The feeding behaviour of an abyssal sea anemone from *in situ* time lapse photographs and trawl samples

Abyssal
Sea anemone
Time lapse photography
Feeding behaviour
Distribution

Abyssal
Anémone de mer
Photographie accélérée
Comportement d'alimentation
Distribution

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ABSTRACT

At 4100 m in the Northeast Atlantic a single specimen of a sea anemone was photographed every 64 minutes for 32 days. The current direction was recorded simultaneously and contrary to published reports on the behaviour of this group, the specimen responded actively by orienting its oral disk into the prevailing current. From trawl samples taken in the same area, the identity of the photographed specimen is suggested as *Sicyonis tuberculata.* This species has been found at depths of 4050-4800 m at up to 213 specimens km^{-2} and contributes about 5% to the wet weight biomass of the megafauna. The stomach contents of these captured specimens were examined and from these and the photographs it is thought that the species feeds 150 times per day on a wide range of material from small suspended particles less than 4 mm across to highly motile megafauna of similar size to itself.

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RÉSUMÉ

Le comportement nutritionnel d'une anémone de mer abyssale, à partir de photographies *in situ* et de prélèvements au chalut

Un spécimen d'anémone de mer a été photographié toutes les 64 minutes pendant 32 jours à 4100 m dans le nord-est de l'Atlantique. La direction du courant était enregistrée simultanément et, en contradiction avec les publications sur le comportement de ce groupe, le spécimen répondait activement en orientant son disque oral face à la direction du courant dominant. Les échantillons prélevés au chalut dans la même zone suggèrent que le spécimen photographié serait *Sicyonis tuberculata.* Cette espèce a été observée à des profondeurs de 4050 à 4800 m, avec une densité atteignant 213 spécimens.km^{-2}; elle représente 5% du poids humide de la biomasse de la mégafaune. Les contenus stomacaux des spécimens capturés et les photographies indiquent que cette espèce se nourrit 150 fois par jour d'une grande diversité d'aliments, allant de petites particules en suspension de moins de 4 mm, jusqu'à la mégafaune très mobile de taille comparable à celle de l'anémone.

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INTRODUCTION

Sea anemones or actinians are found in a wide variety of environments from the intertidal to the abyss. Our understanding of their nutrition has changed considerably in recent years (van Praet, 1985) and several methods of feeding are now recognised. Some species are filter-feeders, taking seston out of the water flowing through their tentacle crown (Sebens, 1981). Others feed macrophagously either on motile prey which blunder into the tentacles or sessile organisms which have lost their foothold due to current action (reviewed in Sebens, 1981). A number of species benefit from a symbiotic relationship with photosynthetic zooxanthellae or bacteria (Steele, Goreau, 1977; Fitt *et al.*, 1982; Herndl *et al.*, 1985) and some species absorb dissolved organic matter across the ectoderm of the column and tentacles (Schlichter, 1978). There is evidence that species previously thought to be carnivorous also feed on plant remains and that there may be a seasonal change in the balance between these two feeding methods (van Praet, 1982).

Many species rely heavily on water currents to supply food, disperse gametes and remove excreta. There may however be a conflict between the benefits derived from increasing current speed and the hazard that individuals may lose their hold of the substrate if the flow is too strong (Wainwright, Koehl, 1976; Vogel, 1984; Koehl, 1984). Changes in current speed induce behavioural changes in many anemones which may reduce this conflict (Robins, Shick, 1979), but in contrast to some other anthozoa such as species of gorgonians or pennatulids (review by Riedl, 1971; Hoare, Wilson, 1977), no species of actiniarian is reported to respond actively to current direction. Sea anemones seem to bend passively with the current whether in the high energy littoral and sublittoral environments (Wainwright, Koehl, 1976) or in the more tranquil deep sea (Heezen, Hollister, 1971; Ohta, 1983).

The present paper describes the behaviour of a single actiniarian specimen at 4 100 m for 32 days based on time-lapse photography. The only previous study known to us using *in situ* photography of anthozoa is that of Eleftheriou and Basford (1983) but in contrast to that study we provide evidence of an active response to current direction by an actinian species. We also provide information on the gut contents of preserved specimens of the same species and report on its abundance and biomass in one area of the North-East Atlantic.

MATERIAL AND METHOD

Bathysnap is an autonomous benthic time-lapse camera and current meter device which is designed to remain on the seabed for up to one year (Lampitt, Burnham, 1983). It is deployed by free fall descent and usually takes photographs of 2 m^2 at a preset time interval using a maximum of 800 frames. The device is recovered using an acoustic command which releases a ballast weight and allows it to rise to the surface under its own buoyancy. It was deployed on 20 July 1982 at a depth of 4 101 m at the mouth of the Porcupine seabight (PSB) in the North-East Atlantic (49°44′N, 14°09′W). The only change from the published design was that the camera angle and height had been adjusted so that 4.8 m^2 of sea-bed was photographed. The height of the flash was also increased, but, although more sea-bed was photographed, there was a considerable loss of definition. Photographs were taken every 64 minutes for 32 days using monochrome thin-based film. Unfortunately, the film ends were destroyed during processing and the data display in the camera did not function so the times at which individual frames were exposed can only be estimated to the nearest day. The current meter (Aanderaa RCM5) logged data every 10 minutes, but due to a technical problem, data were recorded only on current direction and not speed.

The original objective of the deployment was to record changes in the appearance of the sea-bed due to seasonal deposition of detritus (Lampitt, 1985) but, by chance, a large sea anemone was situated within the field of view. It was photographed at 14° to the horizontal, and the orientation of its concave oral disk could be measured on most of the 712 photographs. Tentacular feeding responses and other behavioural events were also recorded.

Having established the probable identity of the specimen photographed (*see* "Results and Discussion") abundance estimates for this species were calculated from 18 trawl samples from the Porcupine seabight and abyssal plain at depths ranging from 3 800 to 4 800 m, obtained using a semi-balloon otter trawl (Merrett, Marshall, 1980) (effective width 8.6 m, maximum mesh size 4.4 cm). Gut content analyses were carried out on about half of the 64 specimens collected in these hauls. Wet weights of the specimens were used to estimate their biomass which could be compared with those of other components of the megafauna.

RESULTS AND DISCUSSION

Description and identification

The specimen photographed (Fig. 1) had a pedal disk diameter of about 8 cm. When fully extended, the oral disk including tentacles measured about 28 cm across. Sixty-four tentacles were visible arranged in an amphicoronate arrangement (Cornelius, Ryland, in prep.) in two rows; each tentacle when extended was about 4 cm long. The mouth which was usually about 1 cm diameter, was 8-12 cm above the sea-bed. The top of the column was weakly noded and was banded horizontally. The pedal disk appeared to be flush with the sediment surface with no solid object visible under it, suggesting the species is one which uses a mud ball to anchor itself to the sea-bed.

Over 1.5 km^2 of sea-bed have been trawled at the mouth of the seabight, collecting about 17 putative species of actinaria, very few of which have been identified. Identification of specimens for which only photographs exist is prone to errors but in this case only one species in the collection has horizontal banding and nodes on the column, has a mud ball in the pedal disk, is of similar size and has a similar number of tentacles (62-92). The species has been identified as the actinostolid *Sicyonis tuberculata* Carlgren by Riemann-Zurneck.

Abundance

Figure 2 shows the abundance of *S. tuberculata* calculated from samples taken at depths between 3 800 and 4 800 m. No specimens were captured in the 102 trawls between depths of 500 and 4 050 m. Between 4 050 m and the greatest depth trawled of 4 800 m there was considerable variability in abundance but no indication that this deepest station was near the lower depth limit of the species (two further specimens not included here

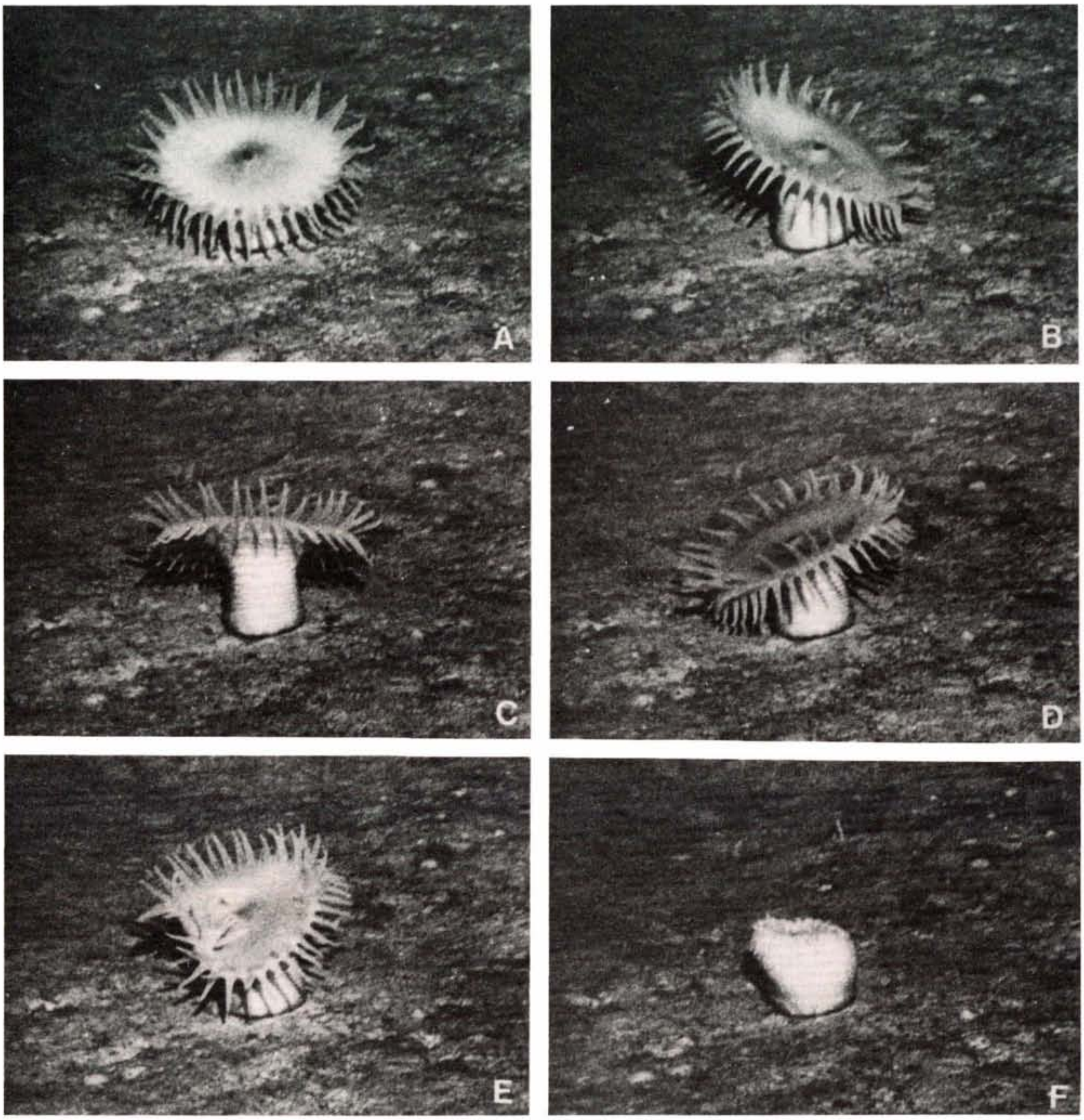

Figure 1

Examples from the photographic sequence of Sicyonis tuberculata *at* 4 101 *m. A-D: Frames separated by about* 3 *hours* (192 *mn*) *on July* 20*th showing rotation of the oral disk in response to the current direction. Three hours after frame D, the orientation was the same as in frame A. E: Example of a tentacular feeding response. F: Complete contraction with only the tentacle tips visible. Such behaviour is indicated in Figure* 3 (*upper*) *by black bars.*

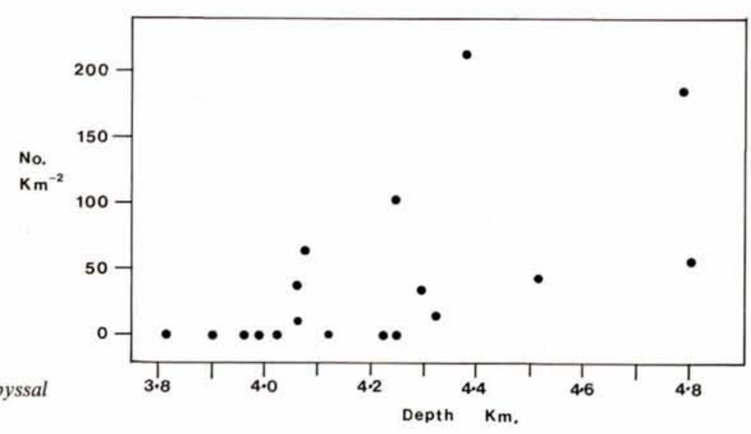

Figure 2

Abundance of S. tuberculata *in the Porcupine seabight and abyssal plain.*

have been captured on the Azores-Biscay rise at 4 090 and 4 560 m). Between 4 050 and 4 800 m observed abundance varied from 0 to 213 km^{-2} with an average of 56 km^{-2}. The mean individual wet weight of the collected specimens after several years in 2% formaldehyde was 146±49 g, giving a mean biomass of 8.2 mg m^{-2}. The ash-free dry weight of deep-sea Actiniaria is about 8% of the wet weight in IOS collections giving an ash-free dry weight biomass of 0.656 mg m^{-2}. The relationship of megafaunal biomass to depth in the Porcupine seabight (Lampitt *et al.*, 1986), estimates wet weight of megafauna to be 163 mg m^{-2} at 4 300 m and of ash-free dry weight to be 7.7 mg m^{-2}. The Actinaria, therefore, contributes about 5% to the wet weight biomass of the megafauna and slightly more to the ash-free dry weight biomass.

S. tuberculata has a wide bathymetric range. It was described originally from 560 m in the Davis Strait (66°N) and 2 340 m in the Denmark Strait (64°N; Carlgren, 1921) and subsequently has been taken between 3 000 and 4 000 m in the North-West Atlantic (52-58°N; Doumenc, 1975). From these records and the present study it should probably be considered a deep-sea species.

Several *in situ* photographs have been published of specimens which are indistinguishable from the specimen photographed in the Porcupine seabight. These were from the South-West Pacific at about 6 700 m (Lemche *et al.*, 1976, Plate 9 *e*), the Antarctic continental rise at 4 840 m (Heezen, Hollister, 1971; Fig. 2.31 ul) and from the North-East Atlantic, probably on the Azores-Biscay rise, at 4 300 m (Feldt *et al.*, 1985; Fig. 9).

Behaviour

The photographs in Figure 1A-1D were taken 3 hours apart on 20 July and show changes in the orientation of the oral disk in response to near-bed currents. Three hours after photo 1D was taken, the posture was the same as in 1A. The anemone therefore completed a 360° rotation in about 12 hours. The direction the oral disk is facing in each frame is shown in Figure 3 (upper) although the time scale is only accurate to 1 day (*see* above). The current direction during the period is shown in Figure 3 (lower) but in contrast to the usual convention, this is illustrated as the direction from which the current is coming. Although the technical problems mentioned above prevented us from calculating the regression between these two directional values, there were two periods when current direction was relatively constant (Fig. 3, 1 and 2). During both periods and particularly the second it is obvious that the oral disk was pointing into the prevailing current. This is also indicated in the 4 tidal cycles before period 1. To our knowledge, this is the first demonstration of an active response to current direction in any actiniarian species. While other anthozoan groups respond in a variety of ways, some actively, the literature suggests that Actiniaria all respond passively. The advantages of active orientation will clearly depend on the diet of the species (as described later in this paper, the species may feed both micro and macrophagously). Suspension feeding of planar Anthozoa is enhanced by orientation normal to the current flow (Leversee, 1976) and Warner (1976) used model structures to show that dish-shaped filters facing into the prevailing current are particularly efficient at collecting suspended particles.

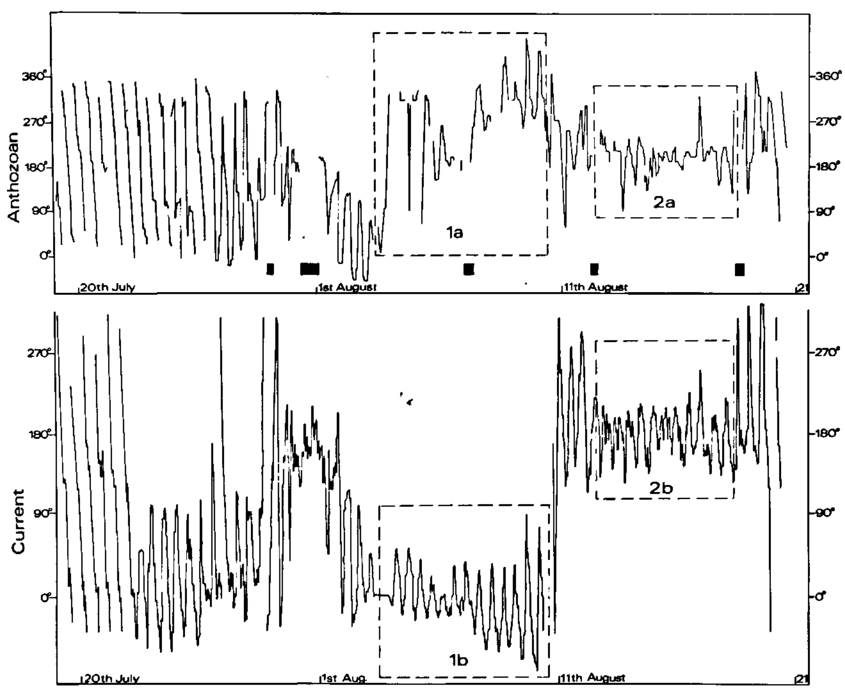

Figure 3

(upper) Orientation of the concave upper surface of the oral disk of the specimens of S. tuberculata. *Black bars indicate periods of complete contraction (Fig. 1F) and other breaks in the record indicate periods when the disk appeared to be horizontal. Two periods when the specimen's orientation was relatively constant are indicated by 1a and 2a; (lower) Direction from which the current is coming. The periods corresponding to those identified on the upper graph are shown as 1b and 2b. Another period of relatively constant current direction around 24th July does not however seem to be associated with a similarly constant oral disk orientation.*

Riemann-Zurneck (1979) suggested that the large oral disk and small pedal disk of another species of deep-sea anemone may enable specimens to orient in the current to collect suspended particles. In the case of *S. tuberculata*, if the disk was orientated downstream the effective capture area would be reduced as a result of obstruction by the column. Megafaunal species may simply swim or walk into the tentacle crown whatever its orientation. However, there is evidence of at least one species drifting over the sea-bed with the current in search of non-motile prey (Lampitt, Burnham, 1983). By facing into the current, with the tentacles above or even touching the sediment, these drifters would be more readily captured than if facing downstream.

If food collected within a few centimetres of the sea-bed is an important component of the diet, one might expect the majority of tentacular responses to be by tentacles nearest the sea-bed. In fact, 31% of the responses were by tentacles in the quadrant of the oral disk nearest the sea-bed which indicates only slightly greater importance of this area over other quadrants (*cf.* 25% in top and 22% in each side quadrant on average). There was no significant difference in the average number of tentacles involved in the feeding response between each of the four quadrants with about 20% of tentacles involved on average.

A further advantage of upstream orientation may be that the current would tend to push the anemone onto the sediment thereby reducing its chances of being washed away. Most Actiniaria are found on hard substrates and those living on soft sediment usually either burrow into the sediment or attach themselves to stable objects such as lumps of rock or other epifauna. *S. tuberculata* improves its stability by means of a ball of sediment in the pedal disk. Such behaviour may not enable the species to resist such high currents as those species on hard substrates but the ambient currents are likely to be much lower in any case. Species using a mud ball as an anchor can presumably colonize a much larger area of seabed than those using a hard substrate.

The advantages of active orientation must be set against the energetic costs of increased muscle activity. These costs may, however, be reduced in deep-sea Actiniara by the structural resilience of the column. Shallow-water species rely mainly on hydrostatic pressure to expand the oral disk and maintain posture (Batham, Pantin, 1950). *S. tuberculata* and many other deep-sea Actiniaria have a very well developed mesogloea (Paterson, unpublished) which may provide support so that less energy need be spent on postural maintenance.

Actiniaria transport food to the mouth by cilia or by tentacles. Tentacular feeding responses were readily visible on the photographs and Figure 1E shows such a response during which up to 30 tentacles were drawn towards the mouth. In common with shallow water tentacular feeders, the mouth moves towards the moving tentacles opening as it does so. Sixty-five such feeding responses were photographed during the deployment (11% of frames) but this is probably much less than the total number which occurred in that period. Hungry shallow-water specimens can complete a tentacular feeding response in 10-15 s (Jennings, 1923) and usually in less than 1 minute (Reimer, 1973) whereas the frame interval used here was 64 minutes. If tentacular feeding responses lasted one minute and 11% of the specimen's time was involved with such a response, 158 feeding events occurred each day. In none of these feeding events was it possible to discern the food particle which suggests they were less than 4 mm in diameter. The photographic resolution was not adequate to detect ciliary feeding and because of the poor state of preservation of captured specimens (*see* below), we have not been able to determine the distribution of cilia over the oral disk or even whether they are present at all.

Another obvious behavioural feature of these photographs was the occurrence of periods of complete contraction. Such periods are common in shallow-water species for short periods of time and usually follow a tidal or a circadian rhythm (Hargitt, 1907; Robbins, Shick, 1979) or are a response to predators or current. On five occasions, identified by black bars in Figure 3 (upper) the specimens contracted completely (*see* Fig. 1F) such that the tentacles were barely visible if at all. The contraction sequence involved a slight or negligible change in posture in one frame followed in the next by complete contraction. The specimens stayed contracted for 1-5 hours and then opened gradually over a period of up to 9 hours. Sometimes atypical behaviour followed for several hours before the usual posture was adopted. Four possible reasons may be put forward for this behaviour which obviously precludes all other behavioural functions. Firstly, it may be a response to the consumption of a large prey item as has been reported for other species (Sebens, 1981). No such items were seen just prior to periods of contraction or at any other time although large prey certainly do contribute to the diet (*see* below). Secondly, it may be a response to very low current speed when the rate of food supply fell below a critical level. Such behaviour is known in the shallow-water anemone *Metridium senile* (Robbins, Shick, 1979) and is associated with a reduction in metabolic rate. Without current speed data it is impossible to assess this suggestion but it seems unlikely since a contracted anemone could not capture megafaunal prey; a conflict not faced by *Metridium* which is restricted to suspension feeding. Conversely the possibility that it is a response to high current speed cannot be assessed, but contracted specimens probably offer less resistance to flow. The photographs show a detrital layer throughout the deployment and this would probably have been resuspended if currents had exceeded the rather low speed of 7 cm s^{-1} (at 1 m above the sea-bed; Lampitt, 1985). A fourth possible explanation for contraction is that it is a defensive response. Actiniaria are prey for a number of species (Webb, 1973; Ottaway, 1977) but once again no potential predators were seen in the photographs.

Gut contents

It is difficult to draw conclusions about the diet of any species from gut content analysis because of differential digestion rates, egestion, poor preservation or adventitious ingestion during capture.

Twenty specimens of *S. tuberculata* were examined and found to contain in their guts sediment of similar composition to that in the pedal disk (planktonic foraminifera and coccoliths). This suggests that the material was ingested adventitiously during capture. Samples collected in April, August, October and November gave no indication of seasonal changes in the diet which might have been expected for a microphagous feeder (Billett *et al.*, 1983; Lampitt, 1985) but such changes as there were may have been masked by the sediment adventitiously ingested. Some specimens contained small pieces of clinker and fish scales. A squid sucker was found in one specimen, the oral part of the echinoid *Pourtalesia* sp. in another and a well digested specimen of the shrimp *Pleisiopenaeus armatus* (Bate, 1881) of total body length 22 cm in a third. In this last case the rostrum of the shrimp had pierced right through the body wall of the anemone which was of pedal diameter 5 cm.

Gut content analysis is not a comprehensive method but in this case it does indicate that *S. tuberculata* feeds both macrophagously and microphagously. This would appear also to be the case for another deep-sea anemone *Actinoscyphia aurelia* which was previously thought to be an obligate detritivore (Aldred *et al.*, 1979) but specimens have now been found to contain echinoderms, polychaetes, gastropods and small Crustacea (Riemann-Zurneck, pers. comm.).

CONCLUSION

In the Porcupine seabight *S. tuberculata* is an important component of the megafauna occurring at an average density over its depth range (4050-4800 m) of 56 specimens km^{-2} (max. 213 km^{-2}) and contributing about 5% to the megafaunal biomass.

In contrast to many, if not all, shallow-water Actiniaria, *S. tuberculata* actively orientates its oral disk into the prevailing current. Food is captured within 12 cm of the sea floor and is ingested using the tentacles probably about 150 times per day. The role of cilia in feeding is unknown. The specimen contracted completely for several hours on five occasions during the deployment and this may have been to digest a large prey item or to resist predation on itself. It includes in its diet highly motile prey of similar dimensions to itself but all the tentacular responses photographed appeared to involve material not large enough to be visible on the photographs (<4 mm in diameter). The nature of the small sized fraction of its food could not be established.

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