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MEDUSAE OF THE AMSTERDAM MID NORTH ATLANTIC PLANKTON EXPEDITIONS (1980-1983) WITH DESCRIPTION OF TWO NEW SPECIES*

by

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ABSTRACT

The medusa fauna of the mid North Atlantic Ocean between 24° and 55° N along approximately 30° W is studied. Two Hydromedusae new to science, *Oceania tydemani* and *Annatiara lempersi*, are described. The differences in fauna south and north of 42° N, and faunal borders near 50° , 48° , 45° , 35° , 30° , and 34° - 37° N are discussed. The vertical distribution and for some species the diurnal migration and subtropical submergence are recorded.

RÉSUMÉ

La faune de Méduses de l'Océan Atlantique Nord central (entre 24° et 55°N; approximativement 30°O) est étudiée. Deux Hydromedusae nouvelles pour la science sont décrites: *Oceania tydemani* et *Annatiara lempersi*. On discute les différences faunistiques au nord et au sud de 42°N, ainsi que les limites faunistiques trouvées au voisinage de 50°, 48°, 45°, 35°, 30°, et de 34° à 37°N. Est mentionnée la distribution verticale et, pour certaines espèces, la migration diurne et la submersion subtropicale.

INTRODUCTION

Winkler (1982) described the Hydromedusae collected in spring during the Amsterdam Mid North Atlantic Plankton Expedition in 1980. Winkler & Van Soest (1981) recorded *Deepstaria* enigmatica from the same cruise and Van der Spoel (1987a) listed some Coronata of the Amsterdam Mid North Atlantic Plankton Expeditions collected in the period 1980-1983. The present paper gives an account of the Medusae collected by these expeditions in spring (1980), summer (1983) autumn (1981) and winter (1982); the data already published are briefly mentioned. Special attention is given to vertical distribution and faunal borders.

Some of the species are illustrated because earlier published figures are frequently diagrammatic. In some cases pictures could be prepared from colour photographs of living specimens which show the normal, not contracted, dimensions of the organism; e.g. *Chromatonema rubrum* (figs. 20, 21) gives a fine example of the effect of fixation and preservation.

MATERIAL AND METHODS

The material studied has been collected during four expeditions between 55°N and 24°N along approximately 30°W in the North Atlantic Ocean (fig. 1) during four seasons in the years 1980 (9/IV-6/V), 1981 (14/IX-14/X), 1982 (1/II-27/II) and 1983 (27/V-24/VI). During these four cruises, stations were sampled as much as possible at comparable geographic localities, but during the winter cruise in 1982 this was impossible due to bad weather conditions preventing part of the transect to be sampled.

Sampling was executed with the RMT 1+8, a combined rectangular midwater trawl developed at the I.O.S. (Baker et al., 1973; Roe et al, 1980) in depth layers of approximately 50 m, 100 m, and 500 m thick between respectively 0 and 100 m, 100 and 500 m, and 500 m and deeper. The mesh sizes of the nets were 0.32 mm and 4.5 mm so that only the relatively large species and specimens were collected. For full data on stations and environmental conditions one is referred to Van der Spoel (1981, 1985) and Van der Spoel & Meerding (1983). Tempertures and salinities given in this paper are all values for the average depth of the samples.

Some species show remarkable differences in vertical distribution at day- and nighttime, but most did not. As still some vertical shifts with the time are expected, where

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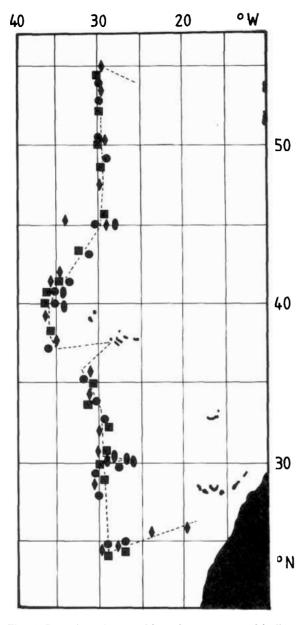


Fig. 1. Investigated area with cruise transect and indication of the position of stations; squares for 1980, diamonds for 1981, ovals for 1982 and circles for 1983.

possible vertical distribution as percentages of total catch per depth stratum, for the population at daytime and at night, is calculated for each species for all stations and it is recorded when an evident percentage of the population crosses a certain depth level between day and night.

The material studied is preserved in the Institute of Taxonomic Zoology (Zoölogisch Museum), University of Amsterdam (ZMA).

RESULTS

Of the total of 72823 specimens 232 could not be identified due to damage. The number of specimens (= spm) collected are given between parentheses.

Class SCYPHOMEDUSAE

 Deepstaria enigmatica Russell, 1967 (1 spm) was collected in spring from a 510-1090 m haul at 24°52' N 29°59' W (Winkler & Van Soest, 1981).

Order CORONATA

Family NAUSITHOIDAE

- (2) Nausithoe atlantica Broch, 1913 (4 spm) was found in the spring, summer and winter cruise between 55°-30°N at depths between 0 and 1010 m, temperature range 4.5-17.4°C (fig. 2).
- (3) Nausithoe spec. (1 spm) was found during the summer cruise between 0-50 m, at 40°54'N.
- (4) Nausithoe punctata Kölliker, 1853 (fig. 3) (8 spm) was found in a sample at 39°59'N in spring between 420 and 510 m depth and two in winter at 30°N between 40 and 505 m. Temperature range 13.3-19.2°C.

Family ATOLLIDAE

- (5) Atolla wyvillei Haeckel, 1880 (171 spm) is a bathypelagic species found along the entire cruise transect (Van der Spoel, 1987a). The temperature and salinity ranges are 3-11.5°C and 34.42-36.21‰, respectively. With Atolla parva, likewise a bathypelagic species, it shares the maximum abundance at temperatures between 8° and 11°C.
- (6) Atolla vanhoeffeni Russell, 1957 (304 spm) is a deep mesopelagic species living less deep than the other two relatives but showing no shallow occurrence at high latitudes, like *Periphylla periphylla* (cf. Van der Spoel, 1987a). The temperature and salinity ranges are 4-14.5°C and 34.42-36.21%, respectively. The temperature curve shows two maxima for abundance, one between 8° and 11°C and one between 12° and



Fig. 2. Nausithoe spec. cf. atlantica from station 65 trawl 13

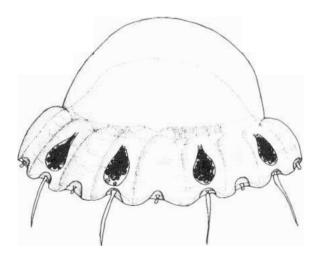


Fig. 3. Nausithoe punctata from station 68 trawl 1.

14°C. This is characteristic as the two other *Atolla* species do not show maxima in temperature preference.

(7) Atolla parva Russell, 1958 (214 spm) is a bathypelagic species found along the entire cruise transect (Van der Spoel, 1987a). The temperature and salinity ranges are 3-13°C and 34.42-36.21%, respectively.

Family PARAPHYLLINIDAE

(8) Paraphyllina ransoni Russell, 1936 (64 spm) was only found in summer between $54^{\circ}20'$ N and $35^{\circ}08'$ N at depths from 90 to 300 m at daytime and 100 to 1750 m at night. The temperature and salinity ranges are $3.5-14.3^{\circ}$ C and $35.01-36.12\%_{00}$, respectively.

Family PERIPHYLLIDAE

(9) Periphylla periphylla (Péron & Lesueur, 1809) (1004 spm) was found in all seasons along the entire transect of the cruises as a mesopelagic species living also at shallow depth north of 42°N (Van der Spoel, 1987a). The temperature and salinity ranges are 3.4-19.8°C and 34.39-36.43‰, respectively. This temperature range is not reflecting real temperature preferences as the majority of the specimens is collected at temperatures between 4° and 11°C. It is notable, however, that this deep- or coldwater species is tolerating temperatures up to 19.8°C.

Order SEMAEOSTOMEAE

Family PELAGIIDAE

(10) Pelagia noctiluca (Forskål, 1775) (fig. 4) (1739 spm) was not found in spring but occurs in high numbers in autumn, while regularly specimens were collected in sum-

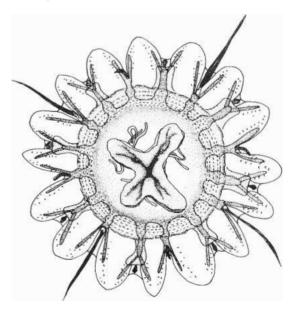


Fig. 4. *Pelagia noctiluca* from station 81 trawl 6, a young specimen.

mer and winter. It is an epipelagic species with its highest abundance in autumn between 200 and 300 m. Vertical migration is not evident. This typically temperate species lives in autumn between 51° N and 24°N, in summer between 45°N and 32°N and in winter between 40°N and 30°N. The temperature and salinity ranges are 6.5-19.4°C and 34.40-36.43‰, respectively.

Class SIPHONOPHORA

- (11) Porpita porpita (Linnaeus, 1758) (3 spm) was only found in autumn between 34°55′N and 27°10′N in a night sample in the upper 50 m and in a day sample from 460 to 870 m. The temperature and salinity ranges are 10.3-22.9°C and 35.59-36.97‰, respectively.
- (12) Velella velella (Linnaeus, 1758) (5 spm) was rarely found, and as young specimens only, in spring between 375 and 500 m at daytime as far north as 45°02'N and in autumn in night samples between 0 and 350 m depth at 45°01'N at 30°08'N. The temperature range is 11.9-15.4°C.

Class HYDROZOA

Order ANTHOMEDUSAE

Family CYTAEIDAE

(13) Cytaeis tetrastyla Eschscholtz, 1829 (fig. 5)
(9 spm) was found in spring at 30°N and in winter at 37°08'N-30°06'N at temperatures of 12.2-23.5°C and salinities of 35.61-36.51%. The depth of two day samples was 40-110 m, the night samples were from depths between 0 and 520 m.

Family CLAVIDAE

(14) Oceania armata Kölliker, 1853 (fig. 6) (14 spm) was found in autumn between 37°08'N and 26°08'N and in summer between 37°00'N and 35°11'N. There seems to be no vertical migration as the day level (40-200 m) was not significantly different from the night level (30-305 m). The temperature range is 12.5-21.1°C and the salinity range is 35.60-37.63%00.

(15) Oceania tydemani n. sp. (fig. 7) (1 spm) was found in autumn at 34°11.4'N, between 60-100 m at a temperature of 18.7°C.



Fig. 5. Cytaeis tetrastyla from station 66 trawl 9.

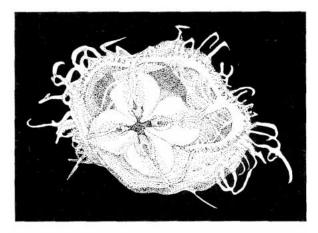


Fig. 6. Oceania armata (after colour photograph) from station 83 trawl 9.

Family BOUGAINVILLIIDAE

(16) Bougainvillia platygaster (Haeckel, 1879) (fig. 8) (78 spm) is a warm water species not found north of 30°N (fig. 9) and in winter restricted to 30°N in the cruise transect, though it is known to occur from 45°S to 40°N in the Atlantic Ocean. In summer it was not collected. This species occurred also in deeper hauls at night (500-1000 m) while at daytime it was only collected shallower than 200 m. Normal diurnal vertical migration seems present as at night the species lives also in the upper 25 m, while it is absent above 40 m at daytime, and 16% of the population crosses daily the 100 m level. The temperature range is 10.5-25.1°C, the

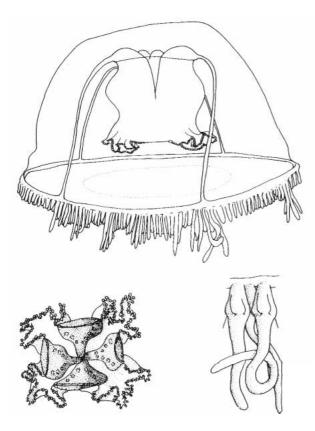


Fig. 7. Oceania tydemani n. sp. from station 48 trawl 13: animal from lateral, mouth with stomach in detail, and tentacles.

salinity range is $35.87-37.93\%_{00}$. The symbiotic occurrence of the medusa *Pegantha trilobata* reported by Winkler (1982) for the spring cruise is also found in the autumn material.

Family PANDEIDAE

- (17) Annatiara affinis (Hartlaub, 1913) (figs. 10, 11) (40 spm), a species mainly occurring in the East Atlantic (fig. 12), was collected in all seasons in Sargasso Sea and North Atlantic Drift waters. Though the day and night vertical ranges 85-1000 m do not differ, 11% of the population migrates upwards through the 300 m level from day to night. The temperature range is 7.8-17.0°C, the salinity range is 35.28-36.45‰.
- (18) Annatiara lempersi n. sp. (fig. 13): the single specimen was collected in summer at

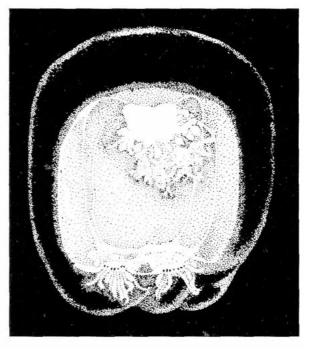


Fig. 8. Bougainvillia platygaster from station 53 trawl 9.

 $31^{\circ}30.9$ N between 300 and 400 m at a temperature of 12.7° C.

- (19) Pandea rubra Bigelow, 1913 (fig. 14) (3 spm) is an epipelagic species (fig. 15) from the upper 300 m in the spring and autumn cruise, living at temperatures of 13.6-19.4°C.
- (20) Pandea conica (Quoy & Gaimard, 1827) (29 spm). For distribution see fig. 16. It was only found in spring and autumn, at night (only one sample) the depth range was 45-95 m, at daytime it was 50-300 m; one specimen was collected in a haul of 300 to 400 m (daytime). The temperature range is 13.9-16.7°C.
- (21) Neoturris pileata (Forskål, 1775). Only two specimens were collected in spring near 35°N in a haul of 200-295 m and one of 320-530 m at temperatures between 12.5° and 15.4°C.

Family CALYCOPSIDAE

(22) Calycopsis gara Petersen, 1957 (fig. 17) (1 spm) was found in spring between 0 and 200 m at 41°01′N and at a temperature of 13.0-15.5°C.

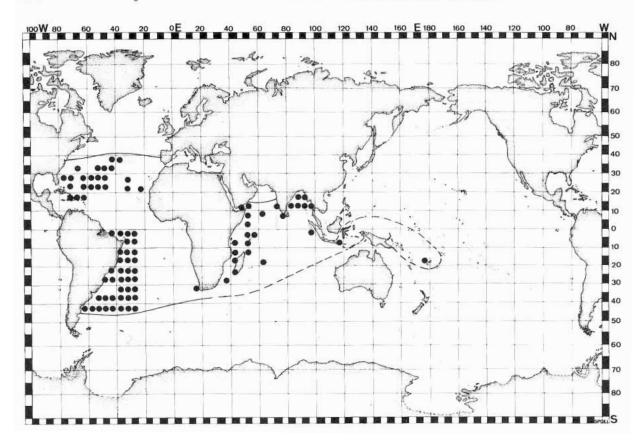


Fig. 9. Distribution of Bougainvillia platygaster.

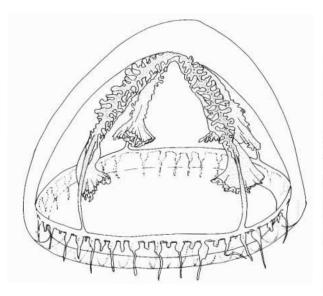


Fig. 10. Annatiara affinis from station 87 trawl 10, 30 mm in diameter.

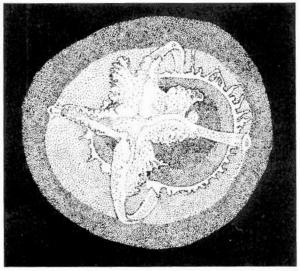


Fig. 11. Annatiara affinis (after colour photograph) from station 88 trawl 9.

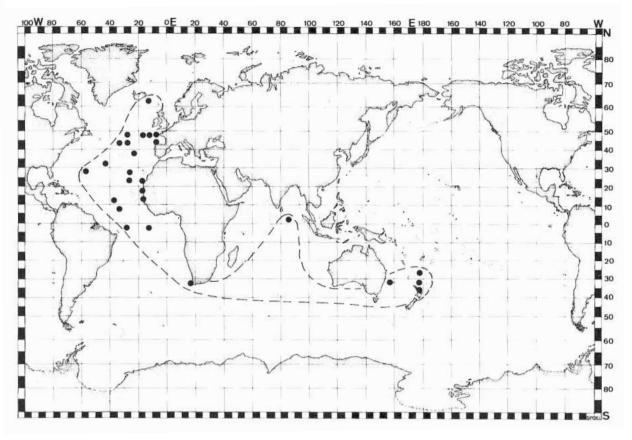


Fig. 12. Distribution of Annatiara affinis.

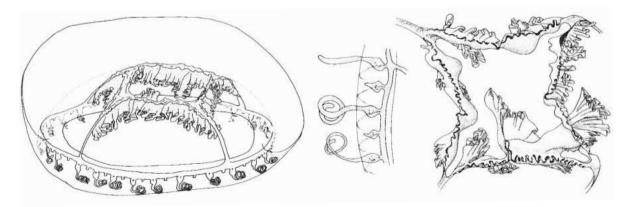


Fig. 13. Annatiara lempersi n. sp. from station 84 trawl 36: animal from latero-apical, part of margin with tentacles, and stomach from apical.

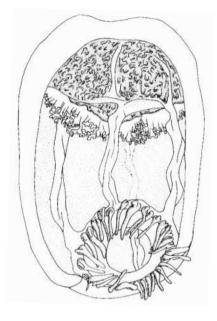


Fig. 14. Pandea rubra from station 84 trawl 35

- (23) Bythotiara murrayi Günther, 1903 (1 spm) was found in spring at 49°00'N between 375 and 500 m at a temperature of 9.3°C.
- (24) Sibogita geometrica Maas, 1905 (figs. 18, 19)
 (6 spm) was found in spring, summer and autumn at 24°44′N, between 44°59′ and 33°28′N and between 41°39′N and 35°07′N, respectively. Vertical migration is evident as all night samples were taken above and all day samples below 200 m. The temperature range is 12.9-16.4°C and the salinity range is 35.85-26.27%00.

Family TIARANNIDAE

(25) Chromatonema rubrum Fewkes, 1882 (figs. 20, 21) (49 spm) is a deep living species (fig. 22) occurring between 400 and 1750 m; probably there is some vertical migration but night samples were too few to

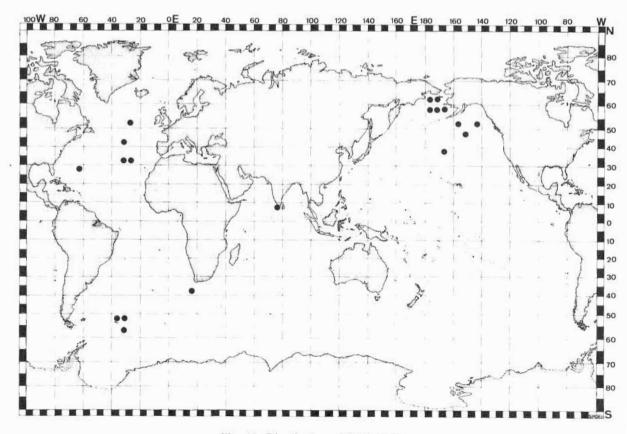


Fig. 15. Distribution of Pandea rubra.

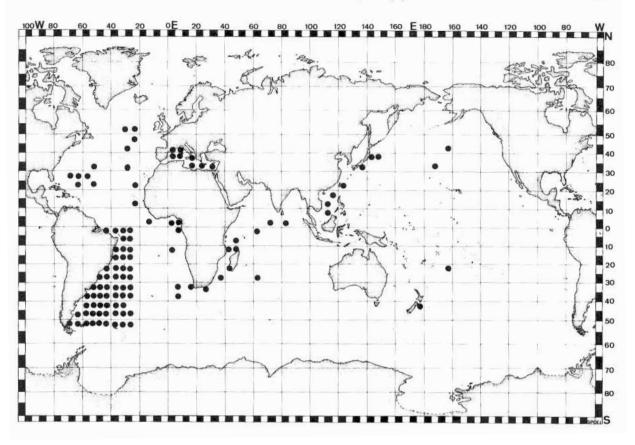


Fig. 16. Distribution of Pandea conica.

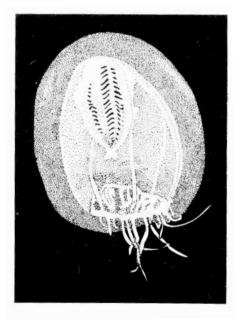


Fig. 17. Calycopsis gara from station 16 trawl-1.

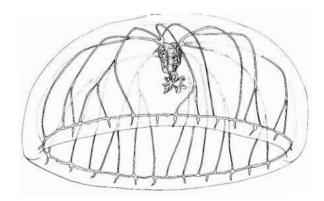


Fig. 18. Sibogita geometrica from station 85 trawl 12.

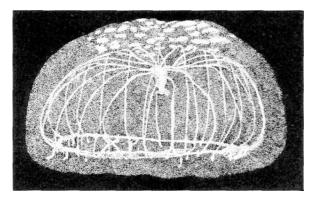


Fig. 19. Sibogita geometrica (after colour photograph) from station 47 trawl 7.

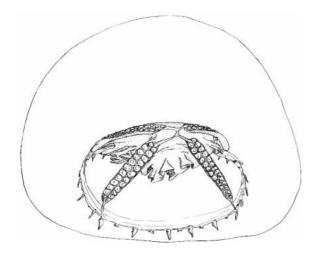


Fig. 20. Chromatonema rubrum from station 76 trawl 26.

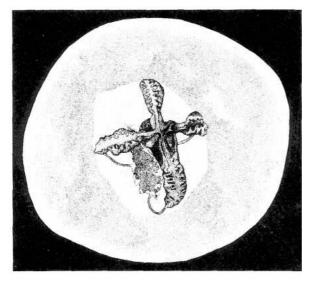


Fig. 21. Chromatonema rubrum (after colour photograph) from station 39 trawl 14.

draw conclusions. The seasonal influence on this species is clear as it retracts during summer to the north and to greater depths. It occurs in spring between 55° N and 39° N, during summer between 55° N and 48° N and during autumn between 55° N and 45° N; in winter it is absent. The temperature range is 3.45- 10.40° C and the salinity range is 34.96- $35.41\%_{00}$. Comparison of a preserved (fig. 20) and living specimen (fig. 21) learns that fixation causes 26% more shrinking of the jelly than of the manubrium.

Order LEPTOMEDUSAE

Family DIPLEUROSOMIDAE

(26) Cuvieria huxleyi (Haeckel, 1879) (1 spm) was found in summer between 45 and 100 m depth at 35°11'N, temperature 16.9°C, salinity 36.29‰.

Family MITROCOMIDAE

(27) Cosmetira pilosella Forbes, 1848 (12 spm) was collected between 50 and 110 m and 440 and 910 m depth at daytime in spring, at temperatures of 10.4-16.4°C.

Family EIRENIDAE

(28) Phialopsis diegensis Torrey, 1909 (1 spm) was collected in winter at 30°02'N between 40 and 115 m, temperature 19.2°C.

Family EUTIMIDAE

(29) Tima flavilabris Eschscholtz, 1829 (252 spm) was only found in spring between 49°N and 24°N in the upper 500 m with the highest concentrations between 0 and 300 m. Vertical migration is found as 80% of the population daily crosses the 100 m depth level. The temperature range is 7.8-19.5°C.

Family AEQUOREIDAE

(30) Zygocanna vagans Bigelow, 1912 (fig. 23) (2 spm) is an epipelagic species collected in the upper 300 m at temperatures of 14-17°C. The Dana Expeditions collected the species at 41°55′N 32°22′W (Kramp, 1959) and in 1980 and 1983 the present material was collected from 41°35′N

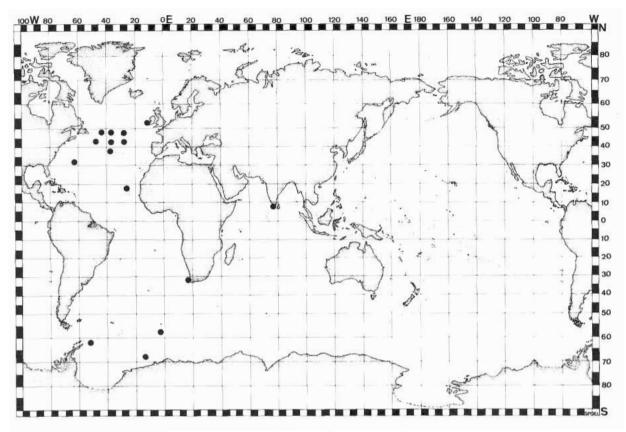


Fig. 22. Distribution of Chromatonema rubrum

 $34^{\circ}57'W$ and $39^{\circ}47'N$ $35^{\circ}32'W$, respectively, so that a very limited stable population near the Azores seems to be present. This small population is the only one hitherto recorded from the Atlantic Ocean, while numerous populations are known from the Indo-Pacific Oceans. The salinity is $36.12\%_{00}$.

(31) Aequorea tenuis (Agassiz, 1862) was only represented by one specimen from 40°58'N 35°27'W between depths of 500 and 1000 m at a temperature of 8.5°C.

Order TRACHYMEDUSAE

Family HALICREIDAE

(32) Halitrephes maasi Bigelow, 1909 (fig. 24) (6 spm) was only found in day samples from 440-1090 m depth in spring and summer between 41°47'N-24°48'N and at 40°58'N, respectively. The temperature range is 9.8-10.5°C.

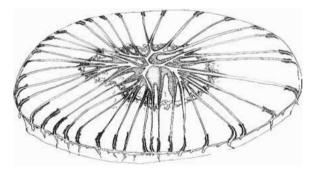


Fig. 23. Zygocanna vagans from the area around the Azores

(33) Botrynema brucei Browne, 1908 (fig. 25) (355 spm) is a deep living species (fig. 26) found in the Atlantic between 60°N and 65°S. It was found in all seasons below 480 m, at temperatures of 3.5-9.4°C and salinities of 34.75-35.15%00. It is a high latitude species with its southern border at

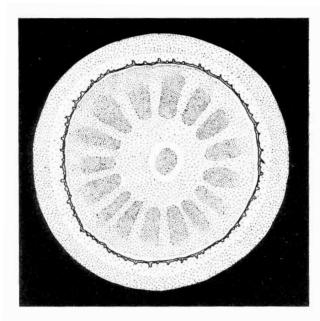




Fig. 24. Halytrephes maasi from station 81 trawl 17.

Fig. 25. Botrynema brucei from station 78 trawl 60.

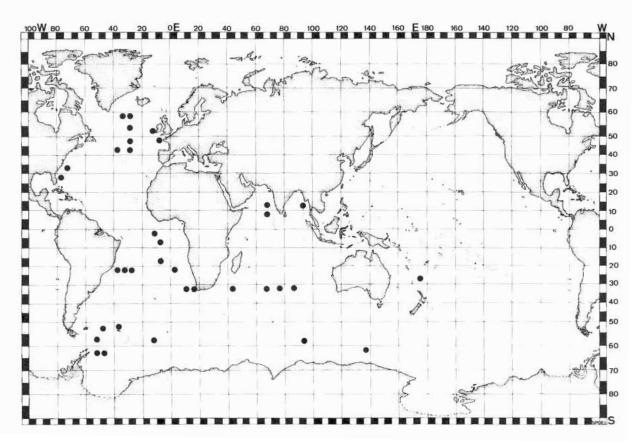


Fig. 26. Distribution of Botrynema brucei.

49°N in spring, at 45°N in summer, and at 40°N in autumn.

- (34) Halicreas minimum Fewkes, 1882 (fig. 27) (547 spm). This species was found in all seasons along the entire cruise transect from 24° to 55°N and only below a depth of 500 m. The temperature range is 3.5-11.0°C, though highest abundances are found at temperatures below 8°C; the salinity range is 34.75-35.87‰.
- (35) Haliscera bigelowi Kramp, 1947 (176 spm) was found in night samples between 330 and 505 m and in daytime samples between 205 and 1020 m. It occurs in spring, summer and autumn. The temperature range is 4.5-19.2°C, most abundant between 8° and 11°C and only sporadic at temperatures above 12°C; the salinity range is 34.74-36.13%₀₀.

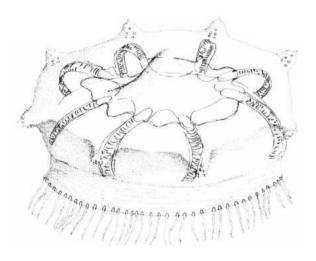


Fig. 27. Halicreas minimum from station 81 trawl 6

Family RHOPALONEMATIDAE

- (36) Rhopalonema funerarium Vanhöffen, 1902
 (27 spm) was only found in winter at 30°00'N at temperatures of 18.5-19.0°C. Though considered to be a bathypelagic species (Kramp, 1959) it is found in a 40-115 m (24 specimens) haul and 395-995 m hauls (3 specimens).
- (37) Rhopalonema velatum Gegenbaur, 1856 (fig. 28) (583 spm) occurred in all seasons

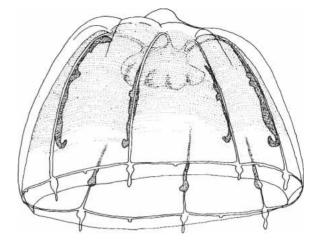


Fig. 28. Rhopalonema velatum from station 84 trawl 36

between 0 and 1760 m depth; the northern limit only changes slightly being at 49°N in spring, at 45°N in summer, at 51°N in autumn and probably at 30°N in winter (the winter cruise, however, sampled too few stations to be sure of this limit). A very slight tendency of vertical migration is found in this eurybathic species as 5% of the population crossed the 50 m level, 11% crossed the 100 m level and 2%crossed the 200 m level daily. The temperature and salinity ranges are 6.15-25.7°C (most specimens are, however, collected between 10° and 20°C) and 35.09-37.10%, respectively. For general distribution see fig. 29.

- (38) Crossota spec. (fig. 30) (1 spm) was found between 500 and 1000 m in summer, at $40^{\circ}45'$ N and at 8.8°C and 35.45% S.
- (39) Crossota alba Bigelow, 1913 (5 spm) was found in samples between 0 and 220 m and between 420 and 1752 m, but there is no indication of diurnal migration. Though the shallow sample from 0 to 220 m was taken by a malfunctioning discrete depth net it is excluded that the depth record is incorrect as the net was never lowered below 250 m, so it is concluded that the species is eurybathic. It occurs in spring at 39°59'N, in summer at 45°N and in winter between 40°55'N and

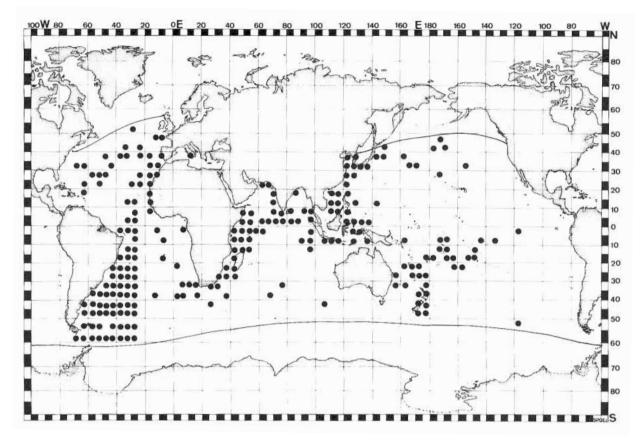


Fig. 29. Distribution of Rhopalonema velatum.

 $29^{\circ}59'$ N. The temperature range is 4.4-16.0°C and the salinity was $35.12\%_{00}$.

- (40) Crossota rufobrunnea (Kramp, 1913) (fig. 31)
 (404 spm) was found in spring between 55° and 40°N, in summer between 55° and 35°N and in autumn between 55° and 48°N. In the day samples the species occurs always below 420 m depth and the single night sample was from 520-1130 m depth (1 specimen). The temperature and salinity ranges are 4.2-9.9°C and 34.75-35.55‰, respectively.
- (41) Sminthea eurygaster Gegenbaur, 1856 (fig. 32) (13 spm) was found in summer and winter at (probably 45°02')-35°11'N and 29°59'-30°03'N, respectively. The temperatue and salinity ranges are 8.2-19.2°C and 35.41-35.75‰.
- (42) Colobonema sericeum Vanhöffen, 1902 (fig. 33) (246 spm) was found in spring between

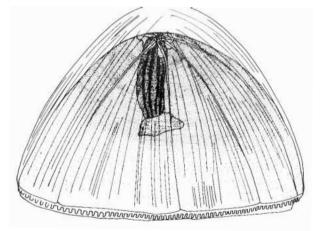


Fig. 30. Crossota spec. from station 81 trawl 6.

55° and 25°N and in the other seasons between 50° and 25°N as a deep living species restricted to depths below 365 m.

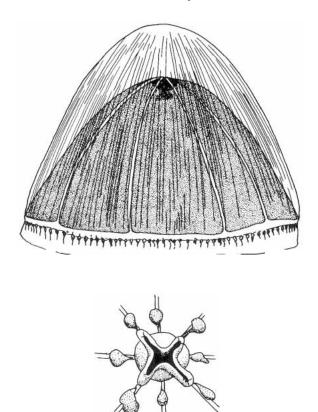


Fig. 31. Crossota rufobrunnea from station 81 trawl 6: animal from lateral and mouth and gonads from aboral.

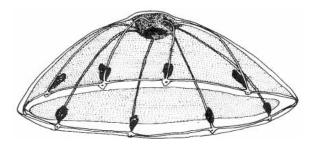


Fig. 32. Sminthea eurygaster from station 84 trawl 6

The distribution in the Atlantic Ocean is between 60°N and 60°S. The temperature and salinity ranges are 4.5-15.2°C and $35.09-36.70\%_{00}$, respectively. The temperatures of 4.5-8.5°C are only recorded for daytime samples; the maxima of abundance are found at temperatures of 9-12°C and at 14°C.

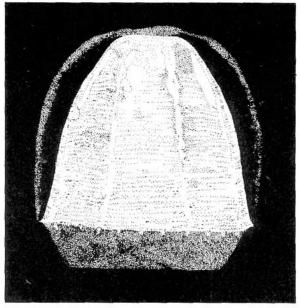


Fig. 33. Colobonema sericeum (after colour photograph) from station 84 trawl 36.

- (43) Pantachogon haeckeli Maas, 1893 (figs. 34, 35) (1650 spm) was most abundant at greater depths. At daytime 1041 specimens were collected of which no one in hauls shallower than 870 m. At night 21 specimens were collected of which 3 between 0 and 100 m and 4 between 360 and 520 m. Thus there may exist some vertical migration. The species was found in all seasons along the whole cruise 55° transect from to 24°N. The temperature and salinity ranges are 3.5-19.2°C and 34.95-35.95%, respectively. This is a widely distributed species in all oceans between 70°N and 70°S (fig. 36).
- (44) Amphogona apsteini (Vanhöffen, 1902) (fig. 37) (6 spm) occurred in summer at 54°20'N and in autumn at 41°44'N, though it is in literature mentioned as a surface form (Kramp, 1959) between depths of 460 and 1750 m. The temperature and salinity ranges are 3.45-10.25°C and 35.03-35.59‰, respectively.
- (45) Amphogona apicata Kramp, 1957 (fig. 38) (8 spm) occurred in summer between 45°02' and 35°09'N and in winter at 29°59'N

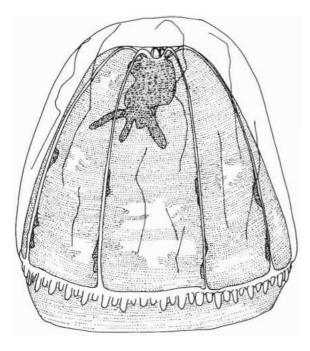


Fig. 34. Pantachogon haeckeli from station 81 trawl 17

Fig. 35. Pantachogon haeckeli from station 78 trawl 60

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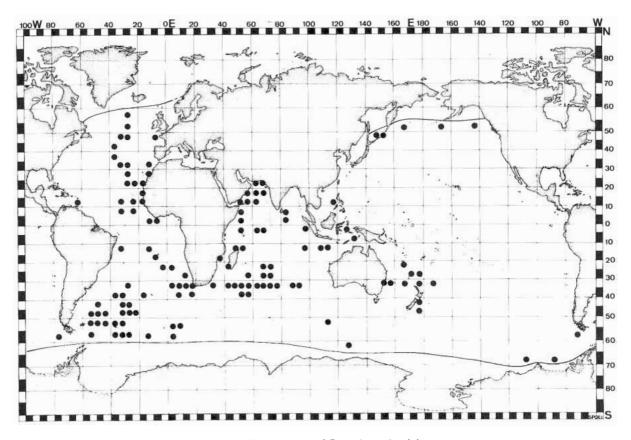


Fig. 36. Distribution of Pantachogon haeckeli

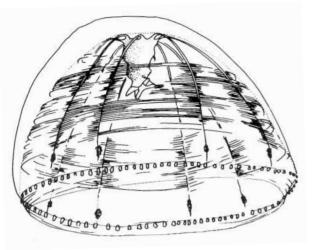


Fig. 37. Amphogona apsteini from station 78 trawl 39

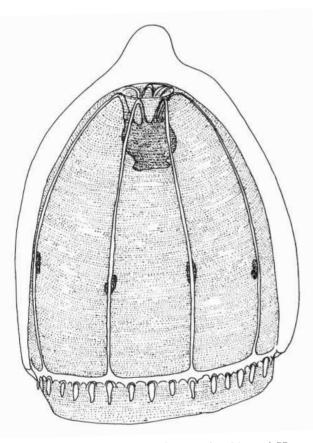


Fig. 38. Amphogona apicata from station 84 trawl 77.

always below 490 m. The temperature and salinity ranges are 6.15-10.3°C and 35.41-33.55‰, respectively.

(46) Tetrorchis erythrogaster Bigelow, 1909 (fig. 39) was only represented by one specimen

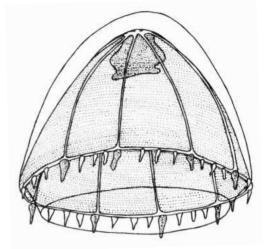


Fig. 39. Tetrorchis erythrogaster from station 78 trawl 39.

between 500 and 1000 m, in summer at 45°02'N. The temperature and salinity were 8.15°C and 35.41‰.

- (47) Aglaura hemistoma Péron & Lesueur, 1809
 (21 spm) was found only in winter at 29°58'N at a depth of 0 to 150 m.
- (48) Aglantha digitale (O. F. Müller, 1766) (figs. 40, 41) (61821 spm) occurred at depths

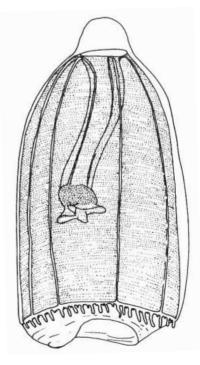


Fig. 40. Aglantha digitale from station 76 trawl 32

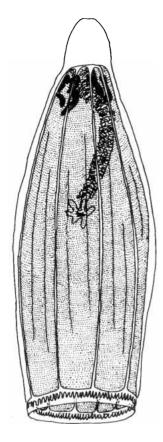


Fig. 41. Aglantha digitale from station 75 trawl 6

between 0 and 1130 m with great abundance between 0 and 100 m and between 500 and 1000 m. In spring it is found from 55° to 39°N, in summer from 55° to 25°N, and in autumn from 55° to 48°N. It is thus a northern species that penetrates the whole area investigated in summer. This southwards penetration is a penetration in deeper layers only. The species occurred south of 40°N only in the twilight samples so that nothing on vertical migration can be concluded, but north of 40°N no migration was found and south of 40°N it occurs only deeper than 500 m. The distribution is probably from 60° to 40°N (fig. 42) in shallow and deeper layers and from 40° to 20°N only in deeper layers. Data on the southern oceans are too scarce to make conclusions, but the same patterns may exist there. The

temperature and salinity ranges are 3.5-18.0°C and 34.72-35.74‰, respectively.

Family GERYONIIDAE

- (49) Geryonia proboscidalis (Forskål, 1775) (8 spm) was found in spring and autumn at night between 40 and 395 m and at daytime between 200 and 1090 m depth at temperatures of 9.8-22.2°C.
- (50) Liriope tetraphylla (Chamisso & Eysenhardt, 1821) (2 spm) was only found in spring in the upper 100 m at temperatures of 17.2°-21.2°C at night.

Order NARCOMEDUSAE

Family AEGINIDAE

- (51) Aegina citrea Eschscholtz, 1829 (figs. 43, 44) (67 spm) is a deep-sea species showing diurnal vertical migration as 42% of the population crosses the 300 m level daily. It seems to live shallower south of 38°N. It is found in spring between 53°00' and 24°44'N, in summer between 54°24' and 24°49'N, in autumn between 50°57' and 35°07'N, and in winter between 40°55' and 39°36'N. The temperature and salinity ranges are 4.5-16.5°C and 35.09-35.81%₀₀, respectively. Always found below 100 m and at daytime mainly below 300 m.
- (52) Aeginura grimaldii Maas, 1904 (fig. 45) (2480 spm) was found at daytime always below 500 m and at night only 5 specimens were collected above this level. In 5 daytime samples below 1000 m 27 specimens were found and in 4 night samples below 1000 m 77 specimens were collected. It is thus a deep-living species without normal diurnal vertical migration. The upper limit of vertical distribution seems to slope down from 40°N towards the south when the single shallow sample at station 85 trawl 15 is neglected. The species occurred along the entire transect 55°N-24°N in all seasons. The temperature and salinity ranges are 3.5-19.2°C and 34.75-3648⁰⁰, respectively.

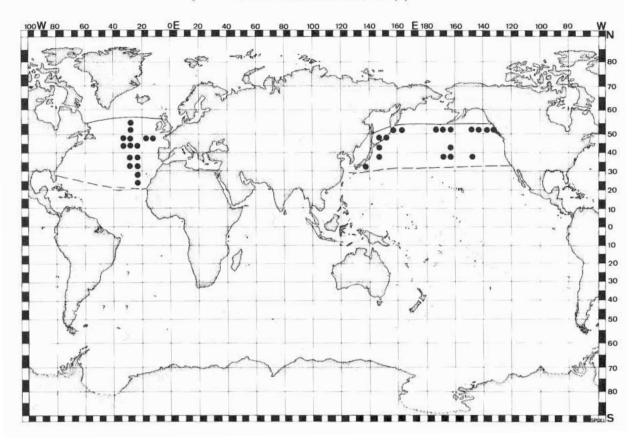


Fig. 42. Distribution of Aglantha digitale.

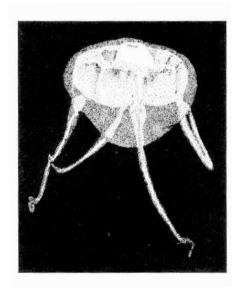


Fig. 43. Aegina citrea (after colour photograph) from station 39 trawl 14.

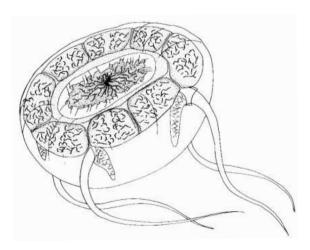


Fig. 44. Aegina citrea from station 84 trawl 37.

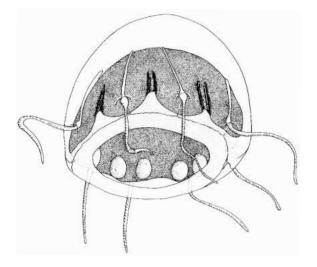


Fig. 45. Aeginura grimaldii from station 81 trawl 6

This species is widely distributed in all oceans (fig. 46) between 60°N and 50°S.

Family SOLMARIDAE

- (53) Solmaris flavescens (Kölliker, 1853) (fig. 47)
 (17 spm) is probably a diurnal migrant as all night samples were from depths of 40 to 115 m and the daytime samples from depths of 195 to 1000 m. It was collected in spring at 37°48'N, in summer at 29°56'N and in winter between 40°57'-30°N. The temperature and salinity ranges are 9.9-19.2°C and 35.69-36.00%, respectively.
- (54) Solmaris solmaris (Gegenbaur, 1856) (13 spm) was collected only in night samples at depths between 0 and 528 m during summer and winter, only south of 42°N. The temperature and salinity ranges are 13.0-20.3°C and 35.80-36.48‰, respectively.

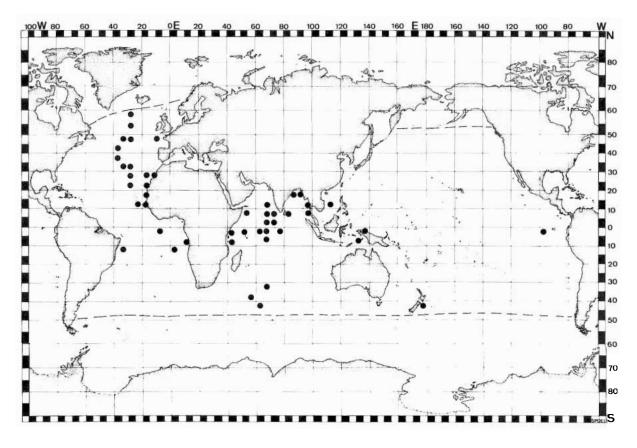


Fig. 46. Distribution of Aeginura grimaldii

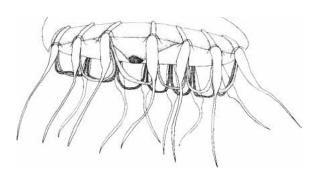


Fig. 47. Solmaris flavescens from station 987 trawl 25

- (55) Solmaris corona (Keferstein & Ehlers, 1861) (1 spm) was collected near the Great Meteor Bank (30°N) in a deep haul between 752 and 1005 m in summer. The temperature was 9.7°C and the salinity was 35.63%₀₀.
- (56) Pegantha laevis Bigelow, 1909 (80 spm) is clearly a vertical migrant as 65% of the population passes daily the 200-300 m depth stratum. It occurred at night between 0 and 500 m but at daytime it was only found in the 100-500 m layer as an upper mesopelagic species. Most records are from spring between 49°01′ and 32°07′N, while a few records in autumn were made between 50°49′ and 35°06′N. The temperature and salinity ranges are 10.9-17.5°C and 35.35-36.02‰, respectively.
- (57) Pegantha martagon Haeckel, 1879 (68 spm) was always more abundant in the night samples as compared to the day samples. Moreover, 8-16% of the population crosses daily the 200-500 m depth level so that vertical migration is tracable. The species occurred in spring and autumn only and was found between 41°31' and 24°48'N and between 37°05' and 25°10'N, respectively. The temperature and salinity ranges are 9.9-19.3°C and 35.53-27.23%00.
- (58) *Pegantha clara* Bigelow, 1909 (23 spm) shows vertical migration as all specimens collected at daytime were from below 200

m and those collected at night were from depths shallower than 200 m. The species was found in spring, summer, autumn and winter in low numbers at 38°00'N-29°48'N, at 44°59'N-41°01'N, at 47°49'N-28°03'N and at 40°55'N-30°02'N, respectively. The temperature and salinity ranges are 12.8-19.2°C and 35.35-36.29‰, respectively.

- (59) Pegantha rubiginosa (Kölliker, 1853) (3 spm) was found in summer and winter at 41°37′ and 29°59′N, respectively and at depths between 103 and 445 m. The temperature is 14.9°C and the salinity is 36.13‰.
- (60) Pegantha triloba Haeckel, 1879 (2 spm) was found only once in winter between 30 and 110 m at 30°02'N with a local temperature of 19.4°C. At this locality also Bougainvillia platygaster was found.

Pegantha spec. (141 spm) are probably damaged specimens of *P. laevis* or *P. martagon*. These specimens were most abundant in spring between $48^{\circ}59'N$ and $28^{\circ}20'N$ but they were also found in autumn between $45^{\circ}03'$ and $28^{\circ}07'N$ and in winter at $40^{\circ}56'N$. A strong migration seems present as 40% of the population crosses the 500 m level and 46% crosses the 100 m level daily.

Family CUNINIDAE

- (61) Cunina duplicata Maas, 1893 (2 spm) was found in summer at 41°39'N and 24°52'N; it was collected at night between 51 and 105 m and at twilight between 515 and 1000 m. The temperatures at these localities were 9.4°-15.4°C.
- (62) Cunina frugifera Kramp, 1948 (2 spm) was found only in summer at 41°34'N at 198-340 m. The local temperature and salinity are 14.2°C and 36.00‰.
- (63) Cunina peregrina Bigelow, 1909 (4 spm) was collected only in one haul of 40 to 115 m depth during winter at 30°02'N, temperature 19.2°C.
- (64) Solmissus marshalli Agassiz & Mayer, 1902 (fig. 48) (5 spm) is a shallow-living species,

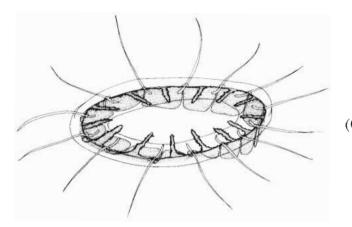


Fig. 48. Solmissus marshalli from station 87 trawl 1.

though considered by Kramp (1959) as deep-living, found between 0 and 200 m, in spring at $28^{\circ}20'$ N, in summer at $29^{\circ}59'$ N, and in winter at $29^{\circ}58'$ N. The temperature and salinity at depth are 19.2° C and $36.75\%_{00}$.

(65) Solmissus incisa (Fewkes, 1886) (65 spm) is a deep-living species (fig. 49). At night the whole population was found below 500 m but at daytime specimens are found as well between 30 and 100 m (1 spm), 200 and 300 m (2 spm), 300 and 400 m (4 spm) and between 400 and 500 m (4 spm), but most animals are from deeper strata. The species is found between 53° and 33°N in spring, between 54° and 24°N in summer, between 55° and 27°N in autumn, and at 30°N in winter. The temperature range is 3.5°-19.4°C and the salinity range is 34.75-35.87‰.

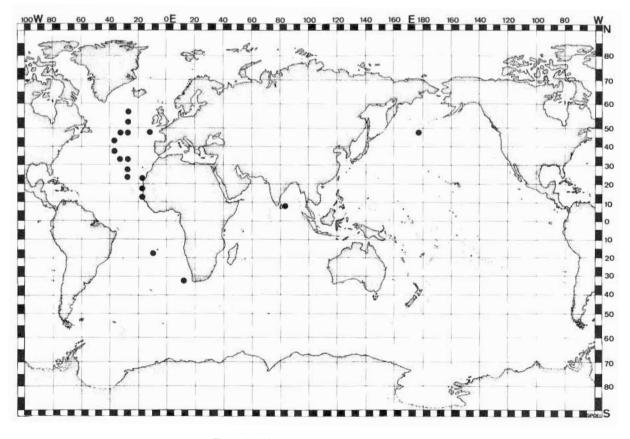


Fig. 49. Distribution of Solmissus incisa

TAXONOMIC NOTES

Sibogita geometrica Maas, 1905

The variability in this species is very large; for a discussion on the validity of the subsp. *occidentalis* Kramp, 1959 one is referred to Winkler (1982) and Van der Spoel & Bleeker (1988).

Crossota spec. (fig. 30)

The specimen from station 81 trawl 6 at 40°56'N between 500 and 1000 m was not attributed to one of the known species though its preservation was good. It had all the characters of the family Rhopalonematidae and of the genus Crossota. There are 8 radial canals in the specimen, the gonads are close to the stomach at the apical point of the canals and there are about 160 marginal tentacles. So the principle characters of C. rufobrunnea are present. The extreme length of the manubrium, reaching halfway the umbrella cavity and the very large oral lips do not occur in C. rufobrunnea, however. As different contractions during fixation preservation may strongly and affect manubrium length, no new species for the present specimen is proposed, the more so as no other discrimating characters have been found.

Oceania tydemani n. sp. (fig. 7)

Description: Umbrella 8 mm in diameter and 5 mm high, manubrium 3 mm in diameter. The medusa is flatly topped. The jelly is thin. Gonads adradial on stomach wall; as they are not fully developed they are seen as small warts only. There is a short peduncle without vacuoles. The manubrium is broad and half as long as the umbrella cavity, quadrangular in cross section. The four lips are only partly lined with nematocysts as the interradial area is lacking nematocysts. There are four simple narrow radial canals. Adaxial ocelli present. No statocysts. The velum is broad. There are 180 solitary marginal tentacles placed in a double, zigzag row.

Holotype: ZMA coll. no. Coel. 5598; 101A project station 48 trawl 13.

Type locality: 34°11.4'N 31°11.3'W, 60-100 m, temperature 18.7°C, 23-IX-1981, daytime sample.

Etymology: The name is given after the oceanographic research vessel H.M.S. "Tydeman", the platform for the 101A project cruises.

The most closely related species is O. armata, but it differs as the lining of the lips with nematocysts is continuous, and the number of tentacles is only up to 100. The discontinuous lining with nematocysts is not in agreement with the diagnosis of the family (Kramp, 1959), but the other characters of the specimen are evidently showing that it belongs to the genus Oceania and family Clavidae.

Annatiara lempersi n. sp. (fig. 13)

Description: Umbrella bell-shaped, 8 mm high and 16 mm in diameter, the jelly is thick and there is no apical projection, exumbrella with nematocyst tracks at each tentacle. Velum small. Stomach short, four-sided but not attached to subumbrella as described for A. affinis, the radial canals do reach only halfway the umbrella and in between the tops of the canals a square is formed by the stomach walls so that the stomach is expanded interradially. The musculature in the umbrella is intact and not distorted so that the configuration of the stomach can not be due to damage. Mouth with strongly folded lips. The four radial canals run from the perradial corners of the interradial square of the stomach to the ring canal. The gonads are probably not yet fully developed, they line the stomach as strongly folded bands. There are 24 hollow smooth marginal tentacles, which are typically curled in the preserved specimen; no abaxial spurs, only a small basal swelling present. One small rudimentary tentacle between each two normally developed tentacles. Abaxial ocelli present on all tentacles.

Holotype: ZMA coll. no. Co. 5932; 101A project station 84 trawl 36.

Type locality: 35°1.0'N 31°30.9'W, 300-400 m, temperature 12.65°C, 6-VI-1983, dusk sample.

Etymology: The name is given in honour of the commander of H.M.S. "Tydeman", KLTZ Ir. A. P. H. M. Lempers.

The most closely related species is Annatiara affinis from which it differs in having only 24 tentacles (28-44 in A. affinis, 32 in the material of station 87), a stomach attached along an interradial square (along a perradial cross in A. affinis).

FAUNAL BORDERS

Winkler (1982) found a faunal boundary zone for epi- and mesopelagic Hydromedusae at 38°-40°N. The latitudinal occurrence of all species is given in fig. 50.

Especially for the spring cruise (1980) (cf. Winkler, 1982) but also for the summer cruise (1983) a faunal border was found near 40° - $42^{\circ}N$. The autumn cruise did not show clear transitions to be based on first and last occurrence of taxa, and the winter cruise made too few stations to use this method. The summer cruise showed high numbers of first and last occurrence at 45° , 42° , 35° , and $30^{\circ}N$.

Mathematically the investigation of first and last occurrence can be refined. However, this and many other methods to detect faunal borders or significant differences between samples are mainly based on statistical methods. For biology, however, it seems appropriate to develop a method based on biological principles.

One can start with the theoretical assumption that species have no value for a sample when they do not contribute to the diversity of the sample and when they do not determine the sample's quality by their dominance. The importance of the species for a sample is thus greater when its distance to the point where its dominance value and its diversity value are zero is greater. This can be expressed in the formula:

$B = \sqrt{(D^2 + C^2)}$

B = the computed value of the species for the sample in which it is present, or the specific loading; C = the value a species adds to the quality of the sample by its dominance; D = the value a species adds to the quality of the sample by its contribution to the diversity.

The dominance value (C) of a species in a specific sample is dependent on the number of specimens relative to the abundance of that species in other samples and on the total number of species in the sample relative to that number in other samples. The following formula is proposed to express the dominance value:

 $C = 100 \times (F \cdot N \cdot \Sigma N)/(F \cdot N_{max} - \Sigma N) \times F/F_{max}$ F = number of species in the sample; N = number of specimens of the species in the sample; $N_{max} =$ number of specimens of the most abundant species in the sample; $F_{max} =$ number of species in the most diverse sample.

The diversity value (D) of a species in a specific sample is likewise dependent on the number of specimens in the sample, but relative to the number of samples in which the species is found and relative to the number of species found in other samples. The following formula is proposed to express the diversity value:

 $D = \sqrt{(1 + A_{max} - A)^2} \times (1 + M - A) \times N$

M = total number of samples in the study; A = number of samples in which the species is found; A_{max} = maximum value for A for the series of samples studied.

The total abundance and diversity of a sample, the sample loading, is the sum of all the specific loadings of one sample. The greater the difference of ΣB of two samples, the greater are the differences in abundance, dominance and diversity of the samples.

The ΣB for a hypothetical series of samples and species is given in table I.

In the equation $\Sigma B = \Sigma \sqrt{(D^2 + C^2)}$ diversity value (D) has a much greater influence on the value of ΣB than the dominance value has, so in the comparisons also $\Sigma \sqrt{C^2}$ is used separately.

The results of this method for the North Atlantic Medusae are shown in figs. 51-54. In spring (1980) (fig. 51) Σ B is on the average much larger north of 40°N than to the south of that latitude. Between 38°N and 42°N the $\Sigma\sqrt{C^2}$ is much larger than at other localities. So

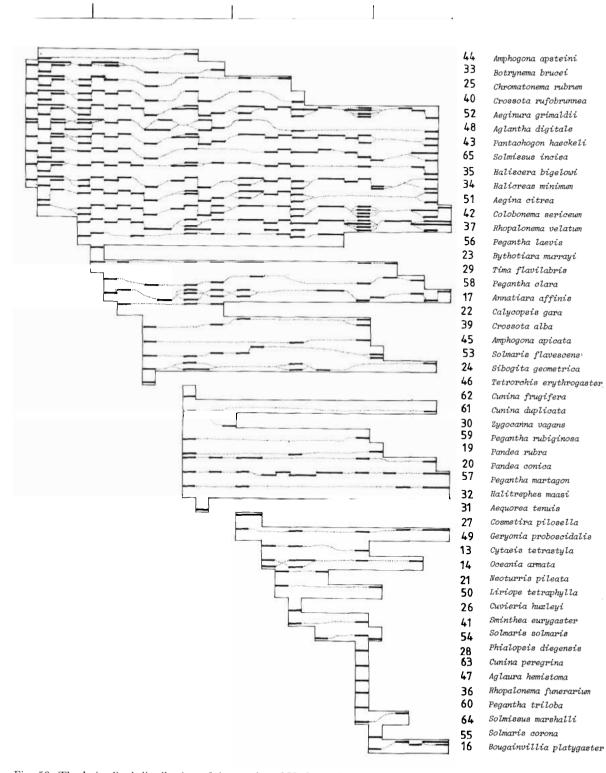


Fig. 50. The latitudinal distribution of the species of Hydromedusae. Along the horizontal axis degrees north, along the vertical axis the species. For each species a bar is used in which a dotted line connects the thick lines, indicating presence, situated: for spring in the top, for autumn above the centre, for winter under the centre and for summer at the bottom of each bar.

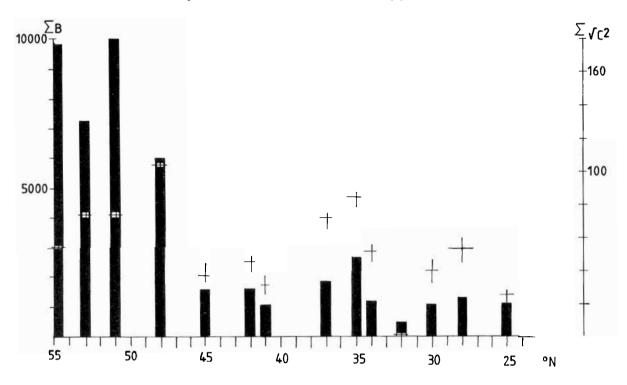


Fig. 52. Diversity abundance analyses for the samples of the 1981 cruise, for explanation see fig. 51



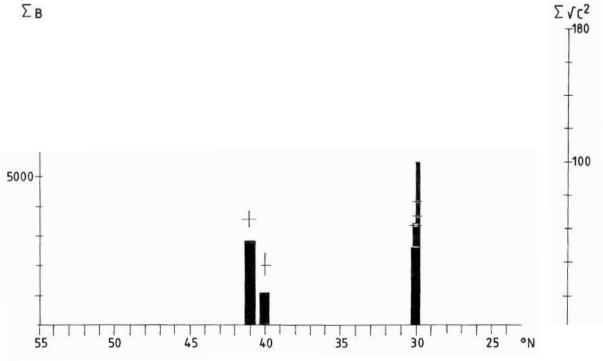


Fig. 53. Diversity abundance analyses for the samples of the 1982 cruise, for explanation see fig. 51.

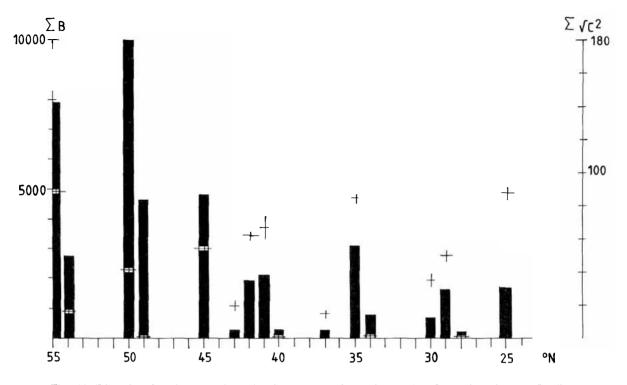


Fig. 54. Diversity abundance analyses for the samples of the 1983 cruise, for explanation see fig. 51

The abundances in spring, autumn, and summer are comparable, though in spring the area south of 40°N shows somewhat higher values. In winter (fig. 53) the ΣB values near 41°N are lower than in summer and autumn, near 30°N the ΣB values are evidently higher than in the other seasons.

As a conclusion it can be stated that the subpolar fauna penetrates in spring southwards to about 40°N and retracts to 50°N in summer, in autumn it again spreads southwards to 48°N and in winter it shows its lowest abundance. In summer the subtropical fauna is most evidently present probably by northward penetration to about 35°N. This pattern deduced from Hydromedusae of the upper 1000 m of the water column is also shown by Radiolaria from the upper 5 m of the water column (Van der Spoel, 1987b).

Chromatonema rubrum is mentioned as a species sensitive to seasonal changes. It is not a temperate species (fig. 22) though it behaves like such a type of element in the North Atlantic. Its seasonal migration consists of withdrawal to colder waters either to the north or to the depth.

BATHYMETRIC DISTRIBUTION

Most bathypelagic eurybathypelagic and species occur in all seasons along the entire transect of the cruise. Exceptions are Paraphyllina ransoni that is only found in summer, Halitrephes maasi that is only found in spring and the bathypelagic species that do not occur south of 42°N: Haliscera bigelowi, Chromatonema rubrum, and more explicitly Botrynema brucei and Aglantha digitale, both species of the higher latitudes showing strong subtropical submergence.

Aeginura grimaldii is also a species with subtropical submergence but as it is frequently recorded from lower latitudes, which is not the case in Aglantha digitale, it is probably sinking to a less deep submergence in the tropical region.

TABLE II

Latitudinal and seasonal differences in distribution, with the division into four ecological groups.

Species	>42°N				<4	2°N		Ecology				
1	Sp	Su	Au	Sp	Su	Au	Wi	Ba	Di	Eu	Ep	*)
Periphylla periphylla	x	x	x	x	x	x	x	x		·		
Atolla vanhoeffeni	х	x	х	х	х	х	х	х				
Atolla parva	x	х	x	х	x	х	х	x				
Atolla wyvillei	x	x	x	x	x	x	x	x				
Annatiara affinis	x	x	x	x	x	х	x		x	x		**)
Halicreas minimum	x	x	x	x	x	x	x	x		,)
Pantachogon haeckeli	x	х	x	х	x	x	х	х	x			
Colobonema sericeum	x	x	x	x	x	x	x	x				
Rhopalonema velatum	x	x	x	x	x	x	x			x		
Aegina citrea	x	x	x	x	x	x	x	x	x			
Aeginura grimaldii	x	x	x	x	x	x	x	x				
Solmissus incisa	x	x	x	x	x	x	x	x		·		
Haliscera bigelowi	x	x	x	x	x	x			•	x	•	**)
Crossota rufobrunnea	x	x	x	x		x		x	•		•	/
Aglantha digitale	x	x	x	x	· x		x		•	x	x	**)
Chromatonema rubrum	x	x	x	x	л			· x	•	л	л)
Botrynema brucei	x	x	x	л	•	·	x	x	·	•	•	
Pegantha laevis				· x	•	· x	^		· x	•	•	
Pegantha martagon	x	•	x		•		•			•	•	
Pegantha clara	х	•	x	x	•	x	•	•	x	•	•	
Pelagia noctiluca	•	x	x	х	X	х	x	•	х	•	v	
Amphogona apsteini	•	x	x	•	х	•	х	•	•	·	х	****)
	•	x	х					x ?	·	•	•)
Nausithoe atlantica	х	•	•	x	·	•	х	1	•	•		
Pandea conica	х	·	·	x	•	х	·		х	•	x	
Zygocanna vagans	х	·	•	x	х	•	•	•	•	•	x	
Tima flavilabris	х	•	•	х	•	·	•	•	x	•	х	
Halitrephes maasi	х	·	•	х	•	•	•	х	•	ว	•	* *)
Bythotiara murrayi	х	•	•					•	•	;	·	**)
Calycopsis gara	х	•	•	х	•	•	•	•	•	•	х	
Paraphyllina ransoni	•	х	•	•	х	•	•	х	•	•	•	* * \
Crossota alba	•	х	•					•	·	х	•	**)
Amphogona apicata	•	х	•	•	х	•	х	х	•	•	•	<i></i>
Sminthea eurygaster	•	х	•	•	х	•	х	•	•	3	•	**)
Sibogita geometrica	•	х	•	Х	х	х			X	•	•	
Solmaris flavescens	•	х	•	х	х	•	х		х	·	·	
Bougainvillea platygaster				х	•	х	х	•	х	•	•	
Pandea rubra		•		х	•	•	х	•	•	•	х	· **)
Geryonia proboscidalis				х		х		•	?	•	•	
Solmissus marshalli	•	•	•	х	х	•	х	·	•	•	х	***)
Pegantha rubiginosa				•	х	•	х	•	•	?	•	
Solmaris solmaris				•	х	•	х	•	х	•	•	
Oceania armata					х	x		•	•		х	
Cytaeis tetrastyla				•	•	х	х	•			?	
Deepstaria enigmatica	,			х			•	х		•	•	
Neoturris pileata				х					?			
Cosmetira pilosella				х					х			
Liriope tetraphylla				х							х	
Aequorea tenuis					х		•	?				
Cunina duplicata					х					•	5	
Cunina frugifera					x						?	
Solmaris corona					х			?				

Species	>42°N			<42°N				Ecology				
	$_{\mathrm{Sp}}$	Su	Au	Sp	Su	Au	Wi	Ba	Di	Éu	Ep	*)
Porpita porpita						х				x		
Cuvieria huxleyi						х	-				?	
Rhopalonema funerarium							х			?		**)
Aglaura hemistoma							х				?	,
Phialopsis diegensis							х				?	
Pegantha triloba							х				?	
Cunina peregrina							х				х	

Table II (contination)

*) Au = autumn, Ba = bathy- and/or mesopelagic, Di = diurnal migrant, Ep = epipelagic, Eu = eurybathic, Sp = spring, Su = summer, Wi = winter. **) According to Kramp these species are bathypelagic. ***) According to Kramp this species is eurybathic. ****) According to Kramp this species is a surface form.

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