

Xenophyophoria (Rhizopoda, Protozoa) in bottom photographs from the bathyal and abyssal NE Atlantic

Xenophyophoria
Bottom photographs
Bathyal
Abyssal
Subtropical NE Atlantic
Xenophyophoria
Photographies du fond
Bathyal
Abyssal
Atlantique NE subtropical

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ABSTRACT

Xenophyophores, giant testate rhizopods, are described from bottom photographs taken with a combined epibenthic sledge-camera system at depths of 1000, 3000, 4000 and 6000 m in the NE Atlantic off West Africa. Seven species, all living on the sediment surface and belonging to three distinct growth form types, are recognized in the photographs. Three species are of a reticulate growth form type (= *Reticulammina* and *Syringammina*), three species are platy and one species is branched. One of the reticulate forms (from 3000, 4000 m) is identified from the corresponding samples as *R. labyrinthica* (Tendal, 1972) but the other species could not be recognized with any certainty in the samples. It is suggested that the 6000 m *Reticulammina*, which is represented in the photographs but not in the corresponding sample, is so fragile that the test is totally disrupted during sampling.

The photographs, taken together with the samples, demonstrate that xenophyophores are as diverse in the Atlantic (18 species now known) as in the other oceans. They are also abundant: *Reticulammina* often occurs in estimated densities of hundreds per 100 m², at most several thousand per 100 m². This is considerably higher than earlier estimates and underlines the view that xenophyophores may, in certain areas, be a dominant element in the abyssal bottom fauna. The present photographs now make it possible better to recognize xenophyophores in previous photographs of the sea floor.

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RÉSUMÉ

Xenophyophores (rhizopodes, protozoaires)
sur des photographies du fond
des zones bathyales et abyssales de l'Atlantique Nord-Est

Des xénophyophores, rhizopodes géants à test, sont décrits d'après des photographies du fond obtenues par un ensemble combinant une luge épibenthique avec un appareil photographique à des profondeurs de 1000, 3000, 4000 et 6000 m dans l'Atlantique Nord-Est au large de l'Afrique occidentale. Sept espèces, vivant toutes à la surface du sédiment et appartenant à trois différents types de formes de croissance, sont identifiées sur les photographies. Trois espèces appartiennent à la forme de croissance de type réticulé (= *Reticulammina* et *Syringammina*), trois espèces sont de forme aplatie et une espèce est ramifiée. L'une des formes réticulées (observée à 3000 et 4000 m) est identifiée à partir des prélèvements correspondants à *R. labyrinthica* (Tendal, 1972) mais les autres espèces n'ont pu être reconnues avec quelque certitude dans les prélèvements. Il est suggéré que la forme de *Reticulammina* de 6000 m observée sur les photographies, mais pas dans le prélèvement correspondant, est tellement fragile que le test est totalement détruit durant le prélèvement.

Les photographies, prises en même temps que les prélèvements, démontrent que les xenophyophores sont aussi diversifiés dans l'Atlantique (18 espèces actuellement connues) que dans les autres océans.

Ils sont également abondants : *Reticulammina* est souvent présent à des densités estimées de plusieurs centaines pour 100 m², et jusqu'à plusieurs milliers pour 100 m². Ceci est beaucoup plus élevé que les estimations antérieures, et renforce l'idée selon laquelle les xenophyophores peuvent, dans certaines zones, constituer un élément dominant dans la faune benthique abyssale. Les photographies réunies permettraient une identification plus facile des xenophyophores sur des photographies des grands fonds océaniques, obtenues précédemment.

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INTRODUCTION

During recent years the photographic recording of deep-sea benthos has undergone considerable technical development and it is now widely used for many different purposes (Hersey, 1967; Isaacs, Schwartzlose, 1975; Thiel, 1970; Holme, McIntyre, 1971; Rice *et al.*, 1979). An important aim is to provide information which cannot be obtained with the methods generally used for sampling the macro- and megafauna.

For certain animal groups, photography may be virtually the only means of obtaining information about their general biology. This is so with the Xenophyophorea, a group of giant, bottom-living rhizopods (Tendal, 1972) which are often extremely fragile and lightly built and have no well-known representatives in shallow water.

Although xenophyophores are not rare, at least in certain deep-sea regions, only a few photographs purporting to show them *in situ* have hitherto been published (Table 1). The kind of information obtainable from such photographs includes environmental features, approximate generic identifications, life position, diversity and density estimates.

METHODS

The present photographs were taken along a series of depth transects from about 1000 m to about 6000 m during cruises 79 (1976), 82 (1977) and 105 (1979) of the RRS "Discovery" off Mauretania, West Africa (Table 2). They were acquired, and the sea floor was simultaneously

Table 1
Xenophyophores hitherto identified in deep-sea bottom photographs.

Presumed genus	Area	Depth (m)	Reference	Plate/figure
<i>Psammetta</i>	SW Pac.	7900-8700	Tendal, 1972	Pl. 16
			Lemche <i>et al.</i> , 1976	Pl. 3
<i>Reticulammina</i>	SW Pac.	800	Tendal and Lewis, 1978	Fig. 4, 6
	NW Atl.	3800-4000	Rice <i>et al.</i> , 1979	Pl. 5-10.
<i>Syringammina</i>	SW Pac.	800	Tendal and Lewis, 1978	Fig. 4-5
<i>Cerelasma</i>	SW Pac.	7900-8700	Lemche <i>et al.</i> , 1976	Pl. 4
	NW Atl.	5300	Tendal, 1980 a (*)	Pl. 1
<i>Stannoma</i>	SW Pac.	6800-8700	Lemche <i>et al.</i> , 1976	Pl. 4
<i>Stannophyllum</i>	SW Pac.	6800-8000	Lemche <i>et al.</i> , 1976	Pl. 5-6

(*) Thiel (1973; 1975) has also published one of these photographs, identifying the organism as a xenophyophore.

Table 2
Photographic stations made during RRS "Discovery" cruises 79 (1976), 82 (1977), and 105 (1979) at depths from 1000-6000 m.

Station No.	Haul No.	Date	Position	Depth (m)	Usable area of photos (m ²)
9128	10	12.11.76	24°18'N, 20°28'W	6059-6059	135
9131	9	19.11.76	20°18'N, 21°43'W	4006-4015	190
9131	10	19.11.76	20°15'N, 21°35'W	3950-3952	200
9131	11	20.11.76	20°09'N, 21°40'W	3921-3921	182
9131	12	20.11.76	20°07'N, 21°26'W	3856-3861	135
9132	7	24.11.76	20°59'N, 18°59'W	3083-3094	
9541	1	15.04.77	20°07'N, 21°25'W	3850-3854	117
9541	3	15.04.77	20°08'N, 21°41'W	3910-3912	88
10153	1	10.-11.10.79	29°06'N, 12°27'W	1065-1090	426

sampled, with a combined epibenthic sledge and camera system (Aldred *et al.*, 1976; 1979; Rice *et al.*, 1979). By means of a pinger, it was possible to determine when the gear was on the bottom and to monitor its operation. An odometer wheel recorded the distance travelled across the ocean floor.

The camera and flash unit were mounted on the frame of the sledge with the optical axis of the camera directed forwards and downwards at a shallow angle (14° to the horizontal). Photographs were taken at 15 or 30 second intervals and cover a trapezoidal area of the sea floor in front of the sledge. On each frame, a photographed area of about 2.6 m^2 was usable. The distribution and size of the xenophyophores was determined by projecting the photographs onto a grid, of which each unit represented a $20 \text{ cm} \times 20 \text{ cm}$ area of sea floor subdivided into $5 \text{ cm} \times 5 \text{ cm}$ squares. Only exposures taken when the sledge was approximately horizontal were used.

RESULTS

Description of the photographs

The 1000 m photographs

Station 10153, haul 1, 1065-1090 m. The bottom is usually flat with scattered biogenic mounds, faecal casts and occasional small depressions. Animal traces are common. The sediment is pteropod ooze.

The photographs show two reticulate growth forms.

Coarsely reticulate form

The single specimen observed corresponds well to the rather coarsely reticulate form found in the 3000 m and the 4000 m photographs and identified as *Reticulammina labyrinthica* (Tendal, 1972).

Finely reticulate form (Fig. 1 A-G)

In form, the specimens are approximately hemispherical, often somewhat flattened or occasionally more domesha-

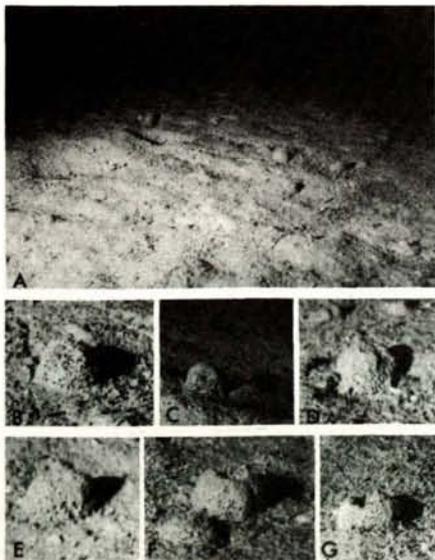


Figure 1
Syringammina at 1000 m. A) Panorama of seafloor showing three specimens (right of centre). B)-G) Individual specimens with estimated diameters of 4-6 cm. Note the crater-like hole in the top part of specimens F) and G).

Table 3

Estimated densities of the reticulate and platy organisms at stations 9128, 9131, 9541 and 10153.

Station No.	Haul No.	Reticulate organisms no per 100 m ²		Platy organisms no per 100 m ²
		Range	Mean	Mean
9128	10	0-380	156	—
9131	9	38-722	228	10
9131	10	38-912	473	22
9131	11	304-2052	969	8
9131	12	76-646	221	6
9541	1	0-346	150	6
9541	3	230-808	473	5
10153	1	0-462	159	—

ped, with an estimated diameter of 1.5 to 7 cm, usually 2.5-5.5 cm, at the base. The rather even surface shows a moderately regular reticulate pattern. The estimated maximum dimension of the spaces in the reticulation is usually $< 5 \text{ mm}$, in most cases between 2 and 4 mm. The organism occurs abundantly with densities up to 460 per square meter (Table 3).

The objects photographed can be identified with reasonable certainty as members of the genus *Syringammina*, partly because they are of the right size and partly because they closely resemble other objects in deep-sea photographs which have already been identified as *Syringammina* sp. (Tendal, Lewis, 1978). The corresponding sample is devoid of xenophyophore remains.

Many specimens are situated in the centre of a shallow depression, about twice as wide as the test, a phenomenon also noted for *Reticulammina* in the deeper localities. Another remarkable feature is a crater-like hole in the top part of many specimens. It may have been made by an unidentified organism, which, or part of which, may sometimes be seen on the border of the excavation.

The 3000 m photographs

Station 9132, haul 7, 3083-3094 m. The bottom is uneven with low mounds and shallow depressions on a scale of about half a metre. The surface is smooth. Animal life is fairly abundant and there is considerable biological disturbance of the sediment surface. The sediment is *Globigerina* ooze with a CaCO_3 content of approximately 40%. Because of the uneven surface, the net was rarely horizontal and so it was difficult to apply the scale grid to these photographs. As a result, no attempt was made to calculate densities and all dimension estimates are highly approximate.

Four growth form types can be recognized:

Regular to convoluted platy form (Fig. 2 A-F)

This often appears as a plate of variable thickness which stands upright above the sediment surface and varies from being regular and approximately fan-shaped to more or less convoluted. The surface of the plate often has rather distinct concentric lines, paralleling the outer margin. In at least one specimen, vague traces of radial ornamentation are visible between these lines. Some

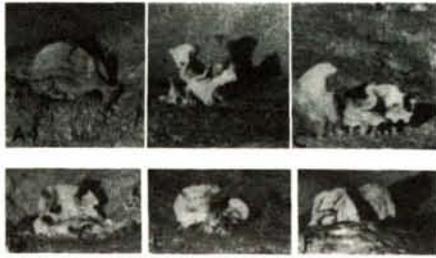


Figure 2
Regular platy forms at 3000 m. The maximum estimated dimensions are 4-6 cm, except for the specimen (or cluster of specimens) shown in F, which is approximately 10 cm across. Note the concentric lines on the specimens shown in A), E), F).

specimens show one, or occasionally several side plates, usually smaller but sometimes as large as the main plate. The free margin is evenly curved and appears rounded in cross section. The basal margin often bears root-like structures, but sometimes directly penetrates the sediment or has the form of a stalk. Estimated size: usually 4-10 cm in width, although there are smaller specimens, some probably <1 cm across.

These organisms are not present in the samples. They are fairly common in the photographs with at least 53 specimens scattered among the 30 frames. They are probably xenophyophores although they do not obviously belong to any of the known genera.

Highly irregular platy form (Fig. 3 A-C)

The test is platy but always irregular with no clearly definable form. The surface is smooth and without ornamentation. At its base, the test directly adjoins the sediment surface without obviously penetrating it. Estimated size: up to about 5 cm across. The organisms are common and usually occur in clusters, within which the single individuals are not clearly recognizable. A *Galatheamina* sp. was dominant in samples from this station, and because half of the recovered fragments were platy, although very small, it may correspond to this form.

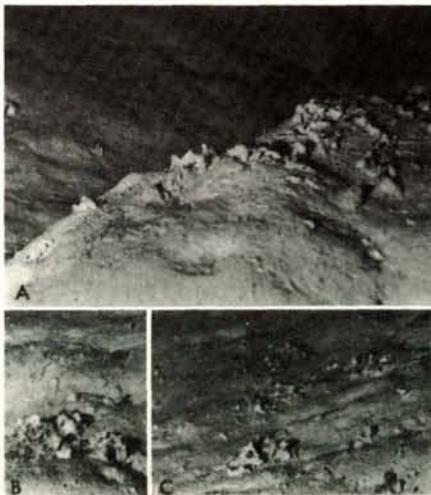


Figure 3
The irregularly platy form at 3000 m. A) Specimens growing on the crest of a small ridge; the visible part of the ridge crest is estimated to be approximately 45 cm long. B) A cluster of specimens, estimated to be about 10 cm across. C) Scattered specimens; the cluster in the foreground has an estimated width of 5-6 cm.

Branched form (Fig. 4 A-C)

The overall shape is hemispherical. The test is composed of a large number of branches which generally radiate from the basal area and seem to be circular in cross-section, with estimated diameter limits of 1 to 7 mm. The branching pattern is somewhat irregular, in principle dichotomous with frequent anastomoses. At the base, there are indications that parts of the test are buried, although special attachment structures are not visible. Very small specimens comprise only a few branches. Estimated size: up to about 12 cm across; very small specimens may be only 1 cm across.

The test structure is reminiscent of *Syringamina* but the branching is more irregular, the branches thicker and the meshes coarser than in the known species. In fact, the samples did yield a heavily fragmented and indeterminate *Syringamina* sp. These organisms are fairly common with at least 57 specimens scattered among the 30 frames.

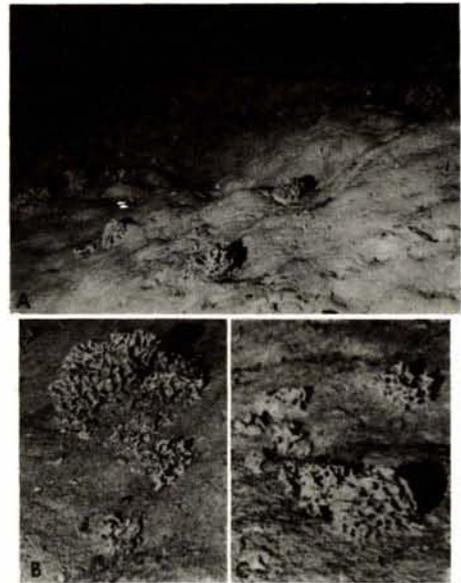


Figure 4
Xenophyophores at 3000 m. A) Panorama showing more than six branched forms, a reticulate form (lower left) and scattered, irregular platy forms; the nearest branched form has an estimated width of 8 cm. The view is oblique because the net was not horizontal. B) Large, partially collapsed branched specimen, estimated to be about 13 cm across. C) Reticulate form, approximately 4 cm wide, with branched forms behind.

Reticulate form

There are 20-25 specimens of a reticulate organism ranging in estimated diameter from 4 to 7 cm. They resemble in all respects the objects identified as *Reticulammina labyrinthica* in the 4000 m photographs. They were not represented in the sample.

The 4000 m photographs

Station 9131, hauls 9-12, 3856-4015 m. The bottom is flat, with scattered biogenic mounds and depressions and considerable biological disturbance. The sediment is *Globigerina* ooze with a CaCO₃ content of approximately 65%.

Two different growth type forms can be recognized.



Figure 5

Xenophyophores at 4000 m. A)-C) *Platy* specimens with large main plate, estimated maximum dimensions 4-5 cm. D), E) Triangular *platy* specimens, estimated maximum dimensions 4-5 cm. F), G) Branched *platy* specimen, estimated maximum dimensions 4-5 cm. H) Large plate, estimated maximum dimension 7 cm. I) Panorama showing numerous reticulate specimens (*Reticulammina labyrinthica*); their density in this photograph is about 1250 per 100 m², the specimen on the lower margin is about 2.5 cm across.

Platy forms

These organisms are uncommon, occurring in densities of 6-22 per 100 m². However, the 30 or so specimens visible in the photographs show considerable variability.

a) with large main plate (Fig. 5 A-C)

At least half of the specimens have a fanshaped main plate, about twice as broad as high, with a rounded or faintly lobed upper edge and raised on a short and broad stalk, up to half the height of the plate. Most of these specimens, in particular the larger ones, bear 1-4 knob-like or plate-like excrescences on the exposed side. Estimated size: the largest main plates are about 5 cm wide;

b) triangular specimens (Fig. 5 D, E)

A few specimens comprise a single plate in the form of a nearly equilateral triangle, raised on a stalk about half the length of the triangle sides. Faint vertical lines on the surface indicate a slightly undulating growth pattern. Estimated size: about 5 cm high;

c) branched specimens (Fig. 5 F, G)

In a few stalked specimens the *platy* part of the test is branched. They range from being dichotomously branched, with the branches and stalk of about equal diameter, to being basically platelike with the branches occurring as outgrowths from the edge of the plate. The tips of the branches seem somewhat twisted. Estimated size: about 5 cm maximum height;

d) large plate (Fig. 5 H)

A single specimen consists of a large main plate with a large side plate. It stands upright on a very short stalk.

The surface has a faint concentric banding. Estimated size: 6-7 cm high.

The *platy* forms are not represented in the samples. The differences in form and branching pattern might reflect different species, but they could just as well represent variation within a single species. In the latter case this variation would be large enough to also cover the regular to convoluted form at 3000 m. In the discussion they are counted as one species at each of the localities.

Reticulate form (Fig. 5 I)

This form has been identified as *Reticulammina labyrinthica* Tendal (1972) and will be described and illustrated fully in a later paper (Gooday, Tendal, in prep.). It occurs abundantly in densities up to about 2000 per 100 m² (Table 3) with hardly a single frame devoid of specimens. There is a broad size spectrum, but it is not possible to measure specimens accurately enough to determine their size distribution. Small specimens display the same form as larger ones. Scattered, fairly low piles (width two or three times height) of approximately circular outline (estimated diameter 5 to 7 cm) with uneven surfaces and sometimes with traces of irregular ridges may be dead, collapsed *Reticulammina* specimens. This form occurs abundantly in the samples, in the form of thousands of fragments.

The 6000 m photographs

Station 9128, haul 10, 6059 m. The bottom is flat and the surface is smooth except for occasional animal traces. The sediment is red clay with a CaCO₃ content of about 1%.

A reticulate growth form type is common (Fig. 6 A-D). In shape and structure it closely resembles *R. labyrinthica* at 4000 m, but the ornamentation is coarser, especially near the top where vertical flange-like ridges are commonly developed. Root-like structures may be pronounced. Estimated diameter: 1-4 cm, usually 2-3.5 cm.

Despite their similarity, we hesitate to identify these specimens as *R. labyrinthica*. Firstly, there are slight differences in the reticulate ornamentation. Secondly, this form is not represented in the samples, which suggests extreme fragility. In the discussion it is counted as a separate species.

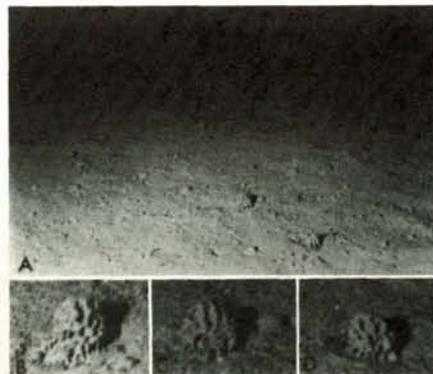


Figure 6

Reticulate form at 6000 m. A) Panorama showing scattered specimens; their density in this photograph is about 350 per 100 m². B)-D) Individual specimens with estimated diameters of 3-4 cm. Note the elongate furrow in C) and the depression surrounding the specimen in D).

The identifications

The identification of the objects in the photographs as xenophyophores is crucial and is based on: a) the xenophyophores in the simultaneously collected samples; b) comparison of the objects with museum material (particularly their size, body form and surface structure); and c) exclusion of other organisms present in the catches. The literature interpreting structures seen in other deep-sea photographs as organisms, casts, organic remains, etc. has also been considered.

The simultaneously collected samples have yielded 12 xenophyophore species (Gooday, Tendal, in prep.) but it is possible to identify with certainty only one of these (*R. labyrinthica* at 4 000 m) in the corresponding photographs. At two stations (1 000 and 6 000 m) xenophyophores were clearly recognizable in the photographs but entirely absent from the material collected. Since the ability of the gear to adequately sample macrobenthic organisms has been previously demonstrated, this discrepancy requires explanation. There are several possibilities:

a) some species are probably too small to be visible on the photographs;

b) some species may live buried in, or under the sediment surface and appear in photographs as a kind of "lebensspuren", if at all;

c) certain very fragile species are perhaps damaged beyond recognition during sampling. Taking this point further, there may be xenophyophores which are so delicate that specimens are simply "blown" into tiny fragments by the pressure wave in front of the sledge. This may apply to the 6 000 m reticulate form. Such species would never appear in catches and could be investigated only by photographic methods;

d) the absence in the catch of the *Syringammma* photographed at 1 000 m possibly reflects the inability of the gear to operate effectively on pteropod oozes. The residue from this station consists almost entirely of pteropod shells. It is easy to imagine these rapidly filling the net to form a loosely interlocking mass preventing further sampling. At two other stations not considered in this paper, xenophyophores are present in bottom photographs but are almost entirely absent from the corresponding pteropod shell dominated sample residue.

A search of the extensive literature showing deep-sea bottom photographs reveals numerous examples of

possible xenophyophores. Many are impossible to identify with any certainty, because of the photographic enlargement or the lighting angle, but there are also some which seem reasonably recognizable. In particular, the experience gained here in studying the numerous *Reticulammina* specimens allows members of this genus to be identified with more confidence. As a result, there is now substantial evidence that this genus is more widely distributed than hitherto recognized (Table 5, Fig. 7).

DISCUSSION

The samples and photographs together demonstrate the presence of 18 species of xenophyophores in the area investigated. The numbers in other relatively restricted deep-sea regions that have been fairly intensively studied are summarized in Table 4. In the three regions (off East Africa, Central and East Pacific) where similar depth ranges were sampled somewhat fewer species were recorded than reported here. Thus, in addition to indicating that the xenophyophore fauna is as diverse in the bathyal and abyssal Atlantic as in the other large oceans, our results also emphasize the value of using the combined method in deep-sea work.

The number of species recognized in the photographs is greatest at 3 000 m (4) and least at 6 000 m (1) with two species being present at both 1 000 and 4 000 m. Larger overall numbers of xenophyophores appear in the 3 000 and 4 000 m photographs than in those from 1 000 and 6 000 m. For particular species, the total number of individuals varies from relatively few (4 000 m platy form) to many hundreds (4 000 m *R. labyrinthica*). Fairly precise density estimates are available for

Table 5

Xenophyophores referable to Reticulammina shown, but previously unrecognized in published deep-sea photographs.

Area	Depth (m)	Reference	Figure
NE Atlantic	1 100	Pratt, 1967	13-9
CE Atlantic	7 000	Pratt, 1962	6
	6 600	Heezen <i>et al.</i> , 1964	9
S. Atlantic	4 350	Ewing and Davis, 1967	24-85
W. Pacific	650	Zenkevitch, 1970	154
E. Pacific	4 600	Menzies <i>et al.</i> , 1973	5-28E
Antarctica	3 400	Simmons and Landrum, 1973	On page 42

Table 4

The number of xenophyophore species known in selected deep-sea regions.

Area	Species number	Depth range sampled	Methods	Author, year
Off West Africa	16	1 065-6 059 m	Trawl sledge photography	This investigation
Off East Africa	13	1 158-5 110 m	Trawl	Tendal, 1972
SW Pacific trenches	7	6 758-8 260 m	Photography	Lemche <i>et al.</i> , 1976
New Zealand	6	652-1 285 m	Trawl photography	Tendal and Lewis, 1978
Central Pacific	13	3 814-5 353 m	Trawl	Tendal, 1972; 1980 b.
East Pacific	8	981-4 758 m	Trawl	Tendal, 1972

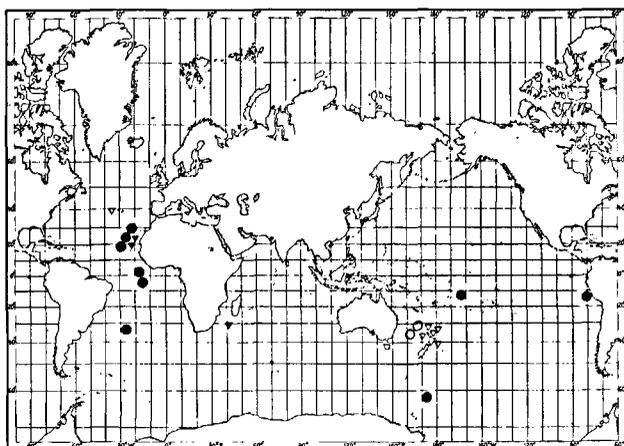


Figure 7
The distribution of the genus *Reticulammina* as improved by identifications in deep-sea bottom photographs: ●, hitherto unpublished photographs, or published photographs in which *Reticulammina* had not been previously recognized; ○, published photographic identifications; ▼, unpublished samples; ▽, published samples.

Reticulammina from 1000, 4000 and 6000 m and the much rarer platy form at 4000 m (Table 3). The previous estimates for xenophyophore densities are tentative and are distinctly smaller than most of those reported here. Lemche *et al.* (1976) and Tendal and Lewis (1978) give figures of about 100 specimens per 100 m² for their most common species *Psammetta* sp. (from 7875-7921 m) and *Syringamma tasmanensis* (from 812-1285 m). In comparison, the mean densities of *R. labyrinthica* run into hundreds of specimens per 100 m² and the maximum value is over 2000 per 100 m². The explanation for the large number of xenophyophores in the present photographs is probably partly technical and partly biological. The photographs themselves are numerous and of high quality while the area investigated is mostly within the optimum depth range for xenophyophores and also lies approximately below a coastal upwelling area, thus receiving an enhanced food supply.

The distribution of *R. labyrinthica* in the 4000 m photographs is random on a scale of meters according to the Clark and Evans (1954) measure. This contrasts with the possible aggregation reported for *Psammetta* sp. and *Stannoma* sp. (Lemche *et al.*, 1976). However, there is some slight indication that the distribution of *R. labyrinthica* is patchy on a larger scale. This species is most abundant around 20°08'N, 21°40'W (9131, haul 12; 9541, haul 3) and least abundant some 26 km away around 20°07'N, 21°25'W (9131, haul 11; 9541, haul 3) (Table 4). Kilometre scale patchiness has been clearly demonstrated for abyssal benthic foraminifera (Bernstein *et al.*, 1978).

The present photographs, supported as they are by simultaneously collected samples, emphasize the view that xenophyophores dominate certain deep-sea benthic communities and must play a considerable ecological role (Tendal, 1972; Thiel, 1975; Lemche *et al.*, 1975; Tendal, Lewis, 1978; Rice *et al.*, 1979). With very little available information about the general biology of the xenophyophores and none about the processes framing their lives, it is impossible to define this role further.

CONCLUSIONS

The main general results of this analysis are that this photographic survey:

- 1) suggests the existence of species so fragile that they have never been brought to the surface in a recognizable condition by any of the generally used types of gear;
- 2) allows a new and better interpretation of some of the objects seen in previously published photographs of the deep-sea bottom;
- 3) is an important supplement to the samples from the area (Gooday, Tendal, in prep.), and reinforces the view that in the Atlantic xenophyophores are as common and diverse as they are in the other two large oceans; and
- 4) clearly shows that members of this often overlooked group may in places be a dominant element in the abyssal bottom fauna.

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