BEAUFORTIA

INSTITUTE OF TAXONOMIC ZOOLOGY (ZOOLOGICAL MUSEUM) UNIVERSITY OF AMSTERDAM

Vol. 32 no. 3

July 30, 1982

THE HYDROMEDUSAE OF THE AMSTERDAM MID NORTH ATLANTIC PLANKTON EXPEDITION, 1980 (COELENTERATA, HYDROZOA)*

J. TH. WINKLER

Institute of Taxonomic Zoology, (Zoological Museum), University of Amsterdam, P.O. Box 20125, 1000 HC Amsterdam, The Netherlands

ABSTRACT

A faunistic description is given of the Hydromedusae collected during the 1980 Amsterdam Mid North Atlantic Plankton Expedition. In all, 30 species have been caught during the sampling period April 11-May 2, 1980. Remarks are made on structural details of some of the specimens collected. Latitudinal and vertical distribution patterns are given and data on the abundance of some species are recorded. For several bathypelagic species a faunal boundary is assessed at about 40°N, probably coinciding with the transition of eutrophic warm temperate water to oligotrophic Sargasso Sea water. This boundary is less sharp in the epi- and mesopelagic zones. Remarkable records are those of *Calycopsis* gara Petersen, 1957, Neoturris pileata (Forskål, 1775), Sibogita geometrica Maas, 1905, Tima flavilabris Eschscholtz, 1829, and Zygocanna vagans Bigelow, 1909.

INTRODUCTION

This paper deals with the Hydromedusae of the Mid North Atlantic. During the first Amsterdam Mid North Atlantic Plankton Expedition these medusae have been collected in the period April 11-May 2, 1980 on board the research vessel H.M.S. 'Tydeman'. The area covered extends from 55°N to 24°N at approximately 30°W. Most specimens were collected in discrete depth samples made between 30 m and 1200 m with the Rectangular Midwater Trawl (RMT1+8). In addition, some specimens were caught with an open ringnet in the upper 150 metres. The reader is referred to Van der Spoel (1981) for extensive information on the stations, hauls and environmental conditions.

The Mid North Atlantic is a thoroughly investigated oceanic area. The knowledge of the distribution of the various oceanic plankton species is extensive, but by no means exhaustive. Kramp (1959) gives an extensive zoogeographical account of the Hydromedusae of the Atlantic Ocean. He distinguished different zoogeographical regions for oceanic species in the epipelagic and bathypelagic zones. He divided the area from 55°N to 24°N into an Arctic, an Atlantic boreal and an Atlantic warm water region. Van Soest (1973) gave an impression of the latitudinal distribution of 21 Hydromedusae species; however, the speci-

^{*} AMNAPE, Project 101A, rep. no 5, supported by a grant of the Netherlands Ministry of Education and Sciences (rep. no 4 appeared in Bull. zool. Mus. Univ. Amsterdam 8 (4)).

mens were caught at different longitudes and in different seasons, which makes it impossible to assess if there is any seasonal influence on the distribution ranges of the different Hydromedusae species.

The aim of the present study is to give an impression of the horizontal and vertical distributions of the different Hydromedusae species in the spring of 1980. Moreover, the author has tried to show that there exist faunal boundaries for different species groups between 55°N and 24°N. Also, additional information about morphological details of some specimens is given, because they had a slightly different shape from that described in the literature.

For simplicity's sake the terms 'epipelagic' and 'bathypelagic' as defined by Kramp (1959) will be used in this paper. Kramp described the epipelagic zone as the upper water layer with its lower limit generally down to 150-250 m; the bathypelagic (the RMT8) and a smaller one on top with an effective mouth area of 0.8 m² and a mesh-size of 0.32 mm throughout (the RMT1). For a full description of the nets and their behaviour the reader is referred to Baker & al. (1973) and Roe & al. (1980). Basically, a sampling scheme was carried out with hauls between 50-100, 100-200 200-300, 300-400, 400-500 and 500-1000 m depth (fig. 1 a).

Some material was caught with an open Rectangular Midwater Trawl (RMT1), which was the same net as the one used in the RMT1+8 combination, and some material was collected with an open ringnet, designed for this expedition. The ringnet has a circular mouth opening of 0.78 m^2 . It is towed through the water at a speed of approximately 2 knots with 80 or 360 metres wire out, which resulted in an estimated fishing depth of 50 and 180 metres respectively and an effective mouth area of ca. 0.55 m². For further details



Fig. I a. Position of the stations and hauls in a vertical profile, giving the opening-closing net samples (solid) and open net hauls (open), and samples taken at night (n), by day (d), at dawn (r) and by twilight (s).

zone then comprises the intermediate and deep water below this epipelagic zone. If the vertical distribution of a particular species in the present collection is restricted to the zone between ca. 0-500 m the term 'epi- and mesopelagic' is used.

MATERIAL AND METHODS

Most material was collected with the Rectangular Midwater Trawl RMT1+8. This trawl is a combined opening and closing net composed of a large net with an effective mouth area of 8 m² and with a mesh-size of 4.5 mm and in the cod end of 1 mm the reader is referred to Van der Spoel (1981).

The material was roughly sorted aboard ship. Almost all the material was fixed with formalin 4% with sea-water and preserved in formalin 2%or propylene phenoxetol plus propylene glycol (Heyman, 1981). Some medusae were preserved in alcohol 70%. The actual numbers of specimens caught are converted into standard numbers, related to a fixed amount (24000 m³) of water filtered. The abundance given in standard concentrations for the different trawls can be compared also when fishing took place with different duration and with different gear. The special

effects of the net size on the net avoidance are then, however, neglected. The formula for calculating standard concentrations for the RMT8 samples is $(3 \times \text{number of specimens})/\text{distance}$ sampled: for the RMT1 samples it is $(10 \times 3 \times 3)$ number of specimens)/distance sampled. The distance sampled is calculated from direct flow measurements. The factor three is used because the distance sampled averaged three kilometres, so the standard concentrations for the RMT8 are as close to the actual numbers as possible. Flow through the nets, depth of the nets and ship speed were such that the mean angle of the mouth of the net will hardly have influenced the amount of water filtered and no special corrections seem necessary (cf. Roe et al., 1980). The formula for calculating standard numbers for the open Rectangular Midwater Trawl RMT1 (RO1) is also $(10 \times 3 \times \text{number of specimens})/\text{distance}$ sampled. For the open ringnet with RMT1 liner

tion data for the different nets have been recorded. The data of the different periods of the day have been taken together, so the influence of day and night on the bathymetrical range has been ignored. The standard concentrations of the different stations give a rough impression of the latitudinal abundances of the species. To show the latitudinal variation in abundance of different species the standard concentrations have been plotted against the latitudes. For a few species the standard concentrations for day and night of all stations are given separately, to show the different bathymetrical ranges of the species by day and by night; for this rough impression the data of the different nets are also given separately.

LATITUDINAL DISTRIBUTION

Table I gives the latitudinal distribution regardless of bathymetrical distribution, of all 30 species



Fig. 1 b. Temperature (°C) profile between 55° and 24°N. Vertical lines indicate XBT and net monitor samples, with their numbers along the y-axis, depth in metres along the x-axis.

(RNR) and open ringnet (RNO) samples the formula is $(43.6 \times \text{nuber of specimens})/\text{distance}$ sampled.

Of each station the bathymetrical range has been considered and the standard concentrations of each station have been calculated. Only the same bathymetrical ranges of the different stations can be compared. Although the abundance given as standard concentrations for the different nets can be compared in the present study, the data of the different nets are given separately, because for some species too great differences in concentracollected in the discrete depth samples and open net hauls. The stations at which a species occurred are marked ' \times '. Only the latitudinal position of the stations is given: for the exact positions of the stations the reader is referred to Van der Spoel (1981).

In spring 1980 the species diversity increased southward between 55°N and 40°N. North of 51°N only 9 species were collected at stats 10 and 11. The species diversity in the bathypelagic zone remained rather constant, but in the epi- and mesopelagic zones it clearly increased. The largest

Table 1. 7	The latitudinal	distribution of	all 30	species	collected i	in the	discrete	depth	samples	and o	open i	net hauls	3.
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station number latitude	10 55°	11 53°	12 51°	13 49°	14 45°	15 44°	16 42°	17 41°	18 40°	19 38°	20 35°	21 34°	22 32°	23 31°	24 30°	25 29°	26 25°	27 25°N
Botrvnema brucei		X		×														
Aglantha digitale	×	x	x	x	x	x	x		х									
Crossota rufobrunnea	×	x		x	×		×		×									
Chromatonema rubrum	×	x		x			x		×		x							
Haliscera higelowi	×	x		x	x		×	x	x		x							
Pantachogon haeckeli	×	x		x	×		×		x	×	×	x	x	x				
Aeginura grimaldii	×	x		x	x		x		x	x	x	×	x	x		x		
Halicreas minimum	×	x		x	x		x		x	x	x	x	x	x			х	
Colobonema sericeum	x	~		x	x		x	×	x	x	x	x	x	x			×	х
Aegina citrea	~	x		x	Ŷ		Ŷ	~	x	Ŷ	x	x	Ŷ	~			x	
Rythotiara murravi				Ŷ					~	~	~	~	~					
Solmissus incisa				Ŷ	×		x				x	×						
Pegamtha laevis				Ŷ	~		Ŷ	×	×	×	Ŷ	Ŷ						
Tima flavilabris				Ŷ	×		Ŷ	$\hat{\mathbf{v}}$	$\hat{\mathbf{v}}$	Ŷ	~			×	x			
Pegamtha spec				Ŷ	Ŷ		Ŷ	Ŷ	Ŷ	Ŷ	×	x	×	x	Ŷ	×		
Rhohalomema velatum				$\hat{\mathbf{v}}$	Ŷ		Ŷ	Ŷ	$\hat{\mathbf{v}}$	Ŷ	Ŷ	Ŷ	Ŷ	Ŷ	Ŷ	x	×	x
Calucobsis gava					Ŷ		Ŷ	Ŷ	~	^	~		~		~	~	~	~
Ammatiana affinis					$\hat{\mathbf{v}}$		÷	Ŷ	¥			×	×					x
Zudocanna nadans							Ŷ	^	^			~						~
Pandea comica							Ŷ	×	×	Y				×				
Halitrephes maasi							Ŷ		Ŷ							×	×	×
Pegantha martagon							^	×	Ŷ		¥	×	×	×	¥	Ŷ	$\hat{\mathbf{x}}$	x
Crossota alba									Ŷ					~	~			~
Gannomia proposcidalis									Ŷ							×	×	×
Cosmetiva pilosella										×								~
Necturnis pileata											×	v						
I iniche tetraphulla											Ŷ						x	
Peramtha clava															×			
Solmissus marshalli															^	×		
Rougainvillia blatugaster																Ŷ	x	×
Sibogita geometrica																	Ŷ	~
number of species	9	9	I	16	14	I	19	10	19	11	14	12	9	9	5	8	10	7

number of species was found at about $41^{\circ}-40^{\circ}$ N; of 19 species were collected at stats 16 and 18. South of 40° N the species diversity suddenly decreased both in the epi- and mesopelagic zones and in the bathypelagic zone. At stats 26 and 27 (at about 25°N) resp. 10 and 7 species were found (table I and figs. 2a, b and c).

SYSTEMATIC ACCOUNT

In the following systematic account a list of material is presented with for each species the stationhaul number, and number of specimens in brackets. Remarks are made on the structural details of some of the specimens collected. The latitudinal and vertical distribution patterns are described.

For a full taxonomic treatment of the species the reader is referred to Kramp (1959), and Russell (1953). General statements about the distributions of the species (indicated with an asterisk) are taken from Kramp (1959), unless otherwise indicated.

Order Athecata (Anthomedusae)

Suborder Filifera

Fam. Bougainvilliidae

Bougainvillia platygaster (Haeckel, 1879) (figs. 3 & 4)

Material: stat. 25-5 (1); 25-6 (2); 25-7 (1); 25-9 (5); 26-4 (1); 26-10 (17); 26-11 (7); 27-3 (2); 27-20 (11); 27-23 (6).

Most specimens have a diameter of 5-11 mm and a height of 4-11 mm. Also some smaller specimens were found with a diameter of 3-4 mm and a height of 3-6 mm. The umbrella is cylindrical with a



Fig. 2 a. The number of species (n) collected at each station between 0-1000 m.



Fig. 2 b. The number of species (n) collected at each station between 500-1000 m.



Fig. 2 c. The number of species (n) collected at each station between 0-500 m.

flatly rounded top and almost vertical sides and thick walls. The manubrium is very flat; there is no peduncle. The oral tentacles bifurcate 4-6 times immediately after their emergence from the mouth margin. The marginal bulbs are slightly triangular, each with 10-13 marginal tentacles in the larger specimens and about 7 in the smaller specimens. On the adaxial side of the marginal ten-



Fig. 3. Bougainvillia platygaster, stat. 26-10. Aboral view of stomach.

tacles there are oval to somewhat stroke- or crescent-shaped ocelli. In the crescent-shaped ocelli the concavity turns outwards. The ocelli did not always have the same shape, perhaps due to the fact that they are easily damaged and lose their pigment. After preservation the colour of the ocelli is dark-red.

To study the position of the gonads two specimens have been cross-sectioned perpendicular to the oral-aboral axis and stained with H.E. In adradial portions of the stomach there are structures carrying medusa-buds at the subumbrellar side. The cross-sections through these structures only showed tissue with many nuclei at the subumbrellar side where the medusa-buds develope. No sexual products were found, so the position of the gonads could not be assessed. Probably the specimens are immature. The medusa-buds are present in groups of one to four buds. The phenomenon of asexual propagation by medusabuds has been extensively described by Kramp (1957a).

Several specimens in the present collection were



Fig. 4. cf. Pegantha triloba, stat. 26-10 A cluster of larvae detached from the subumbrellar cavity of Bougainvillia platygaster.

infected by Narcomedusae larvae, probably of *Pegantha triloba*, a phenomenon described and figured by Kramp (1957a). Mostly two or three clusters of these larvae were attached to the subumbrella inside the triangular pouches between the subumbrella and the aboral wall of the stomach. Also, in several specimens some clusters were found unattached in the subumbrellar cavity. In each cluster always one larva is in a much more advanced stage of development than the other minute buds.

Distribution:

The specimens were mainly collected in the epipelagic zone of the warm water of about 28°N to 25°N. At night, specimens were mostly found just below the surface (depth 0-50 m), during the day they were collected between 50-300 m, with their highest concentration between 100-200 m. Only one specimen was caught between 510-1090 m.

In the Atlantic this species seems to have its principal occurrence in the Sargasso Sea and West Indian waters, but its distribution extends eastwards to the Azores and north-western Africa and southwards to the area east of Brazil and several localities off the east coast of Africa.

Fam. Pandeidae

Annatiara affinis (Hartlaub, 1913)

Material: stat. 14-2 (1); 14-8 (1); 16-2 (4); 16-5 (3); 17-3 (3); 18-2 (1); 18-8 (1); 21-2 (2); 21-10 (1); 22-5 (1); 22-6 (3); 27-6 (1).

Most specimens are in a poor state of preservation; their diameter varies from 13-19 mm, their height from 10-16 mm. Only in a few specimens the number of primary tentacles could be counted: 42-45. They alternate with minute ten-



Fig. 5 a. Annatiara affinis. Horizontal and vertical distributions.



Fig. 5 b. Annatiara affinis. Latitudinal variation of the standard concentration (C.) between 0-500 m for RMT8 and RMT1.

tacles. On the exumbrella are numerous meridional nematocyst tracks.

Distribution: (figs. 5 a, b)

This species has been found from 45° N to 32° N at a depth of 85-405 m. At stat. 14 (ca. 45° N) specimens were caught at a depth of 85-200 m at night, but during the day they were found between 200-300 m. At stat. 18 (ca. 40° N) the same



Fig. 6. Pandea conica, stat. 18-8. Exumbrellar view of umbrella, with a slightly developed apical ectodermal thickening and longitudinal exumbrellar nematocyst ribs.

phenomenon was recorded, but at other stations a clear difference in depth between day and night samples could not be found.

Annatiaria affinis has a wide distribution from 60°N to 42°S in the eastern parts of the Atlantic Ocean; it probably belongs to the deep and intermediate strata.

Pandea conica (Quoy & Gaimard, 1827) (fig. 6)

Material: stat. 16-1 (6); 16-5 (1); 16-6 (3); 16-11 (2); 17-1 (4); 17-4 (1); 18-6 (3); 18-8 (3); 19-13 (1); 19-19 (1); 23-3 (1).

All the specimens lack the characteristic apical process, just like the specimen described and figured by Van Soest (1973). Some specimens only have a slightly pointed apical thickening. The umbrella has a height of 4.5-18.0 mm and a width of 6.5-19.5 mm. The large specimens have 25-34, the smaller ones 16-18 marginal tentacles.

Distribution: (figs. 7 a, b, c)

Most specimens of the present species were collected in the upper strata (depth o-325 m) from 42° to 38°N. Only one specimen was found at about 31°N between 385-500 m. At night the samples with the RMT8 showed a concentration of specimens in the uppermost layers, during the day the specimens were also found slightly deeper. With the Open RMT1 specimens were collected only during the day, just below the surface.

Pandea conica has a wide distribution westwards and southwards in the Atlantic but not further north than the Azores. It has been found near Bermuda, along the west coast of Africa, near



Fig. 7 a. Pandea conica. Horizontal and vertical distributions.



Fig. 7 b. Pandea conica Latitudinal variation of the standard concentration (C.) between 0-500 m for RMT8, RMT1 and between 0-50 m for RO1.



Fig. 7 c. Pandea conica. Vertical distribution by day (white) and night (black) of the standard concentration (C.) between 0-500 m for RMT8, RMT1 and between 0-50 m for RO1.

Patagonia and in the Azores area and it also occurs in the Mediterranean Sea. It is mainly found in the upper strata.

Neoturris pileata (Forskål, 1775) (fig. 8)

Material: stat. 20-4 (1); 21-2 (1).

The specimen caught at stat. 20 fully agrees with the description given by Kramp (1959). However, the dorsal part of the umbrella is damaged and there is no well-developed apical projection. The height is ca. 33 mm and the width ca. 27 mm. The umbrella is bell-shaped, but laterally compressed. The radial canals are ca. 2 mm wide and they have jagged outlines. The ring canal is ca. 1.5 mm wide and also has a jagged outline in some places. There are 84 marginal tentacles.



Fig. 8. Neoturris pileata, stat. 21-2. Exumbrellar view of radial canal with diverticula of irregular length.

A remarkably large specimen was collected at stat. 21. The height is ca. 36 mm and the width ca. 35 mm. The exumbrella is irregular, dorsally it is probably damaged. There is no apical projection. Unfortunately the stomach is badly damaged, the interradial parts of the walls have almost disappeared. The base is very broad, ca. 24 mm, and has a quadrangular shape. The structure of the mouth and lips is difficult to assess; there are remains of lips with much crenulated margins. The manubrium fills the upper half of the subumbrellar cavity. The four radial canals are 4-6 mm wide, they posses 8-9 pairs of diverticula of irregular length, standing more or less at right angles to the canals. The radial canals are joined to the stomach by short mesenteries. The ring canal is 2-4 mm wide, with a slightly jagged outline in some places. The gonads are situated on the stomach wall from the base of the stomach to the mouth lips. In each quadrant they consist of two adradial series of irregular folds directed inwards towards the interradius. On the interradial parts of the remains of the stomach wall there are portions of the gonads consisting of round pits.

There are 84 marginal tentacles with tapering conical bulbs, laterally compressed, clasping the umbrella margin, but not forming conspicuous abaxial spurs. Between two successive tentacles there is sometimes a short tentacular bulb. There are no ocelli. A narrow velum is present. Kramp (1957a) also described a very large specimen (35 mm in diameter and 34 mm high) collected by the Discovery (st. 1606: 26°15'48"S, 12°18'E). It was found in the epipelagic zone. The free distal parts of the radial canals were provided with lateral diverticula of uncommon length, some of them about as long as the width of the canal. According to him the considerable length of the diverticula is most probably the consequence of growth beyond the usual size of this species.

Distribution:

One specimen was collected at about 35° N at a depth of 200-295 m and the other specimen at about 34° N at a depth of 320-350 m.

Neoturris pileata is a common medusa in the north-eastern Atlantic as far north as Iceland and

far southwards off the African coast (as far south as 26° S). Besides, this neritic species is widely distributed in the Mediterranean.

The present specimens probably originated from the Azores coastal area.

Fam. Calycopsidae

Calycopsis gara Petersen, 1957

Material: stat. 14-9 (1); 16-1 (1); 16-6 (2); 17-1 (1).

All the specimens are well preserved. They agree with the description given by Petersen (1957), although most specimens are much larger. The umbrella has a diameter of 10.5-21 mm and a height of 10-22 mm. Petersen (1957) records 11 mm high and 9 mm wide.

Distribution:

The specimens were collected at night between $45^{\circ}N$ and $41^{\circ}N$ to a depth of 200 m. *Calycopsis gara* has only been collected once, by RV "Dana" in the central part of the northern Atlantic (stat. 6683: $50^{\circ}53'N$, $34^{\circ}25'W$, Petersen, 1957), so the present material considerably enhances the knowledge of its size and distribution.



Fig. 9. Sibogita geometrica, stat. 26-8. Aboral view of stomach and the four primary radial canals with lateral branches.



Fig. 10. Sibogita geometrica, stat. 26-8. Oral view of a part of the umbrella margin with two large marginal tentacles and two small marginal tentacles.

Bythotiara murrayi Günther, 1903

Material: stat. 13-6 (1).

Height: 16.5 mm; width: 12 mm. The stomach was torn off the subumbrella during capture; the bifurcation of the radial canals at the base of the stomach was difficult to assess. The marginal tentacles terminate in a large nematocyst cluster.

Distribution:

The specimen was collected at dawn at 49°N between 375-500 m. The present record confirms the Atlantic range as given by Kramp (1959).

Sibogita geometrica Maas, 1905 (figs. 9, 10, 11) Material: stat. 26-8 (2).

Both specimens are well preserved. In one specimen the umbrella has a pumpkin shape; apically there is a slight conical depression. The height is 15 mm and the diameter 21 mm. The jelly is very rigid and about 3 mm thick. The stomach is spherically expanded; it is 8 mm long and 5 mm wide. The gonads are situated on the stomach in eight adradial rows; each row is divided into 16-20 transverse folds. The mouth has four simple lips.

From the stomach base four primary radial canals run straight to the ring canal issuing lateral branches to both sides (fig. 9). At dorsallateral level these branches give rise to other lateral branches of second order. There are 31 radial canals; one radial canal bifurcates near the ring canal. The radial canals terminate into the ring canal, widening triangularly towards the end. Inside these widenings an accumulation of dark coloured "granules" can be found (fig. 10). Nearest to the stomach the radial canals are broad, narrowing after repeated bifurcation, and they broaden again near the ring canal. Sixteen large marginal tentacles emerge opposite corresponding radiating canals. Between 12 pairs of successive large marginal tentacles, opposite radiating canals, small tentacles are directed inwards towards the subumbrellar cavity. Only the proximal portions of the large tentacles are left, the distal portions have snapped off.

Except for the conical depression this specimen agrees with *Sibogita geometrica* as described by Maas (1905) from the collection of the Siboga expedition (stat. 118: 1°38'N, 124°28'E). Maas's



Fig. 11. Sibogita geometrica, stat. 26-8. Aboral view of stomach and the four primary radial canals with lateral branches.

specimen (ZMA COEL. no 3853) is 38 mm high. Although they do not appear in Maas's description and figure, there are, also in his specimen, between the successive large marginal tentacles, small marginal tentacles opposite radiating canals directing inwards towards the subumbrellar cavity. In addition, at the base of the 16 large tentacles an accumulation of coloured "granules" is visible.

The present specimen also largely agrees with a specimen described by Bigelow (1919). On comparing the specimen with Bigelow's description we find the following differences: in his specimen there is no apical depression and there are only 22 radiating canals.

The other specimen of the present collection has a low bell shape; it is laterally somewhat compressed. It agrees with the description given by Kramp (1959). The height is 18 mm and the diameter varies from 28-34 mm. The jelly is rigid and about 3 mm thick. The stomach is small and slender, 3 mm wide and 7 mm high. It is square in cross-section; the base is cruciform. The mouth has four simple lips, perradially slightly pointed. The gonads have 9-10 transverse folds in each of the eight adradial rows. Four groups of primary canals bifurcate irregularly at various levels, giving rise to 32 canals (fig. 11). Three of these canals branch dichotomously just near the ring canal. The bell margin is slightly damaged: only parts of a ring canal are left. Opposite each radiating canal there is a large tentacle, 31 in total. The tentacles have no basal swelling; no accumulation of pigment granules has been found. The distal parts of the tentacles have got lost. Between some successive large tentacles there are remains of a small tentacle; it was not possible to determine whether there are any minute marginal warts.

This specimen also agrees with the specimen collected by the Tridens in the Atlantic (stat. 9: $36^{\circ}26'N$, $23^{\circ}22'W$) and recorded by Van Soest (1973). In his specimen (ZMA COEL. no 6921) there were five groups of primary canals and the system of bifurcations was much more irregular.

Kramp (1959) gave an account of three specimens found in the eastern Atlantic, east of the Azores (collected by the "Dana" in 1922) and in the Bay of Biscay (collected by the "Discovery II") and he described them as belonging to the subspecies *occidentalis*. After examination of material collected by the "Dana", Kramp (1965) concluded, that the Atlantic form is connected with the typical form from Celebes and the Philippines by transitional forms with differences which may only be due to individual variation and which present no reliable difference between the Atlantic and Indo-Pacific specimens. Between the two specimens of the present collection there is, besides the shape of the umbrella and the number of gonadial folds, a remarkable difference in the branching of the radial canals and in the number and rate of development of the large marginal tentacles and the small tentacles.

So, in the present collection one specimen agrees with the Indo-Malayan and tropical form as described by Maas (1905) and the other one agrees with the East Atlantic form as described by Kramp (1959). The present material seems to confirm the opinion stated by Kramp (1965), but an extensive examination of all the material of *Sibogita geometrica* is necessary to draw a decisive conclusion as to the nature of the difference between the Atlantic and Indo-Pacific specimens.

Distribution:

Both specimens were caught at stat. 26 (about 25°N) in the same haul, depth 300-500 m.

In the Atlantic this species has been recorded near the Azores and in the Bay of Biscay.

Fam. Tiarannidae

Chromatonema rubrum Fewkes, 1882

Material: stat. 10-3 (3); 11-1 (6); 13-9 (4); 16-3 (2); 18-10 (1); 20-3 (2).

Some specimens are in a good state of preservation, but mostly they are badly damaged. Their height varies from 6-26 mm, their width from 6-18 mm. The specimen collected at stat. 18 is



Fig. 12 a. Chromatonema rubrum. Horizontal and vertical distributions.



Fig. 12 b. Chromatonema rubrum. Latitudinal variation of the standard concentration (C.) between 500-1000 m for RMT8.

abnormal in having only three perradial lobes on the manubrium extending for half the distance towards the bell margin. Three radial canals terminate into a narrow ring canal; there are 15 marginal tentacles with conical bulbs.

Distribution: (figs. 12 a, b)

In the present collection *Chromatonema rubrum* has been found from 55°N to 35°N between 290-1250 m. The present material shows a decrease in abundance from north to south between 500-1000 m; south of about 40°N only small concentrations are found.

In the Atlantic this bathypelagic species is widely distributed throughout the warm-water region including the boreal region up to its northern limits.

Order Thecata (Leptomedusa)

Fam. Aequoreidae

Zygocanna vagans Bigelow, 1912

Material: stat. 16-5 (1).

This specimen is well preserved. It agrees with the description given by Kramp (1959). The diameter of the umbrella is about 56 mm. The stomach has a diameter of 21 mm. Inside the periphery of the stomach the dichotomous branching takes place; four diverging trunks which bifurcate several times. As a result of the repeated bifurcations 41 radial canals leave the periphery of the stomach, terminating in a ring canal. Two radial canals fuse just near the ring canal. Between each successive pair of radial canals there is a radiating row of 1-8 papillae on the subumbrella. Part of the umbrella margin is slightly damaged; the number of the marginal tentacles is 37. Between the successive tentacles there are rudimentary marginal tentacles.

Distribution:

The specimen was collected at 41°N between 190-330 m.

This neritic species has been found in four widely separated areas: near the Philippines and the Gulf of Panama in the Pacific, and west of Cape of Good Hope and near the Azores in the Atlantic. Kramp's specimen (1959) was caught almost at the same location (stat. 1495, $41^{\circ}55'N$, $32^{\circ}22'W$) and depth (300 m wire) as the specimen of the present collection.

Fam. Eutimidae

Tima flavilabris Eschscholtz, 1829

Material: stat. 13-10 (1); 14-2 (1); 16-1 (47); 16-2 (5); 16-5 (1); 16-6 (17); 16-9 (1); 17-1 (12); 17-3 (10); 17-4 (7); 18-2 (1); 18-4 (5); 18-5 (10); 18-6 (84); 18-8 (38); 18-13 (1); 19-19 (8); 23-3 (1); 24-1 (1); 24-5 (1).

Unfortunately most specimens were badly damaged, particularly the bell margin. Mostly only a peduncle is left. The large specimens agree with the description as given by Petersen (1957). The umbrella of the preserved specimens is flat, the width varies from 20-36 mm. The height of the conical peduncle is about 10-18 mm, the base is broad. The stomach is small, attached to the peduncle along the edges of a perradial cross. The



Fig. 13 a. Tima flavilabris. Horizontal and vertical distributions.



Fig. 13 b. *Tima flavilabris*. Latitudinal variations of the standard concentration (C.) between 0-500 m for RMT8, RMT1 and between 0-50 m for RNO, RNR and RO1.

four perradial lips are pointed with crenulated margins. The four radial canals and the ring canal are narrow. The gonads extend along the radial canals from just above the stomach to almost the bell margin. They are divided into two lateral parts separated by a median groove which is sometimes difficult to discern. The subumbrellar parts are slightly wavy. The peduncular parts are straight. Exact numbers of marginal tentacles, marginal vesicles and marginal warts are difficult to give: in one quadrant the number of marginal tentacles in different individuals varies from 15-19. Between the successive marginal tentacles there are marginal vesicles and marginal warts.

The width of the small specimens varies from 10-15 mm. The height of the peduncle is about

3-5 mm with a broad base, the width 1.5-6 mm. If there are gonads, they are situated on the subumbrellar parts of the umbrella and sometimes on the peduncle.

The number of the marginal tentacles in the specimens which were not damaged varies from 16-20. Between the marginal tentacles there are 2-4 marginal warts and 1-3 marginal vesicles.

Distribution: (figs. 13 a, b, c)

In the present collection *Tima flavilabris* has been principally collected from about $42^{\circ}N$ to $38^{\circ}N$. However, the latitudinal range extends more to the north (49°N) as well as to the south (30°N), although at these latitudes only small concentrations have been found. *Tima flavilabris* was usually found just near the surface (depth 0-100 m) by night, and by day its was caught in the deeper layers (50-300 m).

The species has been found in the Atlantic Ocean, north-west and north of the Azores.

Fam. Mitrocomidae

Cosmetira pilosella Forbes, 1848

Material: stat. 19-19 (6).

The specimens are quite small, 10-13 mm in width. They are badly damaged, especially the umbrella margin, which somewhat hampers determination. The umbrella is hemispherical, but somewhat flattened. The jelly is thick in the apical region, thinning towards the umbrella margin. Remains of a velum have been found. The stomach is small and quadrangular, attached to the subumbrella along the arms of a perradial cross. The base of the stomach is broad. The mouth has four crenulated lips. There are four radial canals with rests of gonads attached on them. The remains of the gonads extend from the middle of the radial canals to the bell margin; the shape of the gonads cannot be assessed. The number of the hollow marginal tentacles varies from 73-76, but in most specimens it could not be ascertained because the bell margin was damaged. The basal bulbs are round to somewhat carrot-shaped. Between the successive tentacles there are 1-8 fexible marginal cirri can be found. In some specimens two marginal vesicles are found per quadrant. There are no ocelli.

Distribution:

These specimens of *Cosmetira pilosella* were collected at 38°N at a depth between 50-110 m.

The species is confined to the north-west European seas and extends southwards from the boreal region down to the Bay of Biscay.



Fig. 13 c. *Tima flavilabris*. Vertical distribution of the standard concentration (C.) by day (white) and night (black) between 0-500 m for RMT8, RMT1 and between 0-50 m for RO1, RNO and RNR.



Fig. 14 a. Halicreas minimum. Horizontal and vertical distributions.

Order Trachymedusae

Fam. Halicreatidae

Halicreas minimum Fewkes, 1882

Material stat. 10-3 (20); 11-1 (115); 13-9 (42); 14-5 (34); 16-3 (11); 18-1 (2); 18-10 (2); 19-22 (1); 20-1 (1); 20-3 (3); 21-6 (4); 22-1 (1); 23-2 (3); 26-4 (4).

The diameter of the umbrella varies from 8.5-26 mm. Nearly all specimens caught in the area from 55°N to 40°N have a more or less flattened umbrella, but the specimens collected in the area from 38°N to 25°N have a bell-shaped umbrella with a conical apical process of varying size. A more detailed study of this variation is in preparation.

Most specimens have lost their stomachs and radial canals with gonads, but they are easy to identify by their rounded perradial lateral exumbrellar processes. Usually there are eight, sometimes 7 or 6 of these processes. The processes have 1-23 small conical papillae. The number of the marginal tentacles per octant varies from 11-60; in many specimens the tentacles have disappeared.

Distribution: (figs. 14 a, b)

All the specimens were collected at the deeper strata between 290-1250 m between 55°N and 24°N. In the present samples *Halicreas minimum* clearly decreases in abundance from north to south. Large concentrations are mostly found between 55°N and 42°N. In the Atlantic this bathypelagic species is generally distributed as far north as the south coast of Iceland and the southern part of the Davis Strait, and southwards the species is distributed almost to the slope of the Antarctic continent.

Haliscera bigelowi Kramp, 1947

Material: stat. 10-1 (1); 10-3 (5); 10-5 (1); 11-1 (1); 13-6 (15); 13-9 (1); 14-1 (1); 14-2 (3); 14-5 (11); 16-3 (6); 17-2 (2); 18-10 (1); 18-13 (1); 20-4 (1).

Diameter of the umbrella is between 7.5-19.5 mm; the height varies between 4.5-9.0 mm. All the specimens are badly damaged; the stomach, the radial canals, the gonads and the umbrella margin are mostly torn off. The umbrella is almost hemispherical; in the upper region the jelly is very thick, thinning towards the sides and the umbrella margin. In the few specimens with a complete umbrella margin there are about 90 marginal tentacles, all of the same shape, though varying in size. They have a flexible proximal position and a stiffer distal portion.

Distribution: (figs. 15 a, b)

In the present collection specimens were caught from 55°N to only 35°N, mainly between 375-1010 m although also specimens were collected between 205-510 m; the concentrations between 300-1000 m decreased from north to south.

In the North Atlantic this bathypelagic species

occurs from the south coast of Iceland to the northern part of the west coast of Africa.

Botrynema brucei Browne, 1908

Material: stat. 10-3 (7); 11-1 (23); 13-9 (12).

Diameter of umbrella: 9-23 mm. In all the specimens the stomach, the radial canals and the gonads have entirely disappeared. However, the specimens are easy to identify by their characteristic shape of the umbrella and the peculiar arrangement of the tentacles which usually remain on the umbrella margin. There are 8 perradial marginal tentacles; between the successive perradial tentacles two adradial groups of 6-12 marginal tentacles are present.

Distribution

The specimens were found in the deeper strata between 290-1010 m from 55°N to 49°N; they are restricted to cold water, probably below the 7°C isotherm.

In the Atlantic Botrynema brucei has a bathy-

pelagic distribution from south of Iceland and Greenland almost to the Antarctic continent.

Halitrephes maasi Bigelow, 1909

Material: stat. 16-3 (1); 18-10 (1); 25-1 (1); 26-4 (1); 27-10 (1).

Diameter of umbrella: 40-55 mm. The umbrella is smooth, saucer-shaped and there are no papillae on the exumbrella. The jelly is soft and thick, thinning towards the umbrella margin. The subumbrella forms a thick lens, in the centre projecting into the stomach cavity; the lens is about 10-20 mm wide. The velum is broad. In all the specimens the stomach, the radial canals and the gonads have entirely disappeared, so that the radial canals cannot be counted. This makes an exact identification impossible. Mostly the marginal tentacles are broken off. The basal stumps usually remain; the number of marginal tentacles is 86-110. The tentacles that are left, all have the same characteristic structure, but they are of different sizes.



Fig. 14 b. Halicreas minimum. Latitudinal variation of the standard concentration (C.) between 500-1000 m for RMT8 and RMT1.



Fig. 15. a. Haliscera bigelowi. Horizontal and vertical distributions.

Distribution:

All the specimens were caught at a depth between 440-1090 m from 41°N to 24°N.

In the northern Atlantic it has been found only in the western parts, in the southern Atlantic it has been mainly caught in the eastern waters.

Fam. Geryonidae

Geryonia proboscidalis (Forskål, 1775)

Material: stat. 18-8 (1); 25-8 (1); 26-4 (3); 27-3 (1).

The umbrella is hemispherical and 3.7-25.6 mm wide. The length of the peduncle varies from 2-8.5 mm. There are 6 broad radial canals. Between the successive radial canals of the large specimens 5-7 centripetal canals issue from the broad ring canal: in the smaller specimens there are only 1-2 centripetal canals. The outline of the gonads is somewhat tube-like.

Just left of the base of each of the six perradial marginal tentacles a small ectodermal string extends for a short distance on the exumbrella towards the apex. Above the base of each ectodermal string a small enclosed marginal vesicle is embedded in the umbrellar jelly. In some specimens the six interradial marginal tentacles extend for a short distance on the exumbrella towards the apex. Above the base of each interradial marginal tentacle there is a small enclosed marginal vesicle embedded in the umbrella jelly.

Distribution:

The distribution of the present collection is rather scattered, bathymetrically and geographically. The specimens were principally caught from about 28°N to 24°N; at night they were caught in the upper layer at a depth of 0-50m, but during the day they were found between 200-1090 m.

In the Atlantic Geryonia proboscidalis is distributed in the epipelagic zone from about 40° N to 35° S, including the Mediterranean.

Liriope tetraphylla (Chamisso & Eysenhardt, 1821)

Material: stat 20-12 (1); 25-5 (1).

Both specimens agree with Russell's (1953) description.

One specimen has a width of 11.5 mm. Its long tapering peduncle has a length of about 10 mm. The outline of the gonads is somewhat heartshaped. Opposite each of the four radial canals there is a long hollow marginal tentacle; just left of the base of each tentacle there is a small enclosed marginal vesicle embedded in the umbrellar jelly. The four short hollow interradial marginal tentacles extend for a short distance on the exumbrella towards the apex of the umbrella. Just above the base of each interradial tentacle there is a small enclosed marginal vesicle, embedded in the umbrellar jelly. There are three centripetal canals in each quadrant.

The other specimen has a width of about 5 mm; the peduncle is 2.5 mm long. There are no centripetal canals. The outline of the gonads is somewhat oval. Just left of the bases of the four radial and the four interradial marginal tentacles a corresponding short ectodermal string extends for a short distance on the exumbrella in the direction of the apex. Above each base of such an ectodermal string a small enclosed marginal vesicle is embedded in the umbrellar jelly.

Distribution:

Both specimens were caught in the epipelagic zone at about 35°N and 28°N.

In the Atlantic this species is widely distributed in the epipelagic zone of the warm-water region and in the Mediterranean Sea: it penetrates slightly into the boreal region.

Fam. Rhopalonematidae

Pantachogon haeckeli Maas, 1893

Material: stat. 10-3 (88); 11-1 (162); 13-9 (16); 14-5 (46); 16-3 (58); 18-1 (4); 18-10 (5); 19-22 (1); 20-1 (3); 20-3 (7); 21-6 (2); 22-1 (2); 23-2 (1).

The specimens agree with the description given by Russell (1953). Most specimens were damaged but the thirty-two exumbrellar furrows, the arrangement of the subumbrellar musculature and the sixty-four solid marginal tentacles, all of the same sizes and structures, are easy to recognize. At almost all the stations sometimes colourless specimens and red-coloured specimens were collected in the same hauls; these are merely forms of the same species (Russell, 1953).

Distribution: (figs. 16 a, b)

All the specimens were collected in the deeper strata (290-1250 m) from 55°N to 31°N. The con-



Fig. 15 b. Haliscera bigelowi. Latitudinal variation of the standard concentration (C.) between 300-1000 m for RMT8 and RMT1.



Fig. 16 a. Pantachogon haeckeli. Horizontal and vertical distributions.

centrations of specimens at a depth of 500-1000 m clearly decrease along the north-south line; south of 40°N only small concentrations were found.

Except in the Mediterranean and in the Arctic seas this bathypelagic species is widely distributed in the Atlantic: from the boreal region it penetrates southwards almost to the Antarctic continent. The species occasionally ascends to somewhat higher layers.

Colobonema sericeum Vanhöffen, 1902

Material: stat. 10-3 (1); 13-9 (4); 14-1 (11); 14-5 (4); 16-3 (4); 16-4 (3); 17-2 (4); 18-1 (4); 18-10 (5); 18-13 (35); 19-22 (5); 20-1 (11); 21-6 (8); 21-10 (2); 22-1 (1); 23-3 (1); 26-4 (3); 27-10 (7).

Almost all the specimens are well preserved. They agree with description as given by Russell (1953).

Distribution:

In the present collection *Colobonema sericeum* was found between 300-1130 m from 55°N to 25°N. The higher concentrations were recorded between 49°N and 33°N.

In the Atlantic this bathypelagic species is commonly distributed throughout the warm-water region, including the boreal region, but not in the Mediterranean nor in the Arctic or Antarctic seas.

Aglantha digitale (O. F. Müller, 1766)

Material: stat. 10-1 (20); 10-3 (6); 10-5 (5); 11-1 (3); 11-4 (546); 11-6 (3); 12-1 (22); 13-1 (86); 13-2 (4); 13-4 (1); 13-9 (18); 13-10 (212); 13-11 (928); 14-1 (2); 14-3 (73); 14-5 (3);

14-10 (92); 15-1 (3); 16-3 (2); 18-1 (2); 18-8 (1).

Height of the umbrella: 7.0-19.5 mm. In many specimens the gonads have disappeared but in some specimens the eight sausage-shaped gonads hang in the subumbrellar cavity from the radial canals close to the base of the peduncle, or the scars of the disappeared gonads are visible on the radial canals. No distinction in the variety *rosea* Forbes, 1848 could be made, because it was not possible to assess the exact number of the marginal sensory clubs.

Distribution

This species was principally found in the epipelagic zone. In this zone specimens are distributed from $55^{\circ}N$ to just north of $43^{\circ}N$; the concentrations do not decrease from north to south. Specimens were also collected from $55^{\circ}N$ to $40^{\circ}N$ in the deeper strata (300-1000 m); these concentrations do not clearly decrease southwards.

In the Atlantic the species is almost generally distributed and very common in boreal and Arctic waters; it has an extensive vertical distribution, though it is rare in the uppermost surface layers as well as in very deep water. Except in the southernmost parts of its range it only occurs in the intermediate and deep strata.

Rhopalonema velatum Gegenbauer, 1856

Material: stat. 13-10 (25); 13-11 (28); 14-2 (3); 14-3 (4); 14-5 (2); 14-10 (1); 16-1 (20); 16-2 (1); 16-3 (1); 16-6 (2); 17-1 (3); 17-4 (7); 18-1 (3); 18-2 (2); 18-5 (9); 18-6 (1); 18-8 (51); 19-1 (2); 19-19 (6); 20-3 (1); 20-12 (2); 21-1 (2); 21-2 (6); 21-3 (2); 21-6 (5); 21-9 (2); 21-10 (3); 22-5 (2); 22-9 (9); 23-2 (1); 23-3 (2); 24-1 (4); 24-2 (80); 24-3 (1); 24-5 (1); 25-4 (3); 25-5 (12); 25-6 (4); 25-7 (2); 26-11 (2); 27-3 (1); 27-7 (1); 27-20 (1); 27-23 (11).

Diameter: 4.0-10.0 mm. In many specimens the radial canals with the gonads or the stomach or both have got lost. The specimens have a characteristic conical process on the summit of the umbrella. There are numerous longitudinal exumbrellar furrows. Many specimens are slightly smaller than stated by Kramp (1959).

Distribution:

In the present collection *Rhopalonema velatum* was found from 49° N to 25° N, principally in the upper strata to a depth of about 300 m. High concentrations were recorded just below the surface (0-50 m) at 49° N, 40° N and about 38° N. Below

a depth of 300 m only small concentrations were recorded.

A slight difference in depth could be assessed between the night and the day hauls made with the RMT8. At night the specimens were principally found between 100-200 m; during the day they are collected somewhat deeper (200-300 m). This difference in depth was less clear in the night and day hauls with the RMT1. The hauls made with the Open Ringnet and the Open RMT1 mainly showed high concentrations of specimens in the upper layers (0-50 m) during the day, in contrast with the hauls made with the Open Ringnet with RMT1 liner which showed great concentrations of specimens in these layers at night.

In the Atlantic Ocean this species is generally distributed and very abundant in the warm region; its northward distribution follows the northern borders of the Gulf Stream and the Atlantic Current



Fig. 16 b. Pantachogon haeckeli. Latitudinal variation of the standard concentration (C.) between 500-1000 m for RMT8 and RMT1.



Fig. 17 a. Crossota rufobrunnea. Horizontal and vertical distributions.

Crossota rufobrunnea (Kramp, 1913)

Material: stat. 10-3 (40); 11-1 (38); 13-9 (49); 14-5 (29); 16-3 (2); 18-1 (1).

Distribution: (figs. 17 a, b)

The specimens were collected from $55^{\circ}N$ to $40^{\circ}N$ in the deeper strata (290-1130 m). The concentrations between 500-1000 m decreased from north to south.

In the Atlantic Ocean this species is very common within a restricted area in the north Atlantic, ranging from the submarine ridges in the north to about 32°N.

Crossota alba Bigelow, 1913

Material: stat. 18-13 (2).

The umbrella has a height of 11-12 mm, the width is about 15-16 mm. On the exumbrella there are numerous meridional grooves, about 30-35 in each octant. In one specimen the stomach is tubular and narrow, in the other it is short and wide, due to its contracted state.

Distribution:

The specimens were both caught at 40°N between 420-510 m.

This bathypelagic species occurs in the East Atlantic from the Bay of Biscay almost to South Africa.

Order Narcomedusae

Fam. Solmarisidae

Of the fam. Solmarisidae only specimens of the genus *Pegantha* Haeckel, 1879, were caught. The identification of the species of *Pegantha* is mainly

based on structures of the umbrella margin: the number of the marginal lappets, the shape of the peripheral canal system and the number and shape of the otoporpae (Kramp, 1959).

Unfortunately, most specimens of *Pegantha* in the present collection are badly damaged, especially their umbrella margins, so exact identification, as well as exact measurements, was often very difficult or impossible.

Pegantha martagon Haeckel, 1879

Material: stat. 16-6 (6); 17-3 (4); 18-4 (2); 18-13 (1); 20-8 (1); 20-12 (2); 20-13 (1); 21-6 (2); 21-10 (2); 22-5 (6); 22-9 (13); 23-3 (1); 24-1 (9); 24-3 (1); 24-5 (1); 26-8 (1); 27-2 (1).

Distribution:

The specimens were principally distributed in the upper layers to a depth of 400-500 m from 42°N to 25°N.

In the Atlantic Ocean this species is distributed as far north as the Azores, mainly in the upper strata.

Pegantha laevis H. B. Bigelow, 1909

Material: stat. 13-2 (1); 16-1 (1); 16-2 (4); 16-4 (1); 16-6 (15); 17-3 (3); 18-2 (1); 18-4 (41); 18-5 (2); 18-6 (1); 18-18 (1); 18-10 (2); 18-13 (4); 19-4 (1); 20-12 (1); 21-2 (1); 21-10 (1); 22-5 (1).

Distribution:

The specimens were collected from 49°N to about 32°N; high concentrations were recorded between

42°N and 38°N, they were mainly found in the upper strata.

In the Atlantic Ocean this species is widely distributed but not very common. It is mainly found in the upper water layers; its distribution extends from Patagonia and South Africa northwards to east and west of the Azores and in the Bay of Biscay.

Pegantha clara H. B. Bigelow, 1909

Material: stat: 24-2 (5).

Width of the umbrella 9.0-17.6 mm. Number of marginal lappets 17-21. Although the specimens are heavily damaged, on some marginal lappets 3-4 long, linear otoporpae have been found.

Distribution:

The present specimens were all found at 30°N between 110-205 m.

In the Atlantic Ocean the species is widely distributed between 50°N and 40°S mainly in the upper layers. It has a predominantly tropical distribution and penetrates slightly into the boreal region.

Pegantha div. spec. indet.

Material: stat. 13-1 (1); 14-3 (1); 16-1 (3); 16-2 (4); 16-3 (1); 16-4 (2); 16-6 (7); 17-1 (1); 17-3 (3); 18-2 (1); 18-4 (27); 18-6 (3); 18-13 (2); 19-22 (3); 20-1 (1); 20-12 (4); 21-3 (2); 21-10 (3); 22-1 (1); 22-5 (3); 22-9 (40); 23-2 (1); 24-1 (3); 24-2 (3); 25-3 (2); 25-4 (2); 25-9 (5).

Fam. Cuninidae

Solmissus marshalli Agassiz & Mayer, 1902

Material: stat. 25-9 (1).

Width: 33 mm. There are 15 tentacles and 15 perradial stomach pouches. These stomach pouches are more or less rectangular; some are wider than long, but most of them are slightly longer than wide.

Distribution:

The specimen was caught at 29°N between 100-200 m.

In the Atlantic Ocean this presumably eurybathic species is distributed only in the eastern part, from the Bay of Biscay to South Africa.



Fig. 17 b. Crossota rufobrunnea. Latitudinal variation of the standard concentration (C.) between 500-1000 m for RMT 8 and RMT1.



Fig. 18 a. Aegina citrea. Horizontal and vertical distributions.

Solmissus incisa (Fewkes, 1886)

Material: stat. 13-9 (1); 14-2 (2); 16-2 (1); 20-1 (2); 20-4 (1); 21-6 (2).

Most specimens are fragmented or heavily damaged. It was difficult to measure the diameter of the umbrella and to count the number of stomach pouches. Two specimens, however, appeared complete: diameter 35-36.5 mm, 22 tentacles. The shape of the complete marginal lappets is rectangular, mostly longer than wide.

Distribution:

The specimens were collected at several stations between 49°N and roughly 34°N between 205-1005 m.

In the Atlantic Ocean this mainly bathypelagic medusa has a range from Scotland and Nova Scotia to South Africa.

Fam. Aeginidae

Aegina citrea Eschscholtz, 1829

Material: stat. 11-1 (1); 13-9 (2); 14-2 (2); 14-3 (1); 14-10 (1); 16-2 (1); 16-3 (1); 18-4 (1); 18-10 (3); 19-1 (2); 19-13 (1); 19-22 (2); 20-3 (3); 21-6 (2); 22-1 (1); 26-8 (2).

Umbrella width: 15.5-18.0 mm. The specimens perfectly agree with the description of the species as given by Russell (1953). In some specimens the distal margins of some of the eight stomach pouches are slightly incised, but mostly they were all quite smooth.

Distribution: (figs. 18 a, b)

Most specimens were collected in the deeper layers (440-1250 m) from 53°N to 25°N. But in the area between 45°N to 38°N also some specimens were caught in the upper layers between 50-410 m.

In the Atlantic Ocean this species is widely distributed in the warm parts where it occurs from the surface downwards to considerable depths; north of about 40°N and south of about 40°S it has, with very few exceptions, only been collected in the deep strata.

Aeginura grimaldii Maas, 1904

Material: stat. 10-3 (116); 11-1 (244); 11-4 (5); Material: stat. 10-3 (116); 11-1 (249); 13-9 (213); 14-5 (165); 16-3 (79); 18-1 (29); 18-10 (31); 19-22 (6); 20-1 (2); 20-3 (17); 21-6 (3); 22-1 (3); 23-2 (1); 25-1 (1).

Many specimens were badly damaged; in several hauls of different stations laterally flattened and oral-aboral flattened specimens were collected. Some specimens have six or seven in stead of the usual eight primary tentacles and sectors. But they all agree with the description of the species as given by Russell (1953).

Distribution: (figs. 19 a, b)

The specimens were collected from 53°N to about 28°N in the deeper layers (290-1250 m). The concentrations between 500-1000 m clearly decreased from north to south; south of about 40°N only small concentrations were recorded.

This distinctly bathypelagic species is widely distributed in the Atlantic Ocean.

Coelenterata indet.

Material: stat. 13-9(1); 14-2(4); 14-9(1); 16-2(1); 16-2(1); 16-3(3); 16-6(1); 17-1(1); 17-2(1); 17-3(1); 18-4(1); 18-7(1); 18-10(2); 18-13(5); 19-22(2); 20-1(2); 21-2(1); 21-6(1); 22-6(1); 22-9(1); 26-8(2); 27-10(3).

DISCUSSION

LATITUDINAL DISTRIBUTION AND FAUNAL BOUNDARIES

A boundary between the transitional zone and the subpolar zone has been described based on the geographical distribution of coccolithophores and a boundary between the transitional zone and the subtropical zone was assessed at ca. 40°N (Angel, 1979). This pattern of zones has been found in a wide variety of zooplankton groups. The boundaries of foraminiferan, euphausiid and mesopelagic-fish communities show a close resemblance to the coccolithophores pattern. However, for ostracods the boundary between the transitional zone and the subtropical zone is found more to the north at ca. 44°-45°N (Angel, 1979). For the mesopelagic fish-family Sternoptychidae Pafortvan Iersel (1981) determined a boundary in spring 1980 at ca. 45°N.

In the present collection of the Hydromedusae a boundary between the subpolar zone and the transitional zone is less clear in both the epi- and meso-pelagic species and the bathypelagic species, although species like *Rhopalonema velatum*, *Tima flavilabris* and *Pegantha laevis* which are common in the epi- and meso-pelagic zone of the warm temperate water and sometimes even the Sargasso Sea, have their northern limits at roughly 49°N.

Also the boundary between the transitional and the subtropical zones is less clear in the epi- and mesopelagic species. From 55° N to about 40° N the species diversity increases, with a peak at 42° - 40° N, but south of 40° - 38° N it decreases and the concentrations of several species in the epi- and mesopelagic zones also decrease (figs. 2 a, b, c). *Tima flavilabris* and *Pegantha laevis* have been collected in small concentrations south of 38° N; on the other hand the concentrations of these



Fig. 18 b. Aegina citrea. Latitudinal variation of the standard concentration (C.) between 100-1000 m for RMT8 and RMT1.



Fig. 19 a. Aeginura grimaldii. Horizontal and vertical distributions.

species also decrease north of 42°N. In addition, a species like *Rhopalonema velatum* does not show a decrease in concentration south of 38°N.

In the bathypelagic zone the species diversity decreases south of 40°N and several species which are commonly distributed in cool and deep water layers clearly decrease in concentration south of $40^{\circ}-38^{\circ}N$ Aeginura grimaldii, Crossota rufobrunnea, Pantachogon haeckeli, Halicreas minimum and Chromatonema rubrum have been collected in very small concentrations south of $40^{\circ}-38^{\circ}N$ (figs. 19-17-16-14 and 12 a, b, resp.). Also Haliscera bigelowi which has a vertical distribution between 300-1000 m, has been recorded in small concentrations south of $40^{\circ}N$ (figs. 15 a, b). Aglantha digitale is not distributed in the deeper water layers at all south of ca. $40^{\circ}N$.

The differences in concentration of these Hydromedusae species south of $40^{\circ}-38^{\circ}N$ is probably the result of the transition from more eutrophic warm temperate water to oligotrophic Sargasso Sea water. Warm temperate water is considered to be found roughly between $50^{\circ}N$ and $42^{\circ}N$; the Sargasso Sea water is situated between ca. $40^{\circ}N$ and $27^{\circ}N$ (Van der Spoel, 1981). Between $49^{\circ}N$ and $25^{\circ}N$ the isotherms between 500-1000 m are rather horizontal. Therefore, temperature cannot be the confining factor in the distribution of these bathypelagic species south of 40° - $38^{\circ}N$.

The oligotrophic condition in the upper layers influences the biomass between 500-1000 m, because the foodchain in the ocean is chiefly vertical. Although the minerals are transported in both horizontal and vertical directions the primary production is only found in the superficial layers. From these water layers the biomass passes downwards along the food chain (Van der Spoel, 1979). As the Hydromedusae are predatory animals and a great part of their food consists of phytophages, the amount of phytoplankton may be of considerable importance for the occurrence and quantity of the medusae (Kramp, 1959). Therefore, the oligotrophic condition may explain the small number of Hydromedusae and the small concentrations of several species south of ca. $40^{\circ}-38^{\circ}N$.

We can conclude that a distinction is possible between a group of species generally occurring in cold and deep water layers (500-1000 m) and a group of species which are commonly distributed in the epi- and mesopelagic zones of the warm temperate water and even of the Sargasso Sea water. The species of the former group all show a decrease in abundance from north to south; almost all of them have a boundary at ca 40-38°N, south of which only small concentrations can be found. The species of the latter group have a less clear boundary at ca. 40-38°N. Some of them are confined to the area between 42-38°N.

MEROPELAGIC SPECIES

The increase of the species diversity from 55° N to 40° N and its peak at 42° - 40° N is mainly caused by an increase of species distributed commonly or only in the epipelagic-mesopelagic zone (figs. 2 a, b, c). The number of bathypelagic species remains rather constant from 55° to 40° N. The increase in species diversity could be the result of neritic species in the epi- and mesopelagic zones, which may have their corresponding hydroids attached

to objects on the bottom within the coastal regions of the Azores.

The neritic Hydromedusa fauna mainly consists of meropelagic Leptolina. Meropelagic Leptolina species such as Zygocanna vagans and Neoturris pileata are bound to the coast, but they are sometimes caught at offshore localities (Kramp, 1959). In the present collection both species have been found in the Azores area, but also other meropelagic species such as Pandea conica and Tima flavilabris may have their hydroids on the coast of the Azores. This would explain the high concentrations of both species recorded at $42^{\circ}-40^{\circ}N$ (figs. 7 and 13 a, b, resp.).

Other meropelagic species such as Sibogita geometrica and Bougainvillia platygaster are possibly transported by the Canary Current, which explains their distribution at about 25°N. According to Van der Spoel (1981) the influence of the Canary Current is traceable south of 27°N. Bougainvillia platygaster is a neritic species of the Mauretanian coasts (Kramp, 1959). Russell (1960) states that the species is in process of becoming an oceanic species; it partly solved the difficulty of finding a suitable substratum for the attachment of the hydroids by asexual propagation. In the present collection all the specimens were immature, but many specimens had medusabuds on the subumbrellar surface of the stomach.

Another explanation for the distribution pattern of Pandea conica can be that the south-east flowing branch of the N. Atlantic Current transports the medusa specimens or their hydroids (attached on objects or loose) from the Bermuda area in the West Atlantic to the Azores area in the East Atlantic. A great abundance of Pandea conica was found at 42°-40°N (fig. 7); the mainstream of the south-east flowing branch of the North Atlantic Current crosses this area (Van der Spoel, 1981). Pafort-van Iersel (in preparation) found a high abundance of the pteropod Clio pyramidata Linnaeus, 1767, forma lanceolata (Lesueur, 1821) at about 41°-40°N. Some Hydromedusa species, probably of neritic origin, are able to spread over the oceans, because they can propagate by asexual budding or, for example, their hydroids may be attached to floating objects (Kramp, 1959). Kramp states that the oceanic distribution of Pandea conica is caused by the fact that its hydroid is attached to the shell of the pteropod Clio cuspidata



Fig. 19 b. Aeginura grimaldü. Latitudinal variation of the standard concentration (C.) between 500-1000 m for RMT8 and RMT1.

(Bosc, 1802). Unfortunately, in the collection of the AMNAPE 1980 no hydroids of *Pandea conica* attached on pteropod shells or other objects have been found. However, on some specimens of the pteropod *Diacria trispinosa* (De Blainville, 1821) forma *atlantica* Dupont, 1978 (stat. 16: 41°56.4'N $35^{\circ}00.7'W$; stat. 20: $35^{\circ}14.4'N$ $31^{\circ}31.6'W$) the hydroid of *Kinetocodium danae* Kramp, 1921, was found attached on both the ventral and dorsal surfaces of the shell, which is in accordance with the description given by Kramp (1921, 1957 b). The medusa *Kinetocodium danae* was not found in the present collection.

GEOGRAPHICAL MORPHOLOGICAL VARIATION

There is a variation in the umbrella shape of *Halicreas minimum*, but due to the lack of specimens, especially south of 40° N it was as yet impossible to decide whether different formae (sensu Van der Spoel, 1971) can be distinguished. If so, the different formae could be related to the warm temperate water and the Sargasso Sea water, shading off into one another at about 40° - 38° N. Van der Spoel (1967) indicated a transitional area at 45° - 40° N at which pteropod formae change into other formae of the same species. A transitional area for chaetognath formae was found between 45° - 40° N at the surface layers, shifting to deeper layers at lower latitudes (Pierrot-Bults, 1975).

Another possible explanation for the variation in the umbrella shape of *Halicreas minimum* may be the relation of the different umbrella shapes to the presence of Arctic intermediate water and Antarctic intermediate water. Both water masses are found below 500 m; the Antarctic intermediate water extends northwards probably to 36° N (Van der Spoel, 1981). The flat umbrella shape has been principally found between 500-1000 m from 55° to 40°N and the bell-shaped umbrella was principally collected at the same depth between 38° N and 25° N.

VERTICAL MIGRATION

Several species, such as Annatiara affinis, Pandea conica, Tima flavilabris and Rhopalonema velatum show some difference in the vertical distribution by day and night. They show vertical migration at night to the upper water layers, but a more detailed examination of the vertical migration was difficult due to the fact that no regular day and night sampling scheme was carried out at each station.

ACKNOWLEDGEMENTS

The author expresses his gratitude to Dr. S. van der Spoel for his assistance in preparing the manuscript, Dr. R. W. M. van Soest is thanked for his constructive comments. The author is indebted to Mr. A. F. de Fluiter who sectioned and stained some specimens of *Bougainvillia platygaster*, and to Mrs. E. van der Zee for her critical reading and preparation of the manuscript. The commander and crew of the oceanographic research vessel "Tydeman" are thanked for their assistance during the cruise.

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Received: December 8, 1981

Institute of Taxonomic Zoology (Zoological Museum), University of Amsterdam P.O. Box 20125, 1000 HC Amsterdam, The Netherlands