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LIFE HISTORY AND RECOLONIZATION AMONG AGGLUTINATED FORAMINIFERA IN THE PANAMA BASIN

by

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With 5 figures, 1 plate and 7 tables

ZUSAMMENFASSUNG

In Kastengreiferproben (spade core samples) von einer 3912 m tiefen Station im Panama-Becken wurde die benthonische Foraminiferenfauna untersucht. Ihre Häufigkeiten und die Verteilung im Mikrohabitat sollten die Unterschiede der lebenden Populationen und die Erhaltung toter Gemeinschaften aufzeigen. Die Gattungen *Dendrophrya, Cribrostomoides* und *Ammodiscus* stellen Formen der Epifauna dar, während *Reophax* vorwiegend zur Infauna gehört. *Reophax*-Arten sind wahrscheinlich verantwortlich für feine, netzförmige Bohrgänge, die in Röntgenaufnahmen beobachtet wurden.

Ein Experiment mit Rekolonisationsbehältern wurde entwickelt, um die opportunistischen Arten benthonischer Foraminiferen zu identifizieren und festzustellen, mit welcher Geschwindigkeit eine Population ein abiotes Substrat besiedeln kann. Der erfolgreichste Kolonisator an dieser Stelle ist *Reophax*, während *Dendrophrya* die geringste Verbreitungskapazität aufweist. Nach 9 Monaten erreichte die Häufigkeit der lebenden Individuen in den Sedimentbehältern ein Zehntel bis ein Drittel der Hintergrundshäufigkeit, wobei sich die Faunendiversität nicht wesentlich von den Kontrollproben unterschied. Die Wiederbesiedelung bei benthonischen Foraminiferen ist rascher als bei Makroinvertebraten.

ABSTRACT

Benthic foraminifera were examined in spade core samples from a 3912 m deep station in the Panama Basin to determine abundance and microhabitat partitioning among living populations and preservation of dead assemblages. The genera *Dendrophrya, Cribrostomoides* and *Ammodiscus* were found to be epifaunal forms, and the genus *Reophax* predominantly infaunal. Species of *Reophax* are probably responsible for fine reticulate burrows observed in x-radiographs.

An experiment using recolonization trays was designed to identify opportunistic species of benthic foraminifera, and to assess the rate at which a population can colonize an abiotic substrate. The most successful colonizer at this site is *Reophax*, while *Dendrophrya* displays the lowest capability for dispersal. After nine months the abundance of living individuals in sediment trays was one-tenth to one-third that of background abundance, but the faunal diversity did not differ greatly from control samples. Recolonization by benthic foraminifera is more rapid than among macrofaunal invertebrates.

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INTRODUCTION

The life history and community structure of deep-sea benthic foraminifera is a subject which has received little attention over the years, yet this information is essential to help assess the rates of disequilibrium processes such as disturbance and succession in abyssal assemblages. Recolonization of substrates by benthic foraminifera has been empirically observed in modern shallow-water environments (Schafer 1983) and in the deep sea (Kaminski 1985). Successive recolonization of the sea floor has also been postulated as the cause of small-scale vertical changes in fossil foraminiferal assemblages in hemipelagic sediments above turbidites in Alpine flysch deposits (Grün *et al.* 1964; Butt 1981). In shallow-water environments, benthic microfaunal communities have been shown to recover from physical disturbance in a few months (Levin 1984), but in the deep sea, rates of recolonization are typically one or two orders of magnitude slower (Grassle 1977, 1978). No experimental study, however, has focused attention on the patterns of benthic foraminiferal response to conditions of community disequilibrium in an abyssal habitat, yet these organisms serve an important role in the trophic structure of deep-sea benthic communities. By studying the life history of benthic foraminifera and estimating the rate at which biological succession takes place, we can better interpret patterns observed in fossil assemblages.

The deep Panama Basin is an excellent environment in which we can test the response of benthic foraminifera to substrate disturbance. The area has no observable nephaloid layer or current-derived bedforms, and x-radiographs have demonstrated that bottom sediment at our station is dominated by biogenic rather than physically formed structures (Aller and DeMaster 1984). Therefore, we can be reasonably certain that the benthic community is not disturbed by bottom currents and that any artificial disturbance introduced in the area will not be augmented by natural causes.

In this study, we document the life history and ecology of benthic foraminifera in the Panama Basin by examining biocoenoses and taphocoenoses in spade cores and recolonization trays placed on the sea floor and assessing the response of benthic foraminifera to community disequilibrium.

STATION LOCATION

The Panama Basin station is located at 5° 20.65'N, 81° 56.19'W at a depth of 3912 m (figure 1). Bottom

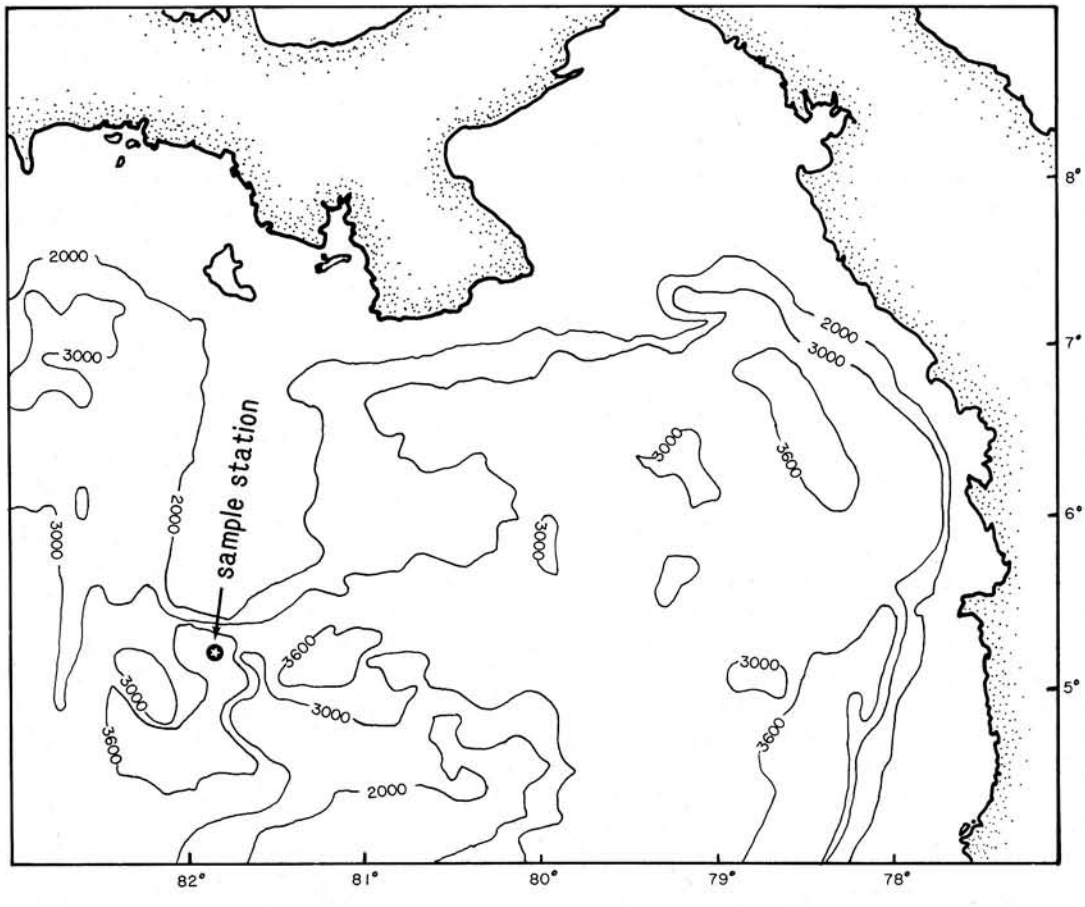

Fig. 1.
Map of study area showing locations of sample station.
Base map from VAN ANDEL et al. (1971), depth in meters.

water potential temperature and salinity in this area are 1.8°C and 34.67°/oo, respectively, and dissolved oxygen concentration is 2.4-2.6 ml/l (Laird 1971; Lonsdale 1976). Bottom current velocities in the area are slow: 2-5 cm/s, and generally east to west in direction (Laird 1971; Lonsdale 1976; Honjo *et al.* 1982). No nephaloid layer is detected, so there is little chance that benthic fauna might be resuspended and advected into sediment trays by bottom currents.

Panama Basin sediments are typically hemipelagic mud, containing about 30% biogenic components ($CaCo_3$, SiO_2). The organic carbon content is around 2.5% and the clay fraction is composed of 50-70% smectite, 15-20% chlorite, 5-10% illite and 10-15% kaolinite (Heath *et al.* 1974). Studies of ^{210}Pb distribution in surface sediments at our site indicate rapid biogenic reworking in the upper few centimeters (Aller and DeMaster 1984). The surface mixed layer is approximately 6 cm thick. Beneath this zone, mixing is about 10 times slower but is present to at least 20 cm depth.

Primary productivity in Panama Basin surface waters displays an east-west spatial gradient between 500 and 1000 mg C/m^2 day, with highest seasonal production in February-March and June-July (Moore *et al.* 1973; Honjo *et al.* 1982). The long term sediment accumulation rate is about 6-10 mg/cm^2 yr based on ^{14}C measurements at the sea floor (Swift 1977).

SAMPLING

The samples examined in this study were collected by the R/V Atlantis II and the submersible "Alvin" in summer of 1982. These consist of surface sediment from two spade cores and three sediment trays, or "mudboxes", which were collected within 100 m of one another. The spade cores were gathered to provide control samples to determine faunal composition and abundance of taxa at this site.

A portion of the sediment collected in spade cores was subdivided into 9 sections 10 x 10 cm in area, and each section was sampled at depth intervals of 0-2, 2-5, 5-10, and 10-15 cm. Another portion of the sediment was allowed to equilibrate to ambient room temperature, then frozen in the ship's reefer at -15°C, to eliminate any biota present. This mud was allowed to thaw and transferred to 30 x 30 x 5 cm fiberglass trays for emplacement on the sea floor. In each recolonization tray, the sediment was approximately 5 cm thick. Sediment from different depth sections of the spade core was handled separately and placed in different sectors of each tray (figure 2). The trays were fitted with a hinged

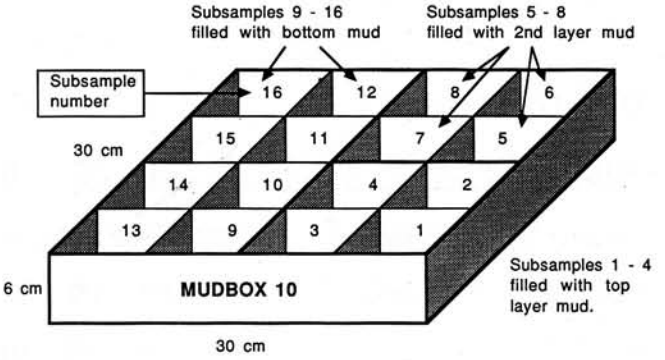

Fig. 2.
Diagram of Mudbox 10 showing configuration of subsamples and the type of sediment used.

PVC lid to prevent loss of mud during emplacement and recovery. The submersible "Alvin" deployed the trays on September 11, 1981, close to the site where spade cores were taken, and once in place on the sea floor, the lids were opened to expose the abiotic mud. After nine months (June 10-12, 1982), the trays were recovered. The Alvin closed the lids on the trays and carried them to the surface for sampling.

Each tray was subsampled in 16 sections 7.5 x 7.5cm in area, and these were not further subdivided with depth. Mud samples from spade cores and trays were fixed overnight in a buffered formalin solution, sieved through a 297 µm sieve, transferred to storage jars and preserved in ethyl alcohol. In the laboratory, preserved samples were stained overnight with Rose Bengal, and prior to picking, samples were again gently sieved and washed into a petri dish with ethyl alcohol. Foraminifera were picked using an eyedropper to transfer specimens to glass vials for storage. All specimens of foraminifera were picked from each subsample and the numbers of live and dead individuals were recorded. With some species, it was necessary to crush specimens or make a small hole in the last chamber with a dissecting needle to determine whether red protoplasm was present. Selected specimens were photographed using a JEOL-35 SEM.

FORAMINIFERAL ABUNDANCE AND DIVERSITY

a) Control Samples

The numbers of living and dead individuals were tallied separately for 4 subsamples (totalling 400 cm^2) from each of two spade cores taken in close proximity to each other (table 1). Spade core 13 was sampled at four depth intervals (0-2, 2-5, 5-10, and 10-15 cm) and therefore provides a more complete data set than Spade core 9, which was only sampled at 0-2, 2-5, and 5-10 cm. No living calcareous benthics were observed in any of the samples, but occasionally, dead specimens of *Pyrgo murrhina*,

Table 1.
Panama Basin, All 112, spade core 9, live/dead individuals.

DEPTH INTERVAL:	0-2 cm				2-5 cm				5-10 cm			
SUBCORE:	**2**	**4**	**7**	**8**	**2**	**4**	**7**	**8**	**2**	**4**	**7**	**8**
Dendrophrya arborescens	37/396	61/362	26/663	8/125	5/32	18/56	3/61	18/36	0/1	0/0	0/2	0/0
Reophax dentiliniformis	2/14	0/6	1/7	3/6	0/22	3/21	10/25	5/17	4/12	1/22	6/23	2/20
Hormosina ovicula	0/6	1/4	0/6	1/5	1/21	1/19	1/15	3/16	0/34	1/30	0/25	2/49
Hormosina distans	0/2	0/0	2/1	0/0	0/0	0/0	0/0	0/0	0/1	0/0	0/0	0/1
Reophax excentricus	0/8	0/6	2/20	1/3	2/13	5/41	10/25	3/11	5/28	4/31	9/20	14/41
Saccammina sp.	0/3	0/3	2/5	2/4	1/12	0/20	0/12	0/19	0/31	0/25	0/30	0/34
Trochammina globigeriniformis	0/7	0/8	1/2	0/4	0/9	1/17	0/16	0/2	0/21	0/15	1/26	1/23
Rhizammina sp. (large)	0/15	2/3	0/3	1/2	0/4	0/6	0/3	0/1	0/1	0/4	0/1	0/3
Lana sp.	5	4	3	2	4	4	2	3	0	1	0	2
Cribrostomoides subglobosus	0/2	2/1	1/2	1/3	0/0	0/1	0/6	0/3	0/8	0/6	0/10	1/9
Recurvoides spp.	2/5	0/3	1/4	0/6	0/6	0/3	4/5	0/3	0/7	0/7	0/7	1/11
Buzasina ringens	0/1	0/0	1/1	0/2	0/1	0/3	0/4	0/0	0/1	0/6	0/1	0/2
Ammodiscus incertus	0/2	0/0	1/2	2/5	1/4	0/2	0/1	0/4	0/8	0/10	0/11	0/12
Ammobaculites sp.	0/1	0/0	0/0	0/0	0/2	0/2	0/2	0/2	0/8	0/1	0/7	0/4
Hormosina globulifera	0/2	0/1	0/1	0/1	0/1	0/1	1/2	0/1	0/2	0/2	0/5	0/3
Eggerella propinqua	0/0	0/0	1/0	0/0	0/2	0/0	1/1	0/1	0/0	0/2	0/1	0/1
Eggerella bradyi	0/0	0/0	0/0	0/0	0/0	0/1	0/0	0/0	0/1	0/0	0/0	0/0
Pelosina sp.	1/3	1/1	0/0	3/3	0/1	0/1	1/1	0/0	1/1	0/0	0/0	0/0

Planulina wuellerstorfi and entosolenians were found. These were rare and were not included in the counts. The living fauna was comprised entirely of agglutinated foraminifera.

The 400 cm^2 area from Spade core 13 contained a total of 497 live individuals of agglutinated foraminifera belonging to 16 species, while 3058 dead specimens belonging to 29 species were found. The same area from Spade core 9 contained 475 live individuals belonging to 18 species, and 3593 dead specimens belonging to 26 species. Only 12.75% of the total agglutinated foraminiferal assemblage was living at the time of collection, as determined by Rose Bengal. This number contrasts with values of 30-40% in abyssal areas in the western North Atlantic determined by Schröder (1986), with the difference probably a result of faster degradation of dead tests in the organic carbon-poor North Atlantic.

The data presented in tables 1-2 show that the major difference in populations between the two spade cores lies in the numbers of *Dendrophrya*, which is more abundant in Spade core 9 by a factor of two, and *Reophax dentaliniformis*, which is three times more abundant in Spade core 13. These differences may be due in part to differential handling and sample quality; (the problems of counting fragments of tubular species are legendary and need not be repeated here). Assuming equal fragmentation, the discrepancy in counts may be partly due to loss of some of the flocculent surface layer in Spade core 13, which would introduce a bias towards infaunal species. However, the cores did not appear to be disturbed, and an equally likely explanation is that the difference in abundance of the two taxa is real, and simply reflects the patchy distribution of species on the sea floor.

Table 2.
Panama Basin, All 112, spade core 13, live/dead individuals.

DEPTH INTERVAL:	0-2 cm				2-5 cm				5-10 cm				10-15 cm			
SUBCORE	**1**	**3**	**9**	**6**	**1**	**3**	**9**	**6**	**1**	**3**	**9**	**6**	**1**	**3**	**9**	**6**
D. arborescens	85/176	75/211	14/98	37/222	7/10	2/14	0/5	1/17	0/1	0/0	0/0	0/0	0/0	0/0	0/0	0/0
R. dentaliniformis	1/11	4/17	2/9	3/10	15/45	19/36	15/30	23/54	5/35	12/52	22/50	11/46	5/27	8/33	6/38	5/50
H. ovicula	3/3	3/6	3/10	0/6	1/21	0/19	1/12	0/20	0/21	0/26	0/36	0/26	0/1	1/12	0/20	0/7
R. excentricus	2/9	1/3	1/2	0/4	3/15	1/15	2/7	3/11	7/17	6/47	3/32	2/38	7/92	2/65	2/54	6/66
Saccammina sp.	2/5	1/1	0/5	0/4	2/8	0/6	0/4	0/11	1/16	0/21	0/27	0/31	0/27	0/19	1/18	0/18
T. globigeriniformis	3/5	1/5	1/8	2/4	0/10	0/14	0/9	0/18	3/28	0/16	0/19	0/18	0/41	0/31	0/21	0/28
Rhizammina sp. (large)	1/3	0/7	0/5	0/4	0/3	0/6	0/10	0/22	0/7	0/19	0/12	0/17	0/3	0/8	0/2	0/4
Lana sp.	3	5	5	3	0	1	2	1	0	1	1	0	1	0	0	0
C. subglobosus	3/0	1/0	0/3	1/2	0/6	0/7	0/3	0/4	0/7	0/7	0/8	0/6	0/7	0/9	0/18	0/10
Recurvoides sp.	0/0	4/1	0/8	0/2	3/9	0/1	0/6	0/3	0/5	0/7	0/9	0/9	0/10	0/5	0/3	0/7
B. ringens	0/0	1/1	1/2	1/0	0/3	0/1	0/0	1/2	0/6	0/5	0/5	0/1	0/4	0/5	0/6	0/3
A. incertus	1/1	0/1	0/0	0/1	0/0	0/0	0/0	0/0	0/3	0/0	0/0	0/0	0/0	0/1	0/3	0/1
Ammobaculites sp.	0/0	0/0	0/0	0/0	0/1	0/1	0/2	0/4	0/3	0/0	0/0	0/0	0/5	0/6	0/2	0/6
H. globulifera	0/0	2/0	0/0	0/1	0/0	0/0	0/2	0/1	0/1	0/2	0/2	0/2	0/2	1/2	0/2	0/0
E. propinqua	0/1	0/2	0/0	0/0	0/2	0/0	0/0	0/0	0/0	0/1	0/0	0/1	0/2	0/2	0/4	0/1
E. bradyi	0/0	0/0	0/1	0/0	0/0	0/0	0/0	0/0	0/0	0/2	0/0	0/0	0/1	0/0	0/2	0/0
Pelosina sp.	0/0	0/0	3/0	0/0	0/0	0/0	5/0	2/0	0/0	0/0	0/0	0/0	0/0	0/2	1/0	0/0

b) Recolonization tray samples

The numbers of living and dead specimens in replicate subsamples from the three recolonization trays are tabulated in tables 3-5. Because the size of the subsamples from the trays differed in area from those taken from spade cores (7.5 x 7.5 cm for the trays versus 10 x 10 cm for spade cores), more subsamples from the trays were counted to obtain comparable data (9 subsamples from a tray corresponds to an area of 506.25 cm^2). The abundance of dead specimens did not differ greatly from tray to tray, and totalled 999 specimens in Mudbox 7, 1029 specimens in Mudbox 11, and 1432 specimens in Mudbox 10.

The numbers of live individuals were small in comparison with control samples, with 48 live individuals in Mudbox 11, 56 individuals in Mudbox 7, and 156 in Mudbox 10. Collectively, only 6.9% of the individuals in trays were alive at the time of retrieval. This compares with 15.6% living individuals in the upper 5 cm of the control samples.

In each tray, sediment from different layers of the spade core was handled separately and placed in different areas of the tray (figure 2). This differential treatment is not reflected in the numbers of dead individuals present in different subsamples. The Shannon-Wiener diversity of live populations from recolonization trays does not differ greatly from that of the control samples, at 2.48 for Mudbox 7, 1.61 for Mudbox 11, and 2.79 for Mudbox 10, versus values of 1.55 and 2.09 for control samples. When Hulburt's Rarefaction Method (Hulburt 1971) is used to calculate $E(S_n)$, the expected number of species at a given sample size (figure 3), the differences in diversity between trays become apparent. At a sample size of 40, the calculated species richness in Mudbox 10 is 10.19, but in Mudbox 11 is only 6.44. The value of $E(S_{40})$ of control samples falls between those of the trays, at 6.86 and 7.73.

The abundance of macrofaunal invertebrates in the trays reflects the same pattern as that of the

Table 3.
Panama Basin, All 112, mudbox 7, live/dead individuals.

SUBCORE :	1	6	7	8	9	11	12	13	14
Dendrophrya arborescens	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
Reophax dentaliniformis	1/7	0/6	2/12	3/11	0/16	2/18	0/7	2/18	5/25
Hormosina ovicula	0/3	1/1	0/1	1/3	0/13	1/11	0/9	1/18	1/9
Hormosina distans	0/0	0/0	0/0	0/1	0/1	0/0	0/0	1/0	0/1
Reophax excentricus	4/34	5/44	4/18	2/44	0/48	0/23	0/11	4/32	5/40
Saccammina sp.	0/2	0/1	0/5	0/6	0/8	0/6	0/1	0/24	0/16
Trochammina globigeriniformis	0/10	0/18	0/20	0/26	0/25	1/17	0/4	1/34	0/38
Rhizammina sp. (large)	0/3	0/1	0/1	0/3	0/13	1/3	0/5	0/12	0/7
Lana sp.	0	0	0	0	0	2	2	0	0
Cribrostomoides subglobosus	0/5	0/2	0/3	0/3	0/5	0/2	0/2	0/12	1/7
Recurvoides spp.	0/3	0/1	0/2	0/2	0/7	0/2	0/0	0/9	0/7
Buzasina ringens	0/3	0/3	0/4	0/0	0/5	1/3	0/1	1/3	0/3
Ammodiscus incertus	0/0	1/1	0/0	1/2	0/2	0/4	0/1	0/14	0/1
Ammobaculites sp.	0/2	0/3	0/3	0/3	0/5	0/0	0/0	0/8	0/8
Hormosina globulifera	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	1/1
Eggerella propinqua	0/0	0/0	0/0	0/0	0/0	0/1	0/0	0/0	0/0
Eggerella bradyi	0/0	0/0	0/0	0/3	0/0	0/0	0/0	0/3	0/0
Pelosina sp.	0/0	0/0	0/0	0/1	0/0	0/0	0/0	0/0	1/0

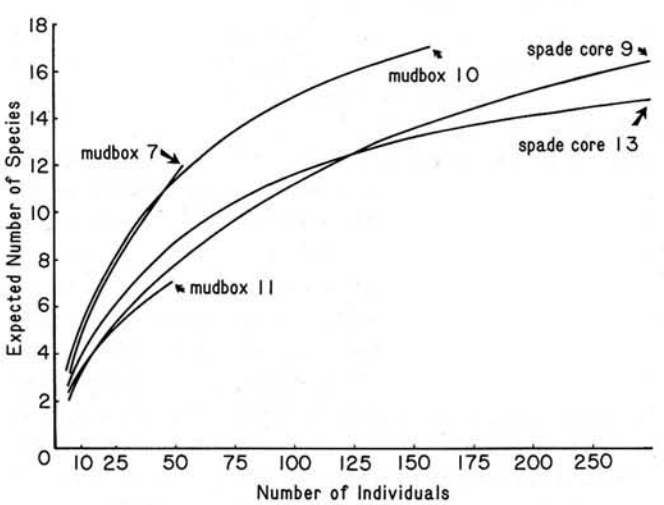

Fig. 3.
Rarefaction curve showing diversity of spade core and recolonization tray samples examined in this study.

foraminifera, with 7 living individuals in Mudbox 11, 11 individuals in Mudbox 7, and 19 individuals in Mudbox 10. About 70% of the individuals are polychaetes, 22% are crustacea, and 8% molluscs. Two new species of spionid polychaete in the genus *Prionospio* are the only species represented by more than two individuals. The mean abundance of macrofaunal invertebrates in the recolonization trays is 1.4 live individuals/100 cm^2. This compares with a mean abundance of 15.6 live individuals/100 cm^2 in control samples from nine Alvin boxcores gathered at the same site.

DISCUSSION

a) Habitat partitioning

A number of studies have suggested microhabitat partitioning as an important factor for the maintenance of diversity in deep-sea benthic

Table 4.
Panama Basin, All 112, mudbox 10, live/dead individuals.

SUBCORE :	3	6	8	9	11	12	13	14	16
Dendrophrya arborescens	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
Reophax dentaliniformis	4/14	1/9	11/21	2/15	3/9	0/17	7/11	12/23	8/23
Hormosina ovicula	0/1	1/4	1/2	0/6	0/0	0/0	0/13	1/10	1/17
Hormosina distans	0/0	0/0	0/1	1/0	0/0	0/0	0/0	2/3	0/0
Reophax excentricus	2/78	7/73	12/140	5/69	5/63	2/71	5/41	9/63	6/50
Saccammina sp.	2/8	0/8	2/10	0/8	0/11	0/7	0/6	0/18	0/7
Trochammina globigeriniformis	0/28	0/33	3/31	0/25	1/23	0/19	0/16	1/27	0/19
Rhizammina sp. (large)	0/8	0/4	1/12	0/5	0/2	0/3	0/5	0/13	2/13
Lana sp.	1	0	0	0	4	2	0	1	0
Cribrostomoides subglobosus	1/4	4/1	0/0	4/2	2/1	1/4	0/3	1/6	2/8
Recurvoides spp.	1/3	0/1	1/2	0/1	0/3	0/0	1/3	1/6	0/2
Buzasina ringens	0/0	0/0	0/0	0/2	1/0	0/1	0/1	0/3	0/2
Ammodiscus incertus	0/0	0/0	0/0	0/2	0/0	0/1	0/1	0/4	2/6
Ammobaculites sp.	0/5	0/6	1/13	1/11	0/7	0/8	0/5	1/6	1/9
Hormosina globulifera	0/1	0/3	0/0	0/2	0/2	0/0	0/0	0/0	0/2
Eggerella propinqua	0/0	0/1	0/0	0/0	0/0	0/0	0/0	0/2	0/1
Eggerella bradyi	0/0	0/0	0/1	0/1	0/0	0/0	0/0	0/0	0/1
Pelosina sp.	0/0	0/0	0/0	1/0	0/0	0/0	0/0	0/1	0/0

communities (Jumars 1975; 1976, Bernstein *et al.* 1978). Under equilibrium conditions, species which do not share the same microhabitat do not compete with one another, and the diversity of the community can be maintained at high levels.

Among deep-water benthic foraminifera, Corliss (1985) has reported vertical stratification of living calcareous taxa in boxcores from the western North Atlantic. Flat, planoconvex genera such as *Planulina* and *Cibicidoides* were found to prefer an epifaunal habitat, while smooth planispiral forms and globular-elongate forms such as *Melonis* and *Chilostomella* prefer an infaunal habitat. A similar relationship between microhabitat and shape is apparent in the observations of Kitazato (1984). In the shallow-water environment of Otsuchi Bay, Japan, the pyriform species *Sigmoidella pacifica* and *Guttalina* cf. *yabei* occupy an infaunal habitat and are reported to move through the sediment. Burrowing behavior has also been observed in the miliolid genus *Quinqueloculina* in shallow-water sediments (Severin *et al.* 1982).

Analogies can be drawn between the test shape of agglutinated foraminifera from the Panama Basin and patterns were observed by Corliss (1985). In our material, the elongate uniserial species *Reophax dentaliniformis* and *Reophax excentricus* clearly prefer, but are not confined to, an infaunal habitat. The elongate shape of the test may be an adaptation for mobility in the mixed layer of the sediment. Agglutinated foraminifera have been suspected as being responsible for causing fine, apparently randomly oriented burrows which are laconically known as "vermicelli bioturbation" (C.D. Hollister, personal communication) observed in x-radiographs from the High Energy Benthic Boundary Layer Experiment (HEBBLE) Site on the lower continental rise off Nova Scotia.

Table 5.
Panama Basin, All 112, mudbox 11, live/dead individuals.

SUBCORE :	4	5	6	8	9	10	11	13	14
Dendrophrya arborescens	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
Reophax dentaliniformis	3/23	3/17	0/12	1/3	1/11	0/5	0/8	2/6	0/7
Hormosina ovicula	1/13	0/3	0/1	0/0	0/2	0/1	0/1	0/2	0/0
Hormosina distans	0/2	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
Reophax excentricus	4/72	5/49	4/53	2/27	2/42	4/35	5/48	2/40	3/39
Saccammina sp.	0/17	0/13	0/11	0/3	0/5	0/11	0/9	0/3	0/5
Trochammina globigeriniformis	0/39	0/17	0/17	0/16	0/21	0/26	0/13	0/16	1/19
Rhizammina sp. (large)	0/11	0/7	0/5	0/3	0/1	0/1	0/2	0/4	0/4
Lana sp.	1	0	1	0	0	0	0	0	1
Cribrostomoides subglobosus	1/11	1/2	0/5	0/4	0/3	0/7	0/6	0/3	0/7
Recurvoides spp.	0/5	0/1	0/3	0/0	0/2	0/2	0/2	0/1	0/1
Buzasina ringens	0/4	0/1	0/2	0/0	0/3	0/5	0/0	0/0	0/0
Ammodiscus incertus	0/4	0/2	0/0	0/0	0/0	0/0	0/1	0/1	0/0
Ammodiscus sp.	0/15	0/3	0/6	0/3	0/11	0/6	0/3	0/3	0/3
Hormosina globulifera	0/0	0/1	0/1	0/0	1/2	0/2	0/1	0/1	0/0
Eggerella propinqua	0/0	0/0	0/3	0/1	0/3	0/0	0/1	0/1	0/1
Eggerella bradyi	0/2	0/1	0/3	0/1	0/0	0/0	0/1	0/0	0/0
Pelosina sp.	0/1	0/0	0/1	0/1	0/0	0/0	0/0	0/0	0/0

A similar type of "vermicelli bioturbation" is ubiquitous in x-radiographs from our site in the Panama Basin, an example of which is shown in figure 4. We attribute the small burrows to *Reophax*, since it is the most abundant macrofaunal-size (2 mm or more) infaunal taxon present at this site.

Several species of agglutinated foraminifera were found living mainly in the flocculent surface layer, which at our site has a thickness of approximately 2 cm. These are komokiacea, *Dendrophrya arborescens*, *Cribrostomoides subglobosus* and *Ammodiscus incertus*. The branching species are assumed to be immobile suspension feeders (Jones and Charnock 1985), and planispiral and disc-shaped forms have been interpreted as being adapted to an epifaunal mode of life (Corliss 1985).

b) Taphonomy

Agglutinated foraminifera construct their tests with an organic cement which in some species contains oxidized iron compounds (Hedley 1963; Schröder 1986), which probably serve as an electron acceptor during the bacterial degradation of organic matter. Some species of agglutinated foraminifera are more susceptible to degradation than others, therefore the composition of the death-assemblage will change with time after the death of the organism. The differential preservation of agglutinated species has a profound effect on the composition of faunal assemblages.

In the Panama Basin, we observe a change from a *Dendrophrya*-dominated assemblage in the surface layer of the sediment to an assemblage dominated by *Reophax* at depth. This is expressed in figure 5. The abundance of *Dendrophrya* drops dramatically beneath the flocculent surface layer, being entirely absent below 5 cm. The absence of dead specimens of *Dendrophrya* in our recolonization trays indicates that degradation of this species is very rapid, taking place in less than nine months. The disappearance of

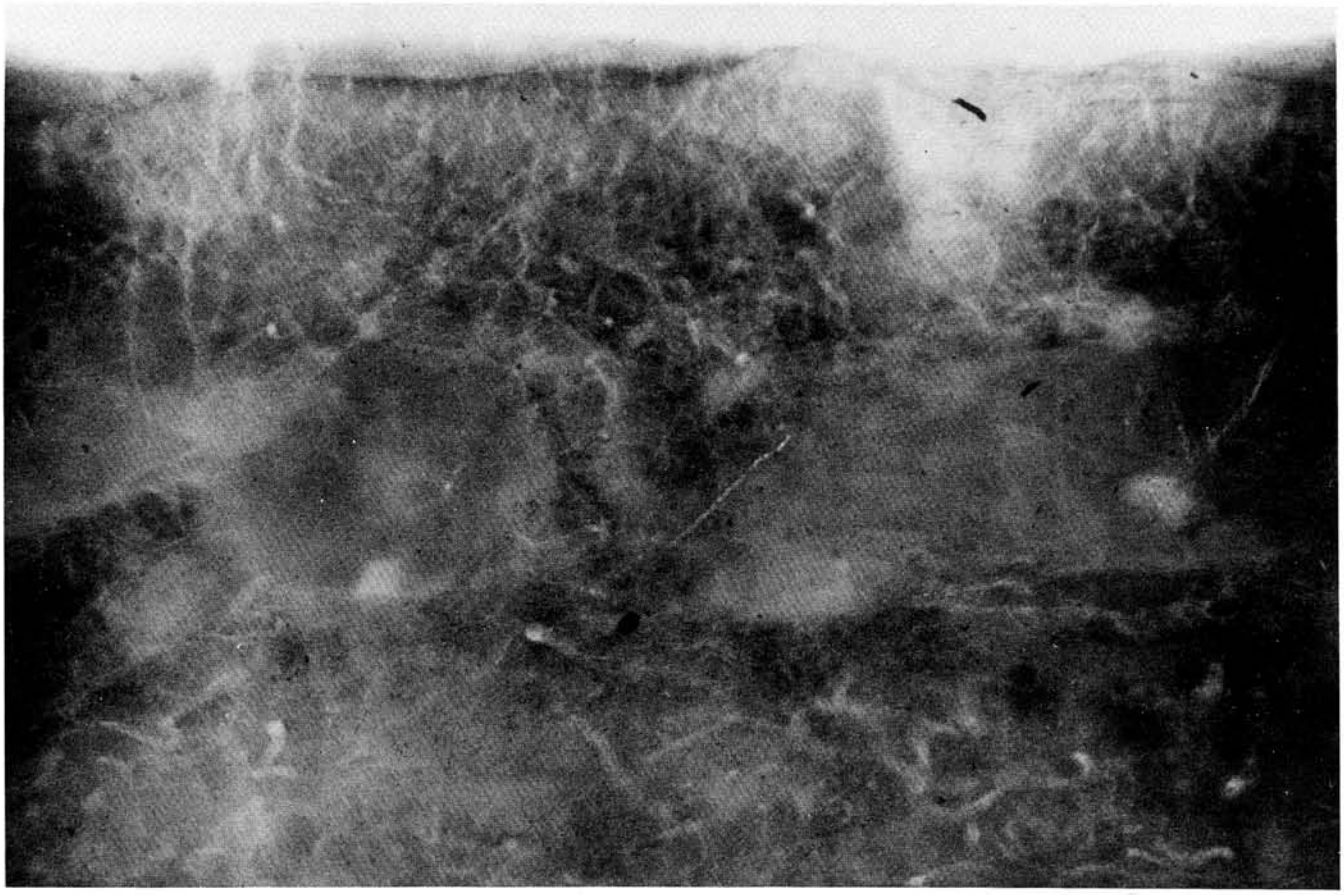

Fig. 4.
X-ray radiograph of sediment surface layer from a spade core collected at our station (courtesy of Robert C. ALLER).
The fine reticulate burrows ("vermicelli bioturbation") are attributed to agglutinated foraminifera. Scale approximately 1 : 1.

Dendrophrya in the trays may have been assisted by the feeding activities of *Reophax*, which is included by Jones and Charnock (1985) in the group of detrital feeding scavengers.

The transition from brownish to grayish-brown sediments at our site is located about 6-7 cm below the surface, indicating reducing conditions, and foraminiferal tests from deeper subsamples are sometimes coated with manganese. In this zone, most empty tests which contain iron compounds in their cement, such as *C. subglobosa*, *H. ovicula*, *Recurvoides*, *Buzasina ringens*, *Saccammina*, *Trochammina globigeriniformis*, *Hormosina globulifera*, and *Eggerella propinqua* are bleached white in color. A good measure of the fossilization potential of agglutinated species is the ratio of living to dead tests in the assemblage. In Spade core 13, the least preservable form is *Pelosina* sp., since 11 live individuals but only 2 dead specimens were found. The most resistant species is *Rhizammina* sp. (large) illustrated in the plate, figure 2, which constructs its test from diatom frustules and other siliceous debris and makes an audible crunching sound when pierced with a dissecting needle.

Table 6 ranks the common species recovered from Spade cores 9 and 13 according to their fossilization potential. The komokiacea are not included because of the difficulty in distinguishing living from dead tests, but are no doubt the least preservable group of benthic foraminifera. From this ranking, it would appear that the presence of iron compounds in the cement increases the preservability of specimens, since the four least preservable species in our samples are not brown in color. Our data are in general agreement with the observations of Schröder (1986) who ranked agglutinated foraminifera from the western North Atlantic in terms of test stability.

c) Recolonization by agglutinated foraminifera

In studies of fossil assemblages from Alpine flysch regions (Grün *et al.* 1964; Butt 1981) and the Norwegian-Greenland Sea (Verdenius and Van Hinte 1983), the simple tubular species were assumed to represent opportunistic species. Small-scale vertical changes in assemblage composition from an astrorhizid-dominated assemblage directly above a turbidite to a more diverse assemblage higher in the hemipelagite was interpreted as evidence of recolonization of the sea floor after a catastrophic event. Verdenius and Van Hinte further elaborated on this subject, describing a "frontier-area subfauna" of primitive forms and a

Table 6.
Agglutinated foraminifera from the Panama Basin ranked in terms of increasing fossilization potential, defined as the ratio of living to dead tests observed in spade core samples.
At the top of the list are species which are least likely to be preserved.

1. *Pelosina* sp.
2. *Reophax dentaliniformis*
3. *Dendrophrya arborescens*
4. *Reophax excentricus*
5. *Hormosina globulifera*
6. *Eggerella propinqua*
7. *Recurvoides* spp.
8. *Buzasina ringens*
9. *Cribrostomoides subglobosus*
10. *Ammodiscus incertus*
11. *Hormosina ovicula*
12. *Trochammina globigeriniformis*
13. *Saccammina* sp.
14. *Rhizammina* sp. (large)

species-rich "mature subfauna" which was interpreted as a later stage of faunal succession. A change from a frontier-fauna to a mature fauna at younger levels in Site 345 was attributed to a reduction in turbidite intensity with time.

More recent studies, however, have interpreted concentrations of tubular species as a result of hydrodynamic sorting. Schröder (1986) reports "countless" tubular fragments in a turbidite layer from the Nares Abyssal Plain. By comparing sedimentological evidence with benthic faunal data, Kaminski *et al.* (this volume) distinguished a redeposited "*Dendrophrya* assemblage" in turbidite clays of the lower Lizard Springs Formation of Trinidad. Considering the epifaunal habitat of *Dendrophrya* in the Panama Basin, this taxon would no doubt be entrained and redeposited by downslope currents. If erosion by a turbidity current occurs mainly in the flocculent surface sediment, we would expect to see concentrations of *Dendrophrya* in the turbidite "d" layer of the Bouma Sequence.

Although we cannot hope to recreate the large-scale devastation of benthic biota caused by a turbidity current, we feel that our recolonization trays provide a good approximation as to which organisms are likely to recolonize a naturally disturbed patch of the sea floor. This experiment is not free of bias, however, because the type of disturbance introduced in mudboxes is unlike anything known in nature. A discussion of the type of experimental bias introduced by our sampling design is given by Smith (1985).

The abundance of living individuals in our mudboxes, summarized in table 7, identifies the opportunistic species. The control sample is the pooled data from the 0-2 and 2-5 cm subsections of both spade cores. Contrary to *a priori* expectations, the tubular species *Dendrophrya arborescens* was found to be a poor colonizer, since no living individuals were found in any of the trays. The best colonizers in our samples were *Reophax excentricus* and *Reophax dentaliniformis*, which is not surprising in view of results of faunal studies conducted at the HEBBLE (High Energy Benthic Boundary Layer Experiment) Site on the lower continental rise off Nova Scotia. At this site, two benthic storms were recorded in early spring of 1983, which disturbed the sediment surface layer to a depth of up to 6 cm. Boxcore samples recovered in June of that year revealed an agglutinated foraminiferal assemblage dominated by species of *Reophax*, including *Reophax dentaliniformis*, which was interpreted by Kaminski (1985) as an opportunistic form.

In the Panama Basin, the species *Reophax excentricus* was present in greater abundance in our mudbox samples than in control samples, which suggests this species is a particularly good colonizer. Other species which display good dispersal capabilities are *Hormosina ovicula*, *Cribrostomoides subglobosus*, *Psammosphaera* sp. and *Trochammina globigeriniformis*.

The mode of colonization of the substrate by the two species of *Reophax* cannot be confirmed without in-situ observation of the living animal. An interesting point is that this species is infaunal, and one would expect infaunal taxa to be less likely to colonize a sediment tray (Smith 1985). Whether this species has free-swimming zygotes as in other benthic foraminiferal species is not known, and we cannot discount the possibility that some or all individuals did not colonize our samples by crawling up the sides of the trays. Crawling behavior in the shallow-water species *Reophax moniliformis* has recently been described by Knight (1986). Knight reports that when a specimen of *R. moniliformis* is placed in an observation cell with its aperture close to a vertical surface, the animal will attach its pseudopodia and climb the wall of the container while holding the test horizontally.

Table 7.
Abundance of live individuals /100 cm² in control samples and colonization trays in the Panama Basin.
Control samples are combined abundance from 0–5 cm layers of both spade cores.

Species	Control	MB 10	MB 11	MB 7
Dendrophrya arborescens	68.3	0.0	0.0	0.0
Reophax dentaliniformis	13.1	9.5	2.0	3.0
R. excentricus	4.6	10.5	6.1	4.8
Hormosina ovicula	2.4	0.8	0.2	1.0
Pelosina sp.	1.6	0.2	0.0	0.2
Recurvoides spp.	1.6	0.6	0.0	0.0
Saccammina sp.	1.3	0.8	0.0	0.0
Cribrostomoides subglobosus	1.1	3.0	0.4	0.2
Trochammina globigeriniformis	1.1	0.8	0.4	0.4
Buzasina ringens	0.8	0.2	0.0	0.4
Ammodiscus incertus	0.6	0.4	0.0	0.4
Bathysiphon sp.	0.6	0.0	0.0	0.0
Rhizammina sp. (large)	0.5	0.6	0.0	0.2
Hormosina globulifera	0.4	0.0	0.2	0.2
Hormosina distans	0.3	0.8	0.0	0.2
Ammobaculites sp.	0.0	0.8	0.0	0.0
Psammosphaera sp.	0.0	1.8	0.4	0.2
TOTAL:	97.8	30.2	9.5	11.1

d) Rates of succession

The total abundance of live individuals in control samples is 97.8 individuals/100 cm^2. However, if we ignore *Dendrophrya*, the abundance of remaining species is 29.4 individuals/100 cm^2. This figure compares well with the abundance in Mudbox 10 (30.2 live individuals/100 cm^2), which suggests that except for tubular forms, nine months may be sufficient time for an agglutinated foraminiferal fauna to recover to background levels of abundance after a disturbance. This finding is in contrast with the density of macrofaunal invertebrates, which did not recover to background levels in any of the trays over the nine month period.

There is evidence in our data that faunal recolonization occurs at different rates. This increases the likelihood that localized disturbance of benthic communities may result in patches of organisms in different stages of succession or contemporaneous disequilibrium (Grassle and Sanders 1973). The expected number of species in a given sample size differs by nearly a factor of two, and abundance differs by a factor of three between MB 10 and MB 11. These differences are greater than those observed in control samples. The observation of patches of agglutinated foraminifera with diversity differing significantly from other patches within an 2 km^2 area was reported by Kaminski (1985) from the HEBBLE Site. The results from both the Panama Basin and the HEBBLE Site indicate that physical disturbance resulting in severe population reduction is an important source of spatial heterogeneity in the distribution of deep-sea benthic organisms.

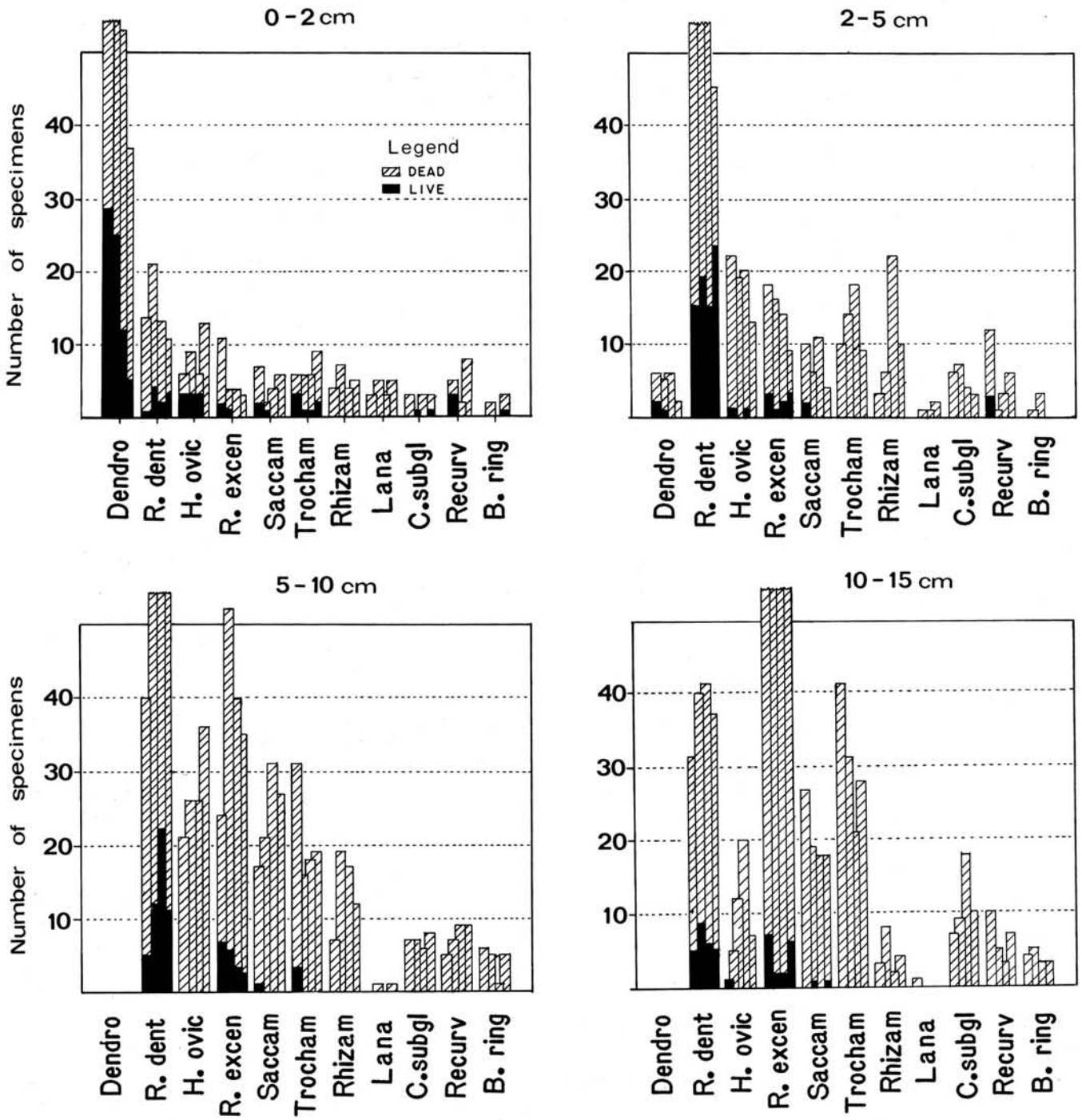

Fig. 5.
Composite diagram showing changing agglutinated foraminiferal populations and dead assemblages with depth in Spade core 13.
The abundance of *Dendrophyra* was arbitrarily divided by three.

CONCLUSIONS

The study of living and dead assemblages in recolonization trays and with depth in spade cores allows us to reconstruct the life history of agglutinated benthic foraminifera in the deep Panama Basin. Tubular and planispiral forms such as *Dendrophrya, Cribrostomoides* and *Ammodiscus*, have an epibenthic habitat, whereas the elongate uniserial genus *Reophax* prefers an infaunal mode of existence and is credited with causing the fine network of burrows observed in x-radiographs. A smaller proportion of the total assemblage was living at the time of collection when compared with data from the North Atlantic (12.75% vs 30-40%).

The tubular species *Dendrophrya arborescens* is a delicate form which disintegrates within nine

months after the death of the animal and possesses poor dispersal capabilities, since it was not found in recolonization trays. This finding contradicts the idea of "primitive" tubular forms being more opportunistic than "advanced" species. The most effective colonizers were two species of *Reophax*, a finding which is corroborated by observations on the lower continental rise off Nova Scotia. The density of taxa in recolonization trays differed from one another by a factor of three, which may suggest recolonization taking place at different rates among different patches of fauna. Recolonization by benthic foraminifera in the deep Panama Basin is more rapid than among macrofaunal invertebrates in the same samples.

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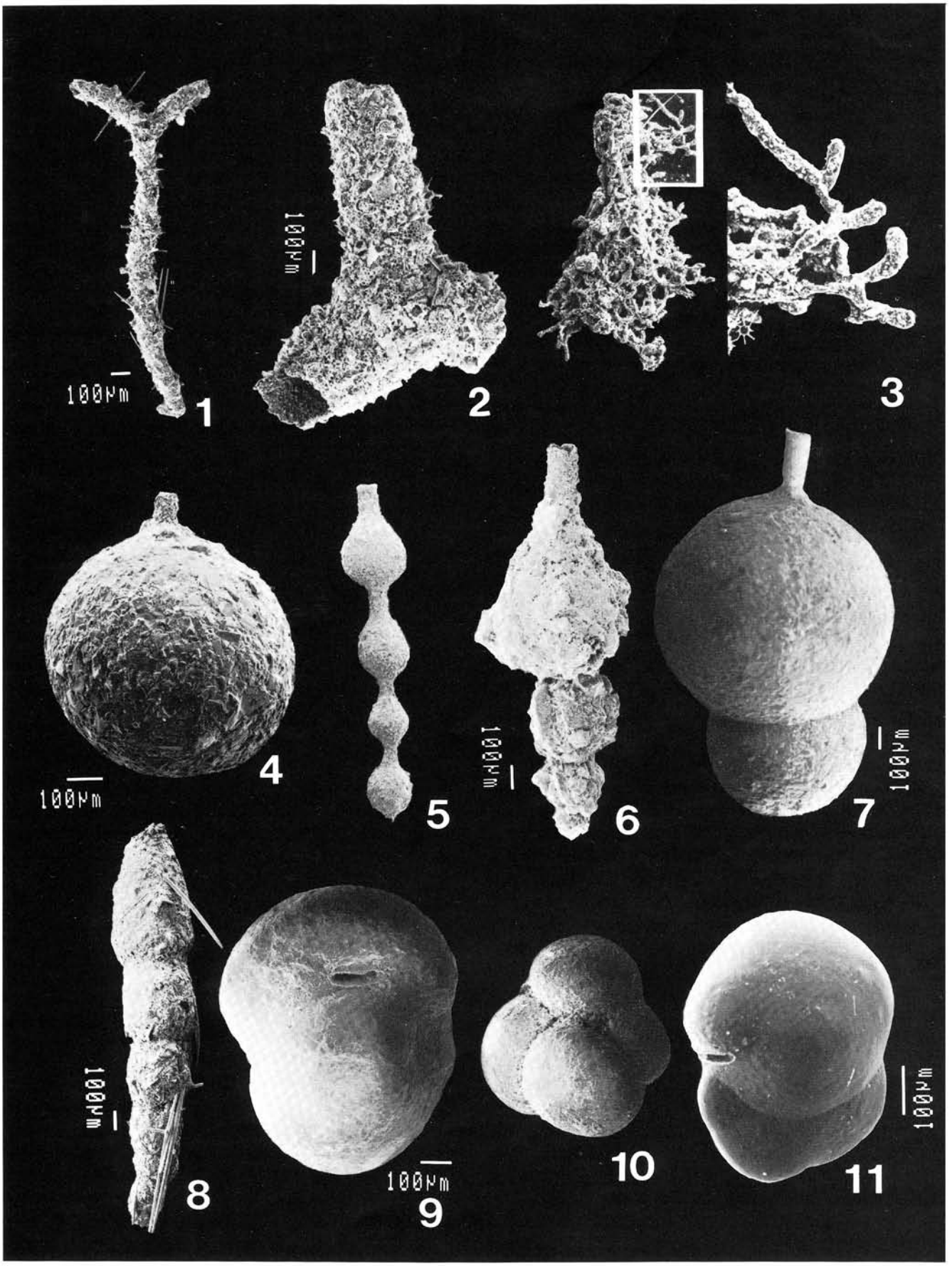
PLATE 1

Figure 1. *Dendrophrya arborescens* (Norman), x35.
Figure 2. *Rhizammina* sp. (large), x46.
Figure 3. *Lana* sp., x43.
Figure 4. *Saccammina* sp., x64.
Figure 5. *Hormosina ovicula* Brady, x40.
Figure 6. *Reophax excentricus* Cushman, x43.
Figure 7. *Hormosina globulifera* Brady, x39.
Figure 8. *Reophax dentaliniformis* Brady, x35.
Figure 9. *Cribrostomoides subglobosus* (G.O. Sars), x50.
Figure 10. *Trochammina globigeriniformis* Parker and Jones, x56.
Figure 11. *Buzasina ringens* (Brady), x85.

All scale bars - 100µm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