Interactions Between Metazoans and Large, Agglutinating Protozoans: Implications for the Community Structure of Deep-Sea Benthos[1]

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SYNOPSIS. Large, agglutinating protozoans belonging to the Foraminiferida (suborder Astrorhizina) and the Xenophyophorea are conspicuous, often dominant faunal elements in the deep sea. A review of known and suspected interactions between these forms and metazoans reveals a potentially significant role for the protozoans in structuring deep-sea metazoan assemblages. Direct interactions include provision to metazoans of (a) hard or stable substratum, (b) refuge from predators or physical disturbance, and (c) access to enhanced dietary resources. In some instances, rhizopod tests may provide a nursery function. Xenophyophore modification of flow regimes, particle flux, bottom skin friction and sediment characteristics appear likely and are believed to account for altered composition and abundance of meiofauna and macrofauna in the vicinity of rhizopod tests. Some analogous interactions are observed between metazoans and biogenic sediment structures in shallow water. However, metazoan-rhizopod associations are hypothesized to be more highly developed and complex in the deep sea than are comparable shallow-water associations, due to rhizopod abilities to enhance scarce food resources and to low rates of disturbance in much of the deep sea. Agglutinating rhizopods appear to be a significant source of heterogeneity on the deep-sea floor and large tests often represent 'hotspots' of metazoan activity. As such, they are hypothesized to have contributed to the origin and maintenance of metazoan diversity in the deep sea by providing distinct microenvironments in which species can specialize.

INTRODUCTION

Among the many differences between shallow- and deep-water faunas of marine sediments are changes in organism size and taxonomic composition. Along a gradient of increasing depth, the average size of infaunal individuals diminishes (Thiel, 1975, 1983; Shirayama and Horikoshi, 1989), and the importance of meiofauna, in particular, foraminiferans, increases. For example, in a comparison of faunal composition at 3 m, 295 m and 2,000 m in the western Pacific Ocean, Shirayama and Horikoshi (1989) found foraminiferans to make up <5%, 15% and nearly 50% of the infauna retained on a 63-μm screen, respectively. Increasing importance of meiofaunal taxa is part of a well-documented trend towards small body size with increasing water depth. However, extraordinarily large species have been reported frequently within selected taxa in deep water (Lipps and Hickman, 1982; Thiel, 1983).

Two groups noted for large body size (0.5 to >10 cm) in the deep sea are the Foraminiferida and Xenophyophorea, rhizopod protozoan taxa which both include agglutinating forms. Representatives from these groups are frequently abundant and conspicuous components of deep-sea faunas (Tendal, 1972; Tendal and Hessler, 1977; Bernstein *et al.*, 1978; Gooday, 1983*b*, 1991; Levin and Thomas, 1988; Gooday and Tendall, 1988; Schröder *et al.*, 1988, 1989; Kaufmann *et al.*, 1989; Levin *et al.*, 1991*a*; Gooday *et al.*, 1992) and their tests often attain sizes much larger than the majority of metazoans with which they occur (Thiel, 1975; Gooday, 1990). The Komokiacea, agglutinating foraminiferans that sometimes attain large size (*e.g.*, on manganese nodules; Mullineaux, 1988) but are often <0.5 cm, will be included in the following discussion because of their numerical importance in many deep-sea settings (Tendal and Hessler, 1977; Schroeder *et al.*, 1989). The natural history of these organisms in the deep sea is poorly known, as the study of live specimens has been initiated relatively recently. Access to deep-water material in good condition has been limited partially by the fragility of tests, and partly

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by a long-standing failure to recognize many specimens in samples as organisms (Tendal, 1972; Tendal and Hessler, 1977).

The intent of this paper is to explore the potential importance of interactions between large, agglutinating rhizopods and metazoans in deep-sea, soft-sediment settings. Some mention will be made of interactions on hard substrates when these substrates occur within a larger sedimentary environment (*e.g.*, Mn nodules). In many areas tests of agglutinating protozoans are the dominant biogenic structure present at the sediment-water interface (Rice *et al.*, 1979; Tendal and Gooday, 1981; Levin and Thomas, 1988; Cartwright *et al.*, 1989; Gooday, 1991; Levin *et al.*, 1991*a*; Gooday *et al.*, 1992). I will briefly discuss the natural history of protozoans in such settings, then focus on their synecology with respect to possible influence on metazoan community organization. Interactions of potential importance include (1) use of protozoan tests by metazoans as substrate and refuge, (2) predation on protozoans by metazoans, and vice versa and (3) indirect interactions involving alteration of metazoan sedimentary and feeding environments by protozoans and their tests. Where possible, I will make comparisons with processes involving biogenic structures in shallow waters.

DISTRIBUTION AND NATURAL HISTORY OF LARGE, AGGLUTINATING RHIZOPODS

Large (≥ 0.5 cm longest dimension), agglutinating species belonging to the Foraminiferida and Xenophyophorea have been reported from all the major ocean basins (Tendal, 1972; Tendal and Hessler, 1977; Gooday, 1990). The greatest densities of large forms occur in regions of high surface production (*e.g.*, beneath upwelling zones), or on sloped topography where particle flux is high (*e.g.*, seamounts, canyons, trenches and continental slopes) (Levin and Thomas, 1988; Gooday, 1990). Areas known to have high densities of large agglutinating rhizopods, and the sizes of the organisms involved, are listed in Table 1. Some of these locations are depicted in Figure 1. Regions with the highest known xenophyophore densities (1–20/m²) include the NE Atlantic off Africa (Fig. 1A) (Tendal and Gooday,

1981), the NW Atlantic continental slope (Fig. 1B) (B. Hecker, personal communication), and eastern Pacific seamounts near the east Pacific Rise (Levin and Thomas, 1988) (Fig. 1C). On one central Pacific seamount, (Magellan Rise, 3,150 m), xenophyophores exhibit average densities of 0.4/m² (Fig. 1D), and comprise >90% of the epibenthic megafauna (Kaufmann *et al.*, 1989). High densities of an infaunal xenophyophore at least 2.5 cm long (3.6×10^3 fragments/m²) were reported by Tendal *et al.* (1982) at 8,260 m in the Ogasawara Trench off Japan. Dense foraminiferan assemblages are reported from the Santa Catalina Basin, where 5 epibenthic species (1–6 cm) occur at 200–300/m² (Levin *et al.*, 1991*a*) (Fig. 1E), in the central North Pacific where komokiaceans dominate (Tendal and Hessler, 1977), and at three locations in the North Atlantic, where species of the tubular foraminiferan *Bathysiphon* are present at densities of 10–175/m² (Gooday, 1983*a*; Gooday *et al.*, 1992) (Fig. 1F).

The two agglutinating rhizopod classes addressed in this review, the Foraminiferida (suborder Astrorhizina) and the Xenophyophorea, are similar in that they agglutinate sediment particles, often selectively, to form elaborate tests with a characteristic structure. Xenophyophores and many of the largest agglutinating foraminiferans occur primarily in deep (>600 m) or high-latitude waters (Tendal, 1972; DeLaca *et al.*, 1980; Gooday, 1990). All xenophyophores and some astrorhizinids (*e.g.*, *Bathysiphon*, *Rhizammina*) are multinucleate. Similarly all xenophyophores and some astrorhizinid foraminiferans (*e.g.*, komokiaceans) produce fecal pellets (stercomata) 10–30 μm in diameter, which may be retained within the test. The Xenophyophorea differ from the agglutinated Foraminiferida in (1) having fecal pellets (stercomata) packaged in strings or masses (stercomare) that are retained within the test and encased by an organic membrane, (2) the presence of barite crystals ($BaSO_4$), termed granellae, within the plasma (Gooday and Nott, 1982) and (3) the presence of an organic tube system enclosing the branched protoplasmic strands.

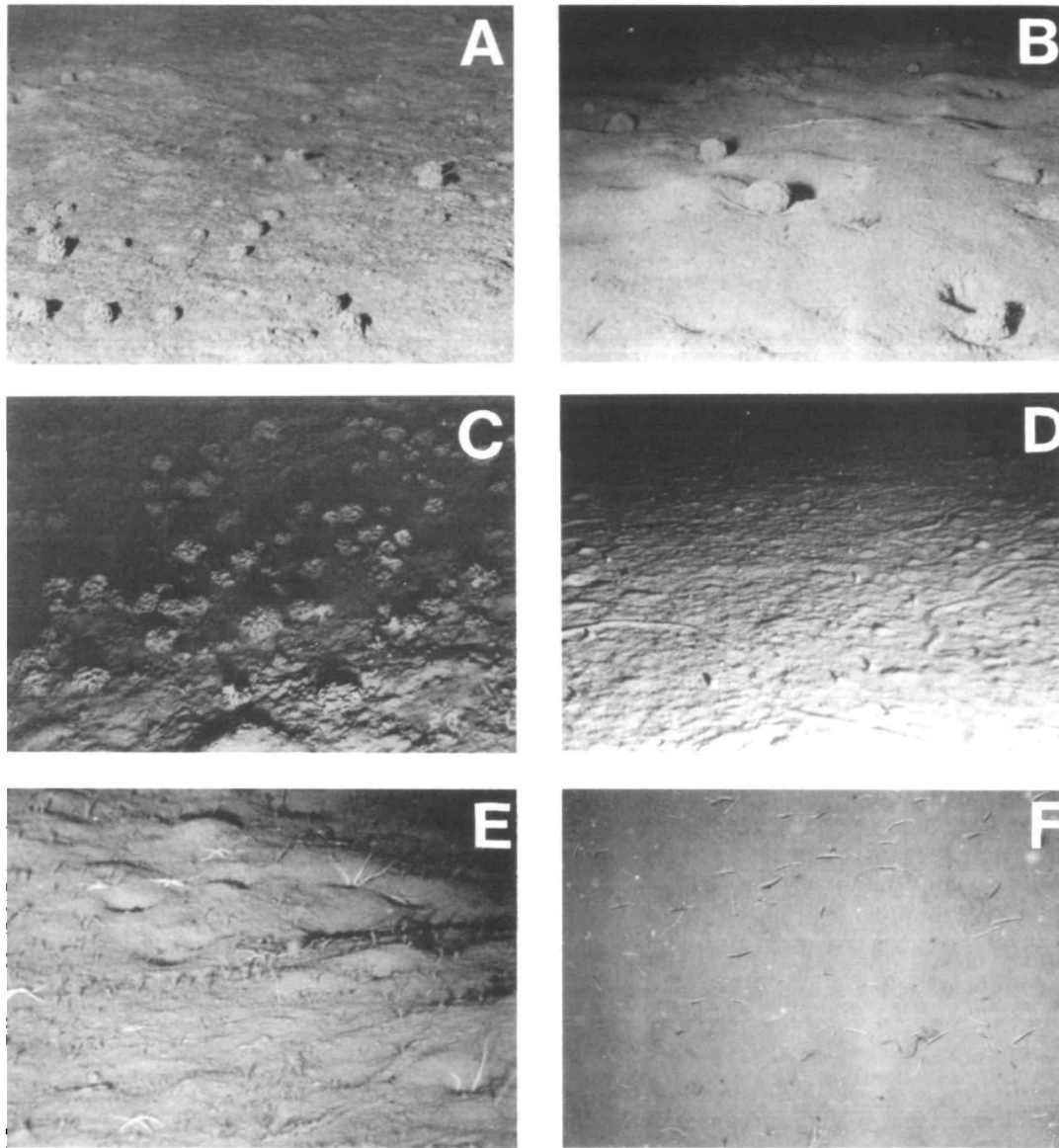Large agglutinating foraminiferans are

FIG. 1. Settings with high densities of one or more agglutinated rhizopod species. A. Xenophyophores *Reticulammina labyrinthica* in the Northeast Atlantic off W. Africa, 3,921 m. Discovery Station 9131, Haul 11. 20°09'N, 21°40'W. (Photo courtesy of the Institute of Oceanographic Sciences, Deacon Laboratory, Benthic Biology Group.) B. Xenophyophores *Syringammina* sp. on the NW Atlantic slope off New Jersey, 2,200 m. 41°N, 73°W. (Photo courtesy of B. Hecker, Lamont Dougherty Geological Observatory.) C. *Reticulammina* sp. on the caldera floor of MOK Seamount, eastern Pacific Ocean, 1,925 m. 09°57'N, 104°35'W. D. Xenophyophores on the cap of Magellan Rise in the central Pacific Ocean, 3,150 m. 07°05'N, 176°52'W. E. Foraminiferans *Pelosina* cf. *arborescens* on the floor of the Santa Catalina Basin, eastern Pacific Ocean, 1,240 m. 33°12'N, 118°30'W. F. Foraminifers *Bathysiphon filiformis* on the NW Atlantic slope, off Cape Hatteras, North Carolina, 850 m. 35°23'N, 74°50'W.

TABLE 1. *Deep-water settings in which large, agglutinating rhizopods (Foraminiferida and Xenophyophorea) are dominant components of the fauna.* *

Location	Depth (m)	Rhizopod taxa	Individual size (longest dimension)	Shape	Densities	Reference
IE Atlantic (off W. Africa)	3,000–4,000 m	*Reticulammina labyrinthica*	3–4 cm	hemispherical, reticulate	3–20/m²	Tendal and Gooday, 1981
IW Atlantic slope, Georges Bank to New Jersey	900–1,500 m	*Syringammina* sp.	4–5 cm	hemispherical, reticulate	1–2/m²	B. Hecker, unpublished data
IW Atlantic Canyons (Lydonia, Oceanographer, Heezen)		*Syringammina* sp.		hemispherical, reticulate	15–20/m²	B. Hecker, unpublished data
astern Pacific Seamounts (MOK, MIB)	1,700–2,200 m	*Reticulammina* spp.	4–8 cm	hemispherical, reticulate	1–18/m²	Levin and Thomas, 1988
Iew Zealand Plateau	800–1,300 m	*Syringammina tasmanensis*	5 cm	hemispherical, reticulate	1/m²	Tendal and Lewis, 1978
anta Catalina Basin	1,200–1,300 m	5 spp. including *Pelosina* cf. *arborescens*, a mud-walled astrorhizinid	0.5 to 6 cm	tubular, branched spherical tubular & spherical	75–100/m² 37–75/m² Total 200–300/m²	Levin et al., 1991a
entral N. Pacific	>4,000 m	agglutinated foraminifers	0.5 cm			Bernstein et al., 1978
entral N. Pacific, Magellan Rise	3,100 m	Psamminidae	~4 cm	flat, fan-shaped	0.2–0.5/m²	Kaufmann et al., 1989
Iest Pacific, Ogasawara Trench	8,260 m	*Occultammina profunda**	2.5 cm	tubular hexagonal network	3.6 × 10³ fragments/m²	Tendal et al., 1982 Swinbanks and Shirayama 1986b
IE Atlantic (off W. Africa)	4,000 m	*Bathysiphon rusticus*	up to 6 cm	tubular	20/m²	Gooday, 1983a
orcupine Seabight, SW Ireland	~1,350 m	*B. folini* *Rhizammina algaeformis*	up to 8 cm	unbranched tubular, tubes branching	3–16/m²	Gooday, 1983a Cartwright et al., 1989
IW Atlantic slope, off North Carolina	600–1,000 m	*B. filiformis*	3–12 cm	tubular	11–35/m² @ 600 m 59–154/m² @ 854 m	Gooday et al., 1992
	500–2,000 m	*B. major*	3–9 cm	tubular	50/m²	
IE Atlantic, Biotrans site	4,000–4,500 m	*R. algaeformis*	up to 4 cm	clumps of tubes	1/core	Cartwright et al., 1989

* All taxa are at least partly epibenthic unless noted otherwise, * = infaunal.

known to feed as carnivores, detritivores, herbivores (on microalgae), suspension feeders, and deposit feeders (Lipps, 1983; Jones and Charnock, 1985; Cedhagen, 1988; Gooday, 1990). They also can take up dissolved organic matter (DeLaca *et al.,* 1981). Xenophyophores have been reported to be primarily suspension feeders (Tendal, 1972), and their presence in regions of high particulate flux and on sloped topography supports this conclusion. Levin and Thomas (1988) proposed that reticulate and folded xenophyophore test morphologies may be adapted to entrain water and suspended particles, thereby permitting tests to serve as passive particle traps. Photographic observations of extensive pseudopodial traces on surface sediments (Lemche *et al.,* 1976) suggest a surface-deposit feeding mode for some species.

DIRECT PROTOZOAN-METAZOAN INTERACTIONS

Use of protozoan tests

The most readily identified association between metazoans and agglutinating protozoans is the habitation of rhizopod tests by a wide range of metazoan taxa. Rhizopod test morphologies are varied and complex (Fig. 2) and test interstices offer considerable living space. Tests may provide: (1) a source of hard or semi-hard substratum in an otherwise soft-bottom setting, (2) refuge from predators or physical hazards, (3) microhabitats suitable for mate location and reproduction or (4) enhanced food supplies. Food resources associated with agglutinating rhizopods may include trapped particulates, protozoan protoplasm or fecal material, other metazoans, or elevated position and access to enhanced particulate flux above the sediment-water interface. Tests can provide the resources mentioned above while the rhizopods are living (Levin and Thomas, 1988; Gooday *et al.,* 1992) or after they are dead (Gooday, 1984).

Protozoans as substrate and refugia

Metazoan use of agglutinated xenophyophore and foraminiferan tests as substrate in the deep sea appears to be widespread. Four detailed investigations have been carried out (Table 2). Examination of tests of living xenophyophores (mostly in the genus *Reticulammina*) on eastern Pacific seamounts (Figs. 1C, 2a–d) (Levin and Thomas, 1988) and tests of living foraminiferans (*Bathysiphon filiformis*) on the upper NW Atlantic slope (Fig. 1F) (Gooday *et al.,* 1992) produced very similar lists of metazoan associates (Table 2), despite the very different morphologies of host rhizopod tests. The average number of metazoans found on each test was 18 and 16 for the two studies, respectively, and all tests had some metazoan associates. Nematodes, harpacticoid copepods, polychaetes, peracarid crustaceans, ophiuroids (on xenophyophores only) and gastropod embryos (on *Bathysiphon* only) comprised the majority of metazoan test inhabitants in these two investigations (Table 2), but many other metazoan taxa were present. In contrast, only 25% of 83 living specimens of epibenthic, agglutinating foraminiferans in the Santa Catalina Basin (SCB) had associated metazoans. The 32 metazoans found on the SCB foraminiferan tests included polychaetes, nematodes, harpacticoid copepods, peracarid crustaceans and sponges (Table 2; Levin *et al.,* 1991*a*). The observation of fewer metazoan associates among the SCB foraminiferans might be due to the tests' smaller size and lesser above-sediment exposure, relative to the xenophyophores or *Bathysiphon filiformis.*

Investigations of the interior of 'dead' foraminiferan and xenophyophore tests produced a different ranking of associates (Gooday, 1984). Sipinculans, which often occupy protected cavities (Barnes, 1974), were by far the most common test inhabitants (86%), while the metazoan groups that dominated in previously mentioned studies comprised most of the remaining test inhabitants (Table 2). Other records of metazoans in foraminiferan tests, reviewed by Gooday (1984), also indicate sipunculans to be the most common inhabitant.

Similar use of biogenic structures such as tubes, burrows, or plant stalks by nonhost invertebrates is well documented in shallow systems. Examples include occupation of echiurid burrows by commensal crabs, polychaetes and bivalves (Reise, 1985), habitation of onuphid polychaete tube caps
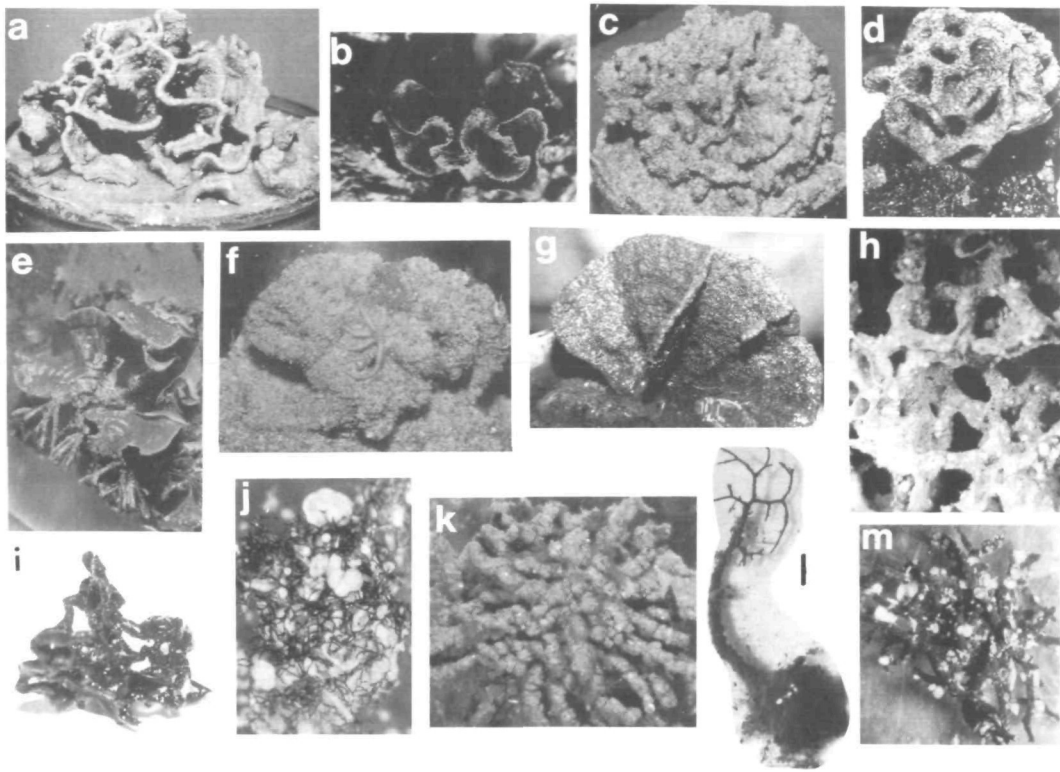
FIG. 2. Examples of agglutinated rhizopod test morphologies. a. *Reticulammina* n. sp. 3 (xenophyophore), 1,924 m, MOK seamount, eastern Pacific, 6 cm diameter. b. *Psammina* sp. (xenophyophore), 3,353 m, Volcano 7 in the eastern Pacific, 4 cm diameter. c. *Galatheammina* sp., 1,775 m, Volcano 6 in the eastern Pacific, 6 cm diameter. d. *Reticulammina* sp. on basalt, 1,952 m, MOK seamount. e. Unidentified xenophyophore (possibly *Stanophyllum* sp.), 5,270 m off Japan, approximately 4 cm long. (Photo courtesy of D. Checkley, North Carolina State University.) f. Unidentified xenophyophore, 1,803 m from MOK seamount, eastern Pacific, 5 cm diameter. g. Unidentified xenophyophore, 2,978 m, Volcano 7 in the eastern Pacific, 7 cm diameter, on a piece of Mn crust. h. *Syringammina* sp. (xenophyophore), from Wilmington Canyon, NW Atlantic, approximately 1,400 m. Reticulations are 2 to 2.5 mm apart. i. Unidentified xenophyophore from Volcano 7, eastern Pacific, 3,005 m, maximum dimension is 3.5 cm. j. Komokiacean *Lana* sp., 1,924 m from MOK seamount, eastern Pacific. Dimension 0.5 cm. k. Mud-walled astrorhizinid, 1,275 m, Santa Catalina Basin, 1 cm diameter. l. Foraminiferan *Pelosina* cf. *arborescens*, 1,275 m, Santa Catalina Basin, eastern Pacific, 3 cm length. m. Unidentified astrorhizinid, 788 m from Volcano 7, eastern Pacific, 1.5 cm longest dimension.

by macro- and meiofaunal forms (Bell and Coen, 1982; Bell and Devlin, 1983), and occupation of dead *Spartina* culms by oligochaetes (L. Levin, unpublished observation).

The exact nature of the metazoan interaction with agglutinated rhizopod tests is often difficult to discern. Some taxa clearly use the tests as hard substrate in an otherwise soft-sediment setting. Tendal (1985) proposed that the xenophyophore *Stannophyllum zonarium* provides an important source of hard substrate to the monopla-

cophoran *Neopilina galatheae* as well as serving as a dietary resource. Attachment of metazoan sediment tubes and egg cases to rhizopod tests appears common. *B. filiformis* tubes on the North Carolina slope support an extensive epifauna and are often covered with sediment tubes and mucous nets (Fig. 3). Eighty-three percent of the attached macrofaunal forms are either gastropod egg cases or a terebellid polychaete, *Nicolea* sp. (Gooday *et al.*, 1992). The terebellid life habits resemble those of a shallow-water congener, *N. zostericola*, which

TABLE 2. *Metazoans inhabiting tests of agglutinating rhizopod protozoans.*[1]

Rhizopod taxon	Xenophyophores (mostly Reticulammina spp.)	Foraminiferans (Bathysiphon filiformis)	Foraminiferans and xenophyophores (mostly Bathysiphon folini)	Foraminiferans (Pelosina cf. arboresans, P. cylindrica, Oryctoderma sp. & 2 mud-walled astrorhizinids)
Location	E. Pacific seamounts	NW Atlantic	NE Atlantic	Santa Catalina Basin
Water depth	1,200–3,350 m	850 m	997–4,414 m	1,240 m
Reference	Levin and Thomas, 1988	Gooday et. al., 1992	Gooday, 1984	Levin et al, 1991a
No. tests examined	27 (living)	20 (living)	16,150 (?)	83 (living)
No. rhizopod spp. examined	8	1	18	5
Percent of tests inhabited by metazoans	100	100	9	25
Total no. metazoans present	485	322	1,011	32
Major metazoan taxa[2]				
Nematodes	35.9%	28.0%	4.2%	31.0%
Harpacticoid copepods	30.5%	17.5%	2.2%	18.8%
Polychaetes	11.5% (16 families)	13.6% (6 families)	4.6% (6 families)	31.3% (5 families)
Ophiuroids	8.2%			
Peracarid crustaceans	6.0%	3.6%	1.5%	9.4%
Molluscs	1.6%	31.0%		
Ostracods	1.4%	1.5%		
Sipunculans	1.0%		8.7%	
Poriferans	1.0%			6.3%

[1] Only taxa comprising ≥ 1% of metazoans within a study are included.
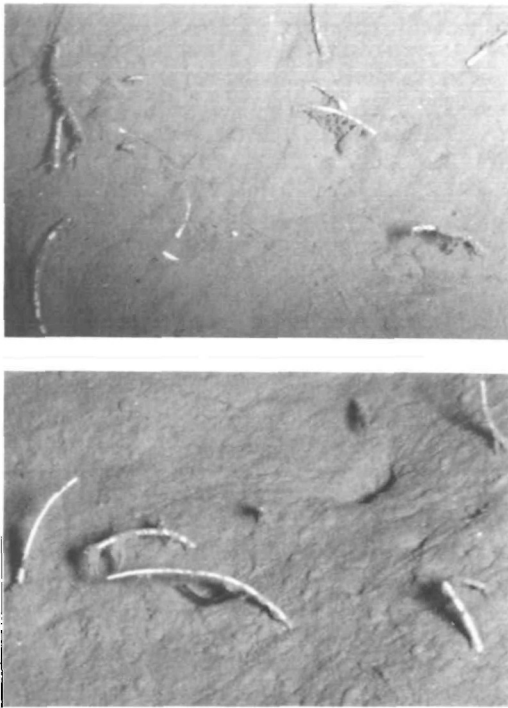[2] Percent of total metazoans collected in that study.

FIG. 3. Two views of *Bathysiphon filiformis* tubes from the NW Atlantic slope off Cape Hatteras, North Carolina, 850 m. Tubes are 6–12 cm in length. Attached sediment tubes (and presumably mucous nets) are made by the terebellid polychaete *Nicolea* sp. Photographs were taken by the Johnson Sealink with an 85 mm camera on dive 2627.

attaches to tubular holdfasts of brown and red algae (Eckelbarger, 1974). Egg cases, an unidentified discoidal anemone, and a medusoid polyp (*Stephanossyphus*) were found attached to 2 specimens of the xenophyophore *Psammina delicata* (Gooday and Tendal, 1988). Gooday (1984) reported the presence of nematode and sipunculan egg clusters in rhizopod tests. A number of soft-bottom species seek protection for eggs on hard substrates in shallow water, including mud snails that lay eggs on oyster shells (Ruppert and Fox, 1988) and killifish that attach eggs to *Spartina* culms (Kneib, 1986).

Two genera of suspension-feeding paludicelline ctenostome bryozoans are commonly found intergrown with agglutinating xenophyophores and foraminiferans, often with the initial zoids deeply embedded within the body of the rhizopod (Gooday and Cook, 1984; Gooday and Tendal, 1988;

Gooday, 1991). The bryozoans *Nolella* spp. were found intergrown with 4% of komokiaceans (mostly *Lana* spp.) and 4–38% of tests of the xenophyophore *Homogammina maculosa* examined from off NW Africa. *Victorella soulei* was associated with the xenophyophore *Reticulammina labrynthica*. These rhizopod-bryozoan associations are not obligatory, as the species investigated are also known to live on sponges (Gooday and Cook, 1984). Gooday and Cook (1984) proposed a mutualistic relationship between *Nolella* aff *monniotae* and its komokiacean host in which the komokiacean may protect *Nolella* from minute predators, while the particle-bearing feeding currents of the bryozoan may enhance the komokiacean diet.

Organisms attached to test surfaces of epibenthic rhizopods are probably benefiting from elevation above the sediment surface as well as from access to hard substrate. They may obtain refuge from infaunal predators, and suspension feeders raised above the bottom gain access to enhanced particle fluxes in the benthic boundary layer above the viscous sublayer (Lutze and Thiel, 1989; Mullineaux, 1989).

Not all metazoans live on surfaces of rhizopod tests. Gooday (1984) reported two nematode species that dwell inside tests between fecal masses and protoplasm of the xenophyophore *Aschemonella ramuliformis*. Harpacticoid copepods were abundant inside the sediment tubes of the xenophyophore *Syringammina* sp. (Levin and Huggett, unpublished observation). Several polychaete species from the eastern and central Pacific, including a flabelligerid, appear to construct sheaths of rhizopod stercomes (Levin *et al.*, 1991b; Riemann, 1983).

The number of metazoan inhabitants has been positively correlated with rhizopod test size (Levin and Thomas, 1988). There is a negative relationship between mesh size of the komokiacean tubule system and the number and size of associated ctenostome bryozoan colonies (Gooday and Cook, 1984). These observations suggest that rhizopod abundance, size and morphology may influence metazoan community structure.

A number of metazoan taxa appear to live exclusively or preferentially in association

with rhizopod tests (Cutler, 1969, 1973), although the associations may result from lack of suitable alternatives (*i.e.,* other tubular cavities). Cutler and Cutler (1980) describe 3 sipunculan species found mainly inside tubes of agglutinating foraminiferans, *Aspidosiphon zinni, Golfingia schuttei* and *G. minuta.* The nematode *Syringonomus typicus* (Leptosomatinae) usually inhabits the cylindrical tubes of the foraminiferan *Rhabdammina abyssorum* (Hope and Murphy, 1969). Gooday (1984) reported finding 40 polychaetes inhabiting dead forminiferan tests. Four-fifths of these belong to two previously undescribed species (a phyllodocid *Mystides bathysiphonicola* and a fauveliopsid, *Fauveliopsis olgae*), that may live primarily or exclusively in foraminiferan tubes (Hartman-Schröder, 1983). The polychaete *Nicolea* sp., which is very abundant on the tubes of living *B. filiformis* at 850 m off Cape Hatteras, North Carolina, is not found in surrounding sediments (Schaff and Levin, unpublished data) and probably lives exclusively on *B. filiformis* tests or other tubular structures. Isopods in the genus *Hebefustis* were reported as rhizopod inhabitants in both Pacific (Levin *et al.,* 1986) and Atlantic Ocean (Gooday, 1984) studies, and may typically seek shelter inside agglutinated tests. Thus, both foraminiferans and xenophyophore tests appear to support specialized metazoan assemblages.

Larger megafauna often reside beneath xenophyophore tests. Most reticulate xenophyophores collected on eastern Pacific seamounts typically had one or more ophiuroids residing under the tests (Levin and Thomas, 1988). A similar phenomenon has been observed in photographs from the NW Atlantic slope (Fig. 1B). Because large numbers of juvenile ophiuroids were collected in and under xenophyophore tests, Levin *et al.* (1986) suggested that rhizopod tests function as a nursery habitat for juvenile metazoans in a manner similar to that in which juvenile abalone and sea urchins seek food and protection beneath large urchin spine canopies in California kelp forests (Tegner and Dayton, 1977).

Predation

The literature contains only a few reports of metazoan predation on large rhizopods,

though such occurrences are probably common. Among the best documented cases is the consumption of the xenophyophore *Stannophyllum zonarium* by the monoplacophoran *Neopilina galatheae* (Tendal, 1985). Radula marks were present on 30% of the *S. zonarium* tests examined, and stercomare and granellare were present in the monoplacophoran gut (Tendal, 1985). Both predator and prey occur exclusively in deep water, and Tendal (1985) has suggested *N. galatheae* may specialize on xenophyophores.

The lysianassid amphipod, *Aristias* sp., is reported to prey on the foraminiferan *Hyperammina palmiformis* (though *H. palmiformis* might be a metazoan [R. L. Manuel, personal communication to A. J. Gooday]) based on the presence of rhizopod tissue in the amphipod gut (Gooday, 1984). Komokiaceans have been found in the gut contents of large, deposit-feeding invertebrates, including several species of the asteroid genus *Eremicaster,* the echiurid *Jakobia birsteini,* and several species of molpadiid holothurians (Sokolova, 1986). In some of these invertebrates foraminiferans and xenophyophores comprised 15–40% of the gut contents, and selectivity for rhizopods was indicated (Sokolova, 1986). Several other deep-sea taxa, including scaphopods (Davies, 1987) and the isopod *Amuletta* (Wilson and Thistle, 1985) are known to be selective predators on foraminiferans. The gut contents of tube-building serpulid polychaetes on manganese nodule surfaces in the central north Pacific included the presence of densely-packed foraminiferan stercomata, and another unidentified polychaete had stercomata incorporated into its tube as well as its gut contents (Riemann, 1983). Polychaete consumption of foraminiferans was inferred from these observations, though the prey was never identified.

Much of the evidence for metazoan predation on agglutinating rhizopods comes from observations of stercomata in metazoan guts. It is unclear whether the predator derives more nutrition from rhizopod protoplasm or from the fecal material. If Tendal's (1979) theory that microbial gardening takes place within rhizopod fecal masses is correct, then the stercomata may represent an exceptionally nutritious food source in

otherwise food-poor settings. Observations of harpacticoid copepods with stercome-filled guts inside *Syringammina* tests (Levin and Huggett, unpublished data) lend support to this idea. Rhizopods are most likely to represent an important dietary resource to metazoans when specialization occurs (as is probably the case for *Neopilina galatheae*) or in locations where rhizopod volume greatly exceeds that of all metazoans combined (*e.g.*, the central north Pacific; Tendal and Hessler, 1977; Bernstein et al., 1978; Mullineaux, 1988).

Rhizopod predation on small metazoans probably occurs (Gooday, 1990), but the frequent occurrence of metazoans on and within protozoan tests suggests that such predation is of minor importance or is highly selective. Squash preparations of *Bathysiphon filiformis* protoplasm from the North Carolina slope revealed polychaete setae and jaws (Gooday *et al.*, 1992), suggesting that *B. filiformis* functions as a carnivore or surface deposit feeder. If rhizopods do prey on small metazoan forms, high densities of epibenthic rhizopods (see Fig. 1) might be expected to inhibit recruitment of metazoan larvae.

Competition

Competition between deep-sea metazoans and large rhizopods for food or space may occur where rhizopods obtain high densities, but this has not been studied. In a shallow mudflat, negative interactions between calcareous foraminiferans and a harpacticoid copepod species have been shown to result from rhizopod exploitation of microfloral food (Chandler, 1989). In deep water, large, epibenthic rhizopods may remove organic-rich particulates from water near the sediment surface before metazoan deposit feeders can obtain access.

INDIRECT INTERACTIONS

Studies of rhizopod interactions with infaunal metazoans (not attached to tests) are scarce, but positive relationships might be expected based on shallow-water investigations of biogenic structures. In intertidal and shallow subtidal settings, elevated densities of infauna are typically observed near sediment tubes, grass culms and similar protruding structures (Eckman *et al.*, 1981;

Eckman, 1983; Gallagher *et al.*, 1983; Luckenbach, 1986). Mechanistic studies point to diminished predation (Luckenbach, 1984), increased sediment stability (Luckenbach, 1986), increased skin friction leading to enhanced microbial activity (Eckman, 1985), enhanced larval deposition (Jumars and Nowell, 1984) and host mucous production (Probert, 1986) as possible sources of infaunal enhancement.

Elevated abundances of macrofauna and meiofauna have been observed in sediments beneath and ≤ 7 cm away from xenophyophore tests on seamounts, relative to those in nearby sediments lacking the rhizopods (Levin and Thomas, 1988; Levin *et al.*, 1986). The taxa exhibiting greatest enhancement were isopods, tanaids, ophiuroids, nematodes, harpacticoid copepods and ostracods. Subsampling within 196 cm^2 boxcores revealed that for many taxa, especially the meiofauna, abundance increases were observed directly beneath the tests or in sediments within a few cm of tests (Levin *et al.*, 1986). Both positive and negative associations between infaunal harpacticoid copepods and the presence of three species of agglutinating foraminiferans in boxcores were reported by Thistle (1979, 1982) in the San Diego Trough. However, neither of these studies documented the mechanisms underlying the association.

Several attempts have been made to ascertain whether rhizopod tests or similar biogenic structures (*e.g.*, cirratulid polychaete mudballs) create special microhabitats for deep-sea metazoans by altering sediment characteristics such as particle deposition, grain size or microbial activity and abundance. Nyholm (1957) was the first to document sediment stabilization by foraminiferans in shallow water. Some xenophyophore species have root-like structures (Fig. 2e) that might be expected to stablize sediments or inhibit predators in the same manner as marsh or seagrass rhizomes (Orth, 1977; Peterson, 1982).

Xenophyophore test structures modify boundary skin friction at the sediment-water interface in a manner and with scaling similar to that described by Eckman and Nowell (1984) for tubes and by Thistle and Eckman (1990) for cirratulid mudballs (J. Eckman, personal communication). Within

the vicinity of xenophyophore tests (several widths), regions of increased and decreased boundary skin friction are present in unidirectional flow, and irregular and folded tests add turbulence and entrain water and particles (Levin, unpublished observation). Thistle and Eckman (1990) have provided evidence for enhanced bacterial abundance near mudballs (1 cm diameter) occupied by cirratulid hosts in the San Diego Trough (1,050 m), and similar microbial enhancement might be expected in the vicinity of occupied rhizopod tests. Experimental work by Eckman (1985) suggests that tubes and other biogenic structures protruding above the sediment-water interface should improve conditions for microbial colonization and growth; however, Thistle and Eckman (1990) found no such effect for uninhabited cirratulid mudballs. Schaff et al. (in preparation) investigated microbial and macrofaunal abundances inside and outside dense patches (75–150/m^2) of B. filiformis tubes (4–12 cm long) at 850 m on the North Carolina slope, but found no significant differences. The observation of rhizopod effects on microbial and metazoan communities may be highly dependent on the species examined, the general environmental conditions (flow regime, organic matter availability), and the scale on which observations are made.

Several lines of evidence suggest that agglutinating xenophyophores may modify particle flux at the sea floor. At bathyal depths on seamounts, xenophyophore tests and sediments beneath them exhibited inventories of excess Th-234 (a naturally occurring radioisotope used as a particle tracer) 3 to 17 times higher than the ambient seafloor sediments (Levin et al., 1986 and unpublished data). These data suggest that the xenophyophores may enhance particle flux to the seabed on 100-day time scales (Levin et al., 1986; DeMaster, personal communication). In contrast, three agglutinating foraminiferans from bathyal depths (Pelosina cf. arborescens, an unidentified mud-walled astrorhizinid, and B. filiformis) revealed no enhancement of excess Th-234 activity associated with tests (R. Pope, personal communication). In photographs from SW Pacific trenches, Lemche et al. (1976)

reported that the bottom around xenophyophores is darker than normal and they attributed this to accumulated sediments. Swinbanks and Shirayama (1986a, b) demonstrated elevated activities of excess Pb-210, a 100-year particle tracer, due to the presence of an infaunal xenophyophore, Occultammina profunda. They identified the stercomata and protoplasm as likely sources of Pb-210 activity. Tendal (personal communication—Deep-Sea Newsletter, 1985) suggested that high levels of radioactivity from these and similar taxa could lead to mutation in organisms that consume xenophyophores.

The scant evidence available suggests that xenophyophores have a greater influence on infaunal metazoans (not living within the rhizopod tests) than do foraminiferans. The large size, intricate (particle-trapping) morphologies, and particle-sequestering behavior of xenophyophores may either directly or indirectly benefit many different taxa. Clearly, much further study is required before the importance of rhizopods to deep-sea metazoan communities will be known. Particularly intriguing topics about which we are completely in the dark include: specialization of metazoan taxa on resources provided by rhizopods such as food or shelter, exploitative and interference competitive interactions, effects on settlement of metazoan larvae, effects on sediment geotechnical properties, and knowledge of the relative importance of passive effects (resulting from structural features of the tests) versus active processes, dependent on the living protozoan.

ANALOGIES AND IMPLICATIONS

Shallow-water systems offer many situations analogous to the biotic interactions I have described for deep-sea rhizopods. There are large, agglutinating rhizopods living in high-latitude shallow sediments (Cedhagen, 1988; Tendal and Thomsen, 1988; DeLaca et al., 1980) that probably have ecological effects similar to their deep-water counterparts. Though few synecological investigations have been carried out on these forms, a study of the foraminiferan Astrorhiza limicola showed relatively few metazoans (3 spp.) associated directly with tests

(Cedhagen, 1988; Tendal and Thomsen, 1988).

Exposed regions of agglutinated polychaete tubes provide habitat heterogeneity on the tube itself (Bell, 1985) and in surrounding sediments (Woodin, 1978; Eckman, 1983, 1985; Luckenbach, 1986). Some of the more elaborate tube caps, such as those formed by onuphid or spionid polychaetes support specialized meiofaunal communities (Bell, 1985). Many shallow sediment structures of biogenic origin alter hydrodynamic and sedimentary microenvironments in ways that influence infaunal composition. Examples include holothurian mounds (Rhoads and Young, 1970), enteropneust fecal casts (Thistle, 1980; Varon and Thistle, 1988), polychaete burrows (Aller and Yingst, 1978), shrimp burrows (Dobbs and Guckert, 1988) and fiddler crab burrows (DePatra and Levin, 1989). Marshgrass and seagrass stabilization of sediments, reduction of currents and addition of hard substrate (Orth, 1977; Thistle et al., 1984) parallel some of the presumed rhizopod functions as well.

Despite the many analogies that can be drawn between shallow- and deep-water community interactions, I hypothesize that metazoan associations with rhizopods and their tests may be better developed and potentially more complex in deep-water settings than are metazoan associations with biogenic sediment structures in shallow water. In the deep sea food is often a limiting resource (Rowe, 1983). Even small enhancements of food resources by rhizopods, whether direct (e.g., trapping of organic matter, gardening of bacteria) or indirect (e.g., hydrodynamic modifications that increase microbial activity), would be likely to benefit metazoans. Also, rhizopod tests may remain intact for longer periods of time in the deep sea, where physical or biological disturbances are less frequent. Specialized associations between rhizopods and metazoans might be more likely to develop in deep water than in shallow water, where biogenic structures can be quite ephemeral. Metazoan-rhizopod associations appear especially pronounced in coarse-grained sediments where natural organic matter availability to infauna is low, and where

other structural refugia are rare (Levin, unpublished observation). Oligotrophic settings such as the central North Pacific, where rhizopods dominate, are also sites where extensive metazoan-protozoan interaction is likely (Bernstein et al., 1978).

Agglutinating rhizopods are a constant, potentially old (Swinbanks, 1982), and often dominant component of the deep-sea fauna. The larger forms clearly create habitat heterogeneity in a range of deep settings. As a group, the agglutinating rhizopods may have contributed to the evolution of metazoan diversity in the deep sea by providing specialized microenvironments (sensu Jumars, 1975; Jumars and Eckman, 1982; Thistle, 1983). In modern deep-sea sediments they serve as hot spots of metazoan activity, and are proposed to be a significant structuring agent for infaunal communities.

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REFERENCES

Aller, R. C. and J. Y. Yingst. 1978. Biogeochemistry of tube-dwellings: A study of the sedentary polychaete *Amphitrite ornata* (Leidy). J. Mar. Research 36:201–254.

Barnes, R. D. 1974. *Invertebrate zoology*. W. B. Saunders Company, Philadelphia.

Bell, S. S. 1985. Habitat complexity of polychaete tube-caps: Influence of architecture on dynamics of a meioepibenthic assemblage. J. Mar. Res. 43:647–671.

Bell, S. S. and L. D. Coen. 1982. Investigations on epibenthic meiofauna. I. Abundances on and repopulation of the tube caps of *Diopatra cuprea* (Polychaeta: Onuphidae). Mar. Biol. 67:303–309.

Bell, S. S. and D. J. Devlin. 1983. Short-term macro-faunal recolonization of sediment and epibenthic habitats in Tampa Bay, Florida. Bull. Marine Science 33:102–108.

Bernstein, B. B., R. R. Hessler, R. Smith, and P. A. Jumars. 1978. Spatial dispersion of benthic Foraminifera in the abyssal central North Pacific. Limnol. and Oceanogr. 23:401–416.

Cartwright, N. G., A. J. Gooday, and A. R. Jones. 1989. The morphology, internal organization and taxonomic position of Rhizammina algaeformis Brady, a large, agglutinated deep-sea Foraminifera. J. Foram. Res. 19:115–125, pls. 1–4.

Cedhagen, T. 1988. Position in the sediment and feeding of Astrorhiza limicola Sandall, 1855 (Foraminiferida). Sarsia 73:43–47.

Chandler, G. T. 1989. Foraminifera may structure meiobenthic communities. Oecologia 81:354–360.

Cutler, E. B. 1969. New species of Sipuncula from the western North Atlantic. Proc. Biol. Soc. Wash. 82:209–218.

Cutler, E. B. 1973. Sipuncula of the western North Atlantic. Bull. Am. Mus. Nat. Hist. 152:103–204.

Cutler, E. B. and N. J. Cutler. 1980. Deep-water Sipuncula from the Gulf of Gascogne. J. Mar. Biol. Ass. U.K. 60:449–459.

Davies, G. J. 1987. Aspects of the biology and ecology of deep-sea Scaphopoda (Mollusca). Ph.D. Thesis, Heriot-Watt University, Edinburgh.

DeLaca, T. E., D. M. Karl, and J. H. Lipps. 1981. Direct use of dissolved organic carbon by agglutinated benthic Foraminifera. Nature 289:287–289.

DeLaca, T. E., J. H. Lipps, and R. R. Hessler. 1980. The morphology and ecology of a new, large agglutinated Antarctic foraminifer (Textulariina; Notodendrodidae nov.). Zool. J. Linn. Soc. 69:205–224.

DePatra, K. D. and L. A. Levin. 1989. Evidence of the passive deposition of meiofauna into fiddler crab burrows. J. Exp. Mar. Biol. Ecol. 125:173–192.

Dobbs, F. C. and J. B. Guckert. 1988. Callianassa trilobata (Crustacea: Thalassinidea) influences abundance of meiofauna and biomass, composition and physiologic state of microbial communities within its burrow. Mar. Ecol. Progr. Ser 45: 69–79.

Eckelbarger, K. J. 1974. Population biology and larval development of the terebellid polychaete Nicolea zostericola. Marine Biology 27:101–113.

Eckman, J. E. 1983. Hydrodynamic processes affecting benthic recruitment. Limnol. Oceanogr. 28: 241–257.

Eckman, J. E. 1985. Flow disruption by an animal-tube mimic affects sediment bacterial colonization. J. Mar. Res. 43:419–435.

Eckman, J. E. and A. R. M. Nowell. 1984. Boundary skin friction and sediment transport about an animal-tube mimic. Sedimentology 31:851–862.

Eckman, J. E., A. R. M. Nowell, and P. A. Jumars. 1981. Sediment destabilization by animal tubes. J. Mar. Res. 39:361–374.

Gallagher, E. D., P. A. Jumars and D. D. Trueblood. 1983. Facilitation of soft-bottom benthic succession by tube builders. Ecology 64:1200–1216.

Gooday, A. J. 1983a. Bathysiphon rusticus de Folin, 1886 and Bathysiphon folini n. sp.: Two large agglutinated foraminifers abundant in abyssal NE Atlantic epibenthic sledge samples. J. Foram. Res. 13:262–276.

Gooday, A. J. 1983b. Primitive Foraminifera and Xenophyophorea in IOS epibenthic sledge samples from the northeast Atlantic. Institute of Oceanographic Sciences Report 156:1–33.

Gooday, A. J. 1984. Records of deep-sea rhizopod tests inhabited by metazoans in the north-east Atlantic. Sarsia 69:45–53.

Gooday, A. J. 1990. Recent deep-sea agglutinated Foraminifera: A brief review. In C. Hemleben, M. Kaminski, W. Kuhnt, and D. Scott (eds.). Paleoecology, biostratigraphy, paleooceanography and taxonomy of agglutinated foraminifera, pp. 271–304. Kluwer Academic Publ., Dordrecht.

Gooday, A. J. 1991. Xenophyophores (Protista, Rhizopoda) in box-core samples from the abyssal northeast Atlantic Ocean (BIOTRANS area): Their taxonomy, morphology, and ecology. J. Foram. Res. 21:197–212.

Gooday, A. J. and P. L. Cook. 1984. An association between komokiacean foraminifers (Protozoa) and paludicelline ctenostomes (Bryozoa) from the abyssal northeast Atlantic. J. Nat. Hist. 18:765–785.

Gooday, A. J., L. A. Levin, C. L. Thomas, and B. Hecker. 1992. The taxonomy, distribution and ecology of Bathysiphon filiformis and B. major (Protista: Foraminiferida) on the continental slope off North Carolina. J. Foram. Res. (In press)

Gooday, A. J. and J. A. Nott. 1982. Intracellular barite crystals in two xenophyophores Aschemonella ramuliformis and Galatheammina sp. (Protozoa: Rhizopoda) with comments on the taxonomic position of A. ramuliformis. J. Mar. Biol. Assoc. UK 62:595–605.

Gooday, A. J. and O. S. Tendal. 1988. New xenophyophores (Protista) from the bathyal and abyssal north-east Atlantic Ocean. J. Nat. His. 22:413–434.

Hartman-Schröder, G. 1983. Zur kenatnis einiger Foraminiferengehause bewohnender Polychaeten aus dem Nordostatlantik. Mitt. hamb. zool. Mus. Inst. 80:169–176.

Hope, W. D. and D. G. Murphy. 1969. Syringonomus typicus new genus, new species (Enoplida: Leptosomatidae) a marine nematode inhabiting arenaceous tubes. Proc. Biol. Soc. Wash. 82:511–518.

Jones, J. W. and M. A. Charnock. 1985. "Morphogroups" of agglutinated Foraminifera. Their life positions and feeding habits and potential applicability in paleoecological studies. Revue de Paleobiology 4:311–320.

Jumars, P. A. 1975. Environmental grain and polychaete species' diversity: Does it have a characteristic scale? J. Mar. Res. 34:217–246.

Jumars, P. A. and J. E. Eckman. 1982. Spatial structure within deep-sea benthic communities. In G. T. Rowe (ed.), Deep-sea biology, pp. 399–451. John Wiley and Sons, New York.

Jumars, P. A. and A. R. M. Nowell. 1984. Fluid and

sediment dynamic effects on marine benthic community structure. Amer. Zool. 24:45–55.

Kaufmann, R. S., W. W. Wakefield, and A. Genin. 1989. Distribution of epibenthic megafauna and lebensspuren on two central North Pacific seamounts. Deep-Sea Res. 36:1863–1896.

Kneib, R. T. 1986. The role of *Fundulus heteroclitus* in salt marsh trophic dynamics. Amer. Zool. 26: 259–269.

Lemche, L. and B. Hansen, F. J. Madsen, O. S. Tendal, and T. Wolff. 1976. Hadal life as analyzed from photographs. Vidensk. Meddr. dansk Naturh. Foren. 139:263–336.

Levin, L. A., S. E. Childers, and C. R. Smith. 1991a. Epibenthic, agglutinating foraminiferans in the Santa Catalina Basin and their response to disturbance. Deep-Sea Res. 38:465–483.

Levin, L. A., D. J. DeMaster, L. D. McCann, and C. L. Thomas. 1986. Effects of giant protozoans (Class: Xenophyophorea) on deep-seamount benthos. Mar. Ecol. Prog. Ser. 29:99–104.

Levin, L. A., L. D. McCann, and C. L. Thomas. 1991b. The ecology of polychaetes on deep seamounts in the eastern Pacific Ocean. Ophelia Suppl. 5:467–476.

Levin, L. A. and C. L. Thomas. 1988. The ecology of xenophyophores (Protista) on eastern Pacific seamounts. Deep-Sea Res. 35:2003–2027.

Lipps, J. H. 1983. Biotic interactions in benthic Foraminifera. *In* M. J. S. Tevesz and P. L. McCall (eds.), *Biotic interactions in recent and fossil benthic communities*, pp. 331–376. Plenum Press, New York.

Lipps, J. H. and C. S. Hickman. 1982. Origin, age and evolution of antarctic and deep-sea faunas. *In* W. G. Ernst and J. G. Morin (eds.), *The environment of the deep sea*, pp. 324–356. Prentice-Hall, Englewood Cliffs, New Jersey.

Luckenbach, M. W. 1984. Biogenic structure and foraging by five species of shorebirds (Charadrii). Est. Coast. and Shelf Sci. 19:691–696.

Luckenbach, M. W. 1986. Sediment stability around animal tubes: The roles of hydrodynamic processes and biotic activity. Limnol. and Oceanogr. 31:779–787.

Lutze, G. F. and H. Thiel. 1989. Epibenthic Foraminifera from elevated microhabitats: *Cibicidoides wuellerstorfi* and *Planulina ariminensis*. J. Foram. Res. 19:153–158.

Mullineaux, L. S. 1988. Taxonomic notes on large, agglutinated foraminifers encrusting manganese nodules, including the description of a new genus, *Chondrodapis* (Komokiacea). J. Foram. Res. 18: 46–53.

Mullineaux, L. S. 1989. Vertical distributions of the epifauna on manganese nodules: Implications for settlement and feeding. Limnol. and Oceanogr. 34: 1247–1262.

Nyholm, K. G. 1957. Orientation and binding power of recent monothalmous Foraminifera in soft sediments. Micropaleontology 3:75–76.

Orth, R. J. 1977. The importance of sediment stability in seagrass communities. *In* B. C. Coull (ed.), *Ecology of marine benthos*, p. 281–300. Univ. So. Carolina Press, Columbia.

Peterson, C. H. 1982. Clam predation by whelks (*Busycon* spp.): Experimental tests of the importance of prey size, prey density and seagrass cover. Mar. Biol. 66:159–170.

Probert, P. K. 1986. Disturbance, sediment stability, and trophic structure of soft-bottom communities. J. Mar. Res. 42:893–921.

Reise, K. 1985. *Tidal flat ecology*. Springer-Verlag, Berlin.

Rhoads, D. C. and K. K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28: 150–178.

Rice, A. R., R. G. Aldred, D. M. S. Billet, and M. H. Thurston. 1979. The combined use of an epibenthic sledge and a deep camera to give quantitative relevance to macrobenthos samples. Ambio Special Report No. 6:59–72.

Riemann, F. 1983. Biological aspects of deep-sea manganese nodule formation. Oceanol. Acta 6: 303–311.

Rowe, G. T. 1983. Biomass and production of the deep-sea macrobenthos. *In* G. T. Rowe (ed.), *Deep-sea biology*, pp. 97–121. John Wiley and Sons, New York.

Ruppert, E. E. and R. S. Fox. 1988. *Seashore animals of the southeast*. Univ. of So. Carolina Press, Columbia.

Schröder, C. J., F. S. Medioli, and D. B. Scott. 1989. Fragile abyssal foraminifera (including new Komokiacea) from the Nares Abyssal Plain. Micropaleontology 35:10–48.

Schröder, C. J., D. B. Scott, F. S. Medioli, B. B. Bernstein, and R. R. Hessler. 1988. Larger agglutinated Foraminifera: Comparison of assemblages from central North Pacific and western North Atlantic (Nares Abyssal Plain). J. Foram. Res. 18: 25–41.

Shirayama, Y. and M. Horikoshi. 1989. Comparison of the benthic size structure between sublittoral, upper slope and deep-sea areas of the Western Pacific. Int. Rev. ges. Hydrobiol. 74:1–13.

Sokolova, M. N. 1986. Data on the feeding of deepwater bottom invertebrates. *In* Academy of Sciences of the USSR, *Feeding of marine invertebrates in natural habitats*, pp. 77–101. P. P. Shirshov Institute of Oceanology.

Swinbanks, D. D. 1982. *Paleodictyon*: The traces of infaunal xenophyophores? Science 218:47–49.

Swinbanks, D. D. and Y. Shirayama. 1986a. A model of the effects of an infaunal xenophyophore on Pb-210 distribution in deep-sea sediment. La Mer 24: 69–74.

Swinbanks, D. D. and Y. Shirayama. 1986b. High levels of natural radionuclides in a deep-sea infaunal xenophyophore. Nature 320:354–357.

Tegner, M. J. and P. K. Dayton. 1977. Sea urchin recruitment patterns and implications of commercial fishing. Science 196:324–326.

Tendal, O. S. 1972. A monograph of the Xenophyophoria (Rhizopoda, Protozoa). Galathea Report 12:7–99.

Tendal, O. S. 1979. Aspects of the biology of Komokiacea and Xenophyophorea. Sarsia 64:13–17.

Tendal, O. S. 1985. Xenophyophores (Protista, Sar-

codina) in the diet of *Neopilina galatheae* (Mollusca, Monoplacophora). Galathea Report 16:95–98, pl. 13.

Tendal, O. S. and A. J. Gooday. 1981. Xenophyophoria (Rhizopoda, Protozoa) in bottom photographs from the bathyal and abyssal NE Atlantic. Oceanol. Acta 4:415–422.

Tendal, O. S. and R. R. Hessler. 1977. An introduction to the biology and systematics of Komokiacea (Textulariina, Foraminiferida). Galathea Report 14:165–194.

Tendal, O. S. and K. B. Lewis. 1978. New Zealand xenophyophores: Upper bathyal distribution, photographs of growth position and a new species. N.Z.J. of Mar. and Freshw. Res. 12:197–203.

Tendal, O. S., D. D. Swinbanks, and Y. Shirayama. 1982. A new infaunal xenophyophore (Xenophyophorea, Protozoa) with notes on its ecology and possible trace fossil analogues. Oceanol. Acta 5:325–329.

Tendal, O. S. and E. Thomsen. 1988. Observations on the life position and size of the large foraminifer *Astrorhiza arenaria* Norman, 1876 from the shelf off northern Norway. Sarsia 73:39–42.

Thiel, H. 1975. The size structure of the deep-sea benthos. Int. Rev. ges. Hydrobiol. 60:575–606.

Thiel, H. 1983. Meiobenthos and nanobenthos of the deep-sea. *In* G. T. Rowe (ed.), *Deep-sea biology, the sea* 8:157–230. John Wiley and Sons Ltd., New York.

Thistle, D. 1979. Harpacticoid copepods and bio-

genic structures: Implications for deep-sea diversity maintenance. *In* R. J. Livingston (ed.), *Ecological processes in coastal and marine systems,* pp. 217–231. Plenum Press, New York.

Thistle, D. 1980. The response of a harpacticoid copepod community to a small-scale natural disturbance. J. Mar. Res. 38:381–395.

Thistle, D. 1982. Aspects of the natural history of the harpacticoid copepods of San Diego Trough. Biol. Oceanogr. 1:225–238.

Thistle, D. 1983. The role of biologically produced habitat heterogeneity in deep-sea diversity maintenance. Deep-Sea Res. 30:1234–1245.

Thistle, D., J. A. Reidenauer, R. Findlay, and R. Waldo. 1984. An experimental investigation of enhanced harpacticoid (Copepoda) abundances around isolated seagrass shoots. Oecologia 63:295–299.

Thistle, D. and J. E. Eckman. 1990. The effect of a biologically produced structure on the benthic copepods of a deep-sea site. Deep-Sea Res. 37:541–554.

Varon, R. and D. Thistle, 1988. The response of a harpacticoid copepod to a small-scale natural disturbance. J. Exp. Mar. Biol. Ecol. 118:245–256.

Wilson, G. D. F. and D. Thistle. 1985. *Amuletta,* a new genus for *Ilyarachna abyssorum* Richardson, 1911 (Isopoda: Asellota: Eurycopidae). J. Crust. Biol. 5:350–360.

Woodin, S. A. 1978. Refuges, disturbance, and community structure: A marine soft-bottom example. Ecology 59:274–284.