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The abundance of deep sea meiobenthos in the Western Pacific in relation to environmental factors

Meiobenthos
Abundance
Deep sea
Western Pacific
Multivariate analysis

Méiobenthos
Abondance
Haute mer
Pacifique Ouest
Analyse multivariée

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ABSTRACT

The relationships between abundance of deep-sea meiobenthos and environmental factors were studied using 12 USNEL box core samples collected in the Western Pacific. Although the environmental factors which have been regarded as important in determining the abundance of deep-sea macrobenthos, *i.e.* water depth and surface productivity, correlated significantly with the abundance of meiobenthos, the correlation coefficient was not necessarily high. To separate important environmental factors from factors of negligible effect, a stepwise method of multiple regression analysis was carried out between abundance of meiobenthos and fourteen environmental factors. In terms of density, the regression equation obtained by the method indicated that calcium carbonate content (*CC*), sorting coefficient (*SO*) and organic carbon content (*OC*) were effective in explaining the statistical variance of meiobenthos. Comparison of standard partial regression coefficients showed that of the above three environmental factors, *CC* has the greatest effect on the density of meiobenthos. In terms of biomass, *SO* was not included in the regression equation, and *OC* and *CC* were found to be equally effective in explaining the statistical variance of meiobenthos. On the basis of the above results, the possible factors controlling the abundance of meiobenthos are discussed.

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RÉSUMÉ

Abondance du méiobenthos profond dans le Pacifique occidental et facteurs de l'environnement

Les relations entre l'abondance du méiobenthos profond et les facteurs de l'environnement ont été étudiés sur 12 échantillons prélevés par le carottier USNEL dans le Pacifique occidental. Bien que les paramètres jugés importants, c'est-à-dire la profondeur de l'eau et la productivité superficielle, soient en bonne corrélation avec l'abondance du méiobenthos, le coefficient de corrélation n'est pas forcément élevé.

Pour mettre en évidence les paramètres importants, une méthode d'analyse par multirégression pas à pas a été appliquée à l'abondance du méiobenthos et à 14 facteurs de l'environnement. En termes de densité, l'équation de régression ainsi obtenue indique que la teneur en carbonate de calcium (*CC*), le coefficient de classement (*SO*) et la teneur en carbone organique (*OC*) permettent d'expliquer la variance statistique du méiobenthos. La comparaison des coefficients de régression partiels montre que, parmi les 3 facteurs de l'environnement, *CC* a un effet primordial sur la densité du méiobenthos. En termes de biomasse, *SO* ne figure pas dans l'équation de régression, et *OC* et *CC* ont le même effet sur la variance statistique du méiobenthos. Les paramètres pouvant contrôler l'abondance du méiobenthos sont discutés à l'aide des résultats ci-dessus.

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INTRODUCTION

After the study of Wigley and McIntyre (1964), who collected meiobenthos at a depth below the continental shelf edge (570 m) for the first time, abundances of deep-sea meiobenthos have been reported from more than 50 stations in the Atlantic Ocean. In the Pacific Ocean, however, only four stations have hitherto been established (Thiel, 1979 *a*). Of these, two stations were situated in the Mariana Trench and the other two in the area of the Central Pacific gyre, and only data on the density of meiobenthos at these stations are reported by Thiel (1975; 1979 *a*). In the present study, precise data on the density and biomass of meiobenthos based on replicate samples as well as the community structure of this size class of organisms are reported at twelve stations in the deep-sea system of the Western Pacific.

Most ecological studies of deep-sea meiobenthos up to now have focused on the description of their abundance in relation to water depth (*e.g.* Dinet, 1973; Coull *et al.*, 1977). On the basis of number of individuals, a strong and negative correlation between abundance of meiobenthos and water depth has been observed, as summarized by Thiel (1979 *a*). At some stations, however, an unexpectedly high density of meiobenthos has been reported and such exceptional cases have been considered to be related, in certain cases, to the high productivity of the surface water (Dinet, 1973), and in other cases, to slow bottom currents which allow organic-rich fine particles to settle on the surface of the sediment (Thiel, 1971). The correlations mentioned above closely follow the rule proposed by Russian scientists (Vinogradova, 1962; Belyaev, 1966; Filatova, 1969; Sokolova, 1972) for deep-sea macrobenthos throughout the world, namely that macrobenthic abundance and trophic structure are mainly controlled by three factors: water depth, surface productivity and distance from land masses. The supply of organic matter to the deep-sea bed is related to these factors. The close correlations of water depth and surface productivity to the organic matter flux in the deep sea are well established (Suess, 1980), and the role of land masses as a source of food was clearly shown by Vinogradova (1962) and Sokolova (1972). In the present study, the applicability of the above rule to the meiobenthic assemblages in the deep-sea system of the Pacific Ocean is investigated.

Although studies of shallow-water meiobenthos have pointed out the importance of sedimentary characteristics as environmental factors (Hulings, Gray, 1976), only a few authors investigating the deep sea (*e.g.* Rachor, 1975; Dinet, 1979; Thiel, 1979 *b*; Dinet, Khripounoff, 1982) have considered chemical and/or physical data rather than mere depth as environmental factors. The greatest obstacle preventing the development of ecological investigations of deep-sea meiobenthos to the analytical level has been the difficulty of quantitative sampling of a sufficient quantity and depth of undisturbed sediment. The rencently devised USNEL box corer (Hessler, Jumars, 1974) has made it possible to overcome such problems. The box corer can sample a large enough quantity of sediment to allow replicate subcores to be taken from one box core for the study of meiobenthos. Furthermore, other large subcores for the study of macrobenthos and subcores for grain size and chemical analyses of the sediment can also be taken from the same box core. Such an approach was used in the present study; all data obtained from the sediments were considered as biotic and abiotic environmental factors for meiobenthos, and the relationships between these environmental factors and the abundance of meiobenthos were comprehensively analysed.

Mesh sieving is the usual method used to separate meiobenthos from organisms of smaller or larger size classes (Uhlig *et al.*, 1973). In most cases, two meshes, corresponding to upper (1.0-0.5 mm) and lower (0.1-0.037 mm) size limits of meiobenthos, have been used for this purpose. Thiel (1972) used not only two meshes (1.0 and 0.04 mm) for the above purpose, but also two additional meshes (0.1 and 0.15 mm) in order to fractionate nematodes into three size classes and then estimate the biomass of nematodes. In the present study, Thiel's method was modified and improved to make six size fractions of organisms using six meshes, the openings of which were 1, 0.5, 0.25, 0.125, 0.063 and 0.037 mm. This multiple sieving technique made available data on the size distribution of organisms. In the present sample, organisms belonging to the "permanent meiofauna" (McIntyre, 1969) or "meiofaunal taxa" (Hessler, Jumars, 1974) are restricted to the size range of 1.0 mm ~ 0.037 mm, and in this size range, meiofaunal taxa predominated over macrofaunal taxa. Therefore, the term "meiobenthos" was defined as the organisms that pass through 1.0 mm mesh and are retained by 0.037 mm mesh, as will be discussed in greater detail elsewhere.

In the present study, the relationships between fourteen environmental factors and two ecological characteristics of meiobenthic distribution were analysed. To simplify such numerous and complicated relationships, the best technique available is multivariate analysis. From the many methods that fall under the heading of multivariate analysis, principal component analysis (DeBovée *et al.*, 1979) and a stepwise method of multiple regression analysis (Coull *et al.*, 1982) have been used previously in the study of meiobenthos, though the results of analysis were not necessarily successful. In the present study, the stepwise method of multiple regression analysis (Wonnacott, Wonnacott, 1981) was carried out, and clearly discriminated the important environmental factors from those which have negligible effects on the abundance of meiobenthos.

MATERIALS AND METHODS

On three cruises of R/V Hakuhō Maru, Ocean Research Institute, University of Tokyo, during 1979 to 1980, 12 sampling stations were established in the Western Pacific Ocean (Fig. 1, Tab. 1). These stations cover four representative topographic environments of the open

Table 1
Station list for box corer.

Cruise	Station	Date	Position		Depth (m)	Sediment	Topography	Chl. *a* of the surface water (mg m^{-2})
KH-79-4	SC-5	1979,8,30	29°16.8'N	144°02.0'E	5 580	Red clay	Ocean bottom	38.5
KH-79-4	SC-6	1979,9,01	23°47.5'N	147°37.4'E	5 820	Red clay	Ocean bottom	20.6
KH-79-4	SC-7	1979,9,05	10°47.3'N	153°43.1'E	5 730	Red clay	Ocean bottom	16.1
KH-79-4	SC-8	1979,9,07	05°00.6'N	156°08.6'E	3 600	Calcareous ooze	Solomon Rise	19.9
KH-79-4	SC-9	1979,9,10	00°17.5'S	158°06.7'E	2 230	Calcareous ooze	Solomon Rise	22.9
KH-79-4	SC-10	1979,9,11	03°19.0'S	159°18.4'E	2 090	Calcareous ooze	Solomon Rise	27.8
KH-80-1	ST.4	1980,3,04	28°14.6'N	142°38.0'E	2 970	Calcareous ooze	Continental slope	62.6
KH-80-1	ST.5	1980,3,01	26°56.9'N	142°55.2'E	4 310	Red clay	Continental slope	35.4
KH-80-1	ST.9	1980,3,03	28°28.3'N	143°19.6'E	8 260	Red clay with silt & sand laminae	Ogasawara Trench	69.8
KH-80-3	SC-14	1980,7,28	32°40.0'N	158°46.7'E	2 430	Calcareous ooze	Shatsky Rise	—
KH-80-3	SC-15	1980,7,30	32°00.1'N	158°38.8'E	3 160	Calcareous ooze	Shatsky Rise	—
KH-80-3	SC-16	1980,7,31	31°43.5'N	157°26.7'E	3 950	Calcareous ooze	Shatsky Rise	—

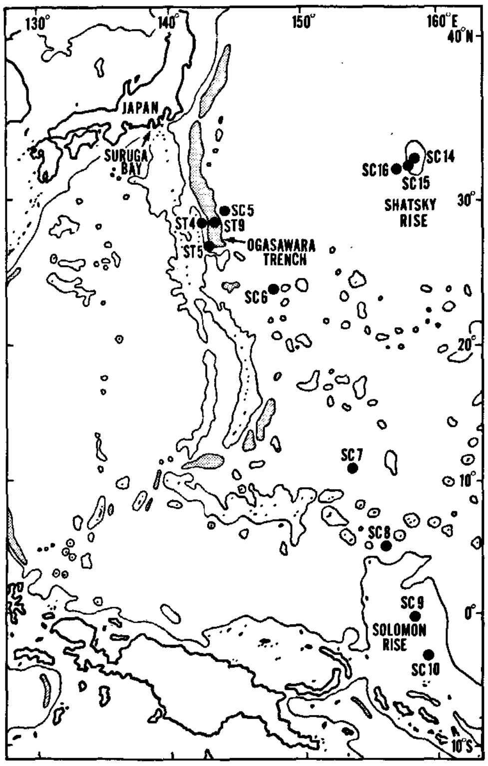

Figure 1
Position of box corer stations for the present study. Contours of 3 000 and 7 000 m are indicated, and the area deeper than 7 000 m (in the trench) is shaded.

ocean: ocean bottom (stations SC-5~7), ocean rise (stations SC-8~10 and SC-14~16), continental slope (stations ST.4 and 5) and trench (station ST.9); they also cover all three biological bathymetric zones (Horikoshi, 1971): bathyal, abyssal and hadal zones (*see* Tab. 1). The component of terrigenous sediment was negligible at all stations except at station ST.9, where silt and sand laminae of probable turbidite origin were interbedded with pelagic "red clay". Although surface productivity is estimated to be low throughout the present sampling area (Koblentz-Mishke *et al.*, 1970), the standing stock of Chl. *a* varied from station to station (Ocean Research Institute, in press *a*; *b*). The sediment type at 5 stations (stations SC-5~7, ST.5 and 9), where water depth was greater than the calcite compensation depth, was "red clay" while that of the other 7 stations (stations SC-8~10, ST.4 and SC-14~16) was "calcareous ooze" containing considerable quantities of biogenic calcite-particles mainly tests of pelagic foraminifers (*e.g.* Globigerinidae).

An USNEL box corer (Hessler, Jumars, 1974) was used to collect sediment. The method of sample treatment is described in detail elsewhere by Shirayama (1982; in press). Briefly, from a box core sample (50 x 50 cm) several subcores were extracted: eight cylindrical subcores ($\Phi = 3.6$ cm *i.e.* 10.2 cm^2) for the study of meiobenthos, two cylindrical subcores of the same size for sediment analysis and eight rectangular subcores (5 x 20 cm) for the study of macrobenthos. In the laboratory on board, the samples for the study of meiobenthos were sliced horizontally to study the vertical profile, and fixed and preserved separately in 5% neutralized filtered seawater formalin with Rose Bengal (0.5 g l^{-1}). The samples for sediment analysis were also sliced horizontally and kept in a freezer. The subcores for the study of macrobenthos were frozen at once without any pretreatment.

In the laboratory on land, the fixed sediments for the study of meiobenthos were sieved using meshes of 1.0, 0.5, 0.25, 0.125, 0.063, and 0.037 mm in size, as mentioned before. From each sample, organisms were sorted under a binocular stereoscopic microscope. For rhizopods, only the whole and fragmented tests stained by Rose Bengal were examined. Although the time for hand sorting of meiobenthos was less than that previously reported (Uhlig *et al.*, 1973) using the multiple sieving technique, it was still considerable and only three out of eight subcores sampled were examined in the present study.

The frozen subcores for the study of macrobenthos were defrosted, sieved using meshes of 1.0 and 0.5 mm, and fixed and preserved separately in 10% neutralized formalin with Rose Bengal. From these fixed samples organisms were sorted under a binocular stereoscopic microscope, classified, counted, and their wet weight measured.

In order to discuss meiobenthic communities as a whole, data on the biomass of these organisms is indispensable, because certain forms of rhizopods, one of the most dominant taxonomic group of meiobenthos, are so fragile that only fragments instead of whole organisms can be counted. To calculate the biomass of meiobenthos, the method of Thiel (1972) was modified in the present study. In the method, it is prerequisite to measure a standard weight per individual of meiobenthos of limited size range. For this purpose, a sample was collected using an Okean Grab in a locality different from those listed above, namely Suruga Bay, on the Pacific coast of Central Japan, at a depth of 510 m. The sample was separated into six size fractions by the multiple sieving technique and was also separated into four groups of organisms, rhizopods, nematodes, copepods, and others. The ash-free dry weight of approximately one hundred individuals belonging to a particular group of organisms and a particular size fraction was measured collectively, and standard weight per individual was determined (values are listed in Shirayama, 1982; in press). Total biomass of the meiobenthic assemblage was calculated by reversing the above process, *i.e.*, for a particular group of organisms the number of individuals in a given size fraction was multiplied by the standard weight per individual for that size fraction, and then the weight of all size fractions for all groups of organisms were summed (for more details *see* Shirayama, 1982; in press).

In addition to routine grain size analysis, the specific density and organic carbon and nitrogen contents of the sediment were determined. Grain size analysis of the sand fraction was carried out using standard sieves, while for the silt and clay fractions, a Coulter Counter was used. From the cumulative percentage curve of the weight of the sediment drawn with respect to the phi scale ($\Phi = -\log_2$ mm), the intercept values corresponding to 5, 16, 50, 84, and 95% cumulatives were obtained, and using these values, *Md* (median diameter), *Mz* (graphic mean diameter), sorting coefficient and skewness were calculated using the formulae in Hulings and Gray (1971).

Water content was measured as the loss of weight of wet sediment by drying at 95°C for 24 hours. Calcium carbonate content was measured as the loss of weight of dry sediment after treatment with hydrochloric acid. Organic carbon and nitrogen contents were measured using a CN corder, "Yanagimoto" model MT-500.

In the present study, organic carbon and nitrogen contents were expressed on the basis of the weight of these atoms per unit volume of wet sediment. The values thus expressed give a measure of the possibility of meiobenthos meeting organic matter. To determine these values, data on the specific density of wet sediment are a prerequisite. Specific density of the wet sediment was measured with a D.O. bottle usually used for measuring dissolved oxygen concentration since the inner volume of this bottle is always constant. After measuring the weight of the empty bottle (W_1) and that filled with water (W_2), the wet sediment was put into the dried bottle, weighed (W_3), and the bottle containing sediment was again filled with water and weighed (W_4). Assuming that the specific density of the water used is 1 g cm^{-3}, the specific density (*SD*) of wet sediment is given as: $SD = (W_3 - W_1)/((W_2 - W_1) - (W_4 - W_3))$.

To measure the dissolved oxygen concentration of the bottom water, two 500 ml water samplers were attached to the frame of the box corer. The samplers were designed to collect water when the box corer hit the bottom. Dissolved oxygen concentration of the collected water was determined using the Winkler method.

RESULTS

For some properties of the sediment, *e.g.* organic carbon content and water content, the change in values with depth in the sediment within the same subcore was considerable, and in some cases the range of values overlapped between two markedly different sediment types, red clay and calcareous ooze (Fig. 2). In the present study, therefore, the mean value throughout the vertical range where meiobenthos were living was chosen as the representative value for each station. On the basis of the results of sediment analysis, especially calcium carbonate content (*CC*), the twelve stations of the present study were divisible into two main groups (*CC*(%): 4.1 ~ 8.7 and 44.8 ~ 92.4), and as expected, they correspond to the red clay and calcareous ooze stations (Tab. 2).

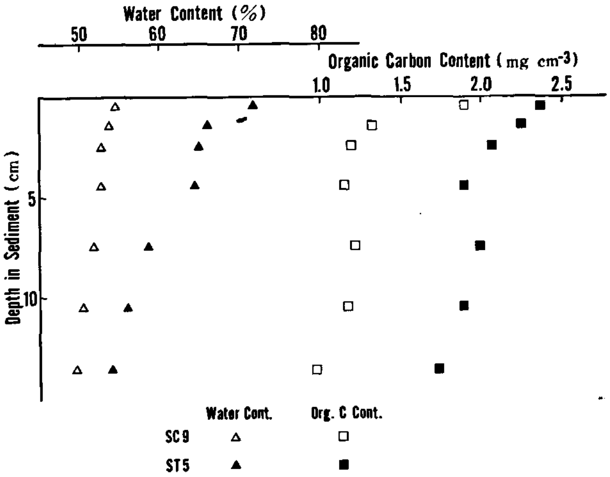

Figure 2

Vertical profiles of two sediment properties: water content (triangle) and organic carbon content (square). Open and filled points denote the data at a calcareous ooze (SC-9) and red clay (ST. 5) stations respectively. Note that the range of values at these two stations with very different sediment types overlap.

On the basis of number of individuals, the community structure of metazoan meiobenthos (excluding rhizopod fragments) in the deep-sea Pacific (Tab. 3) was similar to those in the deep-sea Atlantic, in that nematodes were exclusively dominant and occupied more than 80% of the total, while harpacticoid copepods were subdominant. In more precise comparisons, it was noticeable that tardigrades were rather abundant while ostracods were rarer in the Pacific than in the Atlantic. But these differences were too slight to state that they are the general rule. On the basis of dry weight (Tab. 4), the percentage of nematodes in the metazoan meiobenthos decreased to 43% in average. If rhizopods were included, the nematode fraction decreased more conspicuously to as little as 9.4 to 33% (21% in average). In contrast, rhizopods were found to be so dominant that they occupied more than half of total meiobenthic biomass.

Table 2

List of twelve abiotic environmental factors analysed in the present study.

Station	% sand	% silt	% clay	Median phi	MZ	Sorting coefficient	Skewness	Water content (%)	$CaCO_3$ content (%)	Organic carbon content (mg cm^{-3})	Organic nitrogen content (mg cm^{-3})	Dissolved oxygen concentration (ml l^{-1})
SC-5	10.5	63.6	26.0	7.11	6.84	1.65	-.336	64.1	6.66	2.37	0.312	3.78
SC-6	15.0	65.1	20.0	6.74	6.39	1.96	-.328	64.1	8.05	1.73	0.165	3.30
SC-7	19.0	51.9	29.1	7.17	6.42	2.23	-.503	78.7	8.65	1.09	0.161	3.30
SC-8	38.7	38.4	22.9	5.69	5.26	2.85	-.206	51.5	92.4	0.950	0.0780	3.28
SC-9	55.8	31.1	13.0	3.51	4.19	2.81	.307	51.4	89.9	1.19	0.127	2.75
SC-10	50.9	37.1	12.0	3.98	4.32	2.60	.188	49.0	90.6	0.670	0.0779	2.77
ST.4	25.1	52.2	22.7	6.43	5.99	2.30	-.302	49.1	53.8	1.44	0.141	3.72
ST.5	23.2	59.1	17.7	6.45	6.01	2.07	-.285	57.6	11.4	1.85	0.124	3.10
ST.9	9.62	67.0	23.4	7.12	6.83	1.62	-.341	67.7	4.10	2.14	0.209	3.84
SC-14	21.3	52.3	26.4	7.13	6.26	2.32	-.526	55.7	74.6	2.61	0.244	2.86
SC-15	13.0	53.8	33.2	7.49	6.89	1.87	-.518	54.6	70.9	1.96	0.181	3.36
SC-16	14.4	55.1	30.5	7.30	6.82	1.86	-.441	58.4	44.8	2.13	0.247	3.52

Table 3

Density of meiobenthos (No. 10 cm^{-2}). Mean of three subcores ± standard deviation.

Station	Rhizopods (fragments)	Nematodes	Copepods	*Others	Total (Rhizopods excluded)
SC-5	214 ± 134	257 ± 108	22 ± 15	38 ± 17	317 ± 133
SC-6	87 ± 31	78 ± 17	3 ± 1	8 ± 3	89 ± 20
SC-7	39 ± 19	31 ± 2	3 ± 1	4 ± 2	37 ± 3
SC-8	101 ± 49	126 ± 21	0	13 ± 2	138 ± 23
SC-9	533 ± 93	461 ± 19	39 ± 28	52 ± 16	552 ± 42
SC-10	512 ± 180	384 ± 63	18 ± 3	33 ± 14	434 ± 62
ST.4	231 ± 113	308 ± 33	12 ± 8	47 ± 14	368 ± 20
ST.5	200 ± 105	215 ± 36	26 ± 7	38 ± 23	279 ± 59
ST.9	132 ± 47	389 ± 63	15 ± 1	27 ± 16	430 ± 62
SC-14	1 196 ± 257	1 040 ± 48	71 ± 31	114 ± 8	1 225 ± 82
SC-15	1 041 ± 223	1 195 ± 195	44 ± 25	75 ± 4	1 315 ± 203
SC-16	494 ± 208	755 ± 109	43 ± 30	67 ± 36	864 ± 150

* Others include ciliates, turbellarians, gastrotrichs, kinorhynchs, oligochaetes, polychaetes, tardigrades, ostracods, tanaidaceans and molluscs.

Table 4

Biomass of meiobenthos [ash free dry weight (microgram 10 cm^{-2}) = (mg m^{-2})]. Mean of three subcores ± standard deviation.

Station	Rhizopods	Nematodes	Copepods	Others	Total
SC-5	127 ± 80	47 ± 19	17 ± 16	36 ± 31	227 ± 131
SC-6	61 ± 25	14 ± 2	7 ± 4	7 ± 4	88 ± 35
SC-7	15 ± 3	9 ± 3	1 ± 1	1 ± 1	27 ± 1
SC-8	50 ± 43	18 ± 4	0	10 ± 7	77 ± 48
SC-9	163 ± 25	59 ± 3	55 ± 34	58 ± 67	335 ± 60
SC-10	158 ± 37	41 ± 5	8 ± 3	65 ± 56	271 ± 65
ST.4	126 ± 50	33 ± 2	18 ± 16	173 ± 199	350 ± 229
ST.5	102 ± 77	25 ± 5	21 ± 10	53 ± 62	200 ± 149
ST.9	36 ± 13	64 ± 10	36 ± 53	34 ± 19	169 ± 52
SC-14	396 ± 16	138 ± 7	65 ± 49	275 ± 52	874 ± 43
SC-15	276 ± 69	145 ± 15	29 ± 12	77 ± 67	527 ± 143
SC-16	157 ± 41	87 ± 15	30 ± 12	53 ± 68	328 ± 96

The density of metazoan meiobenthos was least at station SC-7 and highest at station SC-15. The density of macrobenthos was also least at station SC-7 and highest at station SC-10 (Tab. 5). At the deepest station, station ST.9 in the Ogasawara Trench, biomass of macrobenthos was, unexpectedly, highest (*see* Tab. 5). At this station, a species of xenophyophore, *Ocultammina profunda* Tendal, Swinbanks and Shirayama, was very abundant and this species is considered to be responsible for the unusually high biomass at this hadal depth. In the case of meiobenthos, their density was also rather high at station ST.9 compared with the other shallower red clay stations on the ocean bottom such as stations SC-6 and 7 even though xenophyophores

Table 5

Abundance of macrobenthos.

Station	Density (No. m^{-2})	Biomass (wet g m^{-2})
SC-5	367	0.59
SC-6	200	0.33
SC-7	0	0
SC-8	100	0.35
SC-9	1 067	1.20
SC-10	1 466	1.99
ST.4	433	1.68
ST.5	667	1.01
ST.9	1 100	2.35
SC-14	633	0.62
SC-15	233	1.14
SC-16	100	0.83

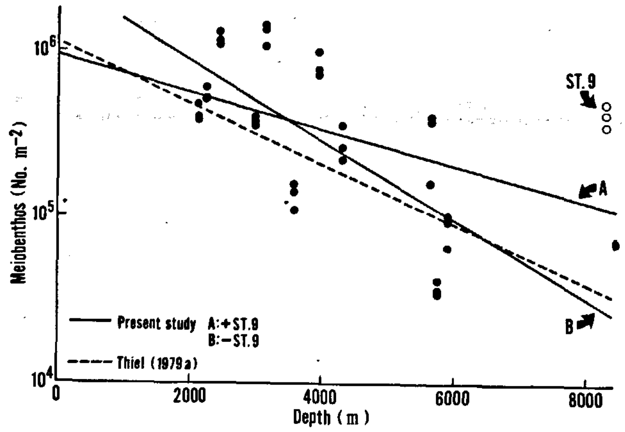

Figure 3

Correlations between the density of meiobenthos and water depth. (A): all data were used ($Y = -0.000\,112X + 5.99$, $r = -0.45$, $p < 0.01$). (B): unusual data at station ST.9 in the Ogasawara Trench (open points) were excluded ($Y = -0.000\,238X + 6.42$, $r = -0.69$, $p < 0.001$). Although both correlations were significant, the correlation coefficients were not necessarily high. Both regression lines of the present study are not different significantly from that of Thiel (1979a: $Y = -0.000\,178X + 6.05$).

were excluded from the density data. In this case, density of meiobenthos and water depth are not negatively correlated. In addition, although the log of meiobenthic density was negatively (−0.000112) and significantly ($p < 0.01$) correlated with water depth (Fig. 3), the correlation coefficient was low ($r = -0.45$). In terms of the log of biomass, meiobenthos decreased with increase of water depth at a similar rate (−0.000107) to that in terms of density, and the correlation coefficient was gain low ($r = -0.45$, $p < 0.01$). If the unusual data at station ST.9 were excluded, the rate of decrease became greater (−0.000238) and the correlation became better ($r = -0.69$, $p < 0.001$). The above results suggest the presence of factors other than water depth which have considerable effects on the abundance of meiobenthos. Within the other two factors thought to be important for macrobenthos, distance from land showed no significant correlation to either density or biomass of meiobenthos ($r = -0.088$ and — 0.0013 respectively), probably because the locations of all stations, except for station ST.9, were sufficiently far from land that no supply of organic matter from land sources can be expected (as mentioned before, at station ST.9, laminae of silt and sand of probable turbidite origin were seen). Although the surface productivity, measured on the basis of Chl. *a* standing stock, correlated significantly with the density of meiobenthos ($n = 27$, $p < 0.05$), the correlation coefficient was low ($r = 0.47$) as in the case of water depth. However, if only a particular type of sediment was considered (*e.g.*, red clay: Fig. 4), Chl. *a* standing stock and the density of meiobenthos were found to be closely correlated (Fig. 4A: $n = 15$, $r = 0.83$, $p < 0.001$). A close correlation was also found between density of meiobenthos and organic carbon content of the sediment (Fig. 4B: $r = 0.88$, $p < 0.001$) for the red clay stations; the latter variable was consequently inferred to have a close correlation to surface productivity. The strict condition that the sediment type must be held constant to obtain a close correlation between density of meiobenthos and nutrient conditions suggests the importance of the nature of the sedimentary particles themselves as an environmental factor.

In order to determine the environmental factors which are important in regulating the abundance of meiobenthos, a stepwise method of multiple linear regression analysis was used in the present study (Wonnacott, Wonnacott, 1981). The regression equation obtained using this statistical method includes those independent variables which significantly increase the proportion of the variance of the dependent variable explained by the regression equation (a probability level of 1% was selected). The analysis was carried out between thirty-six observations of the density of meiobenthos (three for each station) and a total of fourteen independent variables including twelve abiotic factors, *i.e.* median diameter and graphic mean diameter of the sediment, sorting coefficient, skewness, percentages of sand, silt and clay, water content, calcium carbonate content, organic carbon and nitrogen contents and dissolved oxygen concentration of the bottom water, and two biotic factors, *i.e.* density and biomass of macrobenthos. The regression equation obtained was:

$$N_{meio} = 13 \times CC - 663 \times SO + 353 \times OC + 750, \qquad (1)$$

$$r^2 = 0.82$$

$$F = 50 > 4.38 \ (DF: 3{,}32;\ p = 0.01),$$

where N_{meio} is the density of meiobenthos (No. 10 cm^{-2}), CC calcium carbonate content (%), SO sorting coefficient, and OC organic carbon content (mg cm^{-3}). The above equation reveals that calcium carbonate content, sorting coefficient and organic carbon content are those independent variables which are significantly effective in explaining the variance of meiobenthic density. The proportion of the variance of the dependent variable explained by the above equation (r^2), *i.e.* by the combination of the three independent variables incorporated in the above equation, is 82%. The meaning of the F value is the same as that usually used in the analysis of variance, while in the case of multiple linear

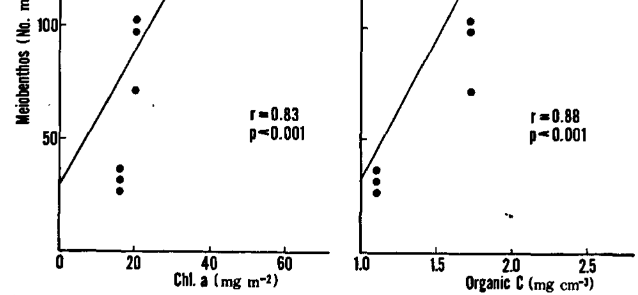

Figure 4

Correlation of the density of meiobenthos to (A): surface productivity (expressed by Chl. a standing stock) and to (B): nutrient conditions (expressed by organic carbon content). Good correlations were obtainable only when the data at five red clay stations were taken up and those at calcareous ooze stations excluded.

regression, the degrees of freedom are given as (P, n-P-1), where P is the number of independent variables incorporated in the regression equation and n is the number of observations (*e.g.* in equation 1, $P = 3$ and $n = 36$).

If variables are standardized (*i.e.* are transformed so that their mean and standard variation become 0 and 1, respectively), the effectiveness of independent variables in explaining the variance of the dependent variable could be compared using the absolute value (*i.e.* the values regardless of sign) of their standard partial regression coefficients. The regression equation using standard variables (indicated by asterisks) is:

$$N^{*}_{meio} = 1.1 \times CC^{*} - 0.61 \times SO^{*} + 0.53 \times OC^{*}. \qquad (2)$$

Comparison of the partial regression coefficients shows that CC is the most effective within the three independent variables of the above equation in explaining the variance of N_{meio}.

In terms of biomass, in which rhizopods were included, the relationships between meiobenthos and the fourteen environmental factors mentioned before were different from those in terms of density. The regression equation in terms of biomass, obtained by the stepwise method of multiple linear regression analysis, was:

$$W_{meio} = 324 \times OC + 4.9 \times CC - 477, \qquad (3)$$
$$r^2 = 0.69,$$
$$F = 37 > 5.32\ (DF: 2, 33; p = 0.01),$$

where $\overline{W}_{meio}$ is the biomass of meiobenthos (mg m^{-2}), OC organic carbon content (mg cm^{-3}) and CC calcium carbonate content (%). In the above equation, it is noticeable that the sorting coefficient (SO) did not appear as an effective independent variable. When variables were standardized, the regression equation was transformed into:

$$W^{*}_{meio} = 0.83 \times OC^{*} + 0.76 \times CC^{*}. \qquad (4)$$

The above equation suggests that the importance of OC and CC at environmental factors, as indicated by their standard partial regression coefficients, is similar.

DISCUSSION

The community structure of dee-sea meiobenthos in the present area, the Western Pacific, does not differ from that in the Atlantic. Furthermore, densities of meiobenthos found in the present study at stations at bathyal and abyssal depths were similar to data hitherto published, in that no significant difference was found between the present study and the review of Thiel (1979*a*) for the regression line between the density of meiobenthos and water depth (*see* Fig. 3). In the hadal zone, however, density of meiobenthos in the Ogasawara Trench (station ST.9) was found to be much higher than all previously published data from the Mariana Trench (Thiel, 1979*a*), the Aleutian Trench (Jumars, Hessler, 1976) and the Puerto Rico Trench (George, Higgins, 1979) even though these data also showed fairly high values; this result emphasizes the importance of conditions other than mere depth in controlling the abundance of meiobenthos.

Previous studies of the biomass of deep-sea meiobenthos treated only nematode assemblages and did not include all meiobenthos, and more particularly rhizopods, despite the high abundance of this kind of Protozoa in the deep sea. However, in the present study, the author was able to calculate biomass of total meiobenthos using the standard weight per individual of a particular group of organisms belonging to a particular size fraction separated by the multiple sieving technique. Although it should be verified whether the standard weight measured using the specimens collected in Suruga Bay is generally applicable to other localities, calculation of biomass on the basis of the standard weight is considered to be practical and accurate enough for present purposes.

Although both density and biomass of meiobenthos showed significant correlation to water depth in the present localities, the proportion of variance accounted for by the regression line (r^2) was only 23 %, and did not become more than half even if the unusual data at station ST.9 in the trench were excluded ($r^2 = 0.48$). In the study of deep-sea macrobenthos, the main factor limiting their abundance is considered to be food availability. In the study of deep-sea meiobenthos, however, the effectiveness of nutrient conditions as a limiting factor has not been supported (Tietjen, 1971; Dinet, 1979; Dinet, Khripounoff, 1982). In the present study, if sediment type remained constant, close correlations were found between the density of meiobenthos and factors related to nutrient conditions, *e.g.* surface productivity and organic carbon content of the sediment. Otherwise, in addition to organic matter content other properties of the sediment seem to be important in regulating the density of meiobenthos.

Although Coull *et al.* (1982) could not find parameters which significantly explained the variance of meiobenthic abundance, the stepwise method of multiple linear regression analysis of the present study yielded a definite regression equation (1) between density of meiobenthos (N_{meio}) and three environmental factors: calcium carbonate content (CC), sorting coefficient (SO) and organic carbon content (OC). Within these parameters, the standard partial regression coefficient of CC was largest, while that of SO and OC were half that of CC. This result suggests that CC has the strongest influence on meiobenthic density. Calcium carbonate content (CC) is considered to be related to two factors: 1) sedimentation rate and 2) larger-sized interparticle pore space. The sedimentation rate at stations ST.4 and 5 was found to be 0.21 and 0.16 cm 1 000 yr^{-1}, respectively, on the basis of the analysis of the ratio of ^{230}Th to ^{232}Th (Yamada, unpublished). In the area of Solomon (stations SC-8 ~ 10) and Shatzky (stations SC-14 ~ 16) rises, the sedimentation rate is reported to be around 1.5 (Berger *et al.*, 1977) and 1.0 cm 1 000 yr^{-1} (Larson *et al.*, 1975) respectively, and at pelagic red clay stations (stations SC-5 ~ 7), it can probably be assumed to be around 0.1 cm 1 000 yr^{-1} (Heezen *et al.*, 1973). If the above values are correct, there is a close correlation between sedimentation rate and calcium carbonate content (*CC*) ($r = 0.93$; $n = 11$; station ST.9 in the Ogasawara Trench was excluded since the rate is unknown and the mechanism of sedimentation is very different). Taking the argument a step further, it may be reasoned that organic carbon flux, which is probably a better measure of food availability for benthic organisms than organic carbon content, is determined by the combination of two parameters, organic carbon of the sediment (*OC*) and sedimentation rate. Since the latter can be indicated by calcium carbonate content (*CC*), as mentioned above, the regression equations (1) and (3) of the present study, which included both *OC* and *CC* as effective independent variables, suggest that food availability is one of the most important environmental factors in controlling the abundance of meiobenthos. In fact the organic carbon flux, represented by the value of *OC* multiplied by *CC*, is closely correlated to both density ($r = 0.81$) and biomass ($r = 0.80$) of meiobenthos.

The other factor, thought to be closely related to calcium carbonate content (*CC*), is the larger-sized interparticle pore space of the sediment, which is considered to be an important habitat niche for meiobenthos (Jansson, 1967). For large pore space to constitute a favourable habitat for interstitial forms of meiobenthos, sedimentary particles should be large and well sorted (Crisp, Williams, 1971). Calcareous sediment contains many tests of planktonic foraminifers, *e.g. Globigerina,* which are much larger compared with the clay-size particles of non-calcareous pelagic sediment; thus a high calcium carbonate content (*CC*) indicates coarser sediment and larger interstitial space. As would thus be expected, *CC* is correlated significantly to both grain size (*i.e. Mz,* $r = -0.67$; $p < 0.05$) and the percentage of larger particles (*i.e.* percentage of sand, $r = 0.74$; $p < 0.01$). Moreover, *CC* is considered to be a better indicator of the quantity of larger-sized pore space than these grain-size parameters for the following reason. The sediment of high *CC* contains many large and intact foraminiferal particles, which contain intraparticle space, *i.e.* space within tests (Hamilton *et al.*, 1982). The intraparticle space can trap a considerable quantity of finer particles, which would otherwise pack and reduce the size of interparticle space, *i.e.* the space between tests. Thus as *CC* increases, both the grain size and intraparticle space increase resulting in greater availability of larger-sized interparticle space which is favourable for interstitial meiobenthos.

The degree of sorting of sediment is another parameter which indicates the effect of finer particles on the size of interparticle space. In the multiple regression equation (1), density of meiobenthos correlated negatively to the sorting coefficient (*SO*). This correlation suggests that well-sorted sediment, the coefficient of which is small, is more favorable for meiobenthos than poorly sorted sediment because in the latter kind of sediment, interstitial spaces made by larger particles tend to be packed with smaller particles. Thus, this correlation also suggests that the quantity of larger-sized interstitial space is an important environmental factor that regulates the density of meiobenthos. In contrast to equation (1), in regression equation (3) based on biomass, sorting coefficient (*SO*) was not included as an effective independent variable. The difference between these two equations suggests that food availability is more important than interstitial space in controlling the biomass of meiobenthos. It is a general rule that if data are expressed on the basis of biomass, then larger-sized animals are given greater weight than smaller-sized ones. Most larger-sized meiobenthos are considered to be non-interstitial forms (Shirayama, 1982; in press), and interstitial space seems to have little influence on their abundance, while food is considered to be a more important environmental factor. Therefore the variables related to nutrient conditions should become more effective in explaining the variance of biomass. In contrast, when data are expressed in terms of density, smaller-sized interstitial forms tend to be given greater weight than larger-sized non-interstitial forms of meiobenthos. Thus, the result that in terms of density (*i.e.*, equation (1)), parameters related to the size of pore space (*CC* and *SO*) were effective in explaining the variance of meiobenthos in addition to those related to food availability (*OC* and *CC*) suggests that pore space has a considerable influence on the abundance of smaller-sized interstitial forms of meiobenthos even in the food-limited deep-sea environment.

CONCLUSION

The low correlation between both water depth and surface productivity and density of meiobenthos in the locality investigated suggests that these factors which *a priori* might be thought important for meiobenthos are not in fact good parameters for estimating the abundance of meiobenthos. In contrast, using the multiple regression equation (1), 82% of the total variance of the density of meiobenthos was explained by a combination of three parameters of the sediment, *i.e.* calcium carbonate content (*CC*), sorting coefficient (*SO*) and organic carbon content (*OC*). The combination of *CC* and *SO* was considered to indicate the availability of larger-sized interstitial space, while the combination of *CC* and *OC* was considered to express the organic carbon flux. Only the latter combination was effective in equation (3) in terms of biomass. This difference between equation (3) and equation (1) suggests that the abundance of larger-sized non-interstitial forms of meiobenthos is limited by the organic matter flux. In contrast, the abundance of smaller-sized interstitial forms is considered to be controlled mainly by the availability of adequately-large interparticle space. Consequently, attention should be paid to factors related to the pore space in the sediment as well as to organic matter flux in future research of deep-sea meiobenthos.

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