

Bathymetric Distribution of Chaetognatha, Siphonophorae, Medusae, and Ctenophorae off San Diego, California¹

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THE SAMPLES STUDIED were obtained at various depths with the BONGO or BMOC open-closing paired zooplankton net (McGowan and Brown, 1966), at 30°30'N, 120°00'W, from 27 August to 8 September 1965.

These collections were taken during night hours (27 August to 8 September 1965), and daylight hours (30 August to 5 September 1965). Quantitative data for each of the species were determined for each of the nets (left and right) for collections at the various strata surveyed; and variations in the number of specimens and in the species were observed at times in the same haul for the samples from the left and right nets. Diagrams were made showing the qualitative and quantitative distribution of the species in the two nets for each of the stratified hauls. However, in the final diagrams the medians for both left and right samples were plotted for each of the stratified hauls.

The data from the collections made at different times and depths during the same half day (dark or daylight) were plotted together. Since the hauls for the same half of the day were made on different dates (there was a lapse of time from one haul to the other), it is obvious that changes might take place at times, either in the depth at which the various species were found or in the quantity of individuals obtained.

In the case of the siphonophores, the nectophores of a physonectes appeared in either the right or left net and in the other net the

pneumatophores with the nectosoma and siphosoma attached. Similarly, in other cases, one of the paired nets contained the bract or the superior nectophore and the other net the gonophores or the inferior nectophore of the eudoxid or paragastric forms of the Diphyidae.

The quantitative distribution of Chaetognatha and Medusae are noted in the diagrams; but in the case of the Siphonophorae, although data on the number of superior and inferior nectophores, gonophores, bracts, pneumatophores, etc. were obtained, because of the peculiar anatomical structure of these organisms it was not convenient to attempt a quantitative representation. In the case of the Monophyiidae and Diphyidae, for instance, it will be easy to establish the number of individuals present from the part obtained in the sample, but this is not so for the Physophorae and Hippopodiidae. Therefore, only the qualitative distribution of the siphonophores was considered in preparing the final diagrams.

During each tow about 10,000 m³ of water were filtered through the net; thus the samples were directly and quantitatively comparable.

Collections were made at the following depths (in meters):

NIGHT	DAYLIGHT
100-10	110-0
100-20	350-250
300-235	460-0
460-410	525-401
500-420	1720-1340
620-530	2300-1880
775-685	2630-2210
840-690	3040-2620
1030-860	
1040-890	
1242-1090	
1710-1450	
2020-1800	
2170-1950	
2320-2100	
2460-2100	

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Several gaps in the bathymetric distribution are obvious, since collections were not obtained at some strata. The most important sampling gap was in the daylight series, of about 800 m (1340–525 m), which interrupts the data on the bathymetric distribution. This lack of data, and the one haul from 460 m to the surface during the daylight series (considered only for the siphonophores), do not permit the location of the upper or lower limits of the distribution of several species.

Quantitative data were obtained by the method explained by Alvarino (1965c and 1966a).

The bathymetric zones considered are: epiplanktonic (upper 200 m), mesoplanktonic (200–1000 m), bathyplanktonic (below 1000 m). The vertical division into zones cannot be static, however, because the stratification of the organisms is controlled by bio-physico-chemical factors.

CHAETOGNATHA

Figures 1 and 2 show the quantity of each of the species found and their distribution for the day and night series, respectively.

The epiplanktonic species observed here were: *Krohnitta subtilis*, *Pterosagitta draco*, *Sagitta bierii*, *S. bipunctata*, *S. enflata*, *S. euneritica*, *S. hexaptera*, *S. minima*, *S. pacifica*, *S. pseudoserratodentata*, and *S. scrippsae*. A typical mesoplanktonic species, *S. decipiens*, also was present in the upper 100 m, but extended to 620 m depth.

Other species characteristic of the mesoplanktonic levels which extended their distribution into the bathypelagic domain were: *S. maxima*, *S. macrocephala*, and *S. zetesios*. The bathyplanktonic species reaching various levels of the mesoplanktonic zone were: *Eukrohnia bathypelagica*, *E. fowleri*, and *E. hamata*.

During the nighttime collections, *K. subtilis* and *S. scrippsae* did not appear in the upper 100 m, but did appear at 500–235 m and 460–235 m, respectively. *S. pacifica* was absent from any level.

The species present in the upper 100 m layers for both night and daylight series, *S. bierii*, *S. decipiens*, *S. euneritica*, and *S. pseudoserratodentata*, were more abundant at night

than during daylight, whereas *S. minima* was more abundant during the day, and the others appeared within the same range of abundance for both periods.

The species spreading from the surface to 300 m depth during daylight were *S. euneritica* and *S. pacifica*, and at night, *S. enflata* and *S. hexaptera*, the latter appearing down to 525 m in the daytime.

Sagitta bierii populated the upper 100 m down to 500 m during both day and night, showing the greatest concentration in the upper 100 m and the lowest between 400 and 500 m at night, whereas during daylight the distribution was homogeneous along the layers it populated; but *S. hexaptera* presented the highest concentration from 300 to 235 m at night, and was homogeneous at daylight down to 525 m depth. *K. subtilis* extended during daylight from the surface to 525 m, with higher concentrations in the upper 100 m, whereas at night it was present only between 235 and 500 m.

The presence of *S. decipiens* in the upper 100 m both at night and by day appears to indicate that upwelling phenomena took place at this location. Two specimens of *S. decipiens* were observed in the left net for the tow from 2630 to 2210 m, and two specimens in the right net from 3040 to 2620 m during the day series. These showed evidence of contamination, however, and were omitted from the figures.

S. scrippsae extended during daylight from the surface to about 500 m, with maximum concentration at 350 to 250 m. At night it extended only from 235 to 460 m, with maximum concentration between 300 and 235 m.

The influence of light in the bathymetric distribution could be understood when observing the vertical distribution of *S. bierii*, *S. decipiens*, *S. euneritica*, and *S. pseudoserratodentata*. However, if the factor of light is responsible for the vertical migration of these organisms, it fails to explain the distribution of *K. subtilis*, *S. enflata*, *S. maxima*, and *S. scrippsae*.

Therefore, the factors influencing the vertical distribution and displacements of the species of chaetognaths may be of various kinds, and interacting: light, temperature, oxygen,

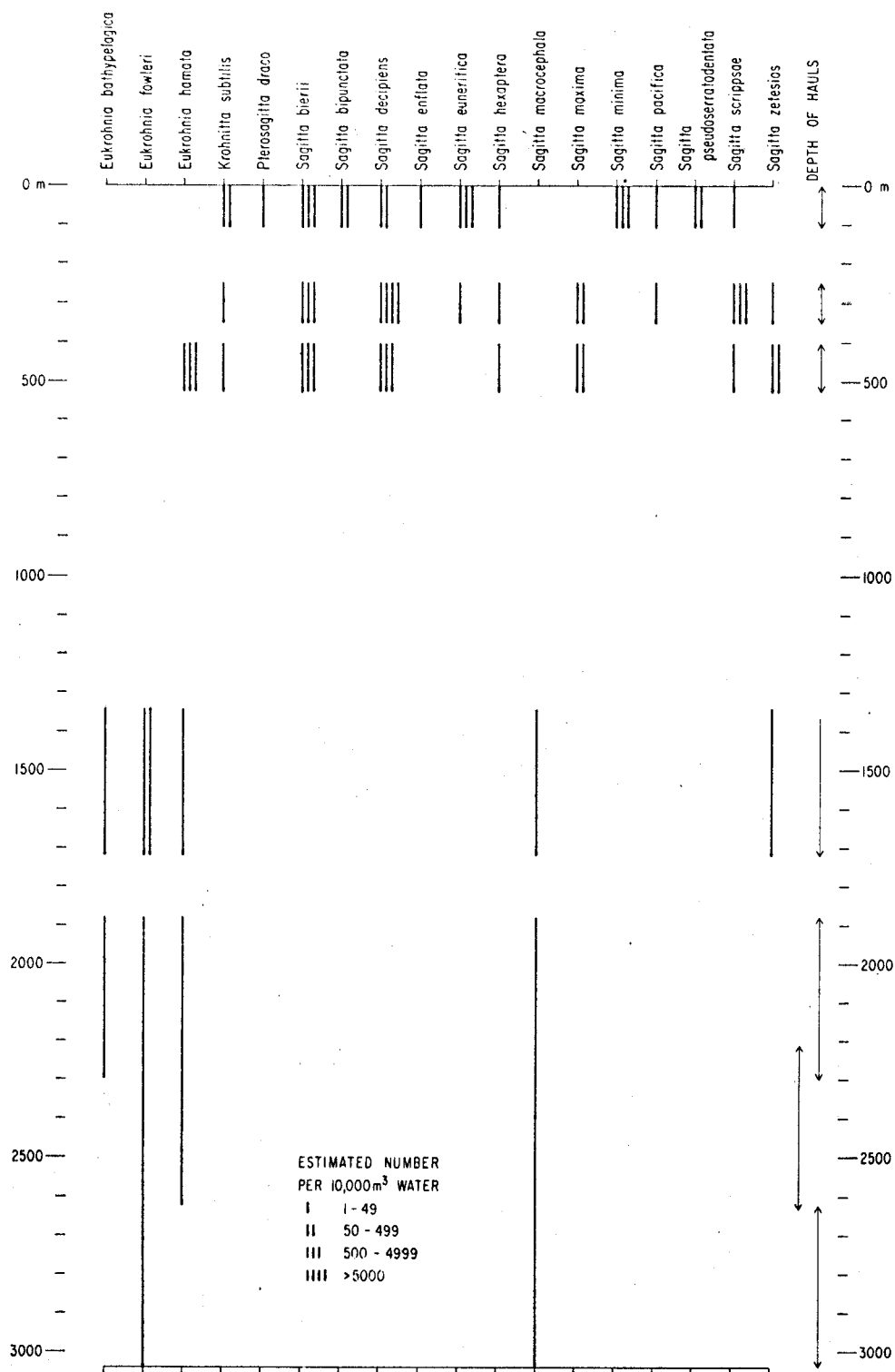


FIG. 1. Bathymetric distribution of Chaetognatha during the daylight series.

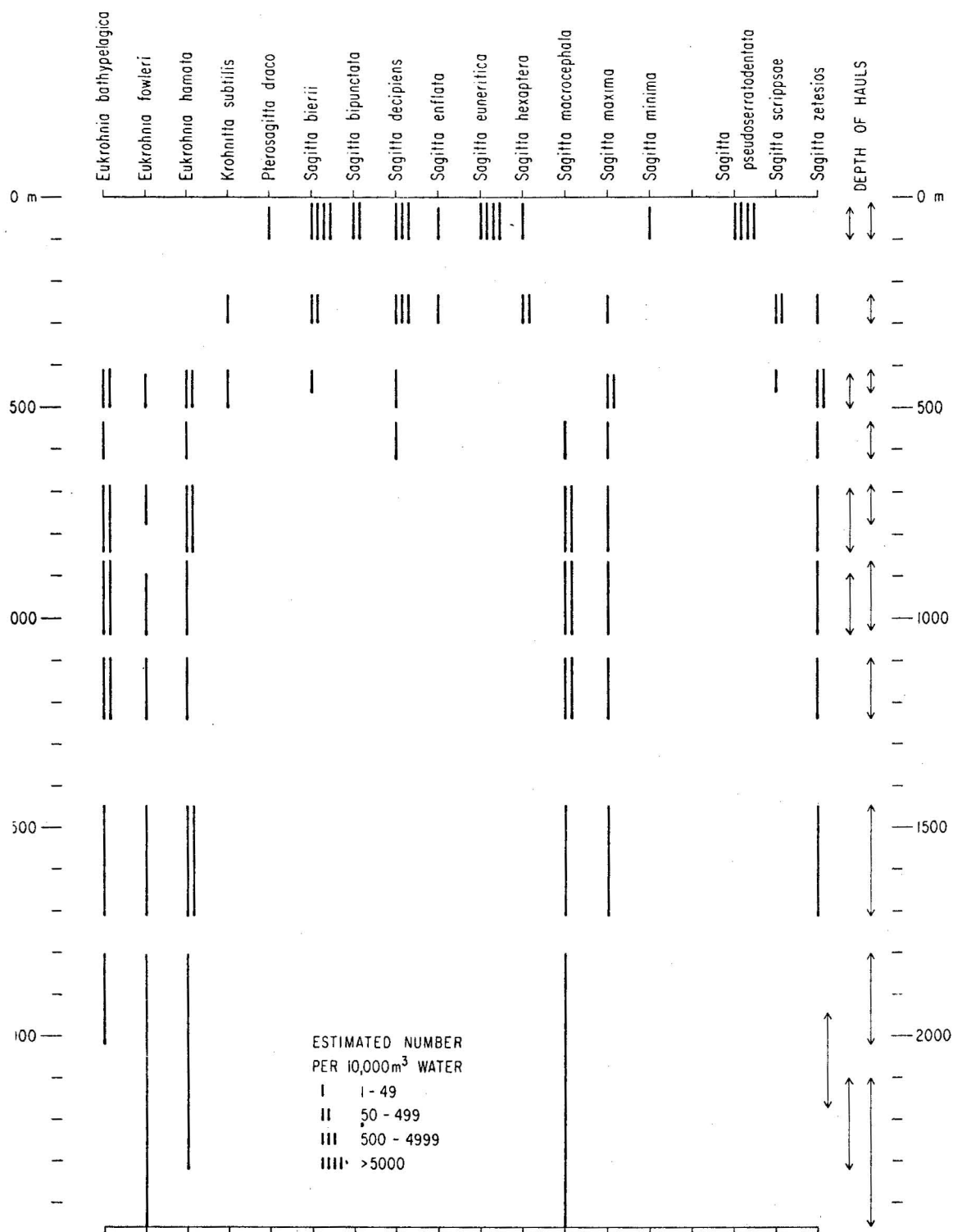


FIG. 2. Bathymetric distribution of Chaetognatha during the night series.

food, hydrostatic pressure, and bio-physico-chemical interrelations with other organisms of the pelagic realm. Also to be considered is the structure of the population, since young individuals appeared to be at levels closer to the surface than were adults (Alvariño 1964a, 1965a).

SIPHONOPHORAE

A greater number of species was observed in the upper 100 m in the daylight series than in the night (Figs. 3 and 4). The species observed in the upper 100 m for both series were *Muggiaea atlantica*, *Chelophyes appendiculata*, and *Eudoxoides spiralis*. These were joined in daylight by *Eudoxia russelli*, *Lensia hotspur*, *L. subtiloides*, *Amphicaryon acaule*, and *Stephanomia bijuga*, and only by *A. ernesti*, *L. multicristata* (extending also to the mesoplanktonic levels), and *Nectodroma reticulata* at night. The last two inhabited the mesoplanktonic domain in daylight.

The daylight haul from 460 to 0 m was included in the diagrams for the siphonophores only, to show the presence of several species at those levels. However, the bathymetric limits cannot be determined for some species; thus, the upper limit of the daylight distribution for *Chuniphyes moserae*, *Ch. problematica*, and *Heteropyramis maculata*, and both upper and lower limits for *L. challengerii* and *Nectodroma dubia*, are not yet established.

The mesoplanktonic species appeared in higher numbers at night than in daylight. Typical mesoplanktonic species such as *L. ajax*, *L. conoidea*, *L. grimaldii*, *Bargmannia elongata*, *Stephanomia rubra*, *Physophora hydrostatica*, and *N. dubia* were not observed at night; and *Nectopyramis diomedea*, *N. thetis*, and *N. natans* were not observed in daylight. Species appearing in the mesoplanktonic levels at night which extend to deeper layers at daylight were *L. achilles*, *Vogtia kuruae*, and *Rosacea plicata*. *Dimophyes arctica* was obtained in the mesoplanktonic levels at night and only at the bathyplanktonic zone during daylight.

Species occupying both meso- and bathypelagic regions were *Ch. multidentata*, *Ch. moserae*, *Ch. problematica*, *Clausophyes galeata*,

Crystallophyes amigdalina, *Heteropyramis maculata*, *L. achilles*, *L. hostile*, *L. lelouvetean*, *L. reticulata*, and *Nectodroma reticulata* (in daylight).

Species observed at the bathyplanktonic levels only were *Clausophyes ovata*, *Ceratocymba dentata*, and *L. havock*.

One specimen of *Velella* (longest axis 70 mm, and sail oriented NW-SE) was obtained with a dip net, 8 September 1965.

One complete colony of *Physophora hydrostatica* was obtained in daylight at depths of 350-250 m.

MEDUSAE

Higher numbers of species were observed during the night series than in the daytime (Figs. 5 and 6). *Liriope tetraphylla* was the only species found for both series in the upper 100 m, presenting a higher number during daylight. *Sibogita geometrica* and *Cunina peregrina* were observed only at night and in the upper 100 m. *Phialidium discoidum* and *Crossota alba* were observed during daylight in these upper strata, and extended from 685 to 1030 m at night.

The mesoplanktonic species were *Sarsia cocometra*, *Zanclea costata*, *Pandea violacea*, *Heterotiara anonima*, *Colobonema sericeum*, *Crossota alba*, *C. brunnea* (extending deeper at night), and *C. pedunculata*.

Species populating both the meso- and bathypelagic levels were *Halicreas papillosum*, *Atolla wyvillei*, and *Periphylla hyacinthina* (observed only at night).

Medusae observed exclusively at the deepest levels were *Homeonema alba*, *Aegina citrea*, and *Nausithoe rubra*.

The medusae showed some degree of stratification related to the size of the specimens; thus individuals of *A. wyvillei* 12-30 mm in diameter appeared at 300-235 m, whereas specimens 75 mm in diameter were found at 1710-1450 m. However, specimens up to 100 mm in diameter were obtained in the 620-530 m level. The size-stratifications for this species appeared to be more clear-cut during the daylight series, when individuals 7-20 mm in diameter appeared in the 460-410 m level, and those 30-60 mm in diameter at 1720-1340 m.

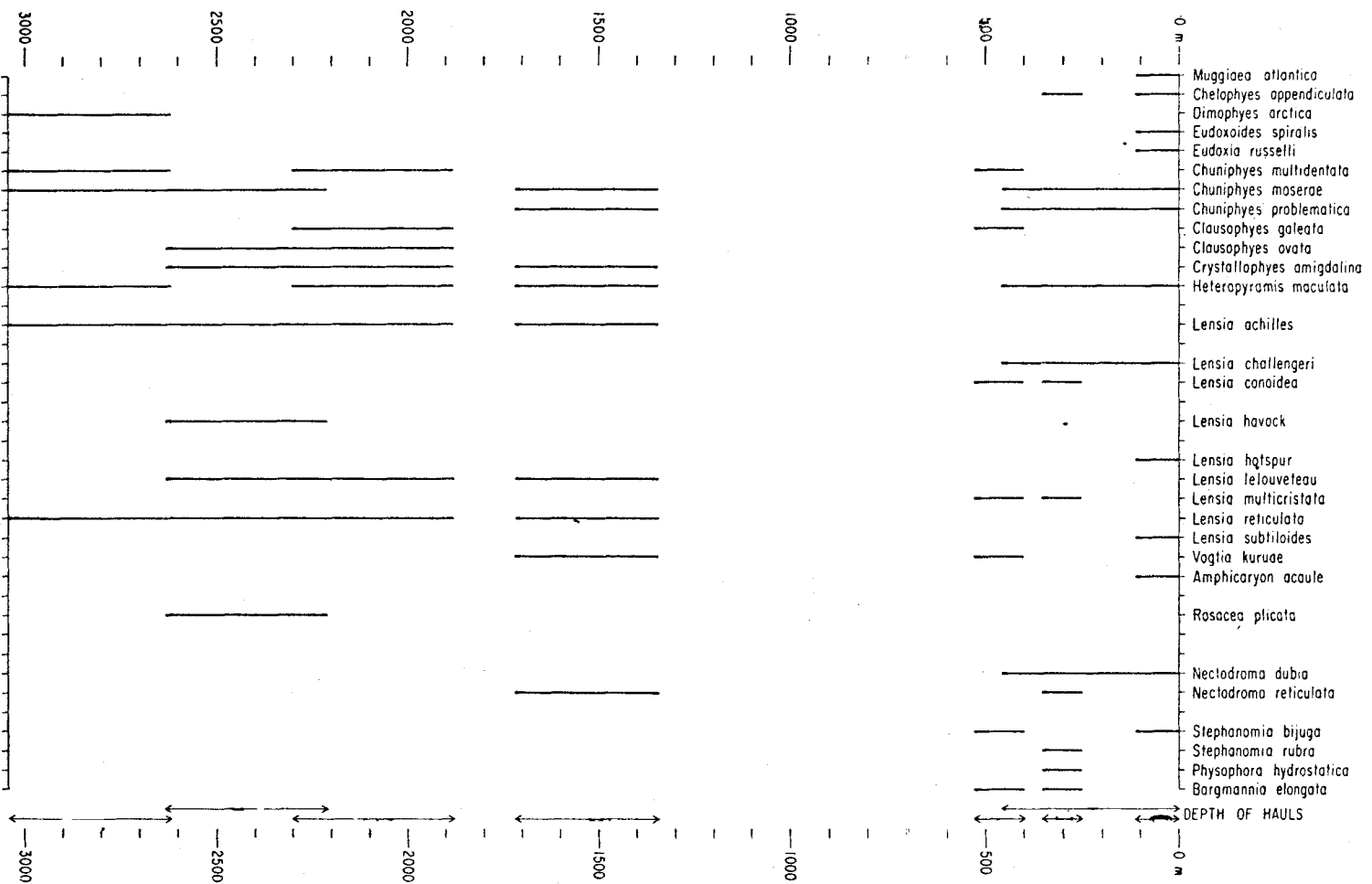


Fig. 3. Bathymetric distribution of Siphonophorae during the daylight series.

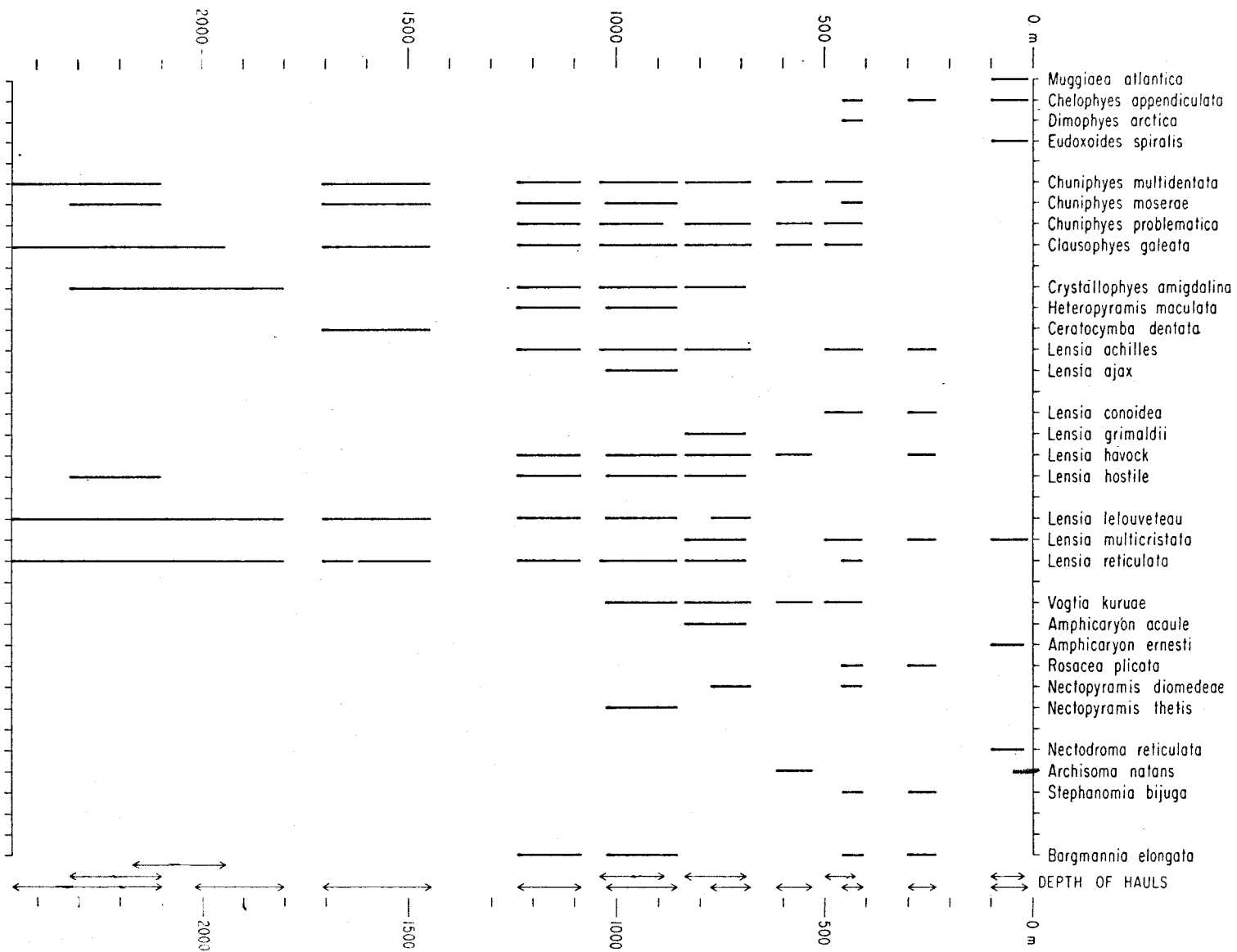


Fig. 4. Bathymetric distribution of Siphonophorae during the night series.

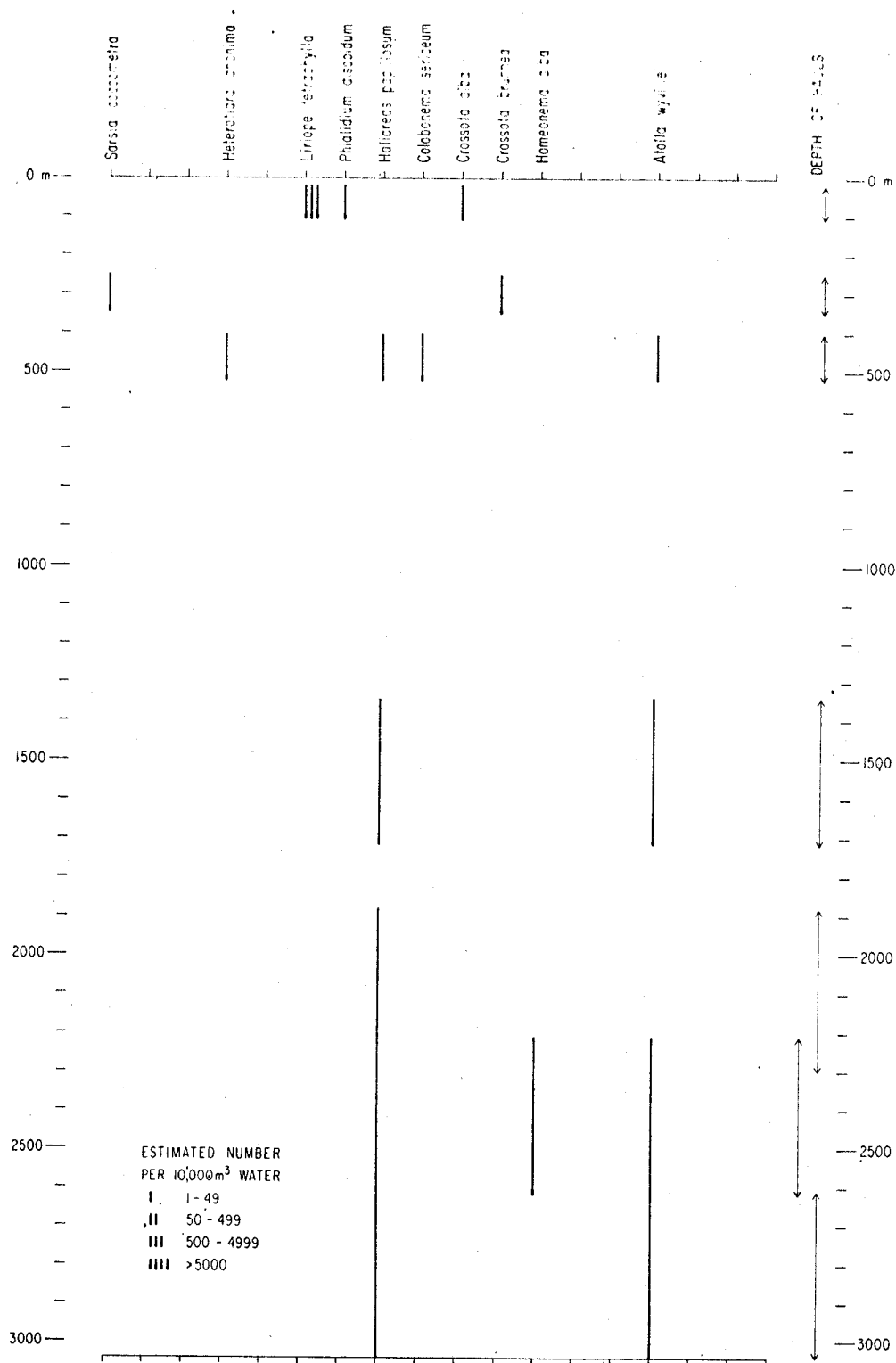


FIG. 5. Bathymetric distribution of Medusae during the daylight series.

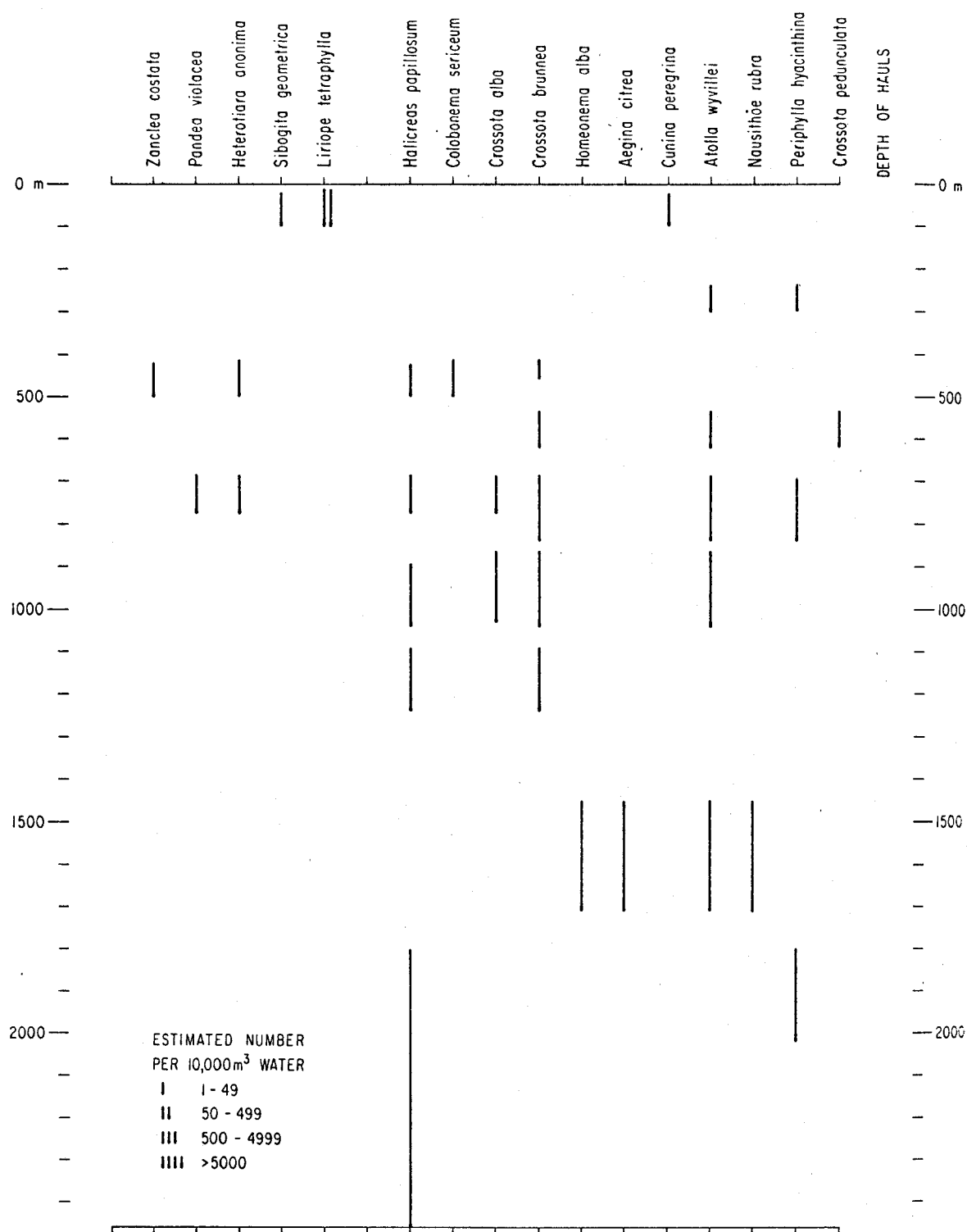


FIG. 6. Bathymetric distribution of Medusae during the night series.

Halicreas papillosum 30 mm in diameter were present at 775–685 m, and those 50 mm in diameter at 1242–1090 m. Specimens of *Periphylla hyacinthina* up to 25 mm high appeared at 300–235 m, whereas at 840–690 m they were 35 mm high. *Colobonema sericeum* up to 40 mm in height were found at 460–410 m, and below this level those 50 mm in height.

CTENOPHORAE

Beroe spp. extended in the night series from 10 m (uppermost sampling) to 500 m, and during daylight from 0 to 525 m.

CONCLUSIONS ON BATHYMETRIC DISTRIBUTION

Several striking features were observed in the bathymetric distribution:

1. The number of species of Chaetognatha and Siphonophorae in the upper 100 m was higher during daylight than at night.

2. The number of specimens for the species of Chaetognatha present both in daylight and at night in the upper 100 m was either of the same numerical magnitude or, in most cases, higher at night.

3. In general, the difference in the number of specimens observed in the right and left net for the upper 100 m was greater during daylight than at night.

Points 1 and 3 suggest either that during

daylight the patches of specimens are denser, or that at night the individuals are scattered throughout a bigger region, thus providing fewer individuals per cubic unit of water. This conclusion appears to be in contradiction with established statements, which maintain that planktonic organisms congregate more at night than in daylight. Another possibility is that they can avoid the net better in daylight than at night. The sky condition at night, when the hauls were taken, was one of darkness, without moonlight; but there are no data on bioluminescence.

Therefore, these preliminary studies appear to indicate that individuals are not evenly distributed, but that there is a small pattern of patchiness included in the total region populated by certain species. By using the paired net it will be possible to detect either this patchiness within the distributional region of the species, or the flocking of individuals when disturbed (a general behavior response observed in nature).

DISTRIBUTION OF THE ORGANISMS AND THE POSITION OF THE SCATTERING LAYER

Unfortunately, samplings were not made at depths at which the scattering records appeared. However, they could be determined easily by correlating records and samples taken at the same time and date. For example, at 1238–

TABLE 1
SPECIES IN THE UPPER 110 M CORRELATED WITH THE SHALLOWER SCATTERING (DAYLIGHT)

GROUP	CONCENTRATION OF INDIVIDUALS PER 10,000 M ³ OF WATER FILTERED			
	GREATER THAN 5,000	4999–500	499–50	LESS THAN 50
Chaetognatha	<i>S. bierii</i>	<i>S. minima</i>	<i>K. subtilis</i>	<i>P. draco</i>
		<i>S. pseudoserratodentata</i>	<i>S. bipunctata</i>	<i>S. hexaptera</i>
			<i>S. decipiens</i>	<i>S. pacifica</i>
			<i>S. enflata</i>	<i>S. scriptpsae</i>
			<i>S. euneritica</i>	
Siphonophorae			<i>M. atlantica</i>	<i>E. spiralis</i>
			<i>E. russelli</i>	<i>L. subtiloides</i>
			<i>Ch. appendiculata</i>	<i>A. acaule</i>
			<i>P. reticulata</i>	<i>St. biiu</i>
Medusae		<i>L. tetraphylla</i>		<i>P. discoidum</i> <i>C. alba</i>
Ctenophorae				<i>Beroe</i> spp.

TABLE 2
SPECIES IN THE 350-250 M LAYER, PARTIALLY COINCIDENT WITH THE
DEEPEST SCATTERING RECORD (DAYLIGHT)

GROUP	CONCENTRATION OF INDIVIDUALS PER 10,000 M ³ OF WATER FILTERED			
	GREATER THAN 5,000	4999-500	499-50	LESS THAN 50
Chaetognatha	<i>S. bierii</i>	<i>S. scrippsae</i>	<i>S. maxima</i>	<i>K. subtilis</i>
	<i>S. decipiens</i>			<i>S. bipunctata</i>
				<i>S. euneritica</i>
				<i>S. hexaptera</i>
				<i>S. minima</i>
				<i>S. pacifica</i>
				<i>S. zetesios</i>
				<i>Ch. appendiculata</i>
Siphonophorae				<i>L. multicristata</i>
				<i>L. conoidea</i>
				<i>N. dubia</i>
				<i>St. rubra</i>
				<i>Ph. hydrostatica</i>
Medusae				<i>B. elongata</i>
				<i>S. cocometra</i>
				<i>L. tetraphylla</i>
				<i>C. alba</i>
				<i>C. brunnea</i>

1550 hours on 5 September 1965, bright and sunny with calm sea, scattering layers appeared at 91 m, 200 m, and 345 m. The species observed coincidentally are detailed in Tables 1 and 2.

The nighttime scattering layer at 2038-2345 hours on 3 September 1965 appeared to be 54.60 m thick at the upper levels, and at a

depth of 218.40 m it was 36.40 m thick. The species observed coincidentally are detailed in Tables 3 and 4.

The siphonophores considered to be most probably responsible for the production of scattering are the Physonectae, those with floats containing gas (CO). Species of that group (*Stephanomia bijuga*, *St. rubra*, and *Physo-*

TABLE 3
SPECIES IN THE 100-20 M LAYER, PARTIALLY COINCIDENT WITH THE
SHALLOWER SCATTERING RECORD (NIGHT)

GROUP	CONCENTRATION OF INDIVIDUALS PER 10,000 M ³ OF WATER FILTERED			
	GREATER THAN 5,000	4999-500	499-50	LESS THAN 50
Chaetognatha		<i>S. bierii</i>	<i>S. euneritica</i>	<i>P. draco</i>
			<i>S. hexaptera</i>	<i>S. enflata</i>
				<i>S. minima</i>
				<i>S. pseudoserrato-</i> <i>dentata</i>
Siphonophorae			<i>M. atlantica</i>	<i>A. ernesti</i>
			<i>E. spiralis</i>	<i>N. reticulata</i>
			<i>Ch. appendiculata</i>	
Medusae			<i>L. tetraphylla</i>	<i>S. geometrica</i>
				<i>C. peregrina</i>
Ctenophorae				<i>Beroe</i> spp.

TABLE 4
SPECIES IN THE 300–235 M LAYER, COINCIDENT WITH THE DEEPEST SCATTERING RECORD (NIGHT)

GROUP	CONCENTRATION OF INDIVIDUALS PER 10,000 M ³ OF WATER FILTERED			
	GREATER THAN 5,000	4999–500	499–50	LESS THAN 50
Chaetognatha		<i>S. decipiens</i>	<i>S. bieri</i> <i>S. hexaptera</i> <i>S. scrippsae</i>	<i>K. subtilis</i> <i>S. enflata</i> <i>S. maxima</i> <i>S. zetesios</i>
Siphonophorae			<i>M. atlantica</i> <i>L. conoidea</i>	<i>Ch. appendiculata</i> <i>L. achilles</i> <i>L. havock</i> <i>L. multicristata</i> <i>St. bijuga</i> <i>B. elongata</i> <i>A. ernesi</i> <i>R. plicata</i>
Medusae				<i>A. wyvillei</i> <i>P. hyacinthina</i>
Ctenophorae				<i>Beroe</i> spp.

phora hydrostatica) were observed at the levels of scattering. It is also probable that the head armature (hooks, teeth, and chitinous plates) of the chaetognaths will contribute to scattering.

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