

Submersible observations of the invertebrate fauna on the continental slope southwest of Ireland (NE Atlantic Ocean)

Bathyal hard ground fauna

Depth zonation

Suspension feeders

Anthozoa

Echinodermata

Faune bathyale de fonds durs

Zonation en profondeur

Suspensivores

Anthozoa

Échinodermata

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ABSTRACT

Relatively little is known of the fauna found on rock substrates in the deep ocean. As a result of the Franco-British deep diving cruise *Cyaporc* in 1986 using the submersible *Cyana* we present observations of a highly diverse sponge, cnidarian and echinoderm fauna occurring between 1 800 and 3 000 m on the steep slopes to the west of the Porcupine Bank and Goban Spur. This fauna is dominated by suspension feeders and appears to show a vertical zonation corresponding to water mass structure. The highest biomass and variety of echinoderms are found between 2 100 and 2 600 m bathed in northward flowing North East Atlantic Deep Water. We present also additional observations of species known from previous sampling programmes but rarely photographed in their natural environment.

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RÉSUMÉ

Observations par submersible de la faune d'invertébrés sur la pente continentale au sud-ouest de l'Irlande (Atlantique NE)

La faune sur fond rocheux à grande profondeur est relativement peu connue. Cette contribution résultant de la campagne franco-britannique *Cyaporc* (plongées profondes avec le submersible *Cyana*) fait état d'une faune hautement diversifiée de spongiaires, cnidaires et échinodermes entre 1 800 et 3 000 m sur les fortes pentes à l'ouest du banc Porcupine et de l'éperon de Goban. Cette faune est dominée par des suspensivores et semble présenter une zonation verticale correspondant aux masses d'eau. La biomasse la plus forte et la diversité d'échinodermes la plus élevée se situent entre 2 100 et 2 600 m dans l'eau profonde de l'Atlantique nord-oriental qui s'écoule vers le Nord. Des observations complémentaires concernent aussi des espèces connues par des campagnes de prélèvements antérieures, mais qui avaient rarement été photographiées dans leur milieu naturel.

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INTRODUCTION

Since the first observations of the "Porcupine" and "Lightning" (Thomson, 1873), the more common fauna of the soft sediments in the deep NE Atlantic Ocean has become well known (Gage *et al.*, 1983; 1985; Laubier and Monniot, 1985). Although soft sediments dominate much of the seabed in the NE Atlantic, there are significant areas between 1 000 and 3 000 m depth along the continental slope where the seabed is very steep and consists of exposed rock. Sampling on steep rock surfaces by conventional methods of trawl, sledge and box core is difficult or impossible. The only rocky areas in this region that have been examined in detail are along the Bay of Biscay (Grasshoff, 1985 *a*; Roux, 1985; Zibrowius, 1985). With the exception of hydrothermal vents (as reviewed by Grassle, 1986) the fauna of rocky areas in other parts of the deep ocean has been poorly described, although there are data accumulating of the fauna associated with rocky areas on seamounts (Genin *et al.*, 1986; Moskalev and Galkin, 1986; Kaufmann *et al.*, 1989; Chave and Jones, 1991). The best way to examine these relatively inaccessible slopes is by surface controlled remote operated vehicles or direct observation from submersible. The latter opportunity arose during the Franco-British diving cruise *Cyaporc* of July and August 1986 when a series of transects from 3 000 to 1 800 m depth were worked up the steep western edges of the Porcupine Bank and Goban Spur. Additional observations were made on soft sediments at 1 760 m on the Goban Spur and at < 1 000 m in the Gollum Channel. Still photographs and video records of these rock slopes revealed areas of dense biological cover dominated by a sedentary fauna rich in poriferan, cnidarian and echinoderm species. Preliminary observations of the echinoderm

Table

Location of dive and dredge stations at which photographs were taken or samples collected.

Dive No.	Latitude N	Longitude W	Depth range (m)
29	49 33.7	13 05.8	1 678-1 683
30	50 19.4	12 51.3	2 634-2 881
31	50 43.9	11 13.2	816-923
32	51 24.5	15 11.0	2 798-1 970
33	51 16.2	15 08.4	1 726-2 820
34	51 20.3	15 15.1	2 164-3 000
35	49 34.0	13 06.2	1 675-1 676
36	50 42.1	11 07.1	468-768
37	49 29.9	13 29.6	2 637-3 000
38	49 34.8	13 06.4	1 672-1 680
39	49 29.2	13 29.4	2 119-3 000
40	50 44.1	11 13.2	922-931
41	50 44.0	11 13.2	906-949
Dredge No.			
1	51 21.50	15 08.98	2 500
2	49 27.40	13 31.251	ca. 2 000+ *
3	49 28.63	13 28.80	ca. 2 000+ *
4	49 32.009	13 34.694	ca. 2 000+ *

* Exact depth unknown owing to steepness of the underwater terrain.

fauna (Tyler and Lampitt, 1988) suggested a zonation related to water masses. Geological observations made during *Cyaporc* have been described elsewhere (Auffret *et al.*, 1987; Auzende *et al.*, 1989; Masson *et al.*, 1989).

This paper presents the analysis of 3000 photographs of these transects and identifies, where possible, the dominant species and relates the distribution of these species to the hydrography of the NE Atlantic. We have included in our figures species for which few *in situ* photographs had previously been taken.

MATERIALS AND METHODS

These observations were made during the Franco-British diving cruise *Cyaporc* in July and August 1986 on the western edges of the Porcupine Bank and Goban Spur and in the Gollum Channel in the Porcupine Seabight using the research submersible *Cyana* (Fig. 1, Tab.). All the areas to be dived had previously been surveyed by *Seabeam* (see Renard and Allenou, 1979) in 1985. Position fixing of the submersible was by triple transponder array with the support ship *Le Suroit* fixing by Satnav (Satellite Navigation). The transects were selected for their geological significance and the observations of the diverse fauna was serendipitous. During each dive *Cyana* descended to its maximum depth of 3 000 m and proceeded upslope. Additional dives as part of an experimental programme were conducted on soft sediment in the Gollum Channel (ca. 900 m) and the Goban Spur (1 760 m). Visual records were made using video and observer-operated single frame camera using ASA 200 diapositive film. With the help of the taxonomic experts consulted (listed in *Acknowledgements*) the fauna observed in the photographs was identified to genus and species level when possible. Some species were collected

Figure 1

Chart of the Porcupine Seabight area showing location of dive sites, dive transects and dredge sites. Depth contours in meters.

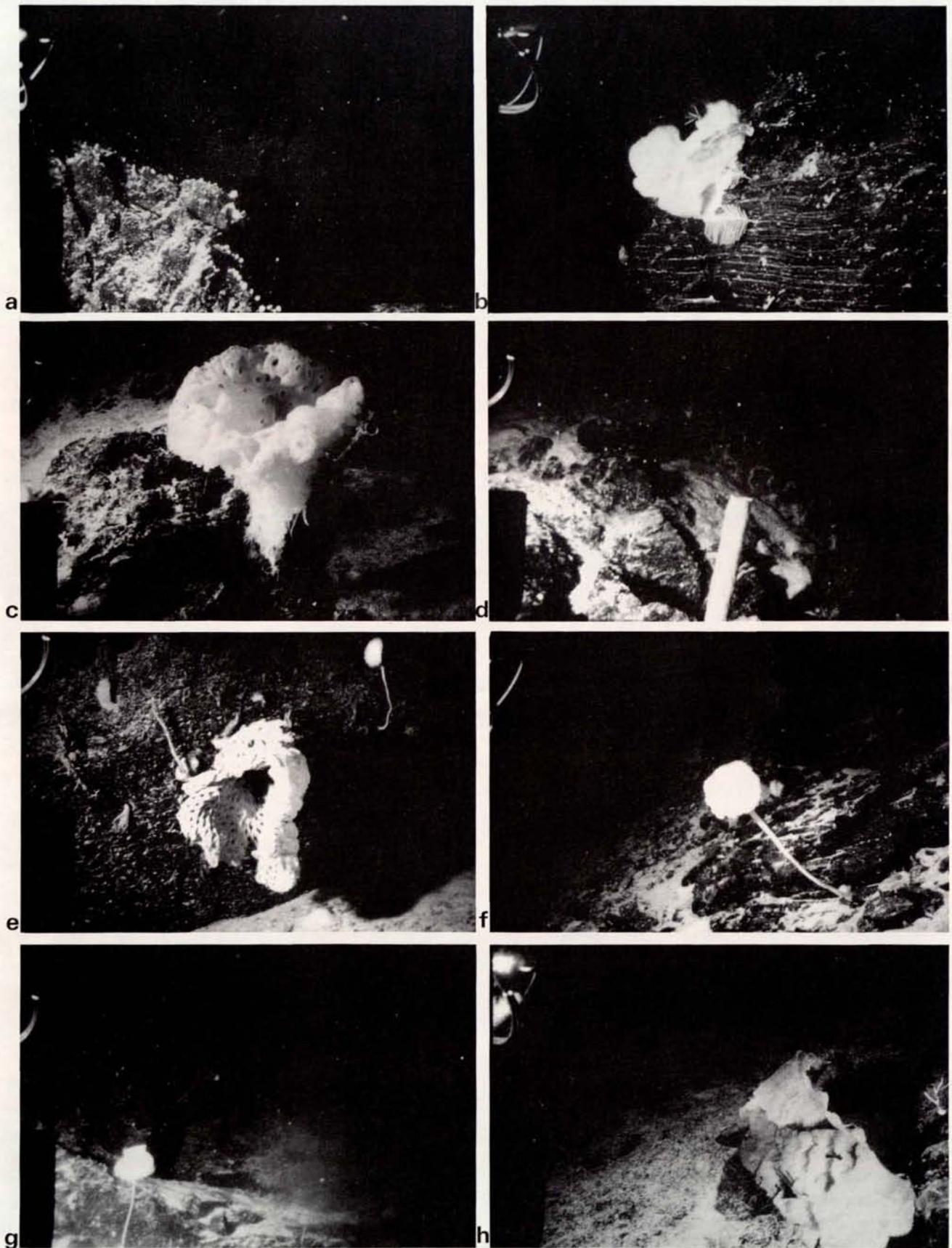


Figure 2

Sponges together with other fauna observed during Cyaporc: a) unidentified small yellow sponge crowded along rock crests (dive 32: 2 672 m); b) ? *Poecillastra*-like sponge and antipatharian *Bathypathes patula* (dive 32: 2 148 m); c) unidentified alveolar hexactinellid (dive 33: 2 084 m); d) ? *Euplectella* sp. (dive 33: 2 605 m); e) unidentified ? lithistid in centre and pedunculate hexactinellid ? *Caulophacus* to the upper right (dive 37: 2 823 m); f) ? *Crateromorpha* sp. (dive 32: 2 119 m); g) ? *Aulochone* sp. (dive 33: 2 595 m); h) large unidentified sponge and axis of gorgonian *Isidella longiflora* to the right (dive 34: 2 969 m).

by the submersible on small rock samples but most sessile species were attached to bed rock and thus not easily dislodged. In addition four dredge samples were taken during the cruise. Where possible species were grouped into depth zones and first and last occurrences noted.

OBSERVATIONS

Along the western edge of the Porcupine Bank between 1 800 and 3 000 m the margin consists of highly metamorphic, probably Caledonian, basement covered by Palaeozoic sediments and an almost tabular Mesozoic cover (Auffret *et al.*, 1987; Auzende *et al.*, 1989; Masson *et al.*, 1989). The northern part of the Goban Spur is composed of sedimentary rocks ranging from Barrenian to Eocene in age. Over all the exposed rock surfaces was a coating of black manganese oxide. Where the slope was less steep the bedrock was covered with a dusting of hemipelagic ooze and at certain levels where the slope of the bed was relatively gentle sediment accumulated. At a number of levels there were scree slopes consisting of rock debris. In the Gollum Channel the sediment consisted of fine sand and silt and showed signs of rippling. Scattered in this channel were isolated boulders up to 1 m diameter possibly deposited as a result of ice rafting.

Rather than present the data according to station we have elected to discuss the main taxa observed in the photographs and their distribution within the transects.

Sponges

The sponges were most common along the deeper rocky transects (> 2 400 m) on the western escarpment of the Porcupine Bank and Goban Spur and were rarely found on the soft sediments of the Goban Spur or Gollum Channel. Sponges are recognizable only as crusts on stones on the shallower soft bottoms of the eastern extremity of Gollum Channel and the eastern rise of the Porcupine Seabight.

Identification of sponges was very difficult. No extensive collections of sponges from the depths surveyed by *Cyaporc* have yet been made. This is particularly true between 2 000 and 3 000 m where the sponge fauna is highly diverse. Because exterior morphological convergences occur the consulted sponge specialists were reluctant to provide more than statements on the resemblances with deep-water sponges that are figured in various works of the classical deep water expeditions.

Among the larger photographed sponges many morphological types can be distinguished. A small yellowish sponge, roughly egg-shaped and attached to the rock by a narrow base occurs on rock crests not invaded by sediment (Fig. 2 a). Large lamellar forms, straight or contorted, may be demosponges *Poecillastra* (Fig. 2 b, 4 g, 5 e). A large globular form (Fig. 5 f) is possibly the demosponge *Geodia megastrella* Carter, 1876. Lamellae or funnels of meshwork may represent lithistids (Fig. 2 e). Hexactinellids are diversified. Narrow cylindrical forms suggest *Euplectella* (Fig. 2 d) whilst large

irregular forms, roughly cylindrical with oblique upper edges resemble *Asconema*. Pedunculate sponges of different types probably represent various genera: globular with a thick stalk; pedunculate with a large oblique top, possibly *Caulophacus* (Fig. 2 e); pedunculate with a point on the distal part, possibly *Hyalonema*; pedunculate with a distal globular alveolar part, possibly *Crateromorpha* (Fig. 2 f); distal part campanuliform on a particularly thin and long stalk, possibly *Aulochone* (Fig. 2 g, 5 b). Another hexactinellid is characterized by a distinctly alveolar structure and an irregular mushroom to funnel shape on a strong pedicel (Fig. 2 c). Various other morphological forms were observed but could not be assigned even to family or higher category (Fig. 2 h).

Hydroids

No hydroids are recognizable with certainty on *Cyaporc* photos. Bushy structures photographed during dive 32 (2 668 m) which resemble gorgonians of the "bottle-brush" type (as in the genera *Thouarella* and *Chrysogorgia*) may in fact be tufts of hydroids attached to some anthozoan (possibly gorgonian) axis.

Rosalinda sp.

A hydroid of the genus *Rosalinda* Totton, 1949, incrusting the calcareous axis of the gorgonian *Isidella elongata* (dredge 3), unfortunately has been preserved dry with its bulky substrate. The hydroid forms a flimsy brownish crust (easily detachable) from which rise tiny, occasionally branched axes, the latter formed of horny material that can also be seen as strands in the crust. According to W. Vervoort (pers. comm.) the incomplete preservation does not allow specific identification, but it might well be *Rosalinda williamsi* Totton, 1949. This species was known only from the scanty type material (incrusting a worm tube and the scleractinian *Desmophyllum cristagalli*) obtained from a cable in the Gulf of Biscay (47° 34' N, 7° 05' W, 440 m; see also Vervoort, 1962; 1964).

Actinians

Several types of actinian photographed during *Cyaporc* are only tentatively identified.

Actinoscyphia saginata (Verrill, 1882)

Several of the large actinians observed on rocky surfaces were characterized by a very enlarged oral disc attached to an elongate narrow base appear to be *A. saginata* (Fig. 3 a). This species is found both in the Celtic Sea and west of Ireland between 700 and 2 177 m (Doumenc, 1975; Riemann-Zürneck, 1978) and on the Galicia Bank, off NW Spain where Boillot (1987) has illustrated it as *Phelliactis robusta*.

Phelliactis robusta Carlgren, 1928

Several photographs show a rather massive actinian solidly attached to stones embedded in soft bottoms and characterized by the oral disc not in the axis of the column (Fig. 3 b).



Figure 3

Actinians, antipatharians and alcyonarians together with other fauna observed during Cyaporc: a) Actinoscyphia saginata (dive 37: 2 380 m); b) Phelliactis robusta (dive 36: 784 m); c) Bolocera sp. with crab near its base (dive 36: 762 m); d) unidentified corallimorpharian anemone (dive 34: 2 898 m); e) Lophelia pertusa with ? Callogorgia verticillata fans (dive 40: 909 m); f) Bathypathes patula (dive 32: 2 412 m); g) bushes of Leiopathes grimaldii and Bathypathes patula to the left (dive 33: 2 049 m); h) several colonies of Anthomastus sp. on rock edge, large stalked crinoid Anachalypsicrinus nefertiti, brisingiid ? Freyella and comatulid crinoid ? Thaumatoocrinus (dive 33: 2 567 m).

P. robusta is found at deep sites in the Celtic Sea (1 797 m) and further north from the north of Scotland to the Denmark Strait (Doumenc, 1975).

Bolocera sp.

Large radial actinians with many tentacles attached to stones appear to be a species of the genus *Bolocera* (Fig. 3 c). In some photographs a crab is present on the stones near the base of the actinian. The poor resolution of these photographs prohibits the identification of the crab but more than one species is believed to occur. From dive 40 there is a strong suggestion that *Paromola cuvieri* (Risso, 1816) is one of the species present. The precise relationship between the actinian and the crab is unknown, but their regular occurrence together suggests that it is not entirely fortuitous.

Unidentified corallimorpharian

A corallimorpharian was observed once on rock (dive 34: 2 898 m; Fig. 3 d). The specimen clearly belongs to this group as its oral disc is surrounded by distinctly knobbed, short tentacles. It may belong to the Sideractidae.

Scleractinians

The deep-water scleractinian fauna of the NE Atlantic is well known especially in the Bay of Biscay and the Rockall Trough (Zibrowius 1980; 1985) and those observed or collected during *Cyaporc* are readily identifiable. Five species are solitary and three are colonial.

Caryophyllia ambrosia Alcock, 1898

One live specimen was collected during dive 35 (1 675 m). The adult of this species usually lives free on soft bottoms whilst the young attach to hard substrates such as pteropod shells. It was not identified with certainty from the photos owing to its small size (1-2 cm diameter) and its rather transparent polyp. *C. ambrosia* is locally abundant in the Bay of Biscay and Celtic Sea and occurs as far north as the Rockall Trough.

Trochocyathus sp.

Because of its small size this species is not recognizable in any of the photographs. A sub-fossil specimen collected during dive 33 (depth unrecorded) is short subconical in shape, on a narrow base, 8 mm high and 10 mm in diameter. Several individuals of the same form, of similar subfossil aspect coated by manganese oxides, had been dredged further south in the Celtic Sea during cruise *Cymor 1* in 1980 (47° 46.25' N, 8° 38.35' W, 2 800 m). This is apparently not one of the two species of *Trochocyathus* described by Zibrowius (1980).

Desmophyllum cristagalli Milne Edwards and Haime, 1848

Two live specimens were observed during dive 32 (1977 m) as well as dead specimens during dive 32 (1906 m) and

during dive 39 (2 462 m). Dead eroded specimens were collected during dives 32 and 33. In the NE Atlantic this species has been recorded as far north as Bill Bailey Bank (61° 04' N, 11° 18' W) and Norway. Of interest is the dead crowded population on vertical rock surfaces covered with manganese oxide. Similar observations were made further south in the Celtic Sea during cruise *Cymor 2* in 1981 suggesting similar ancient populations. These populations resemble those of *D. cristagalli* of the upper Pleistocene preserved *in situ* on deep escarpments (ca. 2 000 m) of the western and eastern Mediterranean (Zibrowius, 1980; Zibrowius and Hove, 1987). The age of the ancient population observed on the western slope of the Goban Spur is unknown as is the cause of its extinction.

Flabellum alabastrum Moseley, 1873

The large compressed scleractinians with a purple polyp that occurred on soft bottoms at 906 m during dive 40 appear to be *F. alabastrum* rather than *F. macandrewi* Gray, 1849, which is similar in shape but smaller and fissiparous. Both species of *Flabellum* have been reported from the Celtic Sea to west of Scotland (*F. alabastrum*) and north to the Shetlands, the Faroes and Norway (*F. macandrewi*). Their depth range overlaps at about 1 000 m, with *F. alabastrum* being the deeper species often being found with *Caryophyllia ambrosia* at ca. 2 000 m.

Javania cailleti (Duchassaing and Michelotti, 1864)

Isolated live specimens of this solitary species were encountered on horizontal and vertical rock surfaces between 2 034 and 2 117 m during dive 32. It is known from the Celtic Sea at depths of 932 to 2 070 m.

Madrepora oculata Linnaeus, 1758

Small live colonies were found between 906 and 915 m during dive 40. As seen during this dive this species commonly occurs with *Lophelia pertusa*. The patches of coral debris encountered at 725 m during dive 36 arise from *M. oculata* and/or *L. pertusa*. This species ranges to south of Iceland and to Norway where it may be found at depths less than 100 m.

Lophelia pertusa (Linnaeus, 1758)

A large colony was observed at 915 m during dive 40 (Fig. 3 e). It bears small live colonies of *Madrepora oculata* and a large gorgonian species apparently *Callogorgia verticillata*. Small live colonies observed on the same dive are most likely *L. pertusa*. This species ranges to south of Iceland and to Norway where it may be found at depths less than 100 m.

Solenosmilia variabilis Duncan, 1873

Live colonies were observed on vertical rock surfaces at 1 816 m during dive 32. *S. variabilis* is the third colonial deep-water scleractinian in the NE Atlantic that builds extensive structures which house a diverse fauna. *S.*

variabilis differs from *M. oculata* and *L. pertusa* by its type of branching and being found at greater depths. It has already been reported from the Celtic Sea and the Porcupine seabight (Zibrowius, 1980).

Zoantharians

Zoantharian colonies associated with pagurids and characterized by large polyps were observed repeatedly on soft sediments in the Gollum Channel during dive 40 (913-937 m). It is highly likely this species is *Epizoanthus paguriphilus* Verrill, 1885, previously sampled by Muirhead *et al.* (1986) from the Porcupine Seabight at similar depths.

Ceriantharians

Ceriantharians were photographed regularly on soft bottoms at 604 to 940 m depth in the eastern end of the Gollum Channel and on the eastern side of the Porcupine Seabight. None could be positively identified.

Antipatharians

There has been considerable new information of the deep-water antipatharians of the NE Atlantic including new records as far north as the Celtic Sea (Grasshoff, 1982 *a*; 1982 *b*; 1985 *a*). Fortunately habitat can contribute to identifying genera and even species. Antipatharians observed during *Cyaporc* were found only during the deeper dives in the Gollum Channel and during the dives along the western escarpment of the Porcupine Bank.

Antipatharians on soft bottoms, characterized by a simple axis in a high spiral (*Stichopathes*), were rarely seen. Forms on rock were common especially around 2 000 m depth and comprise several species in several genera. Those to which we can ascribe tentative identification include:

Antipathes glaberrima Esper, 1792

A colony observed during dive 32 (2 086 m) next to *Bathypathes patula* appears to be *A. glaberrima*. This species has previously been recorded from the Mediterranean and in the Atlantic from Morocco to the Great Meteor Seamount and the Azores (Grasshoff, 1985 *b*).

Antipathes punctata (Roule, 1905)

One specimen was collected at 2 500 m on the west side of the Porcupine bank (dredge 1). This species was originally described from the Azores (1 300 m) and the Cape Verde islands (1 311 m; Roule, 1905) but more recently has been redescribed from 2 100 m in the Bay of Biscay (Grasshoff, 1985 *a*).

Bathypathes patula Brook, 1889

This species, which forms yellow to golden colonies with a single series of simple fleshy branches on each side of the short stem (Fig. 2 *b*, 3 *f*, 3 *g*, 5 *e*), was common bet-

ween 2 086 and 2 412 m during dive 32 and one branch was recovered in dredge 4. *B. patula* has a world wide distribution and has been reported from several stations between 1 980 and 2 282 m in the Celtic Sea (Grasshoff, 1982 *b*).

Leiopathes grimaldii Roule, 1905

This species, which forms large irregular bushes (Fig. 3 *g*), was quite common between 1 813 and 2 049 m during dive 33. It was previously known from between Morocco and the Azores and has been found at shallower depths in the Bay of Biscay (Grasshoff, 1985 *a*).

Alcyonarians

Alcyonarians of the genus *Anthomastus* form pink or red colonies of a few large polyps (Fig. 3 *h*) and were observed repeatedly during *Cyaporc* in the deeper parts of the transects on the western escarpments of the Porcupine Bank between 2 112 and 2 772 m (dives 32 and 33) and on the Goban Spur between 2 171 and 2 988 m (dive 39). One colony was collected. The colonies occur on rock outcrops but also on large stones and small hard surfaces.

Gorgonians

There has been a large amount of data published of the gorgonian fauna of the Bay of Biscay and Celtic Sea (Grasshoff 1982 *a*; 1982 *b*; 1985 *a*; 1986) and this has expedited considerably the identification of gorgonians observed during *Cyaporc*. Together with the sponges and the echinoderms the gorgonians represent the dominant fauna.

The gorgonian fauna is sparse on soft bottoms in the shallow eastern part of the Gollum Channel and on the east side of the Porcupine Seabight and absent from the deeper parts of the Gollum Channel and from the soft sediments of the Goban Spur. However an abundant and diverse gorgonian fauna occurred along the rocky deeper western escarpments of the Porcupine Bank and Goban Spur.

Owing to the diversity and abundance of the gorgonian fauna we have analysed the observations to the lowest taxonomic level possible. Even variations in light, camera angle and distance modify the ability to identify the gorgonians. Some of the more common species include:

Acanthogorgia sp.

Yellow colonies recognizable at *ca.* 2 080 m during dive 33 may belong to this genus. Grasshoff (1982 *b*) reports *A. armata* Verrill, 1879, from 865 to 2 250 m in the Celtic Sea.

Chrysogorgia agassizii (Verrill, 1883)

This species of the "bottle-brush" type appears to occur during dive 33 (1 817 m) and several branches were recovered during dive 34 (depth not recorded). It has been previously recorded from 2 138 to 2 860 m in the Celtic Sea and ranges north to Iceland and Greenland (Grasshoff, 1982 *b*).

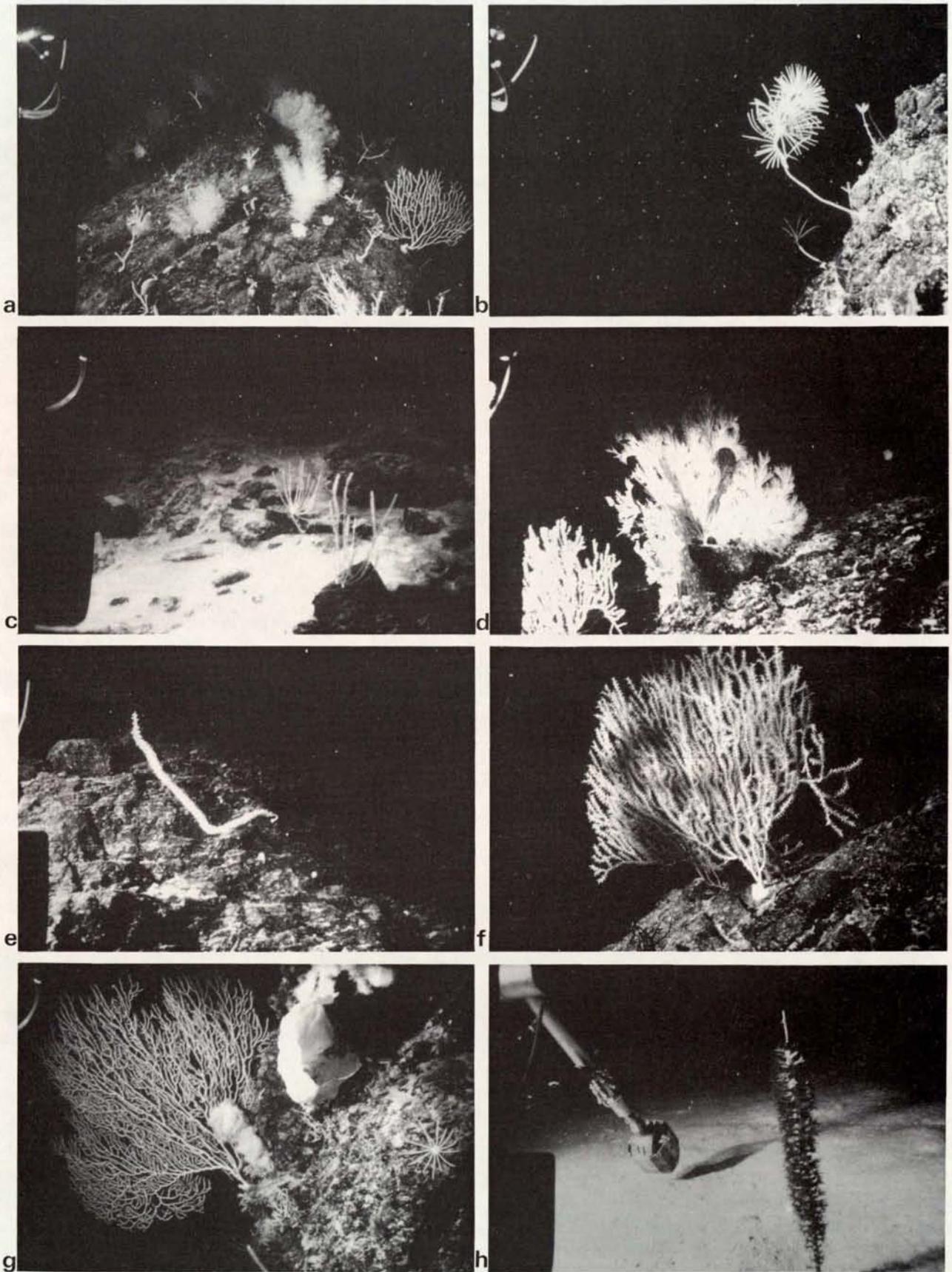


Figure 4

Gorgonians and pennatularians together with other fauna observed during Cyaporc: a) "bottle-brush" gorgonian (possibly Thouarella sp.), fan-shaped colony and lower axes of Isidella longiflora (dive 34: 2 989 m); b) spiraled colony of Iridogorgia sp. between stalked crinoids Conocrinus cabiochi, above, and Porphyrocrinus thalassae, below (dive 32: 2 115 m); c) Primnoid sp. A (dive 33: 2 684 m); d) ? Paramuriceidae to the left and Primnoid sp. B to the right (dive 34: 2 562 m); e) Lepidisis sp. (dive 32: 2 529 m); f) unidentified species of ? Paramuriceidae (dive 34: 2 807 m); g) unidentified species of ? Paramuriceidae, ? Poccillastra-like sponge and brisingiid Freyella (dive 37: 2 847 m); h) Anthoptilum grandiflorum (dive 29: 1 682 m).

"Bottle-brush" gorgonians (Fig. 4 *a*) observed, *e. g.* during dive 32 (2 112 m) and during dive 34 (2 889 m), may belong to the chrysogorgiid genus *Chrysogorgia* or to the primnoid genus *Thouarella*.

Chrysogorgia quadruplex Thomson, 1927

This more irregularly branched species appears recognizable during dive 32 (2 682 m). It has been reported previously from 1 480 m in the Bay of Biscay and between 500 and 2 226 m in the Celtic Sea (Grasshoff, 1982 *b*; 1986)

Iridogorgia sp.

In this magnificent species the monopodial stem forms an upright spiral with simple branchlets arising from its outer side in a single series (Fig. 4 *b*). It was observed at 2 081 and 2 115 m during dive 32. Grasshoff (1985 *a*) records the genus *Iridogorgia* from 2 232 m in the Shamrock canyon photographed during cruise *Cymor 2* in 1981. He tentatively assigned this observation to *I. pourtalesii* Verrill, 1883, a species originally known from the western Atlantic.

Callogorgia verticillata (Pallas, 1766)

Large gorgonian fans seen during dive 40 (*ca.* 910 m) on soft bottom but associated with scleractinian colonies or other hard substrata (Fig. 3 *e*) closely resemble the primnoid *C. verticillata*. The gorgonian branch carried by the crab *Paramola cuvieri* seated on the stone next to an actinian *Bolocera* sp. (dive 40: 911 m) is the same species. *C. verticillata* is known as a more southern species ranging from the Mediterranean to the Great Meteor seamount and the Azores and off Morocco, Portugal and seamounts between Portugal and Madeira (Grasshoff, 1985 *b*; 1986) at depth of < 100 to 1 400 m.

Primnoid sp. A

A very distinct form, apparently not yet recorded in the NE Atlantic was observed between 2 630 and 2 684 m during dive 33. It is characterized by several simple long branches that originate at the same low level near the base (Fig. 4 *c*). It appears to have the distinct whorls of the type characteristic of the primnoids.

Similar colonies have been photographed in the Society Islands, Central South Pacific, during *Cyana* cruise *Teahitia* in 1989.

Primnoid sp. B

The general aspect of this enigmatic form (Fig. 4 *d*) observed at 2 562 m on dive 34 resembles that of *Callogorgia verticillata* but the fans and branches appear more slender.

Primnoid sp. C

One small piece of cylindrical calcareous crust with opposing lateral branches near its base has been collected during dive 32 (2 666 m). As shown previously

(Grasshoff and Zibrowius, 1983; Grasshoff, 1985 *a*; Zibrowius, 1991 *b*), various gorgonians in several families cover their horny axis by a solid calcareous crust, which may spread from the base of the colony upwards along the main stem and even further to lateral branches. After the death of the colony the horny axis decays, but the calcareous crust subsists as a cylindrical tubular structure. It is in this state that the specimen from dive 32 was found. The small piece seems to conform to calcified structures of Primnoidae reported previously, including from deep water in the Celtic Sea.

Lepidisis sp.

Unbranched whip-like isidid gorgonians attached to rock (Fig. 4 *e*), believed to be this genus, have been observed between 2 149 and 2 664 m during dives 32, 33 and 39. Grasshoff (1986) described a new species, *L. cyanae*, from 1 180 to 3 150 m in the Celtic Sea but as this is not the only species of *Lepidisis* in the NE Atlantic we cannot give a precise identification.

Isidella longiflora (Verrill, 1883)

Branched isidid gorgonians (Fig. 4 *a*) are present on hard surfaces on the deeper western escarpments (> 2 900 m) of the Porcupine bank and Goban Spur. We believe this species to be *I. longiflora*, which has been reported down to depths of 4 000 m in the NE Atlantic (Grasshoff, 1982 *b*; 1985 *a*; 1986; Grasshoff and Zibrowius, 1983). Lower parts of the dead colonies are still attached to the substrate (Fig. 2 *h, 4 a*). Such a dead colony was obtained from dredge 3. It has a basal diameter of 23 mm and is 220 mm high and 185 mm wide. Branching occurs from the nodia. The nodia are covered by thick calcareous crusts that hold the internodia together. During dive 33 (2 072 m) the lower part of a large dead axis was collected. It has a maximum diameter of 66 mm near its base and 33 mm at its distal portion and is 190 mm high. Longitudinally it consists of three massive internodia held together by a solid external calcareous deposit at the level of the horny nodia that have disappeared, leaving low transverse lenticular empty spaces within the axis. Seen from the outside, the axis appears homogeneous and continuously calcareous. The piece from *Cyaporc* dive 33 resembles that figured by Grasshoff and Zibrowius (1983; Pl. 7, Fig. 36-37) and by Grasshoff (1985 *a*; Fig. 1 *b*) dredged during cruise *Cymor 1* in the Celtic Sea (2 420 m). This suggests that the colonies of *I. longiflora* can grow to a massive size. Solid calcareous crusts on nodia have also been observed in fossil deep-water *Isididae* (Zibrowius, 1991 *a*).

Paramuriceidae

Large abundantly branched, fan-shaped colonies (Fig. 4 *d, f, g*) were observed below 2 150 m on dives 34, 37 and 39 and represent some of the various species of this family previously recorded from the Celtic Sea (Grasshoff, 1982 *b*; 1985 *a*). There is not enough detail to identify them to genus or species.

Pennatularians

Only one specimen was easily recognizable as a pennatularian (Fig. 4 *h*) and this was seen during dive 29 (1 682 m) on the soft sediments of the Goban Spur. This magnificent specimen is most likely *Anthoptilum grandiflorum* (Verrill, 1879) which ranges to S of Iceland and to depths of 2 700 m. Grasshoff (1982 *b*) reports it from *ca.* 2 175 m in the Celtic Sea.

Polychaetes

Few polychaetes other than serpulids have been collected or observed during *Cyaporc*. Rather large serpulid tubes, several cm long (Fig. 5 *a*), can be seen on a series of photos at 1 813 to 2 117 m depth near the end of dives 32 and 33 along the western edge of the Porcupine escarpment. The tubes appear white against the manganese coated black rock surface. In some cases the tentacle crown can be seen emerging from the tube orifice. The observed tubes are scattered on subvertical rock surfaces or are crowded on subhorizontal rock ledges forming steps (dive 32: 2 034 to 2 032 m), which, for some reason not evident in the photos, are free of sediment accumulation where it would be expected to occur.

It is possible the larger serpulids are *Placostegus* sp. or *Neovermilia falcigera* (Roule, 1898). Tubes of *Placostegus* sp. were taken on rock samples collected at 1 779 m during dive 32. The sculpture of some tubes consists of subvertical, sinuous, narrow lines on the flanks. This suggests a new species distinct from the common *P. tridentatus* (Fabricius, 1779) that lives at more shallow depths in the Atlantic. The presumably new species is known from other records in the Celtic Sea at depths of 1 400 to 2 400 m (Zibrowius, pers. obs.). *N. falcigera* is large and has been collected from the northern part of the Porcupine seabight and characterizes the Pleistocene "Atlantic" deep water fauna of the Mediterranean at *ca.* 2 000 m (Zibrowius and Hove, 1987).

A large serpulid tube, appearing orange to pink in colour, seen during dive 36 (488 m) in the eastern side of the Porcupine Seabight, is possibly *Serpula vermicularis* L., 1767, a species usually found from shallow to bathyal depths in the NE Atlantic.

Empty tubes of *Vermilopsis eliasoni* Zibrowius, 1970, were collected on rock during dive 32 (1 979 m) and on the axis of *Isidella longiflora* during dive 33 (2 072 m). The type locality for *V. eliasoni* is 225 m on Josephine bank, west of Portugal, but it is widely distributed in the NE Atlantic, exceeding depths of 2 000 m in the Celtic Sea.

Pycnogonids

A large specimen of *Colossendeis* sp. was observed during dive 37 (2 863 m). It was striding up the slope carrying a piece of white ? sponge below the body between its legs. It was not ovigerous. *Colossendeis* is fairly common in trawl and sledge samples in the NE Atlantic (Tyler, pers. obs.).

Decapod crustaceans

Nephrops norvegicus (Linnaeus, 1758)

One specimen was observed during dive 36 (553 m).

Paromola cuvieri (Risso, 1816)

Large crabs with long legs carrying a gorgonian branch have been photographed twice during dive 36 (720 m, 534 m). They appear referable to *P. cuvieri*, a deep-water species ranging north to the Hebrides and southern Scandinavia (Manning and Holthuis, 1981).

Neolithodes grimaldii (Milne Edwards and Bouvier, 1894)

This large anomuran was observed twice, at *ca.* 1 670 m on the Goban Spur (dive 35) and at 2 749 m in the Gollum Channel (dive 30). The former specimen was covered with the lepadiform cirriped *Poecilasma kaempferi* (Darwin, 1851), a species that has been shown to have a rapid growth rate in the deep sea (Lampitt, 1990). *N. grimaldii* is often obtained infested with this cirriped epibiont along with the rhizocephalan parasite *Briarosaccus callosus* Boschma, 1930 (Williams and Moyses, 1988; R. Williams, pers. comm.).

Brachiopods

The few brachiopods collected during *Cyaporc* have been examined by B. Laurin: two specimens of *Crania anomala* ? from dive 31 (920 m) and an indeterminate shell debris from dive 33 (2 072 m). Both Hondt (1976) and Logan (1979) reported brachiopods of the genus *Crania* from bathyal depths in the Celtic Sea (47° 33'N to 47° 57'N, 344-825 m), Hondt as *Crania kermes* (Da Costa and Humphreys, 1770), and Logan as *Crania anomala* (Müller, 1776).

Bryozoans

Part of the bryozoan fauna collected during *Cyaporc* has been examined by Hondt (1987). The main species are *Ramphonotus minax* (Busk, 1860) and *Escharella abyssi-cola* (Norman, 1869) from dive 31 (920 m) and unidentifiable fragments of *Stenolaemata* from dive 32 (1 979 m). In addition J.G. Harmelin found bryozoans as epifauna on the large axis of *Isidella longiflora* collected during dive 33 (2 072 m). One species was the anascan *Pyripora catenulata* (Fleming, 1828) but these colonies had very long stolons. An unidentifiable cyclostome of the family Diastoporidae was also present.

Crinoids

The crinoid fauna observed during *Cyaporc* was another highly spectacular group visible. The identifiable species included:

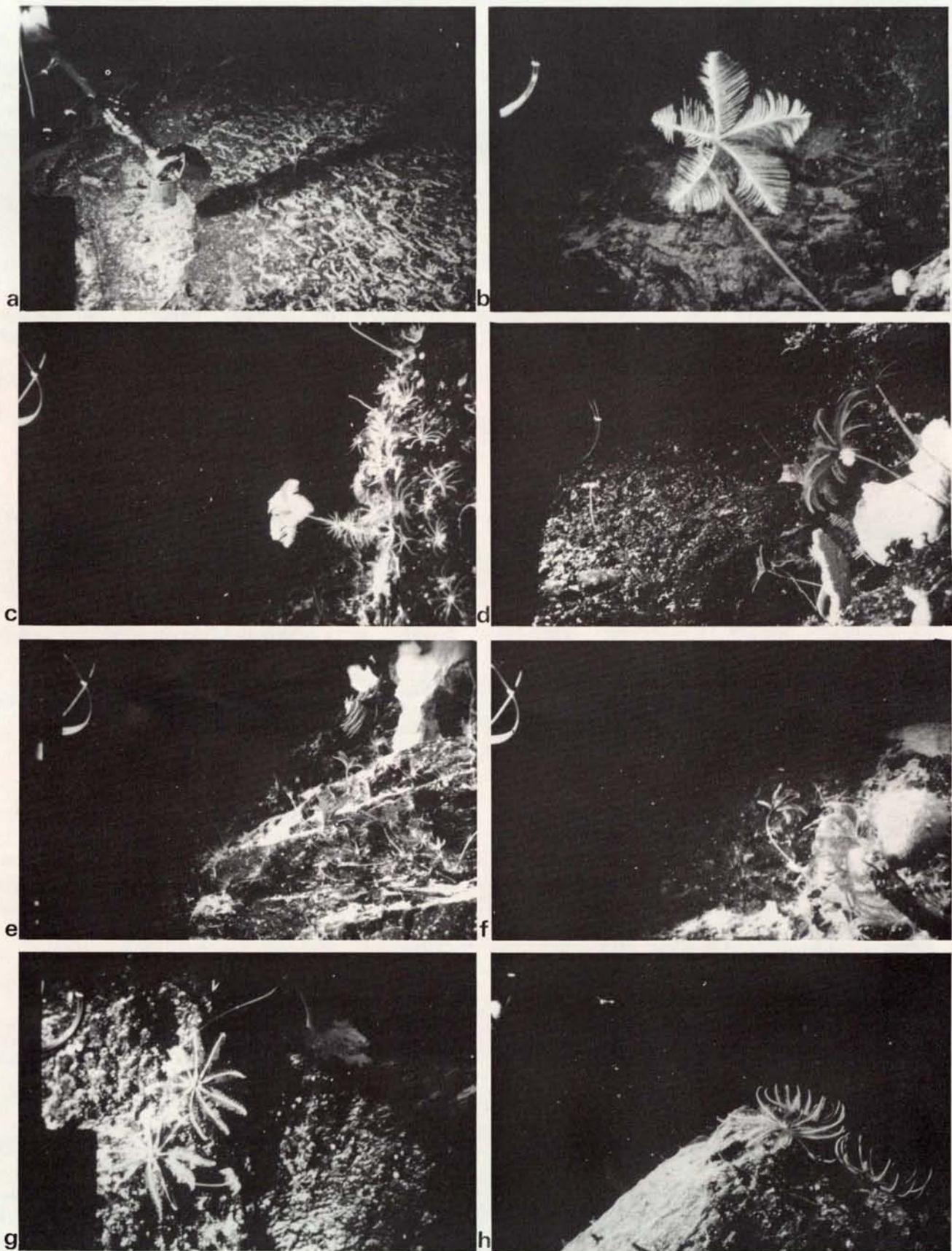


Figure 5

Polychaetes and echinoderms together with other fauna observed during Cyaporc: a) white serpulid tubes contrasted against the manganese-coated rock (dive 32: 2 084 m); b) Anachalypsicrinus nefertiti and pedunculate sponge ? Aulochone in lower right corner (dive 33: 2 481 m); c) ? Thaumatoocrinus jungerseni on the rock surface and part way up the stalk of Anachalypsicrinus nefertiti (dive 32: 2 181 m); d) Porphyrocrinus thalassae and small Conoocrinus cabiochi to the left (dive 34: 2 325 m); e) small Conoocrinus cabiochi (centre and lower right), large Porphyrocrinus thalassae, comatulid ? Thaumatoocrinus jungerseni, large ? Poccillastra-like sponge and antipatharian Bathypathes patula (dive 32: 2 177 m); f) comatulid Trichometra cubensis associated with the sponge Geodia megastrella and Porphyrocrinus thalassae (dive 32: 2 177 m); g) brisingiid Freyella elegans and stalked crinoid Anachalypsicrinus nefertiti (dive 33: 2 688 m); h) Brisingenes multicostata (dive 34: 2 886 m).

Anachalypsicrinus nefertiti A.M. Clark, 1973

This brilliant yellow five-armed species (Fig. 3 h, 5 b, 5 c, 5 g) was observed in great abundance between 2 100 and 2 400 m on the rocky slopes of the deeper part of the Porcupine escarpment (dives 32, 33). This species is orientated with its calyx towards the current and the five arms act as a filter (Fig. 5 b). Clark (1973) first described it from specimens from West of Porcupine Bank (53° 11.2'N, 20° 05.1'W, 2 400 m). Since then it has been recorded from the Bay of Biscay, the Azores and off Morocco over a depth range of 2 150 to 2 800 m (Roux, 1985). The stalk of *Anachalypsicrinus* acts as a support for the comatulid crinoid *?Thaumatocrinus jungerseni* (Fig. 5 c).

Porphycrinus thalassae Roux, 1976

This species is recognized by its bright red crown (Fig. 4 b, 5 d, 5 e, 5 f, 6 c) and is very common in the zone 2 100 to 2 400 m (dives 32, 33). Most of the specimens observed had 10 to 12 arms although the number can vary between 5 and 14 (M. Roux, pers. comm.). Roux (1985) gives the bathymetric distribution of this species as 1 700 to 2 750 m and confines its geographic distribution to the Iberian and Armorican margins. Thus our observations extend its distribution northwards to the Porcupine margin.

Conocrinus cabiochi Roux, 1976

This is also abundant in the zone 2 100 to 2 400 m (dives 32 and 34) and is recognized as a small whitish stalked crinoid (Fig. 4 b, 5 d, 5 e). The depth range corresponds with specimens collected previously during *Cymor* and *Biogas* cruises (Roux, 1985).

Zeuctocrinus gisleni A.M. Clark, 1973

This specimen is not readily seen in photographs (where it may be confused with *Porphycrinus thalassae*) but was taken by dredge 1 (ca. 2 500 m).

?Thaumatocrinus jungerseni A.H. Clark, 1915

Dense patches of this comatulid were observed during dive 32, but it occurred also during other dives (Fig. 3 h, 5 c, 5 e, 6 c). It was described originally from "Ingolf" material collected in the Denmark Strait and SW of Iceland (Clark, 1923; full description preceded by a preliminary one of 1915). More recently it has been found further south in the NE Atlantic, including far W of Porcupine bank (52° 53.3'N, 19° 52'W, 2 734-2 742 m) and off W Africa (Clark, 1980).

Trichometra cubensis (Pourtales, 1869)

At least two specimens of this brilliant red comatulid (Fig. 5 f) were observed associated with a subspheric sponge that was attached to a dead stem of the gorgonian *Isidella longiflora* at 2 177 m during dive 33. *T. cubensis* has a wide distribution in the North Atlantic (Clark, 1980), being associated elsewhere with antipatharians and crinoid stalks (Messing, 1985).

Asteroids

In the deepest parts of each transect, at the base of the Porcupine escarpment and Goban Spur, asteroids were regularly observed, especially brisingiids, which were found mainly on topographic highs or clinging to dead gorgonian stems.

Freyella spinosa Perrier, 1885 [= *F. elegans* (Verrill, 1886)]

This brisingiid is believed to have a world-wide distribution in deep water (Downey, 1986). In the transects examined it occurs most commonly between 2 400 and 2 900 m (dives 33, 37). *F. spinosa* adopts a typical posture in which it extends its arms laterally with the distal parts raised over the adjacent rock surface (Fig. 5 g) or it may elevate itself above the surrounding substratum by attaching to dead gorgonian axes.

Brisingenes multicostata (Verrill, 1894)

This brisingiid was also observed between 2 400 and 2 900 m (dives 34, 37) and maintains a posture where it rests on the rock surface, usually a topographic high, on its disc and the proximal parts of the arms with the distal parts of the arms raised above the surface to make a "bowl" (Fig. 5 h). *B. multicostata* was identified from photos and from a specimen collected during dive 37. These observations extend the range of this species into the NE Atlantic, it being recorded previously from Georges Bank and the Straits of Florida (Downey, 1986).

?Hydrasterias sexradiata (Perrier, 1882)

Only two six-rayed asteroids are known from the NE Atlantic, the forcipulate *H. sexradiata* and the brisingiid *Freyella sexradiata* Perrier, 1894 (see Gage *et al.*, 1983). As the specimen observed (dive 34: 2 639 m; Fig. 6 d) was not a brisingiid, we tentatively identify it as *H. sexradiata*. It has a depth range of 600 to 4 260 m (Gage *et al.*, 1983).

Hymenaster membranaceus Thomson, 1873

A single specimen of this common NE Atlantic species (Gage *et al.*, 1983) was observed in the zone 2 400 to 2 900 m (dive 32).

Ophiuroids

With the exception of the Euryalidae, deep-sea ophiuroids are difficult to identify in photographs owing to the similarity in their outline. In the deep part of the transects ophiuroids were observed occasionally clinging to the branches of gorgonians (dive 34: 2 563 m; Fig. 4 d). Three ophiuroid species could be recognized:

Ophiophycis mirabilis Koehler, 1901

This white species was observed regularly highlighted against the black background of the manganese covered

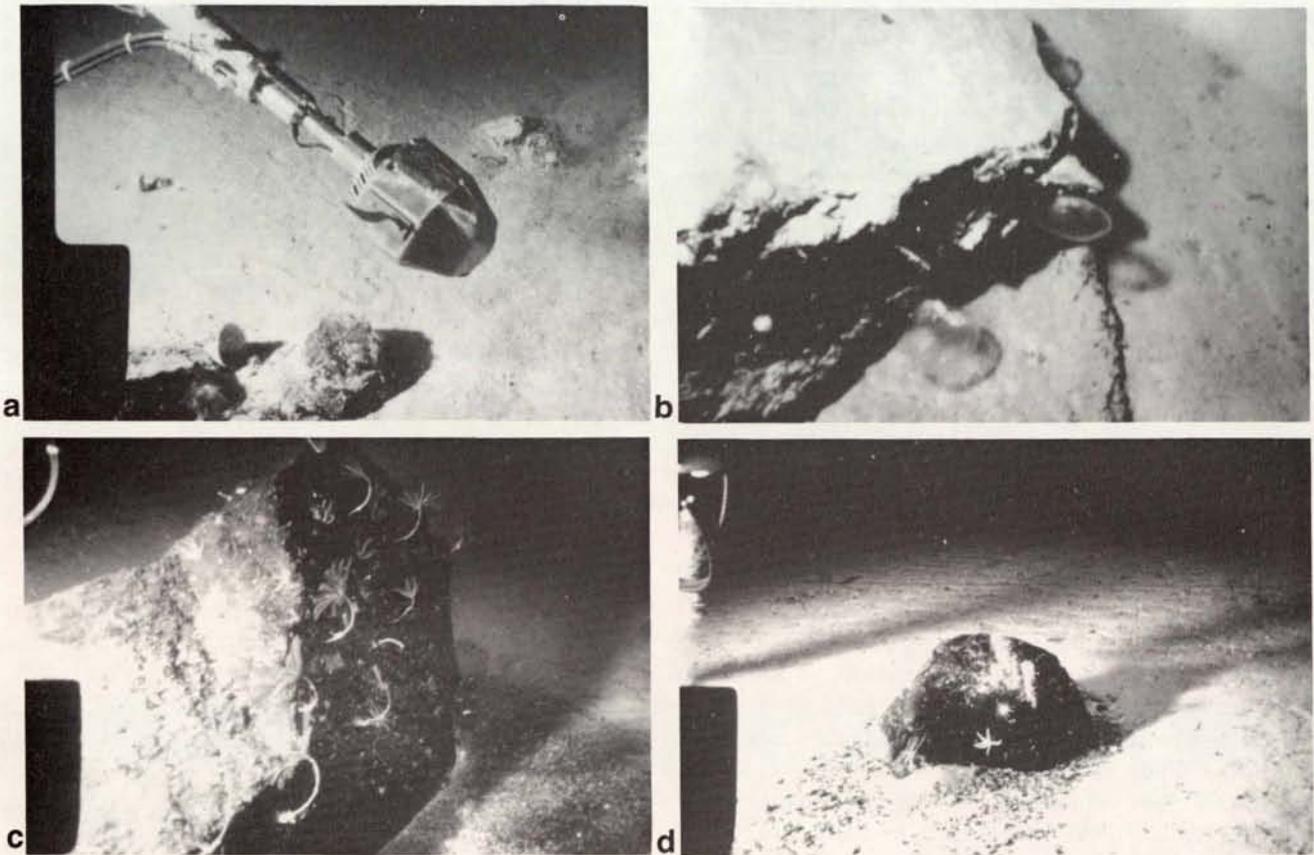


Figure 6

Enigmaticum and evidence of a northward current direction on the slope west of the Porcupine Bank: a) *Enigmaticum* from cruise *Cyaporc* (dive 37: 2 993 m), transparent specimen attached to a piece of rock, to the lower left (below funnel); b) *Enigmaticum* from cruise *Galinaute* (dive 1: ca. 3 000 m), three transparent specimens attached to rock faces; c) current mediated orientation of *Porphyrocrinus thalassae*, together with ? *Thaumatochrinus jungersenii* (dive 39: 2 308 m); d) unidirectional flow past a boulder bearing "bottle-brush" gorgonians, the asteroid ? *Hydrasterias sexradiata* and the echinoid *Echinus affinis* (dive 34: 2 639 m).

rock and was collected on rock samples recovered by *Cyana* (dives 32, 33: 2 150 m). It lives in small hollows wedged in by the stout square-lipped modified arm spines found round the edge of the disc. Paterson (1985) gives the depth range of this species as 1 175 to 1 980 m although Cherbonnier and Sibuet (1972) suggest it occurs down to 2 871 m. It is possible that the paucity of material examined in the past is a result of the difficulty of sampling these steep slopes.

Ophiactis abyssicola (M. Sars, 1861)

This species was found attached to rocks also (dive 32). It is common throughout the NE Atlantic over a depth range of 125 to 4 721 m. Identification can be difficult as the species is very variable (Paterson, 1985).

Ophiomusium lymani Thomson, 1873

This is the dominant ophiuroid on sediment in the NE Atlantic (Gage *et al.*, 1983). Very few were observed on the steep rocky slopes of the Porcupine or Goban Spur except where sediment had accumulated (dive 32: 2 795 m; dive 34: 2 638 m).

Echinoids

Considering the diversity of echinoids found in the NE Atlantic (Gage *et al.*, 1985), very few echinoids were observed during *Cyaporc*. One specimen believed to be *Echinus affinis* Mortensen, 1903, was observed on a boulder at 2 639 m during dive 34 (Fig. 6 b) and *Hygrosoma petersi* (A. Agassiz, 1880) was observed occasionally on sedimentary areas in the zone 2 400 to 2 900 m (dives 32, 33, 39). Its known distribution in the north Atlantic is 730 to 2 870 m (Gage *et al.*, 1985). *Cidaris cidaris* (Linnaeus, 1758) was observed at 912 m during dive 39.

Holothuroids

Although the holothuroids are common on soft bottoms in the deep sea they were observed only rarely during *Cyaporc* and then only associated with sedimentary deposits. *Peniagone azorica* Marenzeller, 1893, was observed in the deepest part of the transect (> 2 700 m) at the base of the Porcupine escarpment (dives 32, 33, 37). It is common in the NE Atlantic between 2 000 and 3 000 m (Le Danois, 1948; Gage *et al.*, 1985). *Laetmogone violacea* Theel,

1879, was found in great numbers on the axial floor of the Gollum Channel down to ca. 1 000 m. Although there was a down canyon current this species did not align itself to this flow as seen elsewhere in other species (Ohta, 1983). The very cosmopolitan species *Benthogone rosea* Koehler, 1896, was found regularly on soft sediments on the Goban Spur (dive 29: 1 760 m).

Enigmaticum

Various photographs taken at depths exceeding 2 000 m during cruises of the French submersibles *Cyana* (*Cymor 2* in 1981 on the escarpments of the Armorican marge; *Cyaporc*) and *Nautile* (*Galinaute* in 1986 on the escarpments of Galicia Bank off northwestern Spain) show an enigmatic organism, which, at first sight, gives the impression of a big "bubble", being highly transparent, several cm in diameter and slightly depressed (wider than high).

The organism (Fig 6 *a, b*) is attached to subvertical rock surfaces by a narrow zone near its equator, shows a horizontal midline along the equator opposite to its point of attachment, and has an otherwise uniform and smooth surface. The narrow attachment, possibly by a pedicel, and the horizontal position of what could be two valves with an anterior commissure could suggest it being a huge brachiopod with a particularly thin and transparent shell. However, in spite of the transparency no typical brachiopod structure (lophophore or brachial skeleton) could be discerned inside with certainty. The big "bubble" appears empty, except near the point of attachment where something of imprecise shape is contained within the presumed shell.

This enigmaticum of a type apparently never collected has been photographed twice during *Cyaporc* (dive 37: 2 834 and 2 993 m). These photos are rather poor (Fig. 6 *a*) and could be interpreted only with reference to more detailed photos of the same organism taken during other cruises (*Cymor 2*, dives 35, 36, 38 on the escarpments of Austell Spur, 48° 23-33'N, 11° 14-17'W, 2 362-2 928 m; *Galinaute*, dives 1 and 5 on the western escarpments of Galicia Bank, respectively ca. 3 000 m and 4 360 m). Photographs from *Galinaute* dive 1 show in considerable detail the structure of three individuals attached to a large piece of rock surrounded by sediment (Fig. 6 *b*).

OBSERVATIONS OF CURRENT FLOW

Although the primary aim of the *Cyaporc* diving programme was geological observation of otherwise inaccessible parts of the Porcupine and Goban slopes, there is photographic evidence of the current direction but not of its speed. In Figure 6 *c* the current is causing the individuals of a group of *Porphyrocrinus* to orientate in the same direction. In Figure 6 *d* the boulder is creating turbulence in a unidirectional flow thus causing erosion of fine grain material downstream of the boulder. By using the heading of the submersible and the orientation of the photograph it is possible to calculate that both photographs indicate a north-

ward unidirectional flowing current at a depth of 2 300 to 2 600 m. This would correspond to the current recognized by Lonsdale and Hollister (1979) and represent the flow of North East Atlantic Deep Water.

DISCUSSION

The fauna of the deep-sea NE Atlantic is one of the best documented for a deep water region anywhere in the world. The first scientific surveys by the Lightning and Porcupine expeditions were carried out to the west of the British Isles in the period 1869-1871. More recently there has been intense activity in the Bay of Biscay (Laubier and Monniot, 1985), the Porcupine Seabight and abyssal plain (Rice *et al.*, 1991) and the Rockall Trough (Mauchline, 1986). However, much of this information concerns the fauna of soft sediments. Observations of the fauna of rocky bottom areas have been made only on the slope bordering the Bay of Biscay (Grasshoff, 1985 *a*; Roux, 1985; Zibrowius, 1985).

The *Cyaporc* diving cruise gave an opportunity to examine both the geology and biology of the steep continental slope and other inaccessible regions north of areas already examined during previous *Cyana* diving cruises. The fauna observed during the present study was not dissimilar to that known for the rocky slopes of the Bay of Biscay but differed considerably from the fauna found in the adjacent Porcupine abyssal plain and Seabight and in the Rockall Trough. The main apparent difference is that the rocky areas are dominated by suspension feeders whilst deposit feeders dominate the soft sediment areas. Even where sediment accumulated on ledges in the rocks, deposit feeding species could be found.

The pattern of suspension feeding by rocky slope species is accentuated in a number of ways. Many of the suspension feeders are on the "edge" of rocks where, owing to a constriction of space, water flow may be accelerated thus increasing the supply of food particles. Many species elevate themselves, or have part of their colony, above the viscous sublayer of the benthic boundary layer as seen on sea-mounts and in other rocky areas (Messing, 1985; Kaufmann *et al.*, 1989). In pennatularians the base of the colony is devoid of feeding polyps. Thus the feeding polyps are in the turbulent log layer of the benthic boundary layer where the current will be rapid enough to supply food particles. In gorgonians the polyps are found all over the colony except at the very base. In the fan-shaped species in this group the fan is held at right angles to the current to present the maximum number of polyps to the direction of flow.

Comatulid crinoids such as ? *Thaumatocrinus jungerseni* were found attached to various points on the stalk of *Anachalypsicrinus nefertiti* and *Trichometra cubensis* was found on top of a sponge. *Freyella elegans* climbed dead gorgonian axes to spread its arms out into the prevailing current. Even *Brisingenens multicostata* lifts the distal parts of its arms into a bowl shape to improve its food collecting

capacity. All these species will benefit from the faster currents in the log layer of the benthic boundary layer as opposed to the retarded flow immediately adjacent to the seabed.

The distribution of the species on the rocky substrata observed during *Cyaporc* suggest a zonation along the western side of the Porcupine escarpment and Goban Spur.

The lowest zone is deeper than 2 900 m and consists mainly of soft sediments characterized by a typical deep-sea soft sediment fauna. The rock fauna at this level includes isidid gorgonians and brisingiid asteroids.

Between 2 900 and 2 600 m is a zone dominated by diverse gorgonians and brisingiid asteroids. The alcyonarian *Anthomastus* is also common.

The next zone (2 600 to 2 100 m) is the most spectacular and is dominated by the crinoids *Anachalypsicrinus nefer-titi*, *Porphyrocrinus thalassae* and ? *Thaumatocrinus jun-gersenii*. This zone corresponds to the "North East Atlantic Deep Water" (Ellett and Martin, 1973; Lonsdale and Hollister, 1979) and represents a generally northern flow. This water mass also covers areas of dense echinoderm fauna on soft bottoms at this depth in the Rockall Trough (Gage *et al.*, 1983; 1985) and Porcupine Seabight (Lampitt *et al.*, 1986) and on rocky substrata in the Bay of Biscay (Roux, 1985). There is, however, no known characteristic of this water mass that would encourage the high biomass of echinoderms. It is possible that the deposition of surface-derived phytodetritus may occur in this area and the northward flowing current which may exceed 7 cm s⁻¹

(Lampitt, 1985) resuspends this material thus making it available for suspension feeders on rocky surfaces. However, there is no evidence to suggest any preferential accumulation of phytodetritus in this zone.

The last recognized zone is shallower than 2 100 m in which there is only limited photographic coverage. A number of species observed also in the deeper zone (2 600 to 2 100 m) were found here but in significantly less numbers.

Until more detailed faunal and hydrographic data are available from this steep rocky area, this apparent zonation and its cause must remain speculative.

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