Ecological observations on the deep-sea anemone *Actinoscyphia aurelia*

Actinaria Actinoscyphia Ecology Bathyal Subtropical NE Atlantic Actinoscyphia Écologie Bathyal Atlantique NE subtropical

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Received 9/2/79, in revised form 16/5/79, accepted 31/5/79.

ABSTRACT

Actinoscyphia aurelia, a hitherto poorly known deep-sea anemone, has been captured and photographed in large numbers off the north-west African coast, in depths between 1000 and 2000 m. After making allowances for the inaccuracies inherent in the use of towed samplers to obtain quantitative results, the indicated densities are some of the highest ever recorded for megabenthic animals at such depths. This could be due to the high sedimentation rate of organic material resulting from upwelling and consequent high primary productivity in this area. In addition, the different size structures of the sampled populations could be explained by slumps, and possibly turbidity currents, which may periodically expose fresh sediment surfaces for repopulation. The ability of *A. aurelia* to exploit these conditions is discussed in relation to its morphology and reproduction strategy.

Oceanol. Acta, 1979, 2, 4, 389-395.

RÉSUMÉ

Observations écologiques sur l'anémone de profondeur, Actinoscyphia aurelia

Actinoscyphia aurelia, anémone de profondeur jusqu'ici peu connue, a été capturée et photographiée en grand nombre à des profondeurs de 1000 à 2000 m au large de la côte nord-ouest d'Afrique. Malgré l'inévitable imprécision due à l'utilisation des engins traînants pour obtenir des résultats quantitatifs, les densités estimées sont parmi les plus élevées jamais signalées pour la mégafaune à de telles profondeurs. Ceci peut être dû au taux élevé de sédimentation de matériel organique résultant de l'upwelling et de la forte productivité primaire qu'il entraîne dans cette zone. De plus, les différences de structure de taille des populations récoltées peuvent être expliquées par des éboulements et par d'éventuels courants de turbidité qui peuvent exposer périodiquement des surfaces sédimentaires vierges pour la repopulation. L'aptitude d'A. aurelia d'exploiter ces conditions sont discutées en relation avec sa morphologie et sa stratégie de reproduction.

Oceanol. Acta, 1979, 2, 4, 389-395.

INTRODUCTION

The genus Actinoscyphia is represented in the North Atlantic by two species, A. saginata Verrill and A. aurelia Stephenson. A. saginata is fairly widely distributed, having been recorded several times from both sides of the Atlantic in depths ranging from 700 to 2200 m (Church, 1971; Grassle *et al.*, 1975; Riemann-Zürneck, 1978). *A. aurelia* has been reported less frequently and, apart from the original description based on material



Figure 1

Known distribution of Actinoscyphia aurelia. All of the stations discussed in this paper are included in the group between 20° and $22^{\circ}N$ to the west of Cap Blanc.

taken off Ireland (Stephenson, 1918), the only published records are those of Doumenc, 1975, Riemann-Zürneck, 1978, and Rice *et al.* (in press) (Fig. 1). The last two records refer to material collected off the north west

 Table 1

 Station data for Actinoscyphia aurelia captures.

African coast from FS Meteor in 1975 and RRS Discovery in 1976 and 1977. Because of the high population densities of the actinians encountered in some of the recent collections, a few ecological speculations on this otherwise rarely taken species seem justified.

MATERIAL AND METHODS

The Discovery and Meteor collections together contain more than 150 benthic samples taken since 1967, in depths in excess of 500 m, between 9°N and 60°N in the eastern north Atlantic. Only 11 of these samples contain Actinoscyphia aurelia (Table 1) and, with the exception of a single sample from off the Azores, all of them were obtained from the north west African coast between about 1 000 and 2 000 m and between 20°N and 32°N. The catches from the two most northerly stations from the African coast (Discovery 8967 and 9017) contained both A. aurelia and A. saginata, but only representative samples were retained so that the relative abundance of the two species is not known. The other samples contained only A. aurelia.

The various samples are not strictly comparable, both because different types of trawl were used on the two vessels and because there has been considerable gear development since the sampling programme began. The Meteor samples were all taken with an Agassiz trawl having a 6 m wide frame carrying two 3 m nets (Thiel, 1970). The early Discovery material (stations 7433, 7840 and 8001) were collected with a simple epibenthic sledge with a mouth width of 2.3 m, while at station 9017 a semi-balloon otter trawl having a head-line length of 14 m was used. None of these types of gear were fished with the intention of quantifying the results, so that although the catches have been used to obtain density estimates

RRS Discovery	Position		Danah			Maria	W-:
number	Lat. °N	Long. °W	(m)	Date	Net	captured	(gm)
7433	38°41.2′	28°27.8′	1 240-1 251	26.10.70	BN 2.4	2	89.8-109.5
7840	21°37.3′	18°04.5'	1 500-1 548	22.3.72	BN 2.4	14	2.6-129.6
8001	22°35.2′	17°37.0′	1 457-1 460	24.7.72	BN 2.4	6	30.0-124.0
8519	24°02.2′	16°59.2′	997-1 037	23.6.74	BN 1.5	3	119.3, 122.2, 235.0
8967	31°25.9′	10°53.7′	1 140-1 222	2.8.76	OTSB 14	2	40.0, 43.0
9017	29°07.1'	12°41.2′	1 341-1 394	18.8.76	OTSB 14	2 (a)	25.6, 51.7
9133	20°57.5′	18°13.7′	2112-2160	25.11.76	BN 1.5	1517 (b)	0.67-44.2
9134	21°54.6′	18°02.8'	1 942-1 949	26.11.76	BN 1.5	269	0.01-67.7
9540	20°55.4′	18°09.8'	2 005-2 009	14.4.77	BN 1.5	271	1.5-34.6
FS Meteor		- Position	Durath			Number	Weight money
number	Lat. °N	Long. °W	(m)	Date	Net	preserved	(gm)
100			2 1 1 0 - 2 0 4 9	26.2.75	AT 152	228	2-48
103	21°24.6′	17°53.6′	1 040-1 023	27.2.75	AT 154	61	16-123

(a) Only a representative sample of this catch was retained.

(b) One quarter of total catch by volume.



Figure 2

Photographs of Actinoscyphia aurelia taken at Discovery station 9134.

the resulting figures are rather tentative. The remaining Discovery samples (8519, 9133, 9134 and 9540) were obtained with a more sophisticated epibenthic sledge (Aldred et al., 1976) with some pretention to be quantitative. The sledge had a mouth width of 2.29 m and was fitted with an opening/closing mechanism which operates when the gear touches or leaves the bottom. A pinger used as an event recorder indicated when the net frame was horizontal (i.e. on the bottom) and when the net mouth was open, so that the beginning and end of the bottom fishing time was accurately determined. In addition, a 35 mm camera, with its optical axis directed towards a point on the bottom 1.5 m ahead of the sledge, took photographs at 15 or 30 second intervals of a trapezoid shaped area of the sea bed, of which 2.6 m² was usable for analysis. These photographs (see Fig. 2) provide data for density estimates which can be compared with those calculated from the net catch (see Rice et al. in press).

The distance travelled by the sledge across the bottom has been estimated from the ship's position at the beginning and end of the fishing period. The primary fixes were obtained from the ship's satellite navigation system with positions between successive fixes being interpolated by a two component log and gyro system. The resulting specific figures have been used in the density calculations although we are conscious that they are only approximations. It is difficult to assign confidence limits to these figures, but the errors involved are unlikely to exceed ten percent.

RESULTS

The estimation of population densities of megabenthic organisms from towed samplers is difficult since such gear is prone to behave erratically (see Rice *et al.*, in press). This usually results in the gear not sampling the entire distance it travels across the sea bed and

the calculated densities, therefore, will tend to be underestimated. Of the 11 samples reported here in which *A. aurelia* occurred (Table 1), only five contained sufficient anemones to justify attempts at such density estimations. The results of these estimates are summarised in Table 2, but since the performance of the different types of gear and the conditions under which they were used varied, the results from these five hauls will be considered individually.

Discovery 9134

As the gear functioned most successfully at this station it will be considered in rather more detail than the remainder. The pinger traces and photographs indicate that the sledge was moving continuously on the bottom during the haul. When, on two occasions, the sledge began to lift, this was quickly countered by paying out a small amount of extra wire, and at the end of the tow the sledge left the bottom very shortly after hauling commenced. In addition, the towing swivel appeared only very occasionally on the photographs, showing that no excess wire was dragging on the bottom. A minimum amount of wire was therefore being used, forming a practically straight line between the gear and the ship. Under these circumstances the net probably followed the ship's movement over the ground quite closely. The ship's satellite navigator indicated that the vessel travelled 1172 m over the ground during the time the net was on the bottom and, making allowances for the wire paid out and hauled in before the gear finally left the sea-bed, the total distance fished by the sledge is estimated at 1047 m, sweeping an area of 2398 m². With a catch of 269 A. aurelia this indicates a density of 0.11 m^{-2} .

Photographs were taken at 30 second intervals during this haul and, from a total of 68 exposures, 39 were considered to be orientated sufficiently well for quantitative analysis. Twenty two of the frames contained anemones, the maximum number on any one frame being 3. They indicate a mean density of 0.35 m^{-2} with 95% confidence limits of 0.22 and 0.45 m^{-2} . Thus, even the lowest estimated density based on the photographs is twice that estimated from the catch size and trawling distance. This discrepancy seems even more serious when the size of the individual specimens is considered, since many of the anemones taken in this haul weighed less than 2 gm (Fig. 3) and at least some of these were probably too small to be seen on the photographs.

Discovery 9133

The total catch of *A. aurelia* at this station was about 100 l of which 25 l, containing 1517 animals, was retained. The sledge travelled a calculated 2432 m indicating a density of 1.09 m^{-2} . Unfortunately no photographs were obtained during this haul because of a fault in the flash unit.

Discovery 9540

The distance travelled by the sledge at this station was calculated to be 960 m, and the catch contained 271 *A. aurelia*. The resulting estimated density of 0.12 m^{-2} must be considered a minimum value since a tear in the net probably allowed part of the catch to be lost. During this haul 94 photographs were taken, but due to the erratic behaviour of the sledge only nine were not obscured by clouds of mud. The number of *A. aurelia* on these unobscured frames varied between 1 and 6 and indicated a mean density of 1.3 m^{-2} .

Meteor 100

The number of *A. aurelia* captured at this station and the resulting densities are only approximations. Using

Table 2

Summary of Actinoscyphia aurelia densities and data on which they are based. See text for details.

Discovery stations

		Distance	un		Density (m^{-2})	calculated from
	Station	by ship over ground	corrected for wire movements	No. of <i>A. aurelia</i> in catch	distance run by sledge	photographs
	9133 9134 9540	2 536 1 172 1 144	2 432 1 047 960	6 068 269 271	1.09 0.11 0.12	0.35 1.3
Meteor stations						
	Station number	Distance run by ship over ground (nautical miles)	Estimated sample volume (m ³)	Number of specimens per litre	Calculated no. in catch	Calculated minimum density (m ⁻²)
····	100 103	2 2	1.0 0.3	60 36	60,000 10,800	5.5 1



photographs of the net when landed, the total catch volume, which consisted almost entirely of *A. aurelia*, was estimated to be 1 m^3 . From a subsample of this catch, 150 *A. aurelia* had a volume of 2.51 and the projected total in the catch would therefore be about 60000. Assuming the attempted ship's speed of two knots over the ground was correct, in a trawling time of 1 hour the net would sample 11000 m², indicating a density of 5.5 m^{-2} .

Meteor 103

Assuming the same distance travelled as at Meteor station 100, a similar rough calculation based on a catch volume of 0.3 m^3 and 36 specimens per litre, results in an approximate density of 1 m^{-2} .

Size and depth distribution

The modal peaks in the five samples containing large numbers of A. aurelia occur at different weights, even though some of the stations were relatively close together (Figs. 1 and 3). Small anemones are virtually absent from four of the samples, but the fifth, from Discovery station 9134, is strikingly different. Almost half of the animals in this sample weigh less than one gram each, while none of the size categories above 4 gm are represented by more than eight specimens.

Stephenson's original material was obtained from depths between 1 197 and 1 607 m, and the combined Discovery and Meteor collections extend the known bathymetric range to between 997 and 2160 m. Specimens exceeding 70 gm are relatively scarce, but it is notable that all of the larger animals were captured at the shallower end of the depth range (see Table 1).

Maturity

A large size range of *A. aurelia* was examined to determine the condition of the gonads. All specimens examined smaller than approximately 8 gm lacked gonads and can therefore be considered as juvenile, whereas the larger specimens always contained at least some mature eggs or sperm, irrespective of season or locality of capture.

DISCUSSION

The population densities of *A. aurelia* reported here are unusually high for a macrofaunal species on the deep continental slope. Indeed, if the calculated density based on the catch from Meteor station 100 is correct, this is by far the largest ever recorded from such a situation. Even if the distance travelled by the trawl has been underestimated by as much as 50% in this case, the resulting calculated faunal density is still remarkable. The results of international research in upwelling areas during the last ten years may help to explain these high densities of suspension feeders. The area from which the samples were obtained, off the coast of Mauretania, is the centre of the west African upwelling region, and is characterised by high levels of primary production; that in the area of Cap Blanc (200 gm.carbon/m²/yr) being one of the highest ever observed (Schulz *et al.*, in press). Food chains in upwelling regions are short (Ryther, 1969) and transport of organic matter to the sea bed must be considerable. This is confirmed, at least in the 500-2000 m depth range, by meiofaunal densities and chloroplastic pigment equivalents in the sediments which indicate high levels of sedimentation (Thiel, 1978, 1979, in press, *a* and *b*).

Benthic biomass is usually considered to decrease with increasing depth (e.g. Filatova, 1969). It is therefore strange that the highest concentrations of these large benthic organisms encountered in the Mauretanian region have been from the deeper continental shelf. This may be due to a lack of food in the upper slope because of water movements preventing detrital settlement. Tides and internal waves in the neighbourhood of the shelf break are known to create the equivalent of 30-50 cm/sec. currents (Fahrbach, Meincke, 1978). These would be fast enough not only to prevent sedimentation, but also to evoke erosion, causing the high concentrations of detritus to settle further down the slope. The northerly directed counter current impinging on the bottom of the upper slope in depths of 100-300 m might also be strong enough to prevent detritus settling out (Thiel, 1978). Furthermore, Mittelstaedt's (1976) model indicates weak downslope transport below the counter current, while Thiel (in press, b) has pointed out that downwelling fronts, which may be orientated either vertically or tilted away from the coast, might also contribute to a downslope transport of organic matter. The organic carbon content of the sediments, the skeletal remains of organisms, the grain size distribution and the observed low levels of meiofauna and chloroplastic pigment densities on the upper slope all support these suggestions (see Diester-Haass, 1978; Bein, Fütterer, 1977; Lange, 1975; Thiel, 1978).

Actinoscyphia aurelia is shown by its gut contents to feed on detrital material. Its Venus fly-trap shape in the natural environment (which is the expression of its unusual morphological bilaterality) together with the directed orientation of the animal as demonstrated by in situ photographs (Fig. 2) suggest that A. aurelia is well adapted to catch detritus in weak unidirectional near bottom currents. However, the macrofauna associated with the large catches of Actinoscyphia do not show any obvious peculiarities, since polychaetes, bivalves, scaphopods, octocorals, decapod crustaceans and holothurians are all present in numbers comparable with those at other stations in the region. The only group occurring in unusually large numbers were the pogonophores, probably taking advantage of the high organic content of the sediment.

Apart from the large numbers of *Actinoscyphia* taken in some of the deep slope samples, the other striking feature of these catches is the very variable size structure of the populations sampled. These differences are difficult to explain, but they may reflect the response of the anemone populations to an unstable environment. Rapid environmental disturbances caused by geological events such as slumps, which are known to occur in the area (Uchupi et al., 1976), and turbidity currents could depopulate quite large areas. If such an area was rapidly repopulated by Actinoscyphia the result would be a population of anemones of roughly the same age and therefore of a rather narrow mono-modal size distribution. From the observed egg size in A. aurelia (app. 150 µm, Riemann-Zürneck, 1978) this species probably produces large numbers of small pelagic larvae and may well be capable of such rapid repopulation, especially in the 2000 m region where the availability of abundant food seems to encourage an opportunistic population explosion. Moreover, the anemones' morphology and life style provide indirect evidence for instability in its habitat. Thus, the unusual ability of the species to stand upright and unattached on the sediment, the enormous development of the column mesoglea which must reduce the overall density, and the rather discoid shape when contracted (Riemann-Zürneck, 1978), all suggest adaptations to enable at least part of the population to survive sediment movement, the animals being swept away rather than buried. Nevertheless, this explanation of the observed Actinoscyphia population size structure is advanced very tentatively because of the great differences between normal biological and geological time scales.

The extensive sediment slumps known to occur in the area (Uchupi *et al.*, 1976) have presumably been separated by decades or centuries. However, relatively small local disturbances (Le Pichon *et al.*, 1975; Marshall, 1978) may occur with frequencies more similar to the biological time scales, where the life cycles usually range from one to a few years. Unless such short-term disturbances are fairly common, the size structure of the anemone populations must normally be regulated by natural successions in relation to ecological conditions, with dense populations of similarly-sized animals resulting from heavy larval settlement in areas with abundant food and little predatory pressure.

SUMMARY AND CONCLUSIONS

Actinoscyphia aurelia has been collected in large numbers from FS Meteor and RRS Discovery at five stations off the north west African coast using techniques which furnish at least some ecological information. The paucity of records since Stephenson's original description suggested that A. aurelia was rather rare. The present material, however, demonstrates that in some areas and at certain depths this is not the case, for the samples reported here represent some of the highest densities of megabenthic animals ever recorded in the deep-sea. The area from which the large samples of A. aurelia were obtained is known to be one of strong upwelling which in turn results in high rates of sedimentation of organic material. The probable detritus feeding habit of A. aurelia is ideally suited to the exploitation of an abundant food supply of this nature.

The different size frequency distributions of the sampled populations may be explained by the rapid repopulation of areas previously denuded by sediment movements if these occur sufficiently frequently to interact with the biological time scales.

Different sampling techniques were used on the two vessels, but only at Discovery station 9134 was it possible to estimate the accuracy of the population density calculated from the catch size. If the density indicated by the simultaneously obtained photographs at this station is correct, the net apparently failed to catch at least two thirds of the anemones in its path. It is difficult to understand how such large sedentary animals, not firmly anchored to the sediment, could be missed in this way, particularly since the sledge's monitoring system indicated that it remained consistently in contact with the sea-bed. However, the results suggest that conventional trawls cannot be relied upon to produce quantitative samples. The population densities reported in this paper, although high compared with the previous reports, must therefore be considered as underestimates of the true values.

Acknowledgements

Our thanks are due to many members of the technical staff at IOS Wormley and particularly to Mr. E. P. Collins, Mr. E. Darlington and Mr. R. A. Wild. We are grateful also to Drs. H. Fechter (München), G. Hartmann-Schroeder (Hamburg), M. Grasshoff, R. Janssen and M. Türkay (Frankfurt) for information on other animals in the Meteor samples. The German research was funded by Deutsche Forschungsgemeinschaft grants Th 124/11-14.

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