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I.O.S.

The use of *in situ* photography in studies of the deep-sea benthos at I.O.S.

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This research has been carried out under contract for the Department of the Environment, as part of its radioactive waste management research programme. The results will be used in the formulation of Government policy, but at this stage they do not necessarily represent Government policy.

NB When this document is issued in the IOS Report Series the benthic photographs will be copied by an offset process and their reproduction will be superior to the copies available here.

INTRODUCTION

The existence of life in the deep-sea was demonstrated, after much doubt and argument, by dredging expeditions undertaken during the mid-nineteenth century, culminating in the Challenger Expedition from 1872 to 1876. Subsequent exploration, mainly using towed sampling gears, built up a picture of a diverse benthic fauna of small and large animals thinly spread on the deep-sea floor. The gross features of faunal distributions and community structure could be determined from these samples, and inferences about life styles of individual organisms could be drawn from anatomical studies and from comparisons with related shallow water forms. Little was known, however, about the small-scale distribution patterns or the behaviour of deep-sea benthic animals since such information is not provided by towed samplers. Gears which collect relatively undisturbed samples of the bottom sediments, such as grabs and corers, may provide such information for the smallest and most abundant benthic organisms, but not for the larger and less common forms.

The use of manned submersibles during the 1960s and 1970s provided much valuable information on deep benthic communities, but these vehicles are expensive to build and operate and are, in any case, themselves strictly limited in their applications. Photographic techniques, employed judiciously, offer a relatively inexpensive alternative to fulfill at least part of the function of submersibles and may provide data which could not be obtained even with the most sophisticated submersibles available.

Because of the technical problems involved, deep-sea photography did not become an extensively used technique until the early 1960s, but since that time a wide range of deep-sea cameras and ancillary equipment has been developed. Cine-photography is still not widely used in the deep-sea because of the high power requirements of the necessary lighting equipment, but most marine laboratories concerned with oceanic biology now employ still photography fairly routinely.

Such photography has been used for three main purposes. First, as a "sampling" technique, both qualitative and quantitative, analagous to the use of such equipment as grabs, sledges and trawls, but clearly with quite different capabilities and limitations. Second, as a means of obtaining information which could not be obtained with more conventional samplers;

for instance, the appearance, attitude and orientation of individual organisms in life, the spatial relationships of groups of organisms, and information on their lebensspuren, that is tracks, trails, burrows and so on. Third, in a time-lapse mode to record sequential events over periods of hours, days or weeks. These categories are not, of course, mutually exclusive and a single photograph, or series of photographs, may provide information in all three.

Since 1975 the benthic biology group at IOS has employed photography extensively, mainly in conjunction with a towed epibenthic sledge (Aldred, Thurston, Rice and Morley, 1976; Aldred, Riemann-Zurneck, Thiel and Rice, 1979; Rice, Aldred, Billett and Thurston, 1979; Rice and Collins, 1980; Rice, Aldred, Darlington and Wild, 1982; Rice and Hartnoll, 1983; Rice and Collins, in press). In addition, time-lapse cameras have been used to record events in large baited fish traps (Thurston, 1979) and, latterly, in conjunction with a current meter forming a deployed system (Bathysnap) capable of monitoring changes on the sea floor (Lampitt and Burnham, 1983; Lampitt, Merrett and Thurston, 1983; Billett, Lampitt, Rice and Mantoura, 1983; Rice 1983; Lampitt in press, _a_ and _b_). Each of these uses has provided important information on the biology of benthic organisms. It is, however, the combination of data obtained by these various techniques, together with catches from nets and traps, which is providing such a powerful tool in our benthic studies.

The following account describes briefly some of the techniques used and the results obtained.

TECHNIQUES

Transect

Towed vehicles carrying cameras to obtain transects of the deep-sea floor have been used many times. Although the photographs obtained from such transects may provide valuable information, the absence of simultaneously obtained catches has frequently made interpretation difficult, particularly in areas not extensively sampled previously. At IOS we therefore decided to link photography and sample collection by mounting a camera on the acoustically monitored IOS epibenthic sledge which had been specifically designed to collect organisms living in, on or immediately above the bottom.

From 1975 to 1978 the sledge had a single net or tier of nets attached to the back of a steel frame 2.3m wide and 0.6m high (Fig. 1) (Aldred et al., 1976). An IOS Mk IV 35mm camera (Rice and Collins, in press) with a capacity of 400 exposures on standard film was mounted beneath the two leading cross-members of the frame directed forwards and downwards to photograph an area of some 2.6m^2 of seabed in front of the sledge. Photographs were taken at 15 or 30 second intervals so that during a normal sledge haul of about 30 minutes on the bottom some 60 to 120 exposures were obtained.

Numerous excellent photographs were taken with this arrangement off the north-west African coast to depths of 6000m and in the Porcupine Seabight down to about 4000m, but because of shallow camera angle, the area covered by each frame was extremely sensitive to the inevitable changes in orientation of the sledge as it travelled across the seafloor. Accordingly, in 1979 the sledge was modified by doubling the height of the frame so that the camera could be mounted higher and more nearly vertical, at an angle of about 30° to the horizontal (Fig. 2) (Rice et al., 1982). This re-orientation reduced the usable area covered by each frame to about 1m^2, but it improved the resolution and decreased the sensitivity to changes in the sledge angle. Since 1979, 74 conventional sledge hauls have been made with this new system in the Porcupine Seabight at depths ranging from about 400 to 4500m.

As a result of our increasing familiarity with the megabenthic fauna of the Seabight, we have recently been able to use the more traditional photosledge technique without simultaneous sample collection by dispensing with the nets on the sledge frame. This has enabled us to increase the length of each tow and, with the development of a new high capacity IOS camera capable of taking up to 1600 photographs, we are now able to leave the gear on the bottom for 6 hours or more and cover a horizontal distance of 10 to 15km. We expect to use this technique increasingly in the future, particularly in the study of faunal boundaries.

Time-Lapse

For time-lapse photography autonomous instruments have been used. These consist of a frame, ballast weight, buoyancy and an acoustic release system.

Such packages free fall to the seabed and are subsequently retrieved by releasing the ballast weight. The IOS camera system has been used within large (3m x 1.5m x 1.2m) fish traps to photograph animals attracted to bait over periods of a day or so (Thurston, 1979; Lampitt _et al._, 1983). More recently cameras have been mounted on a free fall instrument (Bathysnap) (Fig. 3) in the same orientation as on the sledge to photograph an area of sea floor repeatedly while the current speed and direction are simultaneously recorded (Lampitt and Burnham, 1983). Frame intervals have been set at values from 4 minutes to 8 hours depending on the purpose and duration of the deployment (5 hours to 4 months). Sixteen deployments have been successfully accomplished at depths from 512 to 4101m and a wide range of new data has been obtained about rates and types of processes occurring in the deep sea.

RESULTS

The transect photographs have provided a variety of types of information. First, they have been used to check the ability of the epibenthic sledge to collect quantitative samples. The encouraging degree of agreement between the two techniques suggests that we can use the sledge samples with some confidence to estimate the megafaunal benthic biomass, an essential pre-requisite in modelling the deep-sea ecosystems (Rice, _et al._, 1982).

Second, the photographs have provided valuable data on the abundance of a number of organisms which are difficult or impossible to sample quantitatively by conventional methods. Two examples are illustrated in Figs 4 and 5. Figure 4 shows large numbers of foraminiferan-like xenophyophores photographed at a depth of 3900m off the west African coast. These organisms are extremely delicate and are broken into small, and almost unrecognisable fragments in any towed net used to collect them. Indeed, it was their abundance in the photographs which led us to examine the catch residues very carefully and to find xenophyophore material which might otherwise have been missed. Similarly, Fig. 5 shows the sea pen or pennatulid _Kophobelemnon stelliferum_, a representative of a sessile, colonial suspension-feeding coelenterate group which are notoriously difficult to sample adequately because of their ability to bend beneath nets or retract into the sediment. These animals are represented by very small numbers in our samples, but the photographs reveal that in some areas they are present at very high densities. Since there is a strong correlation between polyp number and size/weight in Kophobelemnon, and since the polyps can be readily counted on the photographs, it may be possible to estimate the biomass of the pennatulids from the photographs.

Third, the photographs provide information on the small scale distribution of benthic animals which could not be discerned from the towed net catches (Appendix 1). A particularly dramatic case is that of the small sea cucumber or holothurian Kolga hyalina. This species has occasionally been taken in very high numbers in sledge catches and the simultaneously obtained photographs reveal that the animals are at times clumped into very dense aggregations (Fig. 6) (Billett and Hansen, 1982).

Fourth, the photographs demonstrate close associations between species. Some of these associations, such as that between the hermit crab Parapagurus pilosimanus and the coelenterate Epizoanthus sp. are so close and "unbreakable" that they are obvious in the catches. Others are physically less stable and can only be guessed at from the catches. The presence of large numbers of the spider crab Dorhynchus thomsoni and the hexactinellid sponge Pheronema carpenteri in the same samples suggested some association between them, but this could be confirmed only when photographs were obtained showing the crabs standing, and presumably feeding, on the surfaces of the sponges (Fig. 7). A similar, but less strict, association between Pheronema and the squat lobster Munida tenuimana was also revealed by the photographs. Munida tenuimana occurs fairly abundantly in regions not frequented by the sponge and, from analogy with similar forms known from shallow waters, they are assumed to shelter in shallow burrows excavated within the bottom sediments. However, many photographs of the sponge beds show the squat lobster using the ready made "burrows" formed by the exhalent cavities of the sponge (Fig. 8).

Finally, transect photographs provide information of lebensspuren. Many of the photographs contain tracks, trails, feeding marks and faecal casts, but with no evidence of the animals responsible for them. Occasionally, however, animals are photographed in the process of producing these ephemeral structures and this information, together with data on degradation rates derived from time-lapse photography allows rough calculations of feeding rates to be made (see below).

Time-lapse photography

Time-lapse photography has been used as a method of event-recording, both in isolation and in conjunction with other techniques.

(a) With bait

The use of baited cameras in the deep sea initiated by Isaacs (1969) has revealed the presence of a previously unsuspected element of the fauna of that region. Necrophagous organisms, mainly fish and amphipods, are now known to exist in large numbers in abyssal and hadal zones. Haedrich and Rowe (1978) have indicated that the benthic megafauna cannot subsist solely on the benthic macrofauna and meiofauna and probably, therefore, obtain food from other sources. Some abyssal fish are known to feed on pelagic organisms (Pearcy and Ambler, 1974), and carrion may form a significant input to abyssal benthic food webs. Evidence for such naturally occurring food falls is scant, and their non-appearance in photographic surveys implies a short residence time (or low frequency). The use of baited cameras suggests that this is the case since necrophages arrive quickly at the bait, increase rapidly in numbers, and are capable of rapid breakdown of a food source.

The use of experimental fish traps equipped with time-lapse cameras has provided considerable behavioural data on the necrophagous amphipods attracted to bait (Thurston, 1979). Amphipods begin feeding soon after the bait reaches the bottom, having arrived from a down current direction and from above the horizontal plane in which the bait was suspended.

Data from a subsequent deployment of the fish trap, and from a baited version of Bathysnap, have been combined to document the response of necrophagous amphipods to food falls and the predation of these amphipods by a species of fish (Lampitt et al., 1983). The overall numbers of amphipods and the presence of fish preying on them were related to phases of the tidal cycle (Fig. 9).

Direct observations from submersibles (Wolff, 1971), photographic evidence (Thurston, 1979) and catches from vertical strings of traps (Ingram and Hessler, 1983) suggest that necrophagous amphipods are highly mobile organisms which inhabit the bottom few metres or tens of metres of the water column. Such behaviour conforms to theoretical optimum foraging strategies in the environment, and may explain the rarity of these organisms in sledge and trawl hauls.

Some of the fish and amphipods attracted to bait are known to make considerable forays up into the water column (Smith, White, Laver, McConnaughey and Meador, 1979). These organisms presumably also make extensive longitudinal movements in search of food falls. They form, therefore, a mechanism whereby naturally occurring and man-made substances can be transported both vertically and horizontally. The implication of such transport in terms of dispersal of toxic wastes in the deep sea is considerable.

(b) With transect photography and sledging

Most deep-sea animals are very difficult to recover alive, and are even more difficult to maintain in the laboratory. Consequently, rates of processes are virtually unknown for these animals. Holothurians (sea cucumbers) are abundant in the deep-sea and may form over 90% of the wet weight biomass of the megafauna. _Benthogone rosea_ is a common sea cucumber at mid continental slope depths and, like most other deep-sea holothurians, is a deposit feeder which removes particles from the surface millimetre or so of the sediment.

Transect photographs have provided population density data for _B. rosea_ and their faecal casts in the same area, while time-lapse photographs from Bathysnap enable estimates of the decay rate of the faecal material to be made. The photographs have also been used to estimate the average size of a faecal cast. These data, together with literature values of water content of faecal material from the hindgut, feeding selectivity and assimilation efficiency, and unpublished data on the organic content of the sediments were combined to calculate the assimilation rate (Appendix 2). To date no such calculation has been possible of this fundamental process for any megabenthic species and the consequences of such an important measurement are clearly far reaching.

(c) With coring

Since 1981, use of the SMBA multiple corer (Barnett, Watson and Connelly, in press) has made available totally undisturbed samples of the superficial sediment from the Porcupine Seabight. These cores have provided much background information about the area in terms of sediment particle size, organic content and downslope sediment movement. They have also been a vital adjunct to Bathysnap photographs in understanding seasonal changes, and in the future may provide significant data on bioturbation.

Seasonality. Transect photographs from the Seabight at depths between 1310m and 4100m have often shown dark patches on the seabed during the spring and summer months but never in the autumn and winter, implying seasonal changes in a supposedly aseasonal environment. The dramatic nature of these changes were not appreciated prior to the examination of photographs from a Bathysnap deployment during April/May 1982 at a depth of 2000m. Fig. 10 shows that during most of April there was very little change in the appearance of the seabed, but that over a 32 hour period at the end of the month a substantial deposition of material occurred. Another Bathysnap deployment at the end of May at a nearby locality revealed even more flocculent material on the sea bed. A similar deposition occurred at 4025m in the mouth of the Seabight in 1983, but in this case material became apparently only from mid June. By mid July a layer several centimetres thick was present and this began to disappear in the first half of August.

Although of great interest on their own, the importance of these photographic observations was not fully appreciated until samples of the material were collected using the corer. The material was identified as phytodetritus with a species composition typical of the phytoplankton of the surface waters just prior to its accumulation on the seabed.

The spring phytoplankton bloom in the Porcupine Seabight usually occurs in early April. The Bathysnap results from April 1982 therefore imply a sinking rate of the phytoplankton of several hundreds of metres per day compared with published data on laboratory measurements of sinking rates which suggest maximum figures of no more than a few metres per day (see Billett *et al.*, 1983).

Use of colour film showed that the material sometimes arrives on the bottom as aggregates up to 6mm in diameter. Although these aggregates showed signs of fairly rapid degradation, the corer samples contained similar sized aggregates on which sinking rate experiments were conducted on board ship. Values of 350-1000m/day were recorded, thus substantiating the estimates from the Bathysnap photographs. At 4025m some of the material arrived as aggregates up to 40mm diameter but these have not been identified in the cores.

Once on the seabed the phytodetritus forms a mobile layer which is moved around mounds and hollows by the near-bottom currents, and during some Bathysnap deployments the material was periodically resuspended when the current reached some critical velocity. During one deployment (at 1200m in May 1981) no current meter records were available but variations in the amount of suspended material showed clear evidence of a tidal influence (Fig. 11). A 4000m deployment from which current data were available indicated that resuspension occurred only when the current 1.3m above the seabed exceeded about 7cm/sec.

Bioturbation. The degree to which the active megafaunal animals mix the surface layers of the sediment is of interest to geochemists and geophysicists as well as to biologists. It is difficult to quantify bioturbation from Bathysnap photographs, although Fig. 12 demonstrates large interspecific variations even when the species concerned are of similar size. Regional differences in megafaunal species composition will, therefore, clearly result in considerable variations in the degree of bioturbation over relatively short horizontal distances (~ 1km). During 1983, the vertical profiles of ^{210}Pb and ^{234}Th in cores from three stations in the Porcupine Seabight were measured and used to calculate bioturbation rates. Such measurements reflect the total bioturbation from all size classes of animals, but used in conjunction with Bathysnap photographs it should be possible to partition the total bioturbation to some degree on the basis of animal size classes.

(d) With current meters

The importance of combined photographic and current meter data has been touched on in connection with the resuspension of phytodetritus and the attraction of necrophages to bait. Information on current speed and direction may also be important in interpreting the behaviour of individual megabenthic organisms photographed by Bathysnap and two examples are described here.

Fig. 13 shows a hormathiid sea anemone which was photographed at hourly intervals during a 31 day Bathysnap deployment at a depth of 4100m in July/August 1982. From simultaneously obtained records of the current direction it is clear that the anemone actively orientates its concave (upper) surface into the current (Fig. 14), whereas shallow-water anemones are passively bent downstream by water currents (Koehl, 1977). The Bathysnap photographs certainly provide the only protracted observation of a deep-sea anemone so far made and indicate that such species can react positively to the very low currents which exist a few cm above the seabed (probably less than 1cm/sec).

Fig. 15 shows a deep-sea shrimp, Glyphocrangon sculpta, photographed during a 4 day Bathysnap deployment at 2664m in September 1981. During this deployment two such shrimps moved slowly through the field of view, at an average speed of about 100cm/hour (0.03cm/sec), generally in the same direction as the current but with the long axis of the body orientated at right angles to it. These observations, together with flume tank experiments on dead specimens, suggest that the shrimps were drifting passively with the current in search of the infaunal bivalves and crustaceans on which they feed. Such a foraging strategy is very unusual, if not previously unknown, but may confer several distinct advantages on the species (Lampitt and Burnham, 1983).

(e) Time-lapse photography alone

Although time-lapse photography is most valuable when used in conjunction with other techniques, some useful information not easily obtainable by other means, can be provided by time-lapse photographs alone. For instance, it has been possible to quantify maximum measured rates of movement for a number of benthic organisms from their positions on successive Bathysnap photographs (Appendix 3), though their true maximum speeds may well have been higher, particularly where the inter-frame intervals were long.

Bathysnap deployments have also provided evidence of large infaunal animals which have not been sampled by the towed collecting gears presumably because they withdraw into the sediment on the approach of a sledge or trawl. Out of only 16 deployments below 1000m, covering a total area of $32m^2$, the photographs include three large worms, at least 50cm long and 1cm in diameter, which emerged from burrows and scraped the surrounding sediment surface (Fig. 16). In the absence of comparable organisms in the catches the identity of these worms is uncertain, but they are probably undescribed echiurids. If they are indeed echiurids the total body length may be twice that seen on the surface. In an environment where animals of this size are usually found at densities of less than $1/10m^2$ these worms may be an important, and previously undetected, component of the benthic fauna with considerable effects on bioturbation rates and pore water characteristics.

CONCLUSION

Still photography is a well-established and valuable tool in deep-sea biological studies which forms an important part of the benthic programme at IOS. Transect photographs are of limited use alone, but their value is greatly enhanced in conjunction with results obtained from other techniques. On the other hand, time-lapse photography alone may provide information which is not obtainable by other means, though the value of this technique also becomes much greater when it is used together with other gears. The combination of techniques employed at IOS has already provided important data on the structure and abundance of deep-sea communities, on the behaviour of some of the constituent species, and on the rates of fundamental biological processes. The continued use and refinement of the available systems holds considerable promise for the future.

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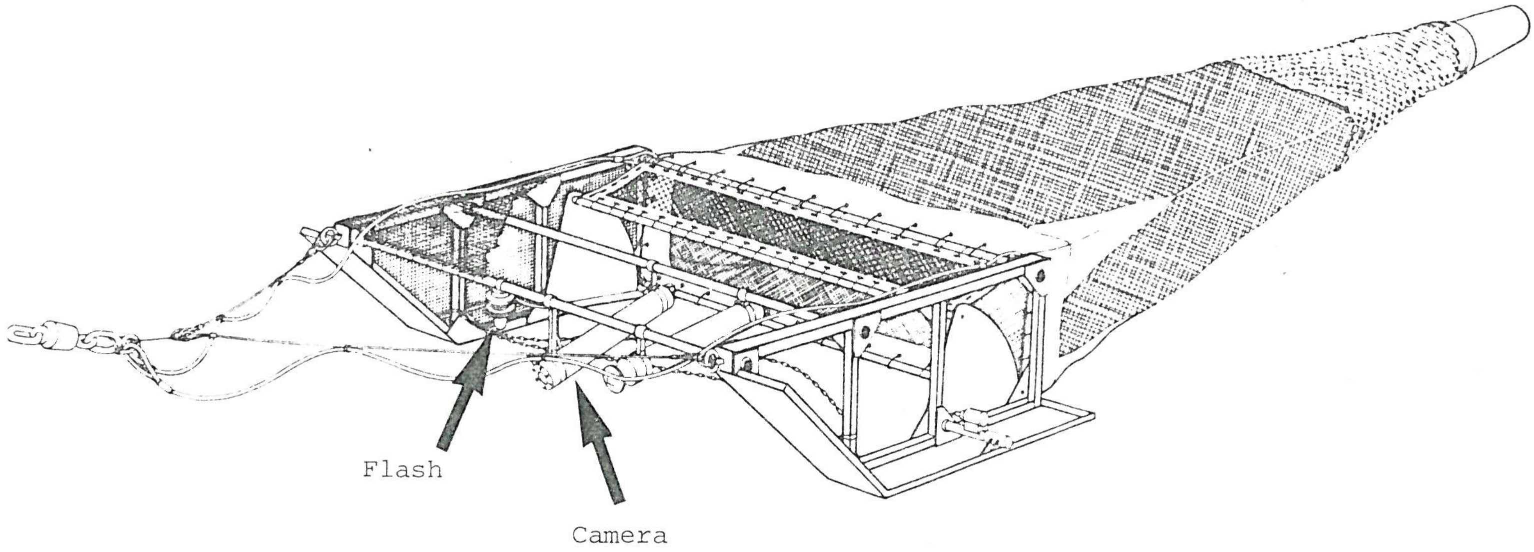

Fig. 1 I.O.S. epibenthic sledge and camera system used from 1975 to 1978.

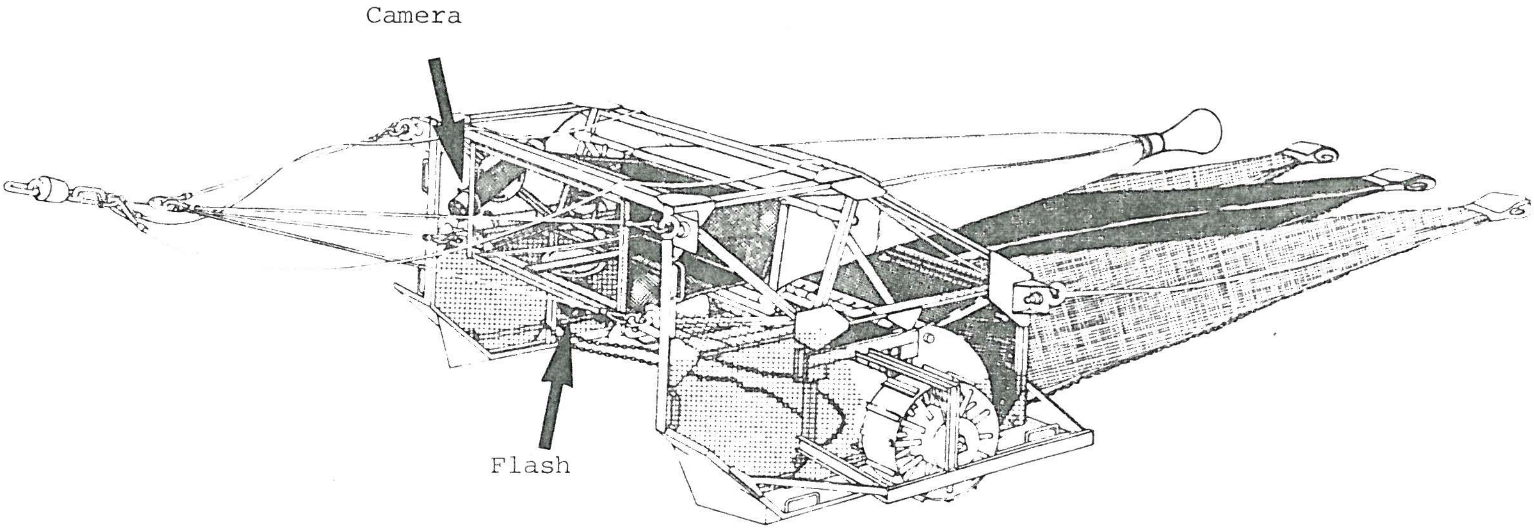

Fig. 2 I.O.S. epibenthic sledge and camera system used since 1979. Note that the camera is mounted higher and at a steeper angle than in the earlier version.

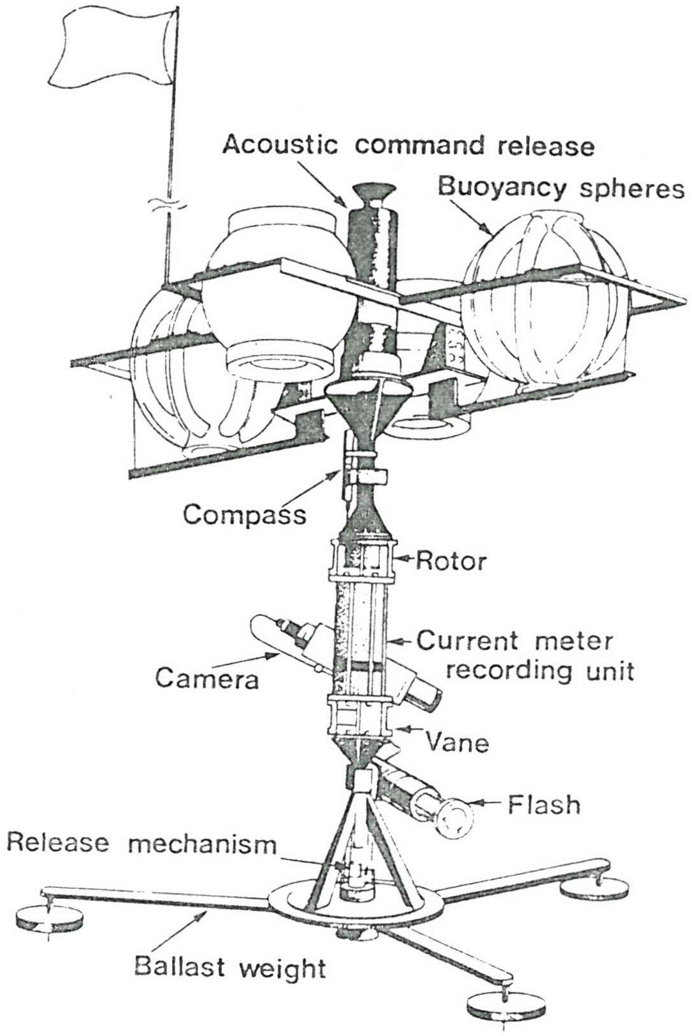

Fig. 3 Bathysnap prior to deployment. It stands 2.4m high and weights 261 Kg. An integral part of the single vertical spar is a modified Aanderaa current meter attached to which is the camera. A 10m polypropylene lazyline with a 25cm float (not illustrated) is attached to the top of the device for use during launching and retrieval.

Fig. 4 Photograph from a depth of 3900m off the north-west African coast (20°10'N : 21°40'W). The near-spherical bodies (1-6cm in diameter) are foraminiferan-like protozoans (Xenophyophores) of the genus *Reticulamina*, which occurred in the photographs at densities of up to 20/m². The black object is the sea-cucumber (holothurian), *Benthodytes typica*.

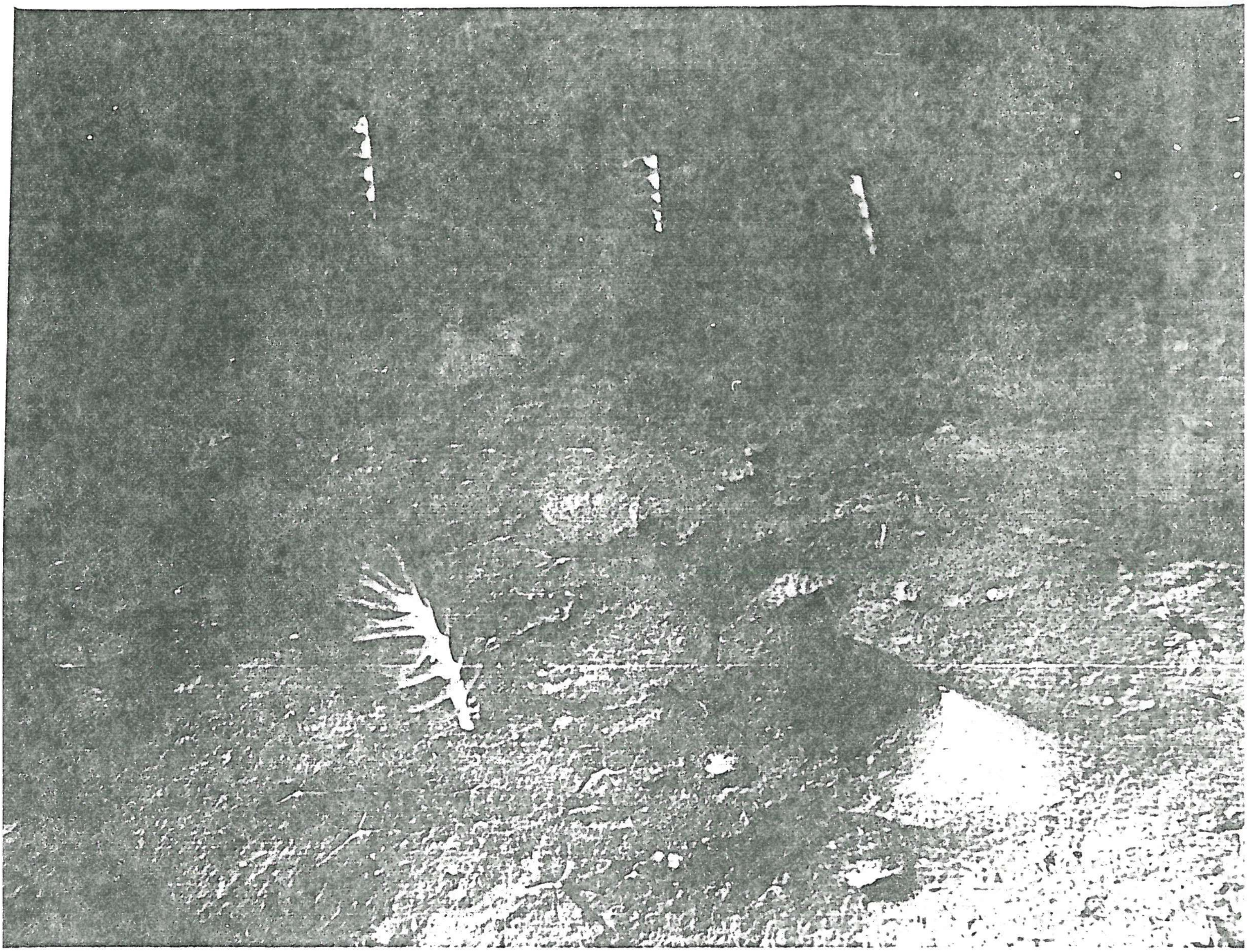

Fig. 5 Juvenile sea-pens (Kophobelemnon stelliferum) photographed in the Porcupine Seabight at a depth of 400m.

Fig. 6 A dense aggregation of the holothurian Kolga hyalina gathered around a sedimentary ring structure at a depth of 3700m at the mouth of the Porcupine Seabight.

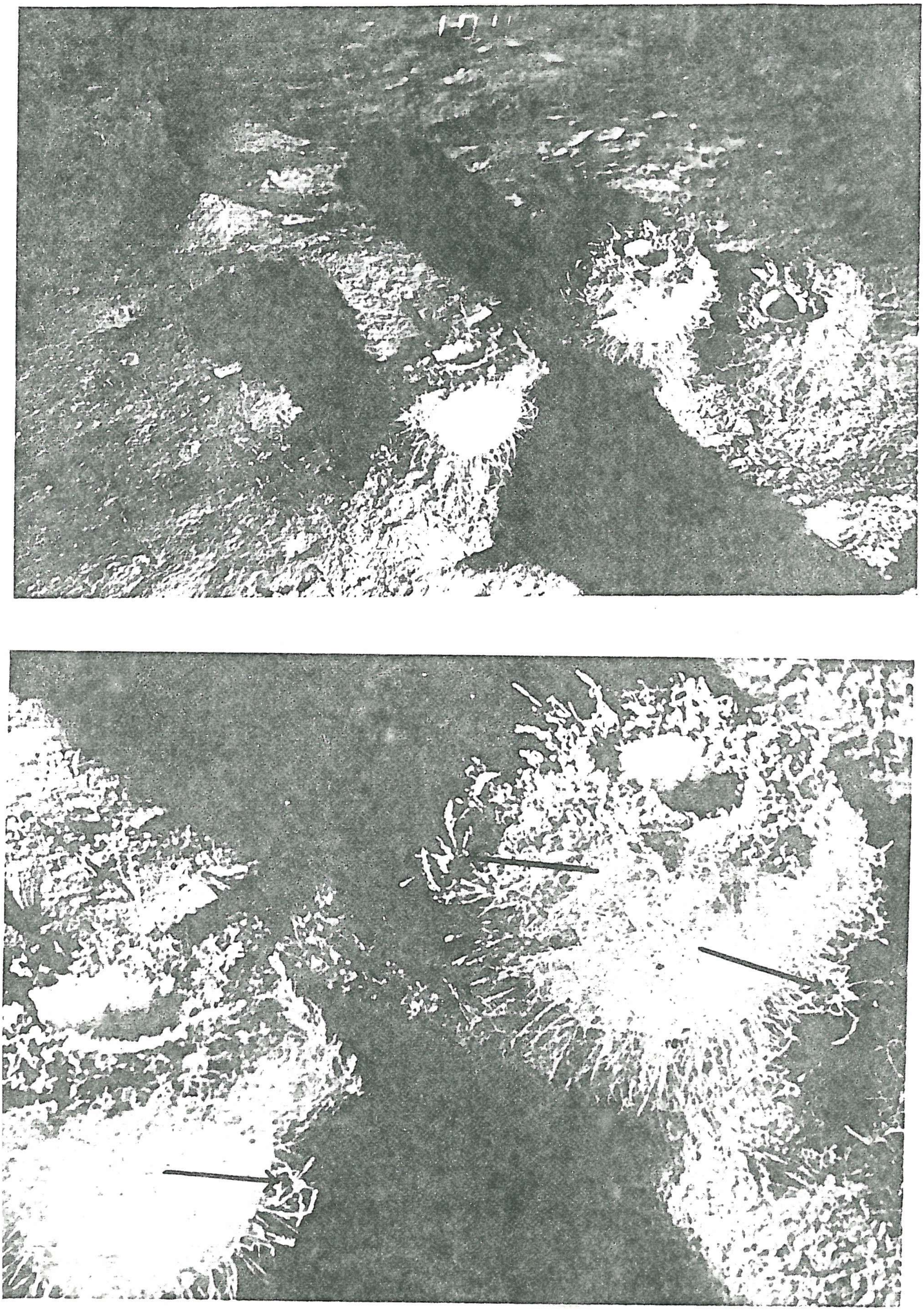

Fig. 7 Hexactinellid sponge, *Pheronema carpenteri*, and the spider crab, *Dorhynchus thomsoni* (arrowed on enlargement) photographed at a depth of 1200m in the Porcupine Seabight.

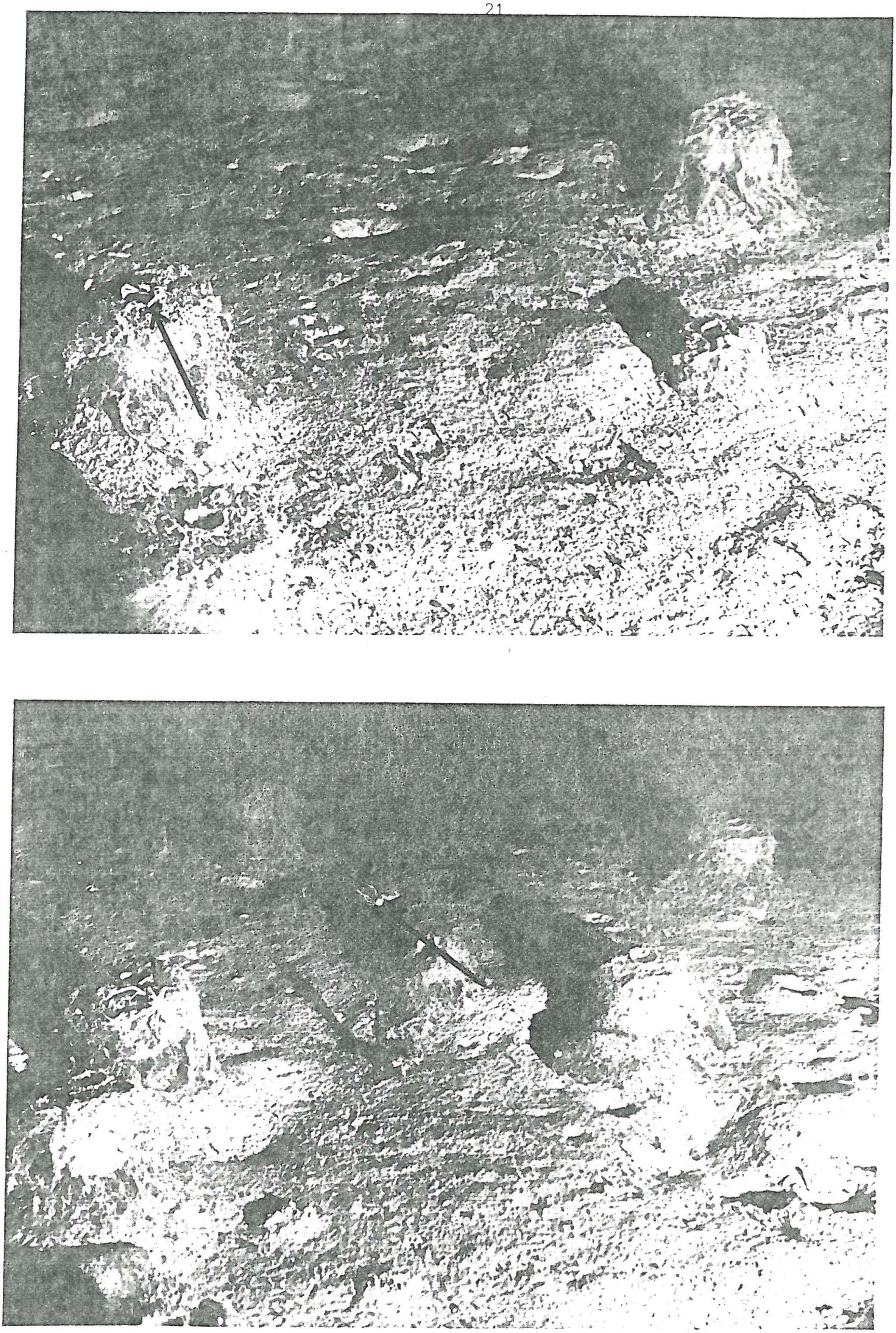

Fig. 8 Squat lobsters, Munida tenuimana, sheltering in the oscular cavity of a Pheronema and in the more usual situation in a burrow in the sediment. Photographed at a depth of about 1100m in the Porcupine Seabight.

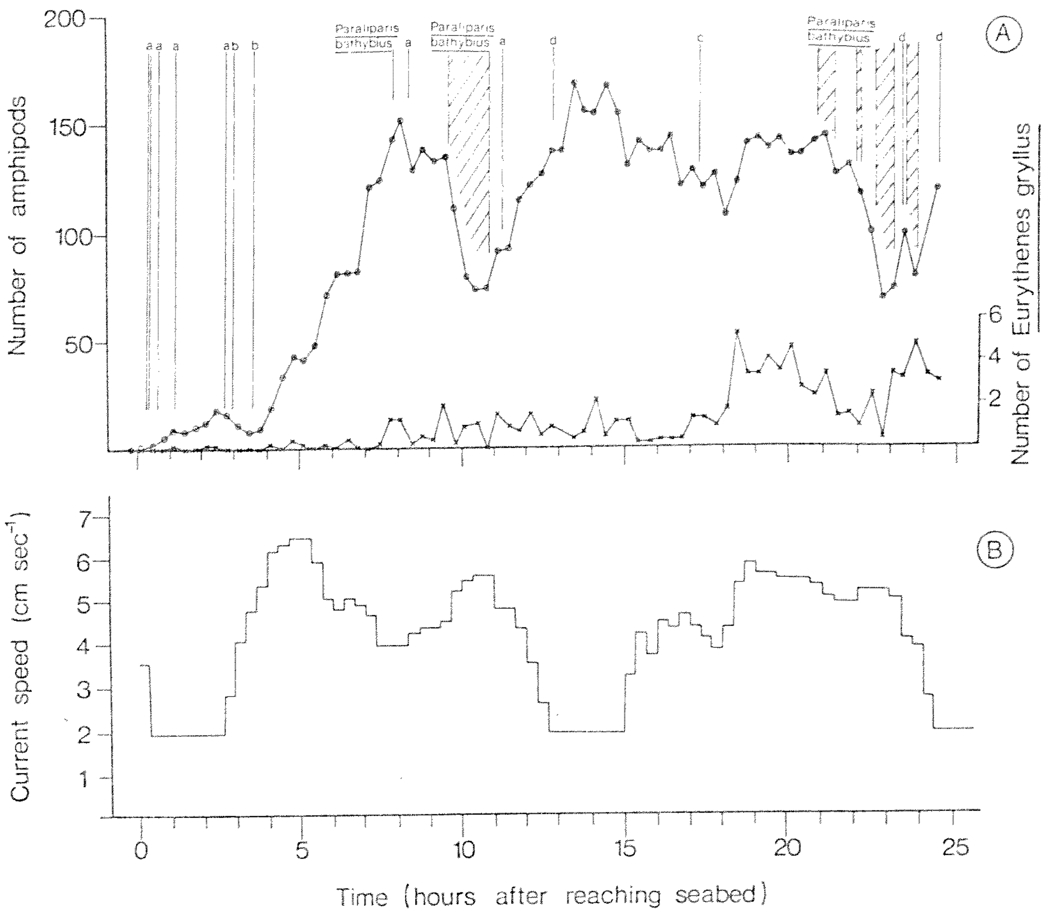

Fig. 9 (A) Numbers of all amphipod specimens and of one species: Eurythenes gryllus visible on bait, and occurrences of the fish predator Paraliparis bathybius. (hatched areas). The presence of other organisms is indicated by the letters (a) Coryphaenoides armatus; (b) Echinomacrurus mollis; (c) Unidentified fish; (d) Pleisiopenaeus armatus.

(B) Current velocities (apparent constant velocities of 1.8cm/sec are artefacts of current meter sensitivity).

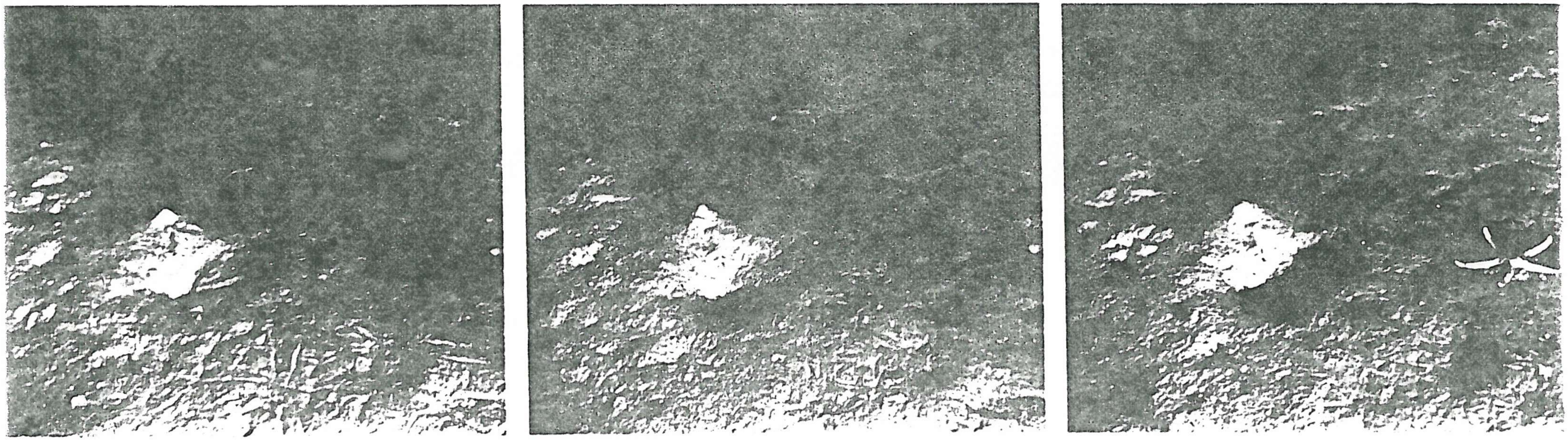

Fig. 10 Area of seabed at 2000m on 3rd April (Left) and on 30th April (Centre) during which time there was little change in the appearance of the seabed. 38 hours later (Right) dark patches of phytodetritus are evident. The asteroid is <u>Plutonaster bifrons</u> with an arm radius (R) of 80mm.

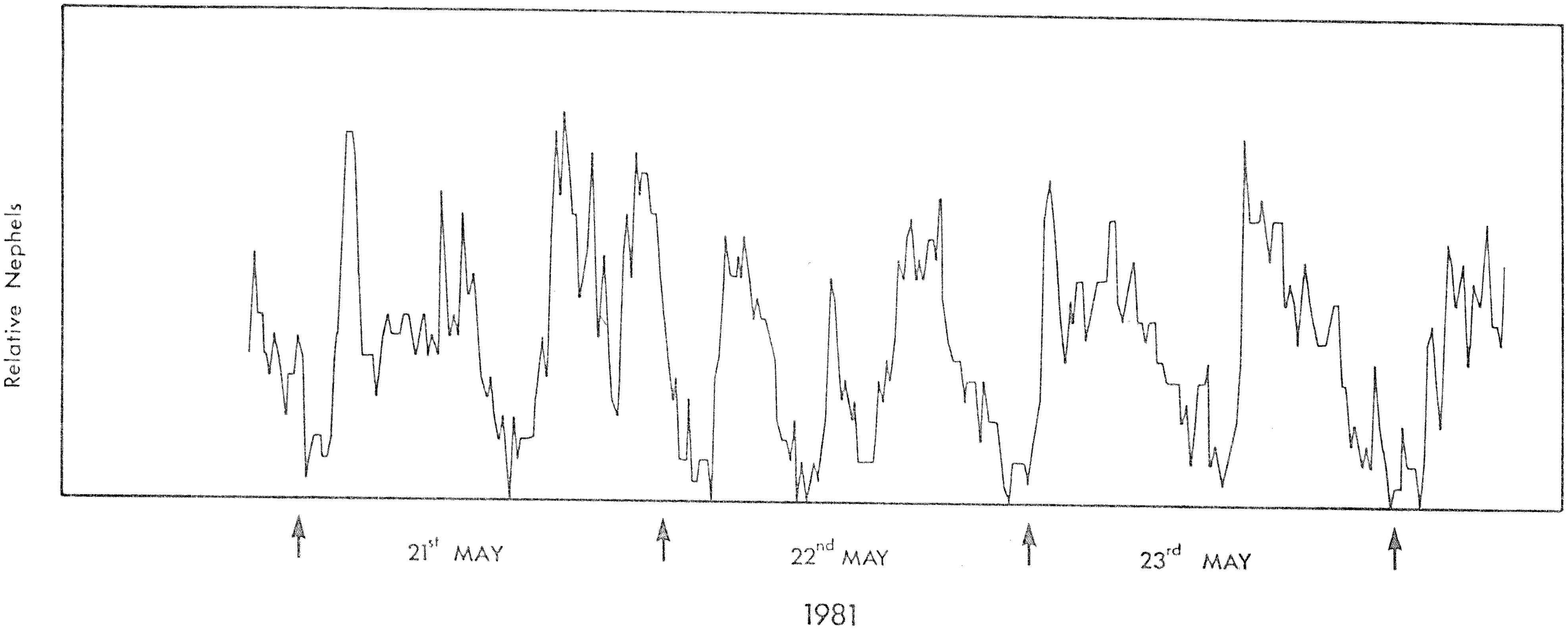

Fig. 11 Variation in the quantity of suspended material within the bottom 1m layer at a depth of 1200m in May 1981.

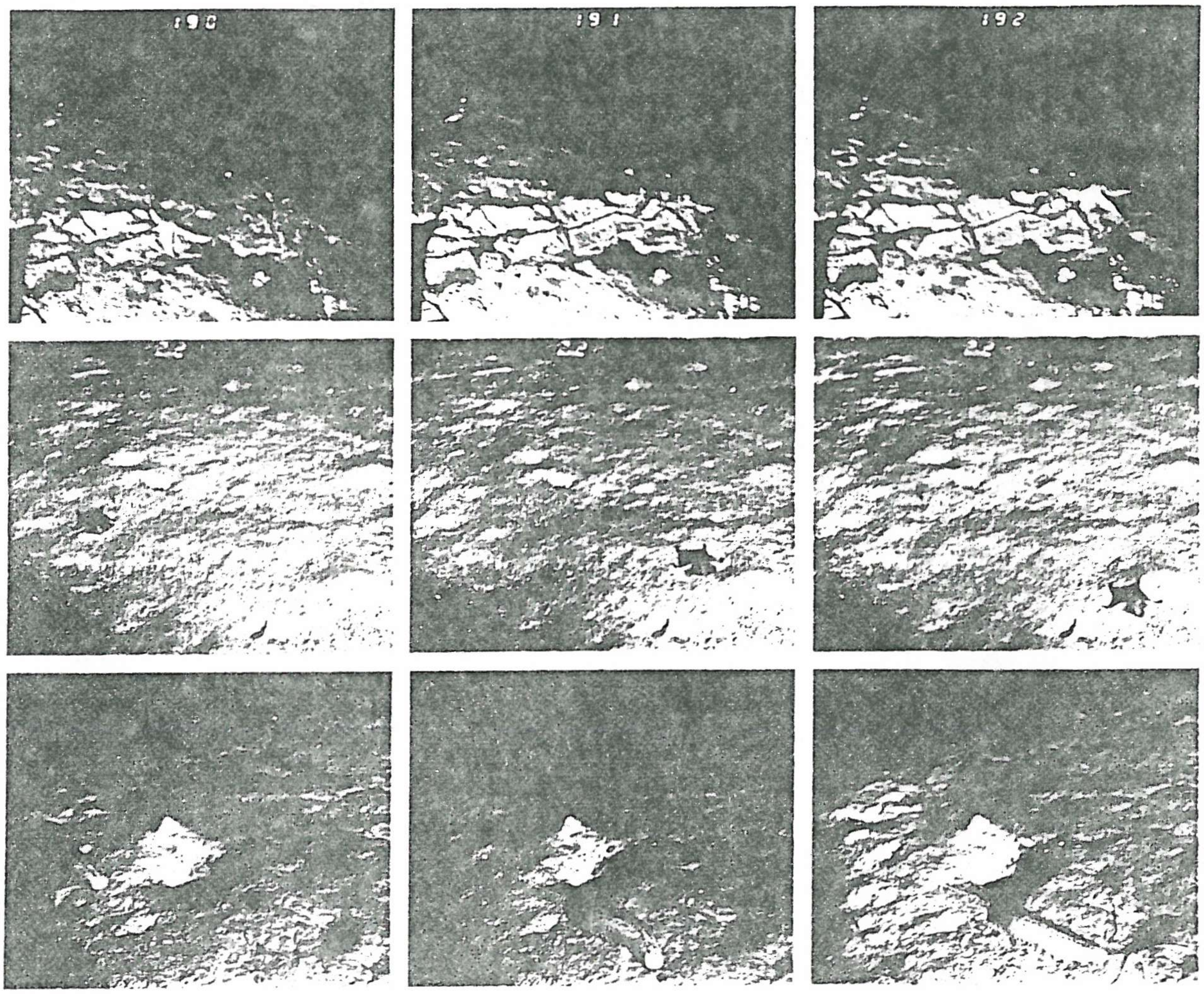

Fig. 12 "Bathysnap" sequences of the asteroids Bathybiaster vexillifer (Top) at 2000m (frame interval 16 mins) and Hymenaster membranaceus (Middle) at 2700m (frame interval 16 mins). The bottom sequence shows the holothurian Benthogone rosea at 2008m with a frame interval of 64 mins. The ophiuroid Ophiomusium lymani appears in the last frame of this sequence.

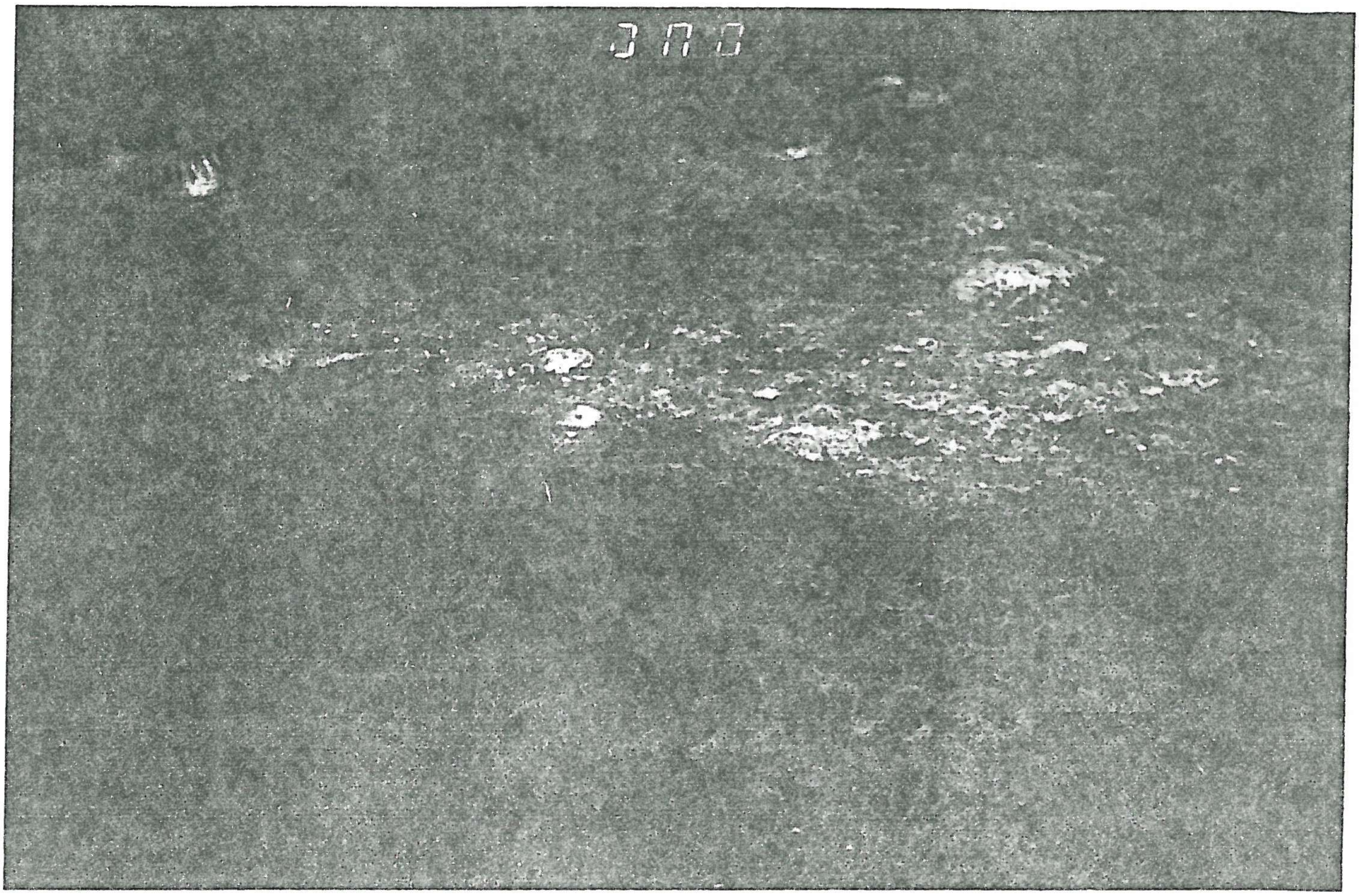

Fig. 13 A hormathiid sea anemone (as yet unidentified) at 4100m photographed for 31 days at hourly intervals.

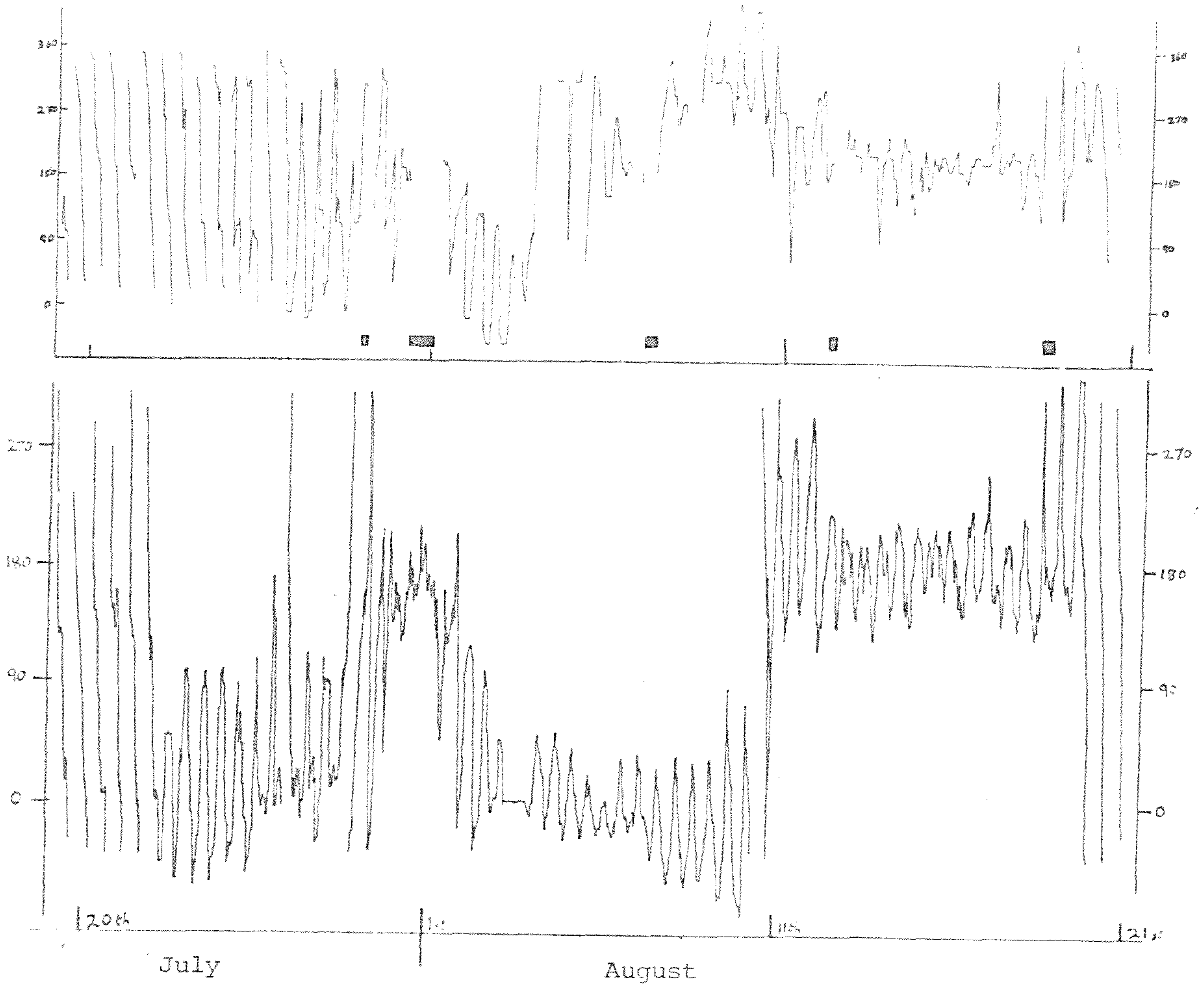

Fig. 14 Orientation of the concave upper surface of an hormathiid sea anemone (upper graph) and the direction from which the nearbed current arrives (lower graph). Due to a camera malfunction it is possible to give the time each photograph was taken only to the nearest day. Nevertheless, the two long periods when the current direction was fairly constant (1-10 and 11-21 August) clearly demonstrate that the anemone orientates its disk into the current. The bars on the upper graph, corresponding to breaks in the orientation record, indicate periods when the anemone had contracted into a tight ball and no disk was evident. Other breaks in the orientation record indicate periods when the disk appeared to be horizontal.

Fig. 15 Two specimens of a glyphocrangonid shrimp. Both have body lengths ≃ 7cm and are probably Glyphocrangon sculpta. Their directions of travel are indicated by arrows.

Fig. 16 An example of one of the large worms photographed by Bathysnap. This one, at a depth of 4040m, reveals 50cm of body length.

APPENDIX 1

Evidence for non-random distributions of a number of benthic species from epibenthic sledge photographs

Station	Species	n	μ	s	f*
50602#1	*Ophiomusium lymani* (brittle-star)	103	1.16	4.62	1895
50609#1	*Ophiura affinis* (brittle-star)	52	21.3	10.72	282
	Kophobelemnon stelliferum (sea-pen)	55	1.74	1.40	62
	Virgularia (sea-pen)	56	0.91	1.23	95
10111#8	*Elpidia* sp. (sea-cucumber)	155	1.04	1.25	232
51208#2	*Pheronema grayi* (sponge)	116	1.14	1.38	193
9756#9	*Kolga hyalina* (sea-cucumber)	45	32.2	97.5	13800
9756#14	*K. hyalina*	46	47.5	115.2	12846
50603#1	*K. hyalina*	172	41.3	2.84	336
50605#1	*K. hyalina*	177	124.8	9.38	1248
10113#1	*K. hyalina*	65	9.3	16.82	1971

n = no. of usable frames
μ = mean density (no./m^2)
s = standard deviation
f* = Fisher's dispersion index (= $\frac{\Sigma(x_i - \bar{x})^2}{\bar{x}}$). The higher this index the more "clumped" is the distribution.

All of the dispersion index figures are significant at the 1% level except that for *Kophobelemnon*. However, the validity of the index in those cases where the mean density is less than 5 is doubtful since the power of the test to detect randomness in this range is poor.

APPENDIX 2

Date	Station	Depth (m)	No. of usable frames	No. of Benthogone	No. of faecal casts	No. faeces/ Benthogone/ day
March '82	51408	2005	84	6	43	0.25
March '82	51407	1500	99	4	38	0.34
April '78	9779#1	1399	89	9	91	0.36
April '78	9775#3	2015	72	2	25	0.45
May '81	51113#2	1535	71	4	33	0.29
July '79	50602	1980	92	2	21	0.38
Sept '79	10111#8	1635	151	9	142	0.56
				36	393 →	0.39

The average dimensions of a faecal cast are 6cm long by 2cm diameter giving a volume of 19cm^3. If the dry bulk density of the superficial sediments = 0.60g cm^{-3} and the water content = 56.9% (Golfe de Gascogne 2100m - Khripounoff 1979) and if the water content of the faeces = 67% (estimated from Sibuet et al. 1982, Massin, 1980). Bulk density of faeces = 0.42g solid cm^{-3}. Dry weight of each cast = 7.98g.

Therefore feeding rate = 3.11g dry sediment per day

Porcupine Seabight sediment ≃ 0.4% organic C of dry weight. From Khripounoff & Sibuet 1980, it is reasonable to assume that B. rosea will feed selectively such that the sediment ingested has 3 times higher organic carbon than the surrounding sediment.

Therefore ingested material = (3 x 0.4) = 1.2% organic C and feeding rate = 3.73mg organic C/day.

If the assimilation efficiency of organic C = 15% (Khripounoff and Sibuet 1980)

Assimilation rate = 5.60mg organic Carbon/day.

A specimen of B. rosea has an organic C content ≃ 510mg

Therefore assimilation rate = 1.1% body C/day.

Bathysnap results show that B. rosea can move at a maximum speed (between frames) of 90cm/h. The width of the feeding path will be about 2cm and this would give a maximum value for the feeding area of 4320cm^2/day. The feeding rate of 3.11g/day gives a volume of sediment ingested of 5.2cm^3/day

Therefore depth of feeding on these assumptions is

$$1.2 \times 10^{-3}\text{cm} = 12\mu\text{m}$$

This value probably has no ecological or behavioural meaning as specimens can probably extract sediment from deeper if it is in a particularly enriched patch, whereas in other places specimens may not feed at all.

APPENDIX 3

	Body length	Maximum speed	
	cm	cm h^{-1}	Body lengths h^{-1}
Asteroidea			
Hymenaster membranaceus	4-9	310	50
Bathybiaster vexillifer	16	100	6
Holothurioidea			
Benthogone rosea	17	89	5
Echinoidea			
Echinus affinis	4	47	12
Gastropoda			
Misc.	4	154	38
Decapoda			
Glyphocrangon sculpta	7	270	39
Vermes	3.2	525	165