Bijdragen tot de Dierkunde, 57 (1): 42-52 — 1987

MEDUSAE OF THE GENERA *PARAPHYLLINA*, *PERIPHYLLA* AND *ATOLLA* FROM THE AMSTERDAM MID NORTH ATLANTIC PLANKTON EXPEDITIONS (1980-1983)*

by

S. VAN DER SPOEL

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

ABSTRACT

The vertical distribution patterns of *Paraphyllina ransoni* Russell, 1956, *Periphylla periphylla* (Péron & Lesueur, 1809), *Atolla parva* Russell, 1958, *A. vanhoeffeni* Russell, 1957, and *A. wyvillei* Haeckel, 1880 are described. A comparison with other bathypelagic taxa shows that there are various upper limits to be drawn for the bathypelagic area. Four typically different vertical distribution patterns are described.

RÉSUMÉ

Les types de distribution verticale de *Paraphyllina ransoni* Russell, 1956, *Periphylla periphylla* (Péron & Lesueur, 1809), *Atolla parva* Russell, 1958, *A. vanhoeffeni* Russell, 1957, et *A. wyvillei* Haeckel, 1880 sont décrits. Une comparaison avec d'autres taxa bathypélagiques montre que les limites supérieures dans le cadre du domaine bathypélagique sont différentes. Quatre types distincts de distribution verticale sont décrits.

INTRODUCTION

To study the vertical subdivision of the water column, especially with regard to the upper levels of the bathypelagic realm, nemerteans (Van der Spoel, 1985a) and coronate medusae have been studied. For the nemerteans it became clear that *Nectonemertes mirabilis* Verrill, 1892 shows different vertical distribution patterns in the different seasons sampled. From the other nemerteans it could be concluded that the upper limit of this bathypelagic group is found between depths of 500 m and 1000 m. For the bathypelagic coronate medusae rather shallow and sometimes restricted occurrences are known. It seems worth while to compare the vertical distributions of the nemerteans and coronates with the bathymetric distribution of the chaetognath *Sagitta planctonis* Steinhaus, 1896 and the fish *Argyropelecus* spp.

The term bathypelagic is ill-defined, and used in different ways as is shown by the citations below:

"The term epipelagic denotes the upper water layers... In the present work it will only comprise the upper 150-200 m... Below this epipelagic layer lies the deepwater with its bathypelagic fauna" (Ekman, 1953: 312).

"If... the transition between this zone" [the mesopelagic] "and the dark underlying bathypelagic zone is the threshold of light...". "The bathypelatic zone is thus uniformly cold and dark..." (Marshall, 1979: 43, 44).

"Chun (1887, 1888) introduced the term 'interzonal species' for animals inhabiting both deep-sea and surface zones. More widely used is the expression 'bathypelagic species' proposed by Haeckel (1891), for designating the migrations of animals found at different depths at different times. Among the Russian authors, Brodskii (1950, 1952), Vinogradov (1954a, 1955a, c) and others apply this term as defined by Haeckel. On the other hand Hjort (see Murray and Hjort, 1912) first used the name 'bathypelagic' in a wider sense to cover all the pelagic animals of the deep-seas" (Vinogradov, 1970: 43).

"The mesopelagic zone is subdivided into shallow mesopelagic (300-700 m) and deep mesopelagic (700-1000 m)" (Boxshall, 1981:

* AMNAPE Project 101A. Report no. 28, supported by the Netherlands Ministry of Education and Sciences. (Report no. 27 appeared in Biol. Oceanogr., 4 (2): 439-445—1987.)

153). This author considers the bathypelagic to start below 1000 m.

Some authors consider the bathy- (and meso-) pelagial to be physicochemically determined water masses, others state that the fauna determines the realm, but most authors use the terms bathy- and mesopelagic for animals as well as for water layers, while sometimes these terms are even used to indicate the behaviour of the animals. This is most confusing; in this paper it is tried to detect, for animals commonly considered to be "bathypelagic" in behaviour and distribution, the upper limit of their vertical range.

MATERIAL

The material studied was collected by the Amsterdam Mid North Atlantic Plankton Expeditions held during four years (1980-1983) in different seasons, between 55°N and 24°N along approximately the 30°W meridian, in depth strata of usually 100 m (500 m below 500 m depth) thickness (Van der Spoel, 1981, 1985b; Van der Spoel & Meerding, 1983). The majority of the samples was preserved in 4% formalin and after approximately one year transferred to propylene-phenoxetol/propylene-glycol (Heyman, 1981). All specimens were identified and measured. The numbers used in this paper for abundances are the actual numbers collected without correction for fishing effort or net type used. As the abundance comparisons are roughly made this method seems to be acceptable.

TABLE I

Records of *Paraphyllina ransoni* (only collected in summer 1983; Tr. = trawl).

Sta.	Tr.	*N*	Position North	Position West	Depth (m)	Time
74	10	2	54°20.9'N	29°53.7'W	1000-1750	at night
75	1	11	52°56.5'N	29°53.8'W	200-300	by day
75	6	34	53°01.0'N	29°51.3'W	90-200	by day
78	55	1	44°58.3'N	29°52.4'W	302-400	at dawn
78	57	7	45°00.6'N	29°55.9'W	398-500	at dawn
81	11	7	41°03.0'N	35°29.3'W	200-300	at night
84	5	2	35°08.6'N	31°23.8'W	100-150	at night

RESULTS

Paraphyllina ransoni Russell, 1956
(Fig. 1)

This rather rare species was hitherto only reported from 48°26'N 09°42'W, 900 m depth (45 specimens), 04°58'N 04°02'W (610 specimens), the shore of Villefranche (1 specimen) and off the West coast of Africa (1 specimen) (Russell, 1970). We found it only during the summer cruise in 1983. The vertical distribution pattern closely resembles that of *Periphylla periphylla* (figs. 2-4), though scarcity of material gives an incomplete picture (cf. table I).

This species occurs over a considerable depth range from 90 to 1750 m and probably more, while its north-south range known so far is from 54°N to 04°N in the Atlantic Ocean. It is striking that this species has only been found in summer 1983.

Periphylla periphylla (Péron & Lesueur, 1809) (Figs. 2-4)

This species, usually considered bathypelagic, can better be described as mesopelagic since its main distribution is found between 200 and 1200 m (see table II). In the deeper trawls from 1000 to 1750 m, made during the summer cruise of 1983, it was absent south of 50°N. The occurrence at shallow depths directly below 50 m is mainly restricted to the night periods in 1980-1982, though during the summer (1983) cruise specimens were also collected above 100 m by day. The vertical range is situated in the North Atlantic mixed waters (cf. Van der Spoel

& Heyman, 1983). A temperature-dependent distribution is not found, but none of the other coronates showed this either.

Between 46° and 42°N the population of *P. periphylla* changes strongly. North of this belt the diameter of the bell varies from 3-235 mm while it ranges from 3-45 mm in the area south of 42°N. Moreover, the samples south of 42°N only provided less than 10 specimens per station, while in the northern area all stations yielded more than 30 specimens. The larger numbers and specimens of greater size north of 42°N, where the species lives also at shallow depths, were not all collected shallower as might have been expected from comparison of the northern and southern area. Still, it cannot be accepted that the deeper and the more southward living specimens are merely expatriated specimens, as smaller specimens south of 42°N all show more developed gonads than do specimens of the same size collected in the north. Moreover, expatriated specimens do usually grow larger than local ones. Kramp (1913) also found, in Greenland waters, specimens of every size at every depth and smaller specimens more abundant in the deeper layers. Stiasny (1934) did not agree with Kramp's findings but his data may have been biased as his material came from different water masses some of which affected by upwelling. Though Mauchline & Harvey (1983) found indications for diurnal vertical migration in both *A. wyvillei* and *P. periphylla*, the present material provided only slight indications for such a phenomenon in the latter species.

The number of specimens collected in each trawl differs strongly in the four seasons, viz.: from an average of 4.7 in winter to 15.3 in autumn.

Atolla parva Russell, 1958
(Figs. 5-6)

In this species specimens with 20 and 24 tentacles at the bell margin were treated separately, as Russell (1959, 1970) mentioned that probably a taxonomic variation is concerned here. The 20-tentacle form seems to have a slightly smaller north-south range than the 24-tentacle form as is shown in figs. 5 and 6. Rarely specimens with 21 (1 spec. Sta. 78-1), 22 (1 spec. Sta. 50-2, 1 spec. Sta. 51-12) and 23 tentacles (1 spec. Sta. 45-11, 1 spec. Sta. 78-39 and 1 spec. Sta. 84-24) were found.

The areas with higher abundance of both types point to a difference; the 20-tentacle form dominates south of 42°N while the other form usually dominates north of 40°N. This is also in agreement with the opinion of Russell (1970) that tentacle numbers are higher (up to 26) in the north. The depth range of both types is 500-1750 m with exceptional occurrences up to 400 m in autumn and spring. Unlike the preceding species, this species shows no shallower occurrence in colder waters. The number of specimens collected per trawl only slightly fluctuates in the different seasons around an average of 4.7 specimens per trawl, with a minimum of 3.3. The variation in size mentioned by Casanova (1977) is not affirmed in the present material; however, the open ocean waters represent other conditions which may explain this difference (cf. table II).

Atolla vanhoeffeni Russell, 1957
(Fig. 7)

This species of the central North Atlantic waters (Russell, 1970) shows its highest abundance between 40° and 45°N. Its vertical range does neither become shallower in the northern part of its range, nor does it seem to be temperature-dependent. The bathymetric range is 400 (300 in spring) — 1000 m. In all samples taken from depths below 1000 m (summer cruise 1983) this species is completely absent, while the other species discussed do occur in these samples. As a consequence this species can be considered deep-mesopelagic, restricted to depths between 300 and 1000 m. Casanova (1981) also found for this species a restricted vertical range between 300 and 400 m in the tropics, while Mauchline & Harvey (1983) found a range of 220-500 m in the Rockall Trough. In the present collections relatively high numbers of this species were

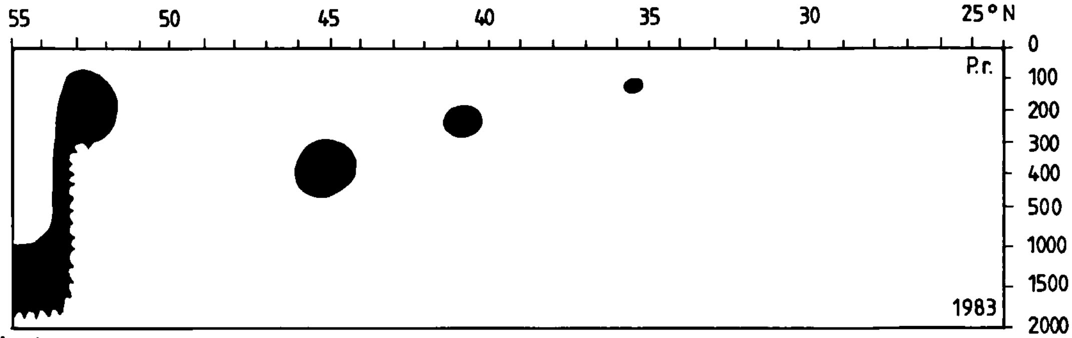

Fig.1

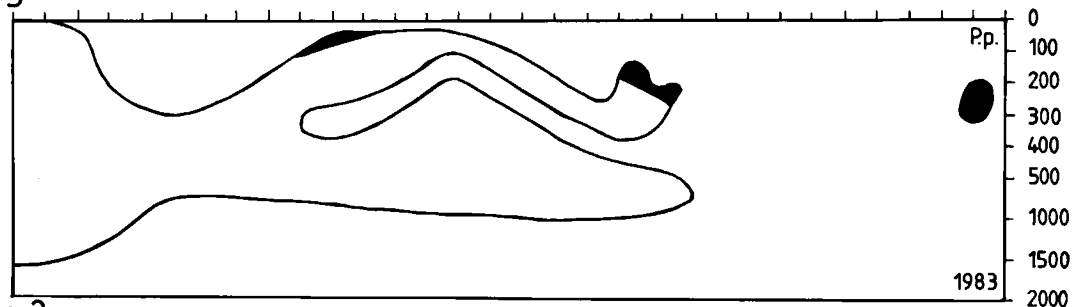

Fig.2

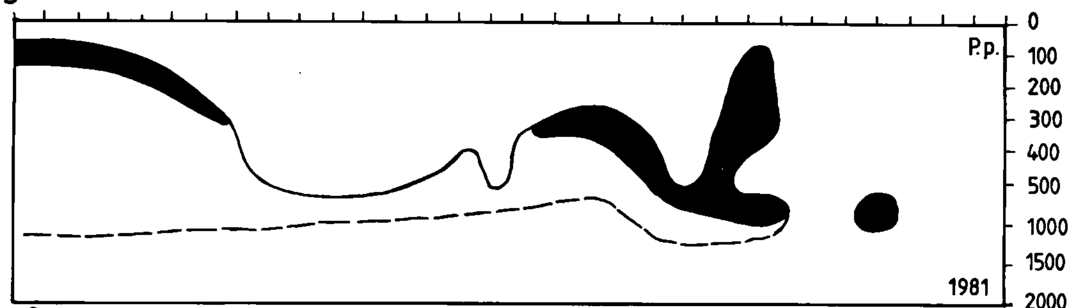

Fig.3

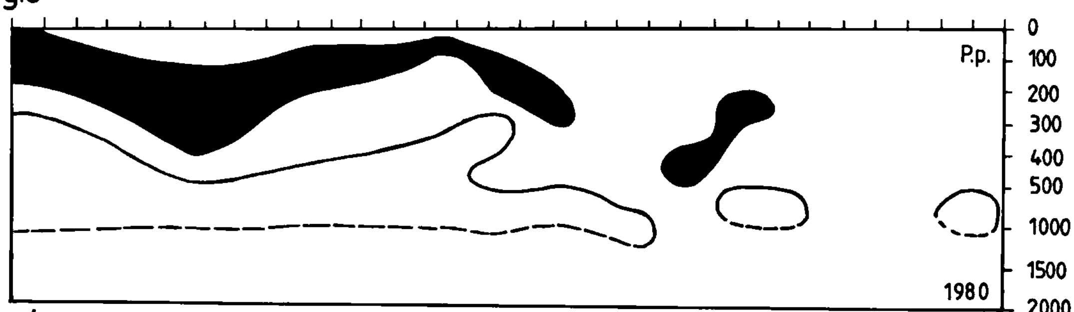

Fig.4

Fig. 1. Vertical distribution of *Paraphyllina ransoni* in summer 1983 along the cruise transect between 55°N and 24°N Depth (m) along the vertical axis.

Figs. 2-4. Vertical distribution of *Periphylla periphylla* along the cruise transect between 55°N and 24°N for summer 1983 (fig. 2), autumn 1981 (fig. 3) and spring 1980 (fig. 4). Depth (m) along the vertical axis. Areas with exclusively night samples are black.

TABLE II

Numbers of specimens of *Periphylla periphylla* (*P.p.*), *Atolla vanhoeffeni* (*A.v.*), *A. wyvillei* (*A.w.*) and *A. parva* (*A.p.*) by station number and trawl. After the number of specimens the average bell diameter (mm) per sample is given. In *A. parva* specimens with 20 and 24 tentacles are treated separately.

Sta.	Tr.	*P.p.*	*A.v.*	*A.w.*	*A.p.* 20 t	*A.p.* 24 t	Position North	Position West	Depth (m)
Spring 1980									
10	1	2-20					54°57.4′	30°00.0′	390-510
10	3	55-?					54°54.0′	30°32.2′	480-1010
10	5	11-152					54°44.9′	29°56.4′	265-400
10	7	14-14					54°43.1′	29°58.9′	0-170
11	1	89-10	1-14	4-31		4-29	53°00.8′	29°58.1′	290-995
11	2	2-145					53°01.3′	29°51.1′	92-210
11	4	3-42					53°08.1′	29°53.9′	40-100
11	7	9-130					53°08.2′	29°55.5′	0-50
13	2	6-14					49°01.1′	30°00.6′	130-220
13	3	37-<20					49°00.9′	29°42.7′	215-310
13	4	93-13	5-9				48°59.8′	29°35.1′	310-400
13	6	1-43	1-7				49°00.7′	29°31.0′	375-500
13	9	31-15	9-17	9-33		3-13	49°00.8′	29°18.5′	480-1005
14	5	15-?	7-8	8-39	2-7	4-11	45°15.0′	29°50.0′	430-1000
14	8	26-12					45°21.8′	29°46.4′	85-200
14	10	1-11					45°24.1′	29°40.6′	50-100
16	3	2-19	2-7	4-39	12-9	3-16	41°47.8′	35°02.8′	490-1000
17	1	3-16					41°01.4′	35°31.3′	45-95
17	2	1-20	24-10				41°10.6′	35°30.9′	330-505
18	1	1-38	3-13	6-30	6-9		39°58.5′	36°24.9′	520-1130
18	2	1-17	21-3				39°52.2′	36°18.1′	265-430
18	4	1-25					39°47.2′	36°16.1′	110-205
18	10	2-11	10-9				39°53.9′	35°38.9′	440-910
19	1	4-14					38°00.6′	35°29.7′	190-320
19	22	1-10	10-10	1-24	9-9	3-7	37°48.5′	35°17.4′	500-1000
20	1		9-9		1-5		35°27.2′	31°51.6′	505-870
20	3	1-14	5-11	13-23	25-11	8-15	35°22.7′	31°44.9′	770-1250
21	3	1-20	3-10				33°47.3′	30°41.8′	390-530
21	6		8-10	2-42	7-9	2-18	33°40.5′	30°40.6′	510-1000
22	1	1-20	5-6		1-9	1-11	32°19.0′	30°03.1′	500-1000
22	6	3-8					32°04.1′	29°54.0′	195-300
23	2	1-11	1-6	1-4	3-9	4-14	30°39.9′	29°59.5′	505-960
25	1		1-30			1-18	28°42.0′	29°59.1′	490-1000
26	4	1-27				1-11	24°52.0′	29°59.5′	510-1090
27	10		1-8			1-15	24°48.6′	28°47.2′	475-1000
Summer 1983									
74	1	2-90					54°20.8′	29°57.1′	296-400
74	4	1-235					54°24.7′	30°00.4′	200-300
74	6	2-130					54°27.1′	30°01.3′	100-200
74	7	9-103					54°23.3′	29°58.3′	5-52
74	10	2-110		4-57	1-7	2-25	54°20.9′	29°53.7′	1000-1750
74	11	2-90					54°18.0′	29°49.6′	50-98
74	12	7-14	1-5				54°22.0′	29°49.0′	400-502
74	15	33-14	1-7	2-71	2-24		54°24.4′	29°48.0′	490-995
75	1	18-33					52°56.5′	29°53.8′	200-300
75	6	12-31					53°01.0′	29°51.3′	90-200
76	26	7-22	1-2	20-28	1-39	5-13	50°21.3′	29°29.7′	500-995
76	30	1-154					50°20.0′	29°20.7′	400-500

TABLE II (continuation)

Sta.	Tr.	*P.p.*	*A.v.*	*A.w.*	*A.p.* 20 t	*A.p.* 24 t	Position North	Position West	Depth (m)
76	31	1-?					50°22.0′	29°23.7′	300-398
78	1		7-9		1-54	1-10	44°58.5′	30°03.8′	500-1000
78	39	3-32	3-9	6-32		2-18	45°02.3′	30°01.3′	500-1000
78	49	1-20					44°59.6′	30°06.9′	196-299
78	53	7-16					44°57.0′	30°01.0′	50-98
78	54	1-35					44°56.8′	29°56.1′	98-200
78	55	2-6	12-9				44°58.3′	29°52.4′	302-400
78	57		12-7				44°58.1′	29°52.1′	0-50
78	60			5-53	5-6	2-35	45°33.1′	29°59.1′	1002-1752
81	6		10-13	7-24		1-21	40°56.2′	35°31.6′	500-1000
81	8	1-24					41°02.3′	35°32.3′	35-100
81	11	7-14					41°03.0′	35°29.3′	200-300
81	14	2-19	10-9				40°59.1′	35°25.4′	280-400
81	16	2-17	29-8				40°56.6′	35°29.6′	400-500
81	17	5-29	3-16	8-18	1-9	1-12	40°58.5′	35°27.5′	505-1000
84	24	1-16	3-13	2-33	3-8	2-11	35°09.6′	31°31.8′	494-1000
84	35	1-40					35°09.2′	31°29.3′	205-305
84	36	1-44					35°11.0′	31°30.9′	300-400
84	37	2-44	5-13	5-29	4-9	1-19	35°11.8′	31°31.4′	505-1000
84	71	1-14					35°09.9′	31°30.6′	200-255
84	72		2-6				35°09.2′	31°26.6′	405-495
84	76	1-10					35°09.3′	31°27.4′	145-205
84	77			7-14	7-9		35°09.6′	31°31.7′	1000-1750
87	35				2-9	1-15	30°00.9′	29°04.0′	500-1000
987	29					2-12	29°59.8′	27°45.7′	752-1005
89	8		2-16			2-9	24°49.5′	30°01.6′	510-1000
89	29		3-14				24°52.8′	30°03.5′	515-1000
89	34	2-35					24°54.3′	30°00.6′	300-400
89	35	2-45					24°49.7′	30°01.7′	190-300
Autumn 1981									
36	8	3-36					55°07.0′	30°10.3′	0-100
36	11	8-68					55°09.5′	30°13.4′	0-390
36	12	98-16	3-13	3-48		3-17	55°07.4′	30°05.4′	0-1140
36	15	5-52					54°13.5′	30°08.8′	0-100
37	4	10-175					53°00.2′	29°57.5′	300-410
37	8	6-143					52°59.2′	29°51.1′	195-280
37	9	27-13	2-18	1-?		8-16	52°58.5′	29°47.4′	400-1000
37	11	4-109					52°56.9′	29°40.7′	100-200
37	12	37-111					52°56.1′	29°37.7′	45-100
38	1	5-168					50°59.8′	29°58.2′	0-415
38	6	3-74					50°58.9′	29°54.8′	0-130
38	8	141-25	4-20	12-30		2-20	50°57.8′	29°50.0′	0-1005
38	11	6-8	7-11	1-11			50°53.8′	29°43.9′	0-520
38	12	8-40					50°50.4′	29°38.6′	0-205
38	14	25-37					50°48.4′	29°35.3′	0-315
39	14	1-17		3-59			47°39.1′	30°13.8′	500-1020
42	6	4-31		4-8	3-6		41°44.4′	34°20.5′	460-870
43	5	2-24	3-14	2-14			41°10.3′	35°42.4′	500-995
43	7	1-23					41°11.1′	35°42.5′	0-421
45	10			8-21			37°08.8′	35°01.0′	505-1010
45	11	1-?			8-13	1-9	37°05.7′	35°06.5′	385-530
45	13	1-25					37°03.8′	35°09.4′	195-380

TABLE II (continuation)

Sta.	Tr.	*P.p.*	*A.v.*	*A.w.*	*A.p.* 20 t	*A.p.* 24 t	Position North	Position West	Depth (m)
47	3	1-31	3-11	1-57		2-9	35°07.7′	31°29.0′	425-855
47	9	2-?					35°06.7′	31°16.4′	360-520
47	12	2-5	1-16	1-51	4-9	1-9	35°07.4′	31°07.3′	750-1170
48	8	1-7	4-10		2-9	2-21	34°12.9′	31°11.9′	500-1150
49	3	2-15		7-11			31°43.1′	29°42.6′	515-1000
49	6	3-16					31°44.5′	29°35.3′	45-107
49	9	1-14					31°47.4′	29°30.0′	200-325
49	10	2-8					31°51.2′	29°25.2′	290-395
50	2			2-19	2-13	2-16	30°05.3′	29°46.7′	730-1200
51	12	1-9	1-13		2-13	2-32	28°07.0′	29°52.8′	500-1050
52	5			1-21			24°57.5′	30°01.2′	490-1005
55	4		7-9	2-8	7-7		27°02.5′	20°17.7′	570-1000
Winter 1982									
62	39	2-13		3-19	4-5	2-8	40°56.3′	35°33.0′	505-980
62	45	13-9					40°56.5′	35°40.0′	195-305
63	27		35-8				39°41.9′	35°46.2′	385-500
63	28		3-8	6-16		1-6	39°36.2′	35°43.1′	505-1000
65	18		1-11				29°60.0′	29°37.5′	400-525
65	20					2-15	29°59.4′	29°34.8′	490-1010
66	1					4-10	30°00.2′	29°29.1′	515-995

taken below 500 m so that the present findings disagree with previously published lower limits of this species in the water column. The number of specimens collected per trawl fluctuated slightly in the four seasons with a minimum average in autumn of 4 specimens per trawl.

Atolla wyvillei Haeckel, 1880 (Fig. 8)

This widely distributed species occurs over nearly the entire cruise transect, except in summer when it is absent south of 35°N. In contrast with the preceding species it occurs below 1000 m. It was always collected in trawls below 500 m, except for two trawls from 430-1000 m and 425-855 m and an inaccurate open trawl; this species can be considered to live usually below 500 m.

In all seasons the highest abundance is found between 45° and 50°N, but numbers are so low that no conclusions can be drawn. The differences in number, averaging 4.7 specimens per trawl, collected during the different seasons are not significant.

CONCLUSIONS

In our records *Periphylla periphylla* is rather a mesopelagic than a typically bathypelagic species; *Atolla parva* and *A. wyvillei* are bathypelagic species, and *A. vanhoeffeni* is in all probability a deep-mesopelagic species restricted to depth levels of 300-1000 m.

No temperature influences regulating the vertical distribution of coronate medusae have been found.

A. parva is a good species. The taxonomic status of the two types with 20 and 24 tentacles at the bell margin cannot be determined on the basis of the present material. Both types occur together in the samples, no essential differences in distribution are found and besides the tentacle number, no other discriminating characters are known.

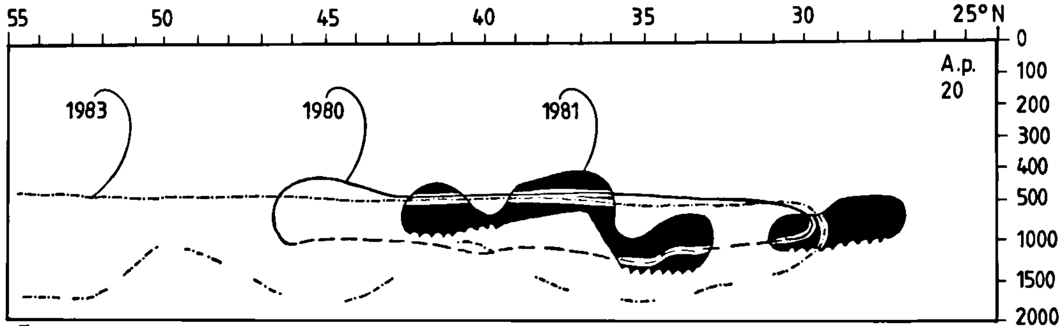

Fig.5

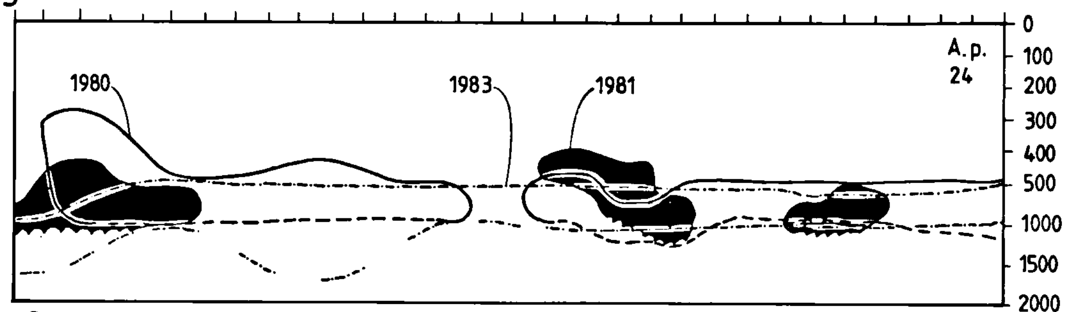

Fig.6

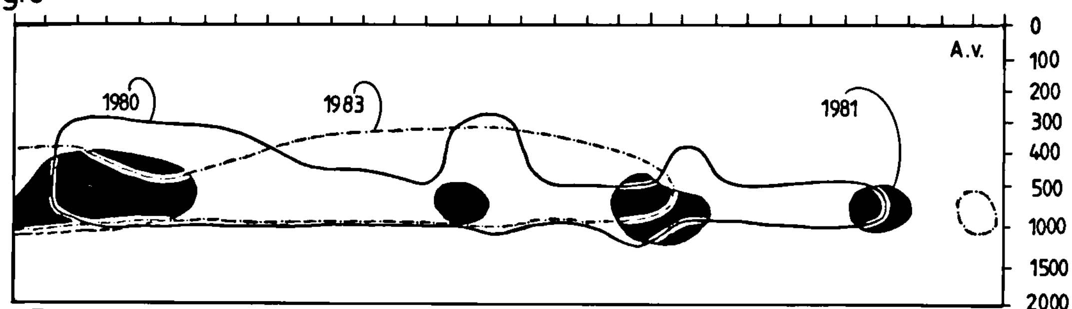

Fig.7

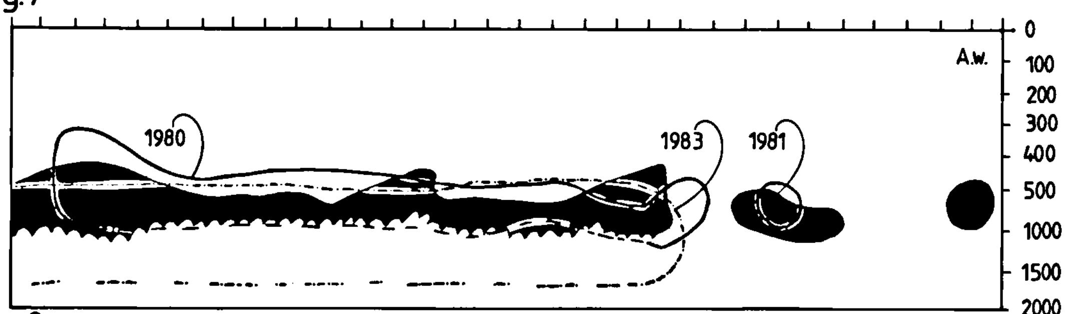

Fig.8

Figs. 5-6. Vertical distribution of *Atolla parva* along the cruise transect between 55°N and 24°N for summer 1983 (-.-.-.-), autumn 1981 (black) and spring 1980 (——), given separately for the 20- (fig. 5) and the 24-tentacle form (fig. 6). Depth (m) along the vertical axis.

Fig. 7. Vertical distribution of *Atolla vanhoeffeni* along the cruise transect between 55°N and 24°N for summer 1983 (-.-.-.-), autumn 1981 (black) and spring 1980 (——). Depth (m) along the vertical axis.

Fig. 8. Vertical distribution of *Atolla wyvillei* along the cruise transect between 55°N and 24°N for summer 1983 (-.-.-.-), autumn 1981 (black) and spring 1980 (——). Depth (m) along the vertical axis.

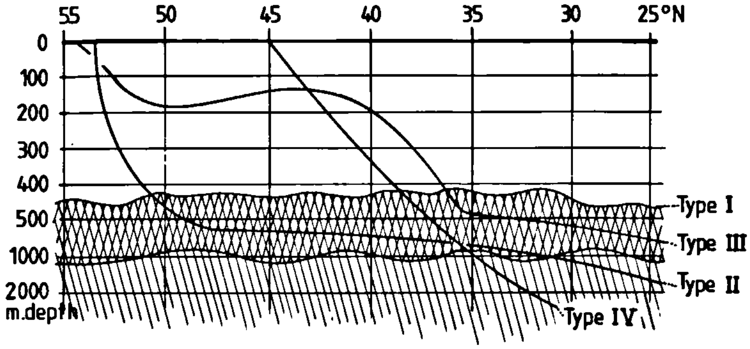

Fig. 9. Diagrammatic representation of the configuration of the four types of upper limits of the bathypelagic realm. The deep-mesopelagic is shown by double hatching (for explanation see text).

The question: "What is the upper level of the bathypelagial?" has more than one answer. At least four types of boundaries can be recognized. In fig. 9 these types are given based on nemerteans, coronates and fishes.

In type I the upper limit of the bathypelagial runs horizontally at a depth of 400-500 m and seems to be independent of hydrographic conditions. This type is shown by *A. wyvillei*.

Type II shows an upper limit between 500 and 1000 m, probably near 700-800 m as found for Chaetognatha (cf. Pierrot-Bults, 1982) and crustaceans (cf. Boxshall, 1981), but in colder waters near 55°N the upper limit ascends. This distribution seems to be temperature-dependent. *Nectonemertes mirabilis* shows this pattern as well (cf. Van der Spoel, 1985a). For type II the term deep-mesopelagic should not be used as species like *N. mirabilis* are living also far below 1000 m.

Closely related to this type is type III, where the range comprises shallower depths already north of 35°N. In some cases this pattern can be temperature-dependent but when, as is shown in fig. 9, the limit stays below 100 m north of 45°N this is not the case. The non-temperature-dependent type III is shown by *Periphylla periphylla*. This pattern is probably not typically bathypelagic, though Stiasny (1934) described this pattern as such.

Type IV, not found for the present medusae, is essentially different from the other three types, though there is a resemblance to type III. In pattern IV, the bathypelagic or mesopelagic representatives start to live at shallower depths north of 30°N and reach the surface near 45°N. *Sagitta planctonis* forma *zetesios* and the fish *Argyropelecus olfersi* are the two most carefully studied examples of this pattern (Pierrot-Bults, 1976; Pafort - Van Iersel, 1981).

In fig. 9 the deep-mesopelagic pattern as shown by *Atolla vanhoeffeni* is indicated by crosshatching. This vertical range seems to coincide partly with the upper layers of the bathypelagial.

Thus it is clear that there is not one single type of upper limit for the bathypelagial, as faunal boundaries are concerned. There is, however, a vertical gradient in which the bathypelagic realm seems to fade out, as is shown in table III. This also explains that there is considerable overlap between the mesopelagial (especially the deep-mesopelagial) and the bathypelagial (cf. table III).

Most bathypelagic representatives in this material are thus found between 1000-1750 m (1130-1750 m south of 40°N), and moderate representation is found between 520-1170 m (855-1170 m south of 40°N), but there are also records though of low diversity between 50-1200 m (52-1200 m south of 40°N).

The term "subtropical submergence" should not be used to describe the variation in depth distribution as shown e.g. by *P. periphylla*, as no submergence of epipelagic forms is concerned, but a shallower occurrence of deeper living

TABLE III

Minimum and maximum depth of shallowest point and minimum and maximum depth of deepest point of the trawls with the total number of bathypelagic taxa (coronates and nemerteans) found together in these trawls; depths in parentheses are for trawls taken south of 40°N only.

Number of bathypelagic taxa	Upper level of net trawls min.	max.	Deepest level of net trawls min.	max.
1	0(5)	752(752)	50(52)	1005(1005)
2	0(200)	510(515)	98(300)	1090(1090)
3	0(385)	500(730)	50(530)	1200(1200)
4	425(425)	570(570)	885(885)	1150(1150)
5	0(750)	750	520	1170(1170)
6	0(520)	1000(1000)	1005(1130)	1750(1750)
7	500(770)	1002	1000	1752(1250)

taxa. It may be difficult to discriminate between subtropical (near 40°N or S) submergence and decreasing depth of bathypelagic forms in the same area (type IV), but it strongly differs from shallower occurrence of deep living forms in polar waters (types II & III).

ACKNOWLEDGEMENTS

The author is much indebted to C. C. Linnenbank, S. H. Lieuw Kie Song and T. Perquin (Organization for the Advancement of Oceanography in the Netherlands, S.B.N.O.) for their efforts in sorting and identifying part of the material. Commanders and crews of H.M.S. "Tydeman" are kindly acknowledged for their neverfailing help during the collecting cruises.

REFERENCES

BOXSHALL, G. A., 1981. Community structure and resource partitioning — the plankton. In: P. L. FOREY ed., The evolving biosphere: 143-156 (British Museum (Natural History) & Cambridge University Press, London/Cambridge/New York/Melbourne).

CASANOVA, J. P., 1977. La faune pélagique profonde (zooplancton et necton) de la Province atlanto-méditerranéenne. Aspects taxonomiques, biologiques et zoogéographiques: 1-455 (Thèse Doct. État Univ. Provence, Marseille).

——, 1981. Nouvelles formulations des règles écologiques connues sous le nom de règle de Bergmann et loi de Jordan. J. Plankton Res., 3 (4): 509-529.

EKMAN, S., 1953. Zoogeography of the sea: i-xiv, 1-417 (Sidgwick & Jackson, London).

HEYMAN, R. P., 1981. Narcotisation, fixation and preservation experiments with marine zooplankton. Verslagen en technische Gegevens, Inst. taxon. Zoöl. (Zoöl. Mus.) Univ. Amsterdam, 28: 1-36.

KRAMP, P. L., 1913. Medusae collected by the "Tjalfe" Expedition. Vidensk. Meddr. dansk naturh. Foren., 65: 257-286.

——, 1947. Medusae. Part III.Trachylina and Scyphozoa with zoogeographical remarks on all the medusae of the northern Atlantic. Danish Ingolf Exped., 5 (14): 1-66.

MARSHALL, N. B., 1979. Developments in deep-sea biology: i-x, 1-566 (Blandford Press, Dorset).

MAUCHLINE, J. & P. F. HARVEY, 1983. The Scyphomedusae of the Rockall Trough, north eastern Atlantic Ocean. J. Plankton Res., 5 (6): 881-890.

PAFORT - VAN IERSEL, T., 1981. The Sternoptychidae (Pisces, Stomiatoidei) of the Amsterdam Mid North Atlantic Plankton Expedition 1980, with a note on specimens intermediate between Argyropelecus aculeatus Valenciennes, 1849 and A. olfersi (Cuvier, 1829). Beaufortia, 31 (4): 97-106.

PIERROT-BULTS, A. C., 1976. Zoogeographic patterns in chaetognaths and some other planktonic organisms. Bull. zool. Mus. Univ. Amsterdam, 5 (8): 59-72.

——, 1982. Vertical distribution of Chaetognatha in the Central Northwest Atlantic near Bermuda. Biol. Oceanogr., 2 (1): 31-61.

RUSSELL, F. S., 1959. Some observations on the Scyphomedusa Atolla. J. mar. biol. Ass. U.K., 38 (1): 33-40.

——, 1970. The medusae of the British Isles, II: i-xi, 1-284 (Cambridge Univ. Press, Cambridge).

SPOEL, S. VAN DER, 1981. List of discrete depth samples and open net hauls of the Amsterdam Mid North Atlantic Plankton Expedition 1980 (Project 101A). Bull. zool. Mus. Univ. Amsterdam, 8 (1): 1-10.

——, 1985a. Pelagic nemerteans of the Amsterdam Mid

North Atlantic Plankton Expeditions (AMNAPE), 1980-1983. Beaufortia, **35** (2): 15-24.

——, 1985b. List of discrete depth samples and open net hauls of the Amsterdam Mid North Atlantic Plankton Expeditions 1982 and 1983 (Project 101A). Bull. zool. Mus. Univ. Amsterdam, **10** (17): 129-152.

SPOEL, S. VAN DER & R. P. HEYMAN, 1983. A comparative atlas of zooplankton. Biological patterns in the oceans: 1-186 (Bunge, Utrecht).

SPOEL, S. VAN DER & A.G. H. A. MEERDING, 1983. List of discrete depth samples and open net hauls of the Amsterdam Mid North Atlantic Plankton Expedition 1981 (Project 101A). Bull. zool. Mus. Univ. Amsterdam, **9** (9): 77-91.

STIASNY, G., 1934. Scyphomedusae. Discovery Rep., **8**: 329-396.

VINOGRADOV, M. E., 1970. Vertical distribution of the oceanic zooplankton: 1-339 (Israel Program for scientific Translations, Jerusalem).

Second draft received: 19 June 1986