stations (stations SC-14 and 15), organisms could be seen in this layer (9-12 cm) only in terms of biomass and not in terms of density (*see* Fig. 3 and 4), since only rhizopods were found in this layer and they were excluded in terms of density. The sediment type at three of the seven stations mentioned above, where meiobenthic distribution was shallowest, was red clay (stations SC-5∼7), while at the other four stations (stations SC-8 and SC-14∼16) it was calcareous ooze, and thus no definite relationship could be seen between the type of sediment and the maximum depth of vertical distribution. Nevertheless, for the index *MD*, indicating the deepest layer of vertical distribution, the stepwise method of multiple linear regression analysis extracted three effective factors from the twelve abiotic environmental factors mentioned earlier and gave a regression equation as follows:

$$MD = -15 \times ON + 2.7 \times DO - 0.12 \times CL + 3.3, \quad r^2 = 0.51, \quad F = 11 > 4.46\,(DF: 3{,}32;\, p = 0.01), \qquad (3)$$

where *ON* is organic nitrogen content (mg cm^{-3}), *DO* dissolved oxygen concentration of the bottom water (ml l^{-1}) and *CL* weight percentage of the clay fraction of the sediment (%). When variables were standardized, the regression equation was transformed into:

$$MD^* = -0.55 \times ON^* + 0.53 \times DO^* - 0.42 \times CL^*. \qquad (4)$$

On the basis of the above equation, the effectiveness of three independent variables in explaining the variance of *MD* was found to be nearly the same. Nutrient conditions, represented by *ON*, were found to be effective in accounting for the variance of *MD*. But the partial regression coefficient was, unexpectedly, negative, indicating that meiobenthos tend to invade deeper layers of the sediment in food-limited environments. The positive coefficient of *DO* suggests the possibility of oxygen availability as a limiting factor for *MD*. If this element regulates the maximum depth of vertical distribution, then negative correlation coefficients for *ON* and *CL* are understandable. In nutrient rich conditions, *i.e.* at stations where *ON* is high, oxygen consumers, *e.g.* meiobenthos, should be abundant, and in fine clay-rich sediment, the permeability of interstitial water should be low; in both cases, therefore, aerobic depth in the sediment should be shallow.

The importance of the role of oxygen in the regulation of *MD* is again suggested by another equation which was obtained using four biotic factors as well as the twelve abiotic ones.

$$MD = 1.6 \times W_{macro} - 0.0018 \times N_{meio} - 8.0 \times ON + 7.4, \quad r^2 = 0.67, \quad F = 21 > 4.46\ (DF: 3{,}32;\ p = 0.01), \qquad (5)$$

where W_{macro} is biomass of macrobenthos (g m^{-2}), N_{meio} density of meiobenthos (No. 10 cm^{-2}) and *ON* organic nitrogen content (mg cm^{-3}). Using standardized variables, the regression equation was transformed into:

$$MD^* = 0.60 \times W^*_{macro} - 0.40 \times N^*_{meio} - 0.29 \times ON^*. \qquad (6)$$

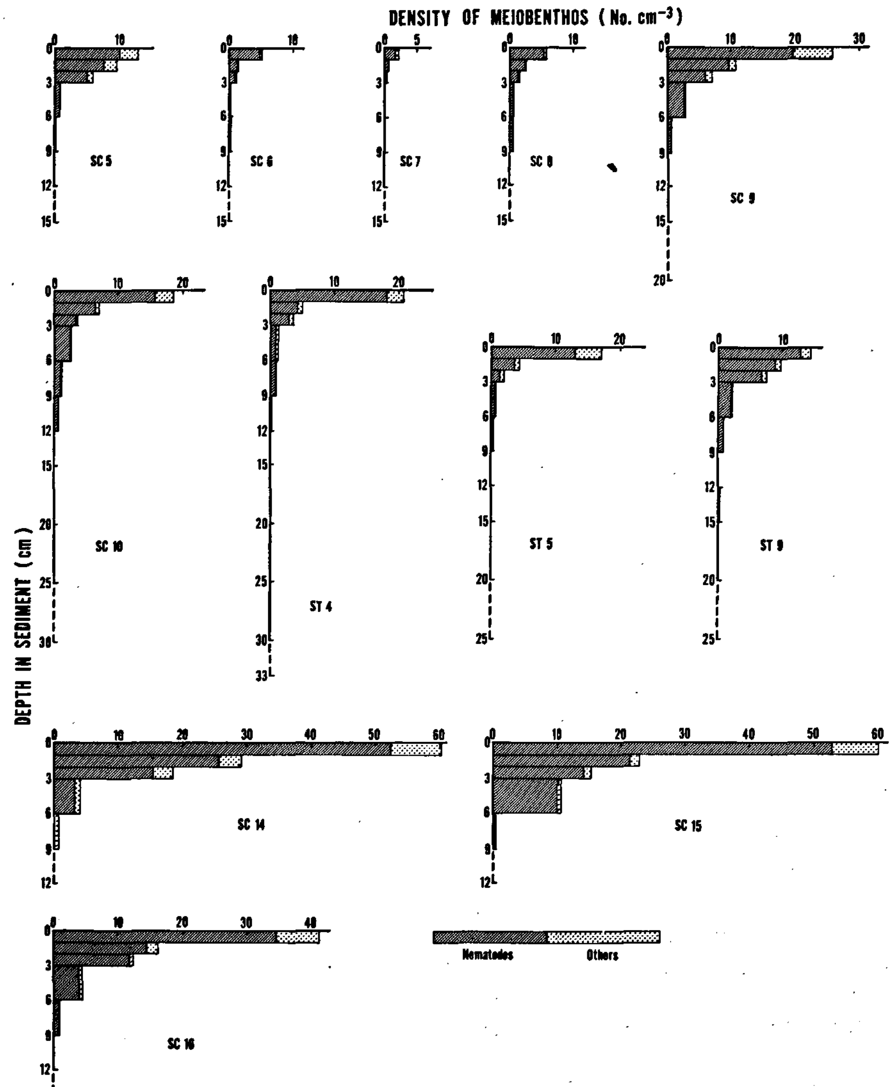

Figure 4

Vertical distribution of deep-sea meiobenthos in the sediment profile. Values are expressed in terms of density. A broken line indicates the sediment layer in which organisms could not be found. At stations SC-14 and 15, organisms were seen in the layer between 9 to 12 cm in terms of biomass (see fig. 4), but not in terms of density, since in this layer only rhizopods were found and they were excluded in terms of density.

The above equation indicates that the effect of W_{macro} on MD is the strongest and that of N_{meio} follows. All relationships between MD and the three independent variables in the above equation are considered to indicate that oxygen availability is the factor limiting maximum depth of distribution of meiobenthos in the sediment. The positive partial regression coefficient of W_{macro} can be interpreted as indicating that bioturbational activity of macrobenthos facilitates the diffusion of oxygen into the depths of the sediment, while the negative correlation coefficient of N_{meio} suggests the role of meiobenthos as oxygen consumers. The negative coefficient of ON might be related to the consumption of oxygen during the oxidation of organic matter by microbenthic bacteria and/or chemical processes.

DISCUSSION

The general concept that benthic organisms are concentrated in the surface layers of the sediment was found to hold true for the deep-sea meiobenthos of the locality investigated. At all stations, the density of organisms was highest in the surface layer of the sediment, and decreased exponentially with increase of depth in the sediment. At seven of the twelve stations examined in the present study, meiobenthic organisms disappeared below the 9-12 cm layer, and the number of individuals found in layers deeper than 12 cm never became greater than 1% of the total meiobenthos. These results suggest that 12 cm is a deep enough sampling depth for practical purposes when studying the abundance of meiobenthos. However, for the purpose of describing the vertical distribution of meiobenthos throughout their complete habitat range, sediments should be examined to a depth of at least 30 cm, since nematodes and foraminifers were found in the layer between 25 to 30 cm at station ST.4 of the present study.

The two properties of the vertical distribution of meiobenthos, analysed in the present study, seem to be regulated by different environmental factors. On the basis of the regression equation (1), it was suggested that in environments where food availability, especially organic matter flux, is limited, meiobenthos tend to be concentrated in the surface layer of the sediment. Although exceptional cases have been found near and around oceanic ridges, *e.g.* the Galapagos Rift (Karl, 1980), where primary production is found below the euphotic zone, most deep-sea organisms depend for their food resources directly or indirectly on organic matter produced in the surface water and transported to the sea floor in particulate organic rich matter, especially fecal pellets (Hinga *et al.*, 1979; Tanoue, Handa, 1980). Therefore, food availability is considered to be highest in the surface of the sediment, where fresh food settles, and this condition could be seen in the vertical profile of organic nitrogen content of the sediment (*see* Fig. 2). Although the organic matter content is not much less at red clay stations than at calcareous ooze stations, if sedimentation rate is considered, the flux of organic matter is probably much lower at the red clay stations of the present study; at these stations, competition for food may well be keen and meiobenthos would be expected to be concentrated in the nutrient rich surface layer of the sediment to catch the freshly settled particulate organic matter.

The regression equation (3) showed that index of maximum depth (MD) tends to be shallower at the stations where environmental conditions, especially nutrient conditions represented by organic nitrogen content (ON), seem more favourable for meiobenthos. This unexpected result pointed to the possibility that oxygen is a depth limiting factor. The findings from the regression equation (5) that MD was positively and negatively correlated to the abundance of macro- and meiobenthos respectively also suggest that MD is correlated to oxygen availability as mentioned before. The deepest aerobic layer is thought to be determined by a combination of the rate of consumption of oxygen by the sediment, especially by micro- and meiobenthos, and the rate of diffusion of oxygen molecules into the sediment, which is facilitated by the bioturbation of macrobenthos (Revsbech *et al.*, 1980). In the present study, the oxygen concentration of the pore water was not measured. However, the aerobic depth in the sediments could be determined from vertical profiles of manganese oxide, the abrupt increase of which is thought to correspond to the level of maximum penetration of free oxygen into the sediment (Froelich *et al.*, 1979). From this point of view (manganese data are given courtesy of Dr. D. D. Swinbanks, Ocean Research Institute, University of Tokyo) MD and the depth of oxidized sediment are significantly ($p<0.001$) correlated (Fig. 5) and this supports the view that oxygen determines the maximum depth of distribution of meiobenthos.

The possibility that oxygen regulates the maximum depth of vertical distribution of organisms has also been suggested for the deep-sea macrobenthos in Suruga Bay (Shirayama, Horikoshi, 1982). Considering this result for deep-sea macrobenthos and the present results, it might be possible to say that the maximum depth of vertical distribution of deep-sea benthos in the sediment is generally regulated by oxygen availability in the sediment. Furthermore, it should be noticed that since oxygen availability is strongly affected by biological activity, at least one characteristic of benthic distribution is controlled by biological interactions even in the deep sea.

CONCLUSION

In the present locality, more than 99% of total meiobenthos were concentrated in the surface 12 cm of the sediment, while at one station they could still be found in the layer between 25 and 30 cm. These results suggest that for the study of the abundance of deep-sea meiobenthos, a sampling depth of 12 cm is enough, while for the purpose of describing the vertical distribution of meiobenthos within the sediment, samples should be examined to a depth of at least 30 cm.

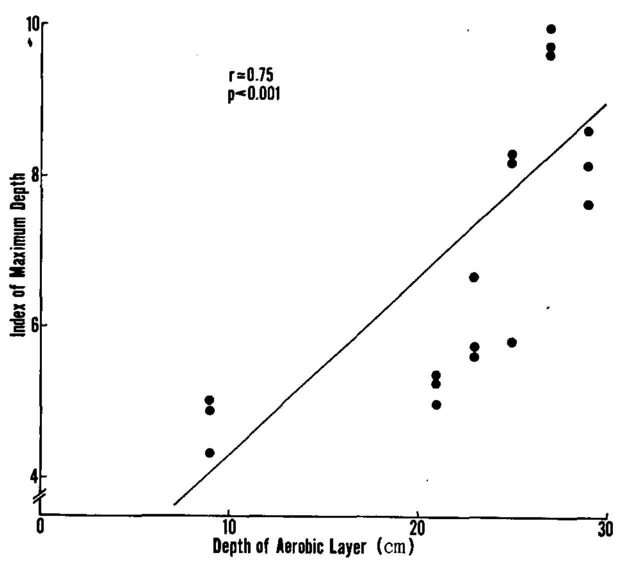

Figure 5

The relationship between index of maximum depth of meiobenthic distribution (MD) *and the depth of aerobic layer of the sediment estimated by the vertical profile of manganese oxide distribution.*

The stepwise method of multiple linear regression analysis between the indices *DC* (degree of concentration to the surface) and *MD* (maximum depth of vertical distribution) and sixteen factors revealed that these indices are controlled by different environmental characteristics. The index *DC* is controlled mainly by factors related to the organic matter flux, and organisms were concentrated more strongly in the surface of the sediment at stations where food is limited and competition for food is supposed to be keen. On the other hand, *MD* was considered to be limited by oxygen availability at depth in the sediment, which is considered to be regulated primarily by a combination of opposing biological processes, *i.e.*, consumption of oxygen by meio- and microbenthos and bioturbation of macrobenthos which facilitates the diffusion of oxygen. The relationships between *MD* and oxygen availability stress the importance of biological processes in modifying the physico-chemical environment which consequently affects the distribution of deep-sea benthic organisms.

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