

NOTE

Effects of giant protozoans (class: Xenophyophorea) on deep-seamount benthos

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ABSTRACT: Biogenic sediment structures have been proposed to enhance diversity in deep-sea sediments. To evaluate this hypothesis we examined the influence of xenophyophores, giant sediment-agglutinating protozoans, on the structure of metazoan communities inhabiting sediments of deep (1000 to 3300 m) seamounts in the eastern Pacific Ocean. Xenophyophores provided habitat for 16 major metazoan taxa. Sediments immediately surrounding xenophyophores exhibited elevated faunal densities and species richness relative to control sediments collected 1 m from the tests. Amphipods were exclusively associated with the protozoan tests or sediments beneath them. Crustaceans, molluscs, and echinoderms exhibited enhanced infaunal densities in the presence of xenophyophores but polychaetes did not. Both horizontal and vertical distributions of infauna appear to be influenced by these protozoans. ^{234}Th measurements suggest that xenophyophores and their associated fauna increase the particle flux of fine-grained material to the seabed and enhance subsurface mixing on a 100 d time scale. We propose that xenophyophores alter hydrodynamic conditions and provide deep-sea metazoans with substrate, food, and refuge. The resulting habitat heterogeneity may contribute to maintenance of high benthic diversity.

The benthic fauna of the deep sea is noted for unusually high diversity relative to shallow-water fauna (Hessler & Sanders 1967, Sanders 1968). Among the many explanations offered for elevated deep-sea diversity (reviewed in Rex 1983), the habitat heterogeneity hypothesis (Jumars 1975, 1976) has received much recent attention (Thistle 1979, 1983, Jumars & Eckman 1983, Gooday 1984). Biologically produced sediment structures, such as mounds, tubes, tests, fecal casts, burrows, and tracks, may enhance diversity in one of 2 ways. Biogenic structures may persist for long periods under highly stable conditions in the deep sea and provide microhabitats within which species can specialize on different resources (Jumars 1975, Thistle 1979, Gooday 1984). In shallow environments, where the frequency of disturbance is orders of magnitude higher (Thistle 1981), such structures are likely to be obliterated rather quickly. Alter-

natively, local disturbances in the deep sea may allow species with similar resource requirements to coexist below carrying capacity (Grassle & Sanders 1973, Jumars & Eckman 1983).

One important group of biogenic structures in the deep sea is comprised of the tests produced by giant, sarcodine protozoans of the class Xenophyophorea (Tendal 1972). Xenophyophores are common epifauna at depths greater than 500 m in regions of the Atlantic, Indian, and Pacific oceans exhibiting high surface productivity or topographic relief (Tendal 1972, Levin unpubl.). Xenophyophores agglutinate sediments to form large tests (0.5 to 25 cm diameter) which protrude above the seabed (Tendal 1972). In this paper we examine the influence of xenophyophores on the composition, diversity, and spatial distribution of sediment-dwelling assemblages on deep (1000 to 3300 m) seamounts in the eastern Pacific Ocean. We evaluate whether xenophyophores, which are abundant on seamounts (Levin 1984), provide the sort of habitat heterogeneity which could contribute to maintenance of high faunal diversity.

Most of our knowledge of xenophyophores has been derived from analyses of bottom photographs (Lemche et al. 1976, Tendal & Lewis 1978, Tendal & Gooday 1981), or from haphazard collection of specimens (often damaged) in benthic sled hauls (Tendal 1972, Gooday 1983, 1984) or box cores (Tendal et al. 1982). Use of the submarine ALVIN has allowed observation and collection of intact xenophyophores.

Materials and methods. Box cores, each containing 4 square subcores ($7 \times 7 \times 15$ cm), were collected from 7 sites on 4 seamounts in the eastern Pacific Ocean off Mexico (Table 1). One pair of cores was taken at each site. One core in each pair sampled a xenophyophore and underlying sediment, the other was taken less than 1 m away over sediment with no visible biogenic structures. Six xenophyophore tests were recovered

Table 1. Dive sites and faunal abundances for a study of xenophyophore effects on infauna. Paired box cores (196 cm²) were taken at each site, 1 over a xenophyophore and 1 as a control

Alvin Dive	Sea-mount	Lat.	Long	Sample depth (m)	% Silt-clay	Substrate	Number of individuals per core					
							Macrofauna	Polychaetes	Molluscs	Pterocarid crustaceans	Echinoderms	Meiofauna
							xc/cc	xc/cc	xc/cc	xc/cc	xc/cc	xc/cc
1389	6	12°45'N	102°35'W	1775	12.2	Foram sand	28/22	11/18	1/0	8/2	4/0	53/46
1390*	6	12°40'N	102°35'W	3009	83.2	Metalliferous mud	43/32	19/19	4/1	8/5	1/3	274/243
1393	7	13°20'N	102°30'W	1790	24.7	Foram sand	35/20	13/17	4/1	8/0	7/0	22/24
1394	7	13°15'N	102°31'W	2850	75.2	Metalliferous mud	35/20	13/13	3/1	11/2	3/0	234/75
1395**	7	13°27'N	102°37'W	3353	-	Metalliferous mud	15/22	5/13	0/1	6/1	0/0	85/70
1397	5	12°56'N	103°29'W	1247	30.1	Mn, Fe oxides	35/27	14/17	5/1	2/0	4/2	19/20
1469	NW Bonanza	31°11'N	122°15'W	2776	67.4	Calcareous ooze	21/13	18/6	0/0	2/1	0/0	118/37
Total							212/156	93/103	17/5	45/11	19/5	805/515
$\bar{x} \pm 1$ SD, Xeno core							29.5 $\pm 9.4/$	13.3 $\pm 4.3/$	2.3 $\pm 2.1/$	6.4 $\pm 3.1/$	2.7 $\pm 2.4/$	115.0 ± 94.2
Control core							22.3 ± 5.5	14.7 ± 4.2	0.9 ± 0.4	1.6 ± 1.6	0.7 ± 1.16	73.6 ± 71.6
Paired t test: $t_6 =$							2.83	0.57	2.52	4.86	1.76	1.85
P =							<.05	NS	<.05	<.01	NS	NS

xc = xeno core
cc = control core
* The xeno core may contain some test inhabitants
** Some organisms were lost from the xeno core due to incomplete closure

intact. Sediments were sectioned at 0 to 2 and 2 to 10 cm intervals prior to sieving. All material was preserved in 10 % buffered formalin. Infaunal data reported are for macro- and meiofaunal taxa retained on a 297 μ m screen. Within-core distributions of infauna were examined for 2 box cores in which a xenophyophore was collected within a single subcore. Six additional xenophyophores were recovered in cylindrical pushcores (7 cm diam \times 15 cm). All material from the xenophyophore tests was sieved through a 63 μ m screen in the laboratory.

Two cylindrical cores (7 cm diam \times 15 cm), collected on Dive 1469, were sectioned at 1 cm intervals to a depth of 5 cm for analysis of ²³⁴Th. ²³⁴Th is a naturally occurring radioisotope with a half life of 24 d which can be used to establish rates of sedimentary processes on a 100 d time scale (Aller & DeMaster 1984). After adding a ²²⁸Th/²³²U spike to monitor chemical yield, ²³⁴Th was extracted from 5 to 10 g of dried sediment over a period of 5 h using a near-boiling 6N HCl solution. Thorium was isolated using ion exchange and TTA extraction techniques. The activity of ²³⁴Th was measured by detecting the beta decay of ²³⁴Th and its short-lived daughter, ²³⁴Pa, on a low-level beta counting system.

Results and discussion. Five types (genera?) of xenophyophore tests were collected on the seamounts

including 2 reticulate forms from foram sands (Fig. 1 A, B, C) and 3 platy xenophyophores from metalliferous muds (Fig. 1 D, E) and calcareous ooze (Fig. 1 F). A semifossilized hexactinellid skeleton was sampled from hydrothermal deposits (Dive 1397) and has been included in this discussion because of the similarity in functional effects.

We found 109 macrofaunal individuals and 79 meiofaunal individuals inhabiting the 12 xenophyophore tests. Polychaetes and ophiuroids each comprised 31 % of the macrofauna, followed in abundance by isopods (15 %), amphipods (4 %), and sipunculans, tanaids and sponges (each 3 %). Gastropods, bivalves, echinoids, tardigrades, and ascidians were each represented by 1 or 2 individuals. Meiofaunal taxa included nematodes (57 %), harpacticoid copepods (39 %) and ostracods (4 %). Thirty-three % of all the macrofauna and 39 % of all the meiofauna reported were found in the largest test examined (Fig. 1 B). A previous report of metazoans inhabiting rhizopod tests (Goody 1984) documents many of the same taxa but cites dominance by sipunculans, which were preferentially associated with a particular foraminiferan. We observed a family grouping of 10 nannoniscid isopods (*Hebefustis* sp.) within the largest test, suggesting that the tests provide a semipermanent residence. However, some specimens recovered from the tests, such as pardaliscid

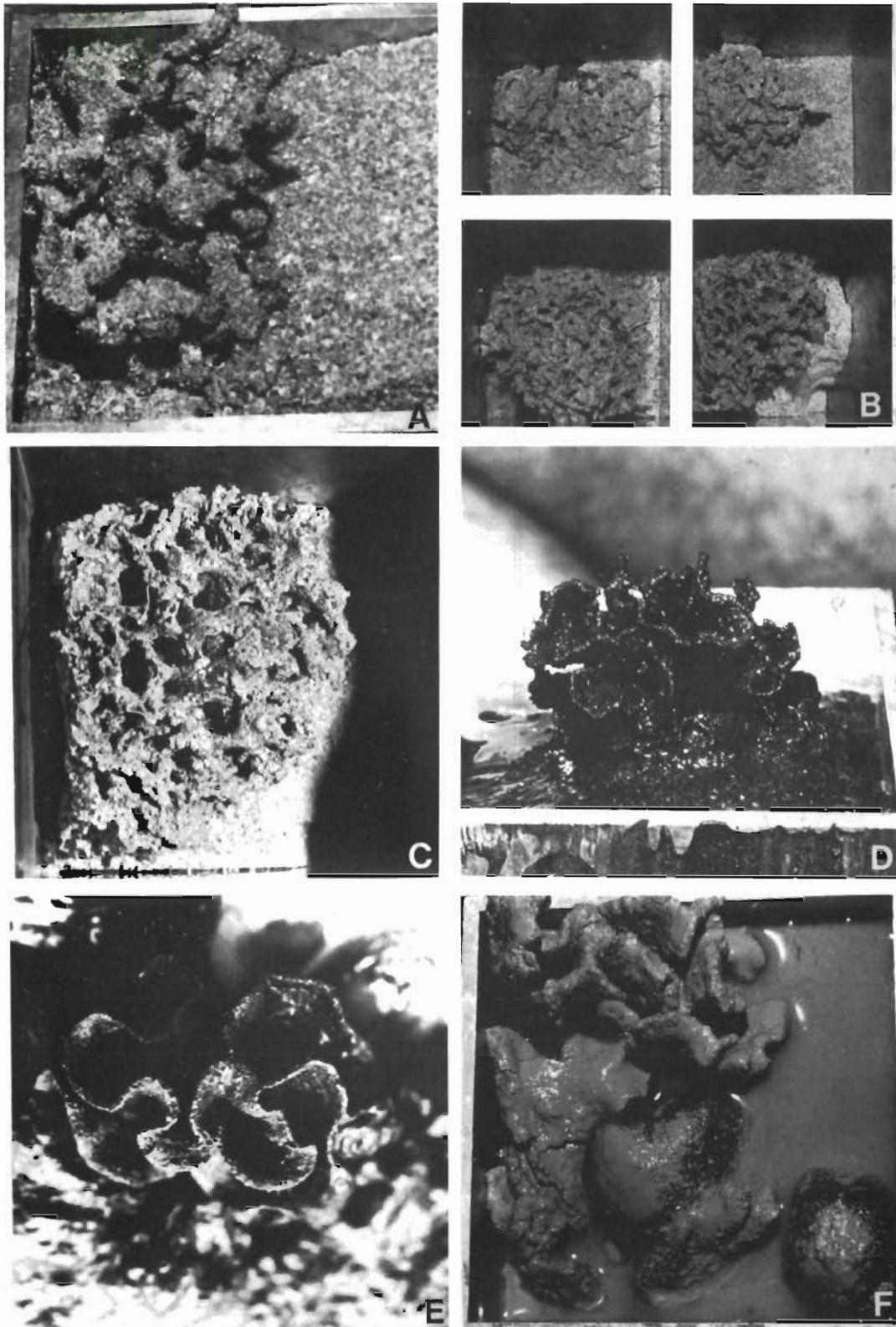


Fig. 1. Xenophyophore tests collected in box cores. (A) Dive 1389, *Galatheimmina* sp., 6 cm longest dimension, 1775 m. (B) Dive 1393, *Reticulammina* sp., 13 cm diameter, 1790 m. (C) Closeup of lower right replicate shown in (B). (D) Dive 1394, *Psammmina* sp.A., 4 cm diameter, 2850 m. (E) Dive 1395, *Psammmina* sp.B., 4 cm diameter, 3353 m. (F) Dive 1469, unidentified, 5 cm longest dimension, 2776 m. Identifications by O. Tendal

amphipods and polynoid polychaetes, are highly mobile forms.

Sediments beneath and near xenophyophore tests contained more macrofauna ($\bar{x} = 29.5$ individuals core⁻¹) than control sediments ($\bar{x} = 22.3$ individuals core⁻¹) ($t_6 = 2.83$, $p < 0.05$). The total abundance of polychaetes was unaffected by the presence of xenophyophores, but molluscs (bivalves, gastropods, aplacophorans and polyplacophorans), peracarid crustaceans (amphipods, isopods, and tanaids), and echinoderms (ophiuroids, echinoids, and holothuroids) were each 3 to 4 times more abundant in sediments beneath xenophyophores than in control cores (Table 1). Amphipods (10 individuals), collected at 5 sites, were found exclusively associated with xenophyophores. Amphipods may have been more likely to escape from control sediments during sampling due to the absence of a refuge. Macrofaunal species richness was higher in cores with xenophyophores (126 infaunal species) than in control cores (91 infaunal species). Rarefaction analysis (Smith & Grasse 1977) indicates increased macrofaunal diversity beneath xenophyophores at 3 sites and no difference from controls at 4 sites. Differences in species composition which are observed between xenophyophore and control assemblages (there being only 25 % species overlap) collectively enhance the overall diversity of seamount sediments.

Small-scale (< 15 cm) horizontal distributions of infauna were examined for 2 box cores (Dives 1389 and 1394) in which the xenophyophore tests were re-

covered cleanly within 1 of 4 subcores (Fig. 2). In both cores total faunal density and species richness were enhanced in the xenophyophore-bearing subcore (Fig. 2). It should be noted that elevated species richness in the xenophyophore-bearing subcores was simply a result of higher faunal abundances. No diversity differences (based on rarefaction analysis) were detected among subcores within each of the 2 box-cores. Preferential association with the xenophyophore (within a box core) was observed for peracarid crustaceans in coarse- ($\chi^2_1 = 16.7$, $p < 0.005$) and fine-grained ($\chi^2_1 = 5.12$, $p < 0.025$) sediments and for harpacticoid copepods ($\chi^2_1 = 87.2$, $p < 0.005$) and nematodes ($\chi^2_1 = 23.7$, $p < 0.005$) in fine-grained sediments (Fig. 2). For these taxa the xenophyophore influence probably occurs within a few centimeters of the test.

The presence of xenophyophores in cores correlates with an upward shift in the vertical distributions of infauna. In foram sands the top 2 cm of the control box cores contained only 42 % of the total macrofauna and 46 % of the total meiofauna. Near-surface sediments beneath xenophyophores (0 to 2 cm) contained a significantly greater proportion of the macrofauna (75 %) and meiofauna (76 %) (arcsin transformation, $p = 0.0002$). Macrofaunal and meiofaunal densities in the 2 to 10 cm fraction of xenophyophore-bearing cores were half those in control cores despite higher overall (0 to 10 cm) infaunal abundance in the former group. In metalliferous muds the vertical distribution of macrofauna was unaffected by the presence of xenophyophores. However, a greater proportion of meiofauna

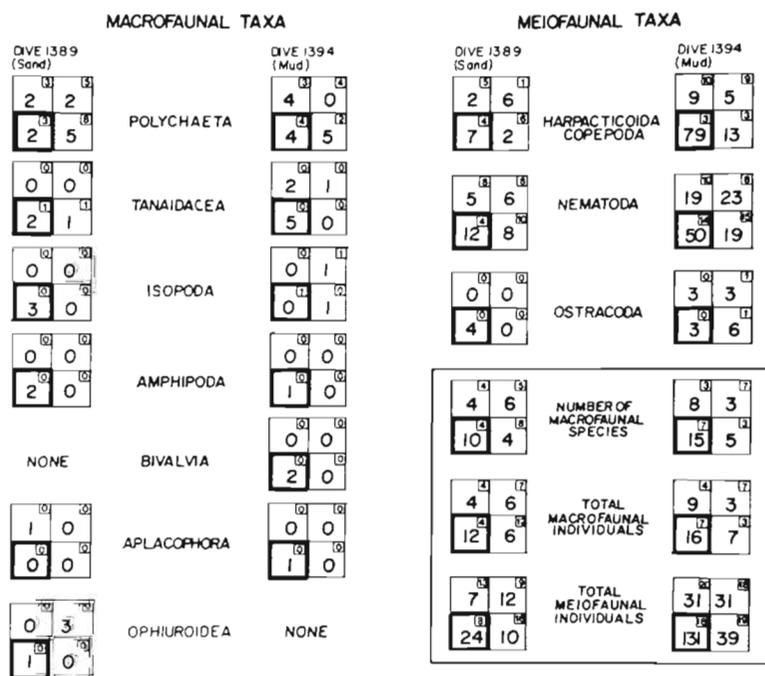


Fig. 2. Distribution of infauna among subcores ($7 \times 7 \times 10$ cm) within 2 ALVIN box cores. In each of the 2 cores the xenophyophore was located within a single subcore (bold lines). Numbers given are the infauna retained on a $297 \mu\text{m}$ screen. Numbers in the upper right of each subcore are values for control cores taken approximately 1 m away. Chi square analyses of numbers of individuals and numbers of species within versus outside the xenophyophore-bearing subcore are as follows. Total number of macrofaunal species: Dive 1389, $\chi^2_1 = 3.55$, $0.1 < p < 0.5$; Dive 1394, $\chi^2_1 = 9.04$, $p < 0.005$. Total number of macrofaunal individuals: Dive 1389, $\chi^2_1 = 4.76$, $p < 0.05$; Dive 1394, $\chi^2_1 = 8.01$, $p < 0.005$. Total number of meiofaunal individuals: Dive 1389, $\chi^2_1 = 11.63$, $p < 0.005$; Dive 1394, $\chi^2_1 = 122.50$, $p < 0.005$. Although macrofaunal species richness was elevated in the xenophyophore-bearing subcores, rarefaction analyses indicate no diversity enhancement in those subcores

occurred in the top subsample from the mud cores containing xenophyophores (84 %) than in control cores (78 %) ($p = 0.0240$).

Several hypotheses can be advanced to explain xenophyophore influences on metazoan composition, abundance, and distribution. The xenophyophore tests provide additional living space, above and possibly below the sediment-water interface, by increasing the amount of surface area available. One common test inhabitant, a flabelligerid polychaete, has been found in a sheath constructed of xenophyophore fecal material (stercomata). The tests may function as a structural refuge from large epifaunal predators and grazers, as was proposed by Gooday (1984). Small ophiuroids were extremely abundant (25 individuals) in the reticulate test shown in Fig. 1B. Camera sled photographs showed large (5 to 10 cm) ophiuroids frequently residing beneath xenophyophore tests and urchin traces which markedly detour towards and circle xenophyophore tests (Levin unpubl.). Juveniles and small individuals in the deep sea may gain protection from their association with xenophyophore tests in the same manner that juvenile urchins and abalone gain refuge from predators under urchin spine canopies in California kelp forests (Tegner & Dayton 1977). Portions of the rhizopod tests anchored beneath the sediment surface may also inhibit predation on infauna by epifauna and stabilize sediments as seagrass roots do in shallow water (Orth 1977, Peterson 1982).

Xenophyophore protoplasm (Tendal 1985) and stercomata (Tendal 1979), other test inhabitants, and trapped organic particulates, may serve as additional food sources in an environment where food is generally believed to be a limiting resource (Rowe 1983). Stercomata are accessible to metazoan test inhabitants which burrow into test surfaces (e.g. nematodes) and may become exposed when portions of a test break. Stercomata are thought to have elevated bacterial growth rates (Tendal 1979), of great potential value to sediment-ingesting species. Feeding on xenophyophores has been reported for monoplacophorans (Tendal 1985) and may extend to many other taxa. In addition, the test structures themselves are likely to alter the hydrodynamic and sedimentary regimes in their immediate vicinity, much as do tubes or other biogenic structures (Nowell & Jumars 1984). Resulting microhabitat differences could alter patterns of microbial growth, faunal recruitment, and feeding (Jumars & Nowell 1984), and thereby select for differing lifestyles.

Passive modification of near-bottom flow and active behavior of xenophyophores and their associated fauna may modify particle flux from the water column and the distribution of particles within the seabed. ^{234}Th (a naturally occurring tracer of water-column

particulate material deposited during the past 100 d) was measured in 2 cores collected from the caldera floor of NW Bonanza seamount (2776 m). One core was collected over a xenophyophore, whereas the other was a control core collected 1 m away. Sediments within and beneath the xenophyophore test contained 3 times the ^{234}Th activity of control sediments (4.4 dpm cm^{-2} versus 1.3 dpm cm^{-2}) (Fig. 3), suggesting enhanced deposition of fine-grain particles in the vicinity

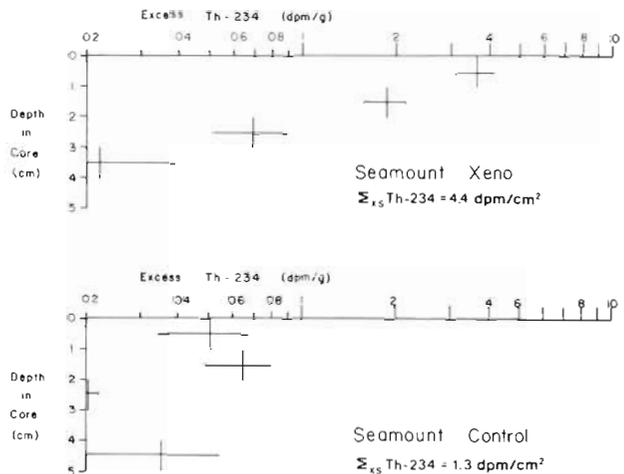


Fig. 3. ^{234}Th profiles for 2 sediment cores (7 cm diam \times 15 cm deep) collected on the Mn nodule covered floor of NW Bonanza Seamount ($31^\circ\text{N } 122^\circ\text{W}$), 2776 m. The upper profile is from a core collected over a xenophyophore similar to that in Fig. 1F. The xenophyophore occupies the top 1 cm. The lower profile was collected from control sediments 1 m away

of the xenophyophore during the 100 d prior to collection. Excess ^{234}Th activity was observed to a depth of 3 cm in the core containing the xenophyophore, indicating that particles from the sediment-water interface have been transported to this depth on a 100 d time scale. Assuming that ^{234}Th penetration into the seabed is a result of biological mixing, the mixing intensity can be characterized by modeling the slope of the ^{234}Th profile. The ^{234}Th data from the xenophyophore core yield a mixing coefficient (D_b) of $17 \text{ cm}^2 \text{ yr}^{-1}$, which is an order of magnitude greater than typical open-ocean mixing coefficients (DeMaster & Cochran 1982), but comparable to values from Panama Basin (Aller & DeMaster 1984). Enhanced abundances of infauna associated with the xenophyophore at that site (see Table 1, Dive 1469) are probably responsible for the high intensity of mixing.

Further study and experimentation are needed to determine which processes are responsible for the faunal patterns described above. It is likely that other agglutinating protozoans, such as komokiacean foraminifera, exert similar influence on deep-sea communities. From our preliminary findings we conclude

that xenophyophores, which often attain densities of 1 to 10 ind m^{-2} (Lemche et al. 1976, Tendal & Lewis 1978, Levin unpubl. obs.), are an important source of sedimentary and faunal heterogeneity, and as such, may contribute to maintenance of high benthic diversity in the deep sea.

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