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The Diel Migrations and Distributions within a Mesopelagic Community in the North East Atlantic. 7. Siphonophores

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CONTENTS

1. INTRODUCTION

IN MANY studies of marine planktonic ecosystems the rôle played by gelatinous organisms often receives little attention despite the fact that they can be the predominant organisms in the macroplanktonic–micronektonic size groupings. There are, however, many inherent problems in establishing the contribution of such animals to an ecosystem, not least of which is the difficulty of obtaining quantitative estimates of their abundance or biomass. For instance, the fragility of siphonophores results in their incomplete capture by nets, whilst many ctenophores are totally destroyed either during collection or on preservation (HARBISON, MADIN and SWANBERG, 1978). A consequence is that there are few studies on the diel vertical migration of these animals, and indeed on the more general aspects of their vertical distribution. In the case of siphonophores, MOORE (1949, 1953) considered their diel and seasonal distributions in the Bermuda and Florida Current regions, and established that many siphonophores species do undertake diel vertical migrations. PUGH (1974) considered the vertical distribution of siphonophores in the Canary Island region and concluded that, in many cases, the diel vertical migration made by several slow-swimming species described overall a sinusoidal pattern, with little "stationary time" (PEARRE, 1979) at either of the day or night

depth extremes. This concept was discussed further by PUGH (1977) and illustrated by data from a series of eleven hauls made over a 24 hr period at a depth of 250 m (see ROE, 1974). The possible factors which might play a part in initiating or controlling the diel vertical migrations of siphonophores were considered. MUSAYEVA (1976) also considered the diel vertical migrations of siphonophores and their relation with hydrographical conditions, and MARGULIS (1974, 1976) discussed the zoogeographical distribution of siphonophores, in the Atlantic Ocean, and related these to water masses.

In a wider sense it is often difficult to assess the rôle of gelatinous organisms in the flow of energy through the marine food chains. Much work has been carried out on siphonophores to try to understand their feeding behaviour, diet and metabolism, e.g. BIGGS (1977), PURCELL (1981b, 1983), but there is less information on which animals prey on these siphonophores. Occasionally, as reported in this series of papers, identifiable remains of siphonophores are found in fish or crustacean stomachs, but more often an amorphous mass is encountered which once could have been some gelatinous organism. NAVARRO (1927) reported *Sardinella* feeding on siphonophores.

This paper is one of a series which consider the diel vertical migration patterns of various planktonic groups found at a site (ca. 44°N 13°W) in the North-east Atlantic Ocean.

2. METHODS

The siphonophores considered here were identified from a set of 97 samples derived from four series of hauls, at depths of 100, 250, 450 and 600 m, each fished over separate 48 hr periods. The sampler used was an RMT (1 + 8) combination net (BAKER, CLARKE and HARRIS, 1973), and details of the sampling procedures are given in an associated article (ROE, ANGEL, BADCOCK, DOMANSKI, JAMES, PUGH and THURSTON, 1984). For the purposes of this study, only the siphonophores in the RMT 8 (mesh size – 4.5 mm, mean volume filtered 32.2×10^3 m^3) net catches were considered. Any identifiable piece of a siphonophore was enumerated. Most siphonophores like other hydrozoan coelenterates, demonstrate an alternation of generations, although both phases are planktonic. However, the sexual stage in the physonect siphonophores is small and ephemeral, while that of the calycophoran species clearly can be identified, as an eudoxid stage. Both the asexual (polygastric) and sexual (eudoxid) phases have been counted and estimates of their abundance made as outlined in the Appendix to this paper. The estimates of population abundance were converted to numbers per 10^3 or 10^4 m^3 of water filtered, with the assumption that the filtration efficiency was 100%. The fragility of the individual siphonophore specimen results in its being broken up into several, or myriad, parts on contact with the netting and there is likely to be a loss of material during collection which could result in an underestimate of numbers. None the less, although it may be difficult to make quantitative estimates of siphonophore numbers from net samples, in such a study as this the characteristics of the gear were the same throughout and so the sampling errors are consistent such that there is no reason why the change in the siphonophore population over each 48 hr period cannot be considered without undue bias.

At all stages in the presentation of the siphonophore data it should be borne in mind that the four depth horizons were not sampled concurrently, but consecutively over a period of thirteen days between 6th and 19th April 1974, with some other sampling interspersed between. Thus, although the data will be presented as a set of histograms, one for each depth interval and arranged one above another in depth order, in actuality the data are not so closely comparable.

However, as ANGEL (1984) points out, there is also no evidence to suggest that a comparison of these data in this way would lead to any serious errors in interpretation.

The time period (GMT) encompassed by each series of samples is:

100 m	1001	6–iv	to	0948	8–iv
250 m	0910	10–iv	to	1003	12–iv
450 m	0717	17–iv	to	0819	19–iv
600 m	0950	13–iv	to	0935	15–iv

In addition to these series, reference will be made to some other sampling programmes carried out on the same *Discovery* Cruise (Cr. 61). Firstly, the day and night depth distribution of siphonophores was determined from a series of one or two hour hauls fished over 100 m depth horizons from the surface to 1,000 m. This series is referred to as the "Miniseries" in this paper, and the details of the sampling programme are given in ANGEL (1977). Secondly, a "Repeat" series, when the three 100 m depth horizons between 300 and 600 m were sampled, by day and by night, on seven occasions during Cr. 61, and on another five occasions over the next year. Thirdly, the earlier series of eleven hauls made over a 24 hr period at 250 m (see PUGH, 1977). This "24 hr series" was carried out on a *Discovery* Cruise in 1972 at a site, 30°N 23°W, further to the south in the sub-tropical warm waters of the North-east Atlantic Ocean.

3. RESULTS

3.1. *Total siphonophore population*

The total population of siphonophores in each RMT 8 net sample was assessed as outlined in the Appendix, and normalized to numbers per 10^3 or 10^4 m^3 of water filtered, as discussed in the Methods section. Figure 1 illustrates the relative contribution of the siphonophores to the total numbers of individuals from all the taxa identified from the RMT 8 catches. In three of the 48 hr series, the 100 m one apart, the siphonophores were the numerically dominant organism in all the samples, even allowing for a possible reduction in estimated numbers, particularly in the 250 m series, as mentioned in Appendix 1. If one also considers the other identified gelatinous organisms, i.e. medusae and ctenophores, then these made little contribution to the overall numbers except for the medusae in the daytime hauls of the 100 m series. Together they averaged 0.37, 2.98 and 4.94% of the 250, 450 and 600 m 48 hr series total populations respectively, as compared with 81.9, 69.7 and 71.1% respectively for the siphonophores from the RMT 8 catches. In the 100 m series the siphonophore contribution to the often low total numbers of organisms varied widely between 7.3 and 97.2%, while the medusae were significantly, at the 0.1 to 1% level, more abundant during the daytime and on two occasions were the predominant taxa in the RMT 8 samples, notwithstanding the fact that the overall number of organisms were very low.

In rank order of abundance, comparing directly the catches made by both the RMT 1 and RMT 8 nets and normalizing the data to numbers per 10^3 m^3, despite possible differences in, for instance, the filtration efficiencies of the two nets, the siphonophores overall were the fourth most abundant taxon, after copepods, chaetognaths and ostracods, in the total catches from the three deeper 48 hr series, and were fifth ranked in the 100 m series, being displaced by euphausiids. However, by day the siphonophores also ranked fourth at 100 m, with small

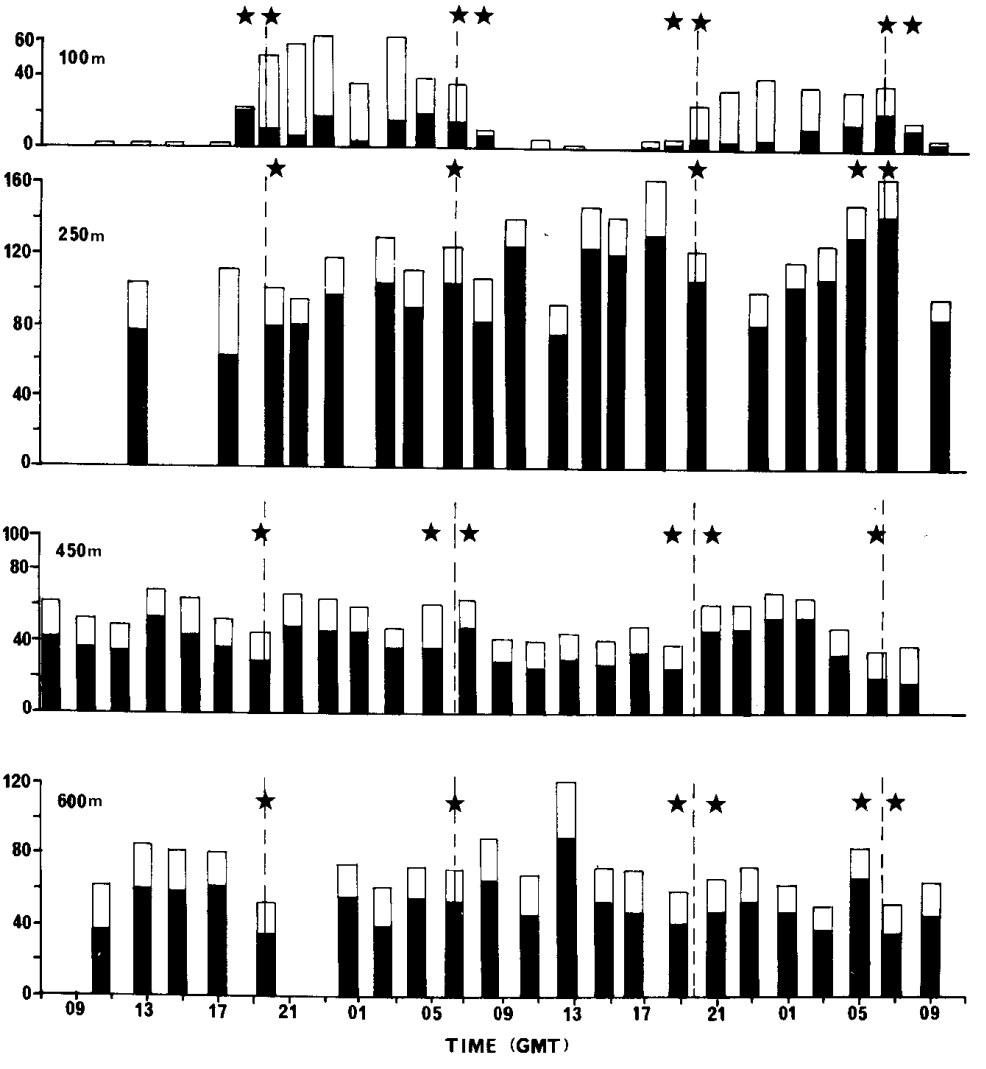

FIG. 1. The relative contribution of siphonophores (black) in each haul for each of the 48 hr series to the total number of animals of all the taxa identified from the RMT 8 samples. Left ordinate: – numbers per 1,000 m^3 of water filtered. The times of sunrise and sunset are indicated but it should be noted that the four 48 hr series were sampled consecutively not contiguously. The hauls which were not included in the calculation of the day or nighttime mean populations are indicated by an asterisk (★) – see text for details.

euphausiids third and the ostracods reduced to fifth place as much of their population underwent a diel vertical migration (ANGEL, 1984) such that they regained their third ranking at 100 m by night despite the enhancement of euphausiid numbers by the diel migration of the larger animals. A similar situation prevailed at 250 m where, by day, siphonophores were more abundant than ostracods, while in the 450 m series the diel migration of the euphausiids resulted in that taxon being more abundant than siphonophores during the daytime.

The number of siphonophores, standardized to unit volume, in each haul and for each depth series is shown in Fig. 2, together with the number of siphonophores species present in each haul. The relative contributions of the polygastric and eudoxid stages to the total are shown, except in the 100 m series where the latter stage was present only in very small numbers. It is of particular interest to compare, in Fig. 2, the three deeper 48 hr series. In the 250 m

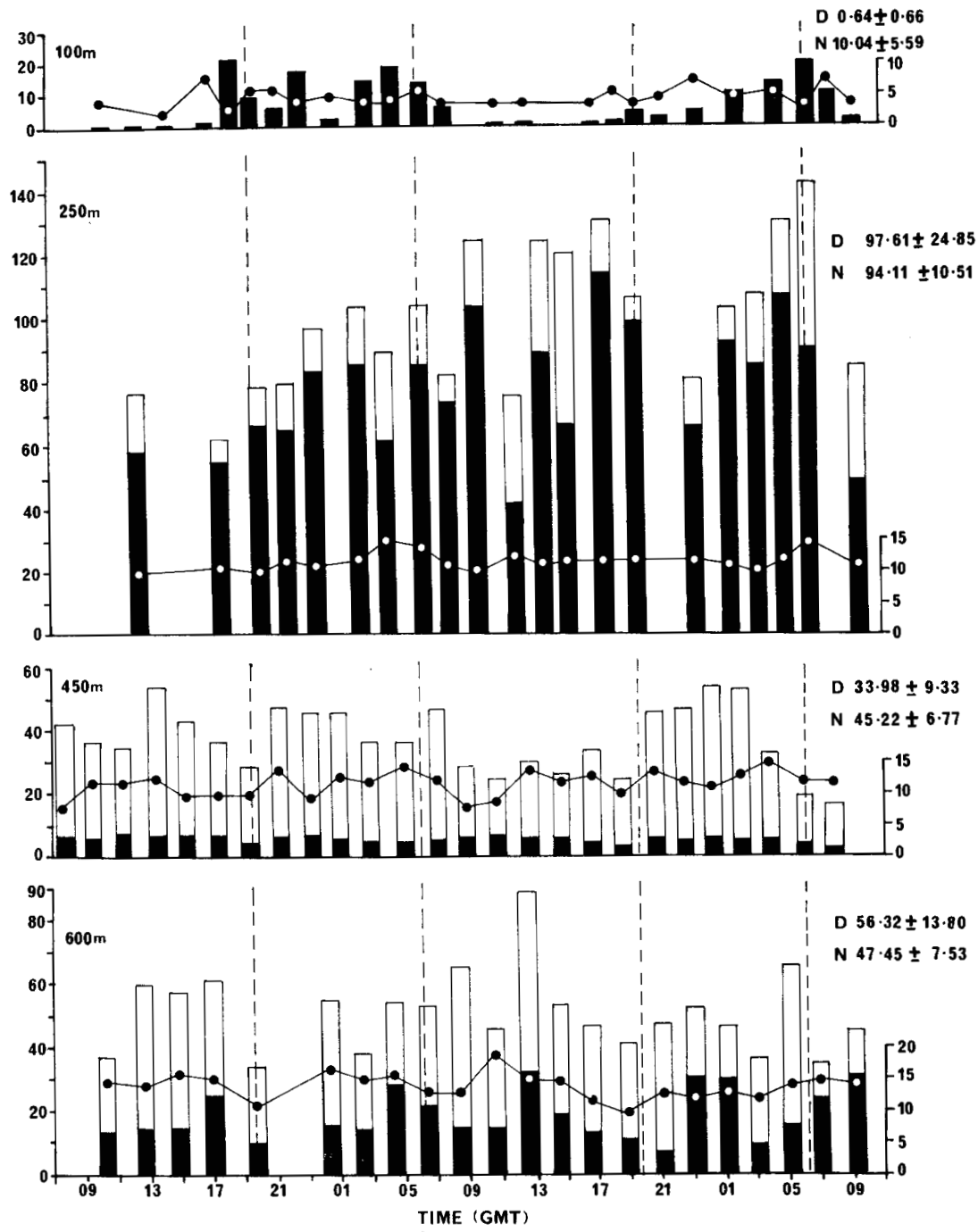

FIG. 2. The relative contribution of the polygastric stage nectophores (black) and eudoxids to the total number of siphonophores (histograms) and the number of siphonophore species found in each haul (•). The combined mean numbers and their standard deviations, by day (D) and by night (N) are shown for each depth sampled. Left ordinate: – numbers of individuals per 1,000 m^3 of water filtered. Right ordinate: – number of species per haul. See also legend to Fig. 1.

series the siphonophore population generally contained a preponderance of nectophores of *Rosacea plicata* and *Chuniphyes multidentata*†, while the eudoxid stage of the latter species was present in relatively small numbers. However, in the 450 m series these eudoxids predominated,

†For authorities see Table 1.

TABLE 1. THE SIPHONOPHORE SPECIES CAUGHT DURING THE FOUR 48 HR SERIES

The diurnal (D) and nocturnal (N) mean numbers per 10,000 m^3 of water filtered are shown for each species and for each depth horizon sampled. In addition the percentage contributions of the specific populations to the total number of siphonophores caught during each 48 hr series and for all four series combined are shown together with the overall ranked order of abundance of each species

Species	100 m			250 m			450 m			600 m			Overall	
	D	N	% of Total	D	N	% of Total	D	N	% of Total	D	N	% of Total	% of Total	Rank
Apolemia uvaria (LESEUER ?1811)	–	–	–	–	0.31	0.02	–	0.32	0.04	0.05	0.18	0.02	0.02	21
Halistemma rubrum (VOGT, 1852)	4.66	1.07	4.04	0.13	0.10	0.01	0.17	–	0.03	0.05	–	0.003	0.18	13
H. striata TOTTON, 1965	–	1.25	0.94	–	–	–	–	–	–	–	–	–	0.04	20
Nanomia cara AGASSIZ, 1865	–	0.78	0.59	–	–	–	–	–	–	–	–	–	0.02	22
Bargmannia elongata TOTTON, 1954	–	0.14	0.11	3.51	9.18	0.85	0.17	0.08	0.04	–	–	–	0.36	12
Physophora hydrostatica FORSKÅL, 1775	0.19	0.33	0.38	–	–	–	–	–	–	1.04	0.26	0.14	0.05	19
Amphicaryon acaule CHUN, 1888	–	–	–	–	–	–	–	–	–	0.03	0.03	0.006	0.006	26
Maresearsia praeclara TOTTON, 1954	–	–	–	–	–	–	–	–	–	0.13	0.16	0.03	0.007	25
Rosacea plicata sensu BIGELOW, 1911	0.32	1.81	1.58	247.85	264.68	32.24	9.29	7.77	2.42	8.16	6.41	1.49	15.36	2
Praya dubia (QUOY ET GAIMARD, 1833, 1834)	0.05	–	0.03	–	–	–	–	–	–	–	–	–	0.001	32
P. reticulata (BIGELOW, 1911)	–	–	–	0.03	–	0.002	–	–	–	–	–	–	< 0.001	35
Prayoides intermedia LELOUP, 1934	–	–	–	0.03	–	0.002	–	–	–	–	0.07	0.006	0.002	30
Desmophyes annectens HAECKEL, 1888	–	0.07	0.05	0.24	0.10	0.02	–	–	–	–	–	–	0.01	24
Nectopyramis thetis BIGELOW, 1911	–	–	–	0.10	0.38	0.03	0.24	0.35	0.08	0.09	0.13	0.02	0.08	17
N. diomedeae BIGELOW, 1911	–	–	–	–	–	–	0.05	0.03	0.01	0.06	0.03	0.01	0.004	29
Vogtia serrata (MOSER, 1925)	0.23	0.04	0.19	4.42	13.25	1.19	19.13	18.96	5.37	6.76	7.02	1.39	2.09	5
V. spinosa KEFERSTEIN and EHLERS, 1861	1.82	1.46	2.36	30.01	21.02	3.11	0.57	0.74	0.18	0.29	0.14	0.04	1.43	8
V. glabra BIGELOW, 1918	–	–	–	1.59	9.63	0.77	8.18	1.28	1.41	0.19	0.33	0.05	0.65	9
V. pentacantha KÖLLICKER, 1853	0.02	0.02	0.03	7.14	7.27	0.90	0.09	–	0.01	0.05	–	0.006	0.38	11
Lensia conoidea (KEFERSTEIN and EHLERS, 1860)	27.65	93.01	89.17	4.45	1.63	0.36	1.55	0.70	0.33	0.88	0.42	0.14	8.11	3
L. multicristata (MOSER, 1925)	–	–	–	7.59	15.77	1.54	0.73	0.54	0.18	19.50	18.65	3.87	1.73	6
L. fowleri (BIGELOW, 1911)	0.05	–	0.03	–	–	–	–	–	–	–	–	–	0.001	31
L. achilles TOTTON, 1941	–	–	–	–	0.23	0.02	1.12	1.40	0.35	0.06	0.33	0.04	0.10	16
L. meteori (LELOUP, 1934)	–	–	–	–	0.03	0.002	–	–	–	–	–	–	< 0.001	33=
L. hostile TOTTON, 1941	–	–	–	–	–	–	0.14	0.32	0.06	4.44	5.39	0.99	0.44	10
L. grimaldi (LELOUP, 1933)	–	–	–	–	–	–	0.53	0.51	0.15	2.12	0.92	0.32	0.12	14
L. panikkari DANIEL, 1970	–	–	–	–	–	–	–	0.03	0.004	–	–	–	< 0.001	33=
L. lelouveteau TOTTON, 1941	–	–	–	–	–	–	–	–	–	0.08	0.16	0.02	0.006	27
L. exeter TOTTON, 1941	–	–	–	–	–	–	–	–	–	0.79	1.41	0.22	0.06	18
Dimophyes arctica (CHUN, 1897)	0.07	0.09	0.12	0.90	1.92	0.19	10.56	9.60	2.85	13.90	12.71	2.71	1.54	7
Clausophyes ovata (KEFERSTEIN and EHLERS, 1860)	0.02	–	0.01	0.14	0.10	0.01	0.22	0.33	0.08	101.43	113.41	21.66	5.82	4
C. massiliana PATRITI, 1969	–	–	–	–	–	–	0.02	–	0.003	2.02	2.33	0.44	0.12	15
Chuniphyes multidentata – Nects.	0.05	0.04	0.06	403.09	466.17	54.99	8.29	11.17	2.71	14.07	13.19	2.77	23.42	1
LENS and VAN RIEMSDIJK, 1908 – Eudoxids	0.02	0.03	0.04	9.07	45.47	3.74	269.37	329.03	83.67	327.80	297.03	63.60	37.79	
Heteropyramis maculata MOSER, 1925	–	–	–	–	–	–	0.05	0.11	0.02	–	–	–	0.005	28
Enneagonum hyalinum QUOY ET GAIMARD, 1827	0.15	0.20	0.25	0.03	0.08	0.007	–	–	–	–	–	–	0.01	23

usually contributing ca. 80% (79.7 ± 4.5%) to the total numbers, and there was a concomitant reduction in the number of nectophores of both the aforementioned species. A similar situation in the 600 m series except that a considerable number of nectophores of another species, *Clausophyes ovata*, reduced the percentage contribution of the eudoxids even though the latter were present in roughly the same numbers as in the 450 series (Table 1). These differences in the distribution of the eudoxids and nectophores of *C. multidentata* will be discussed in more detail below, but they illustrate the conjecture (see Appendix 1) that for the most part, the components of the eudoxid stage were separate entities and had been released from the stem of the polygastric stage.

In Fig. 2, and subsequent histograms showing the variations in the population of siphonophores over the four 48 hr periods of sampling, the mean number of animals by day (D) and by night (N) are given for each depth, together with the standard deviation of that mean. Those hauls whose greater part fell within $1\frac{1}{2}$ hr of sunset or sunrise (see Fig. 1) were excluded from this analysis in an attempt to overcome the problem posed by those slow-swimming species of siphonophores which describe a diel sinusoidal pattern of depth change when vertically migrating (PUGH, 1977). Although a somewhat arbitrary assumption, it does allow a better comparison of the daytime and nighttime populations present at any one depth. It is difficult also to apply orthodox statistical methods to data sets such as these which are not necessarily distributed normally, but it is possible to test for differences between these mean populations using a two-tailed Student's '*t*' test. In addition it is necessary to distinguish between temporal patchiness in the data, i.e. the presence of a repeated diel vertical migration, from spatial heterogeneity in the distribution of the population. In an attempt to investigate this, LLOYD's (1967) 'patchiness' coefficient, C was calculated using the data standardized only to the mean volume of water filtered by the net.

Thus

$$C = \frac{\overset{*}{x}}{\bar{x}} = 1 + \frac{V - \bar{x}}{\bar{x}^2}$$

where $\bar{x}$ is the overall mean density of the population at any one depth; V, the variance of this mean; and $\overset{*}{x}$, the sample estimate of 'mean crowding'. The standard errors for this coefficient, estimated by moments, is given by

$$S.E. = \frac{V}{\bar{x}^2}\sqrt{\frac{2\overset{*}{x}}{n\bar{x}}} = \frac{V}{\bar{x}^2}\sqrt{\frac{2C}{n}}$$

where n is the number of hauls in that 48 hr series.

As an indication of the patchiness which might be expected from a relatively stable population of siphonophores, the coefficient, C, has been calculated from the data obtained from another set of 24 samples taken over a 36 hr period at 1,000 m (ANGEL, HARGREAVES, KIRKPATRICK and DOMANSKI, 1982), at which depth there were no indications of diel vertical migration by the siphonophore population. It was found that for most species this coefficient was significantly different, at the 5% level, from random indicating that there was some degree of spatial heterogeneity in their distributions. One species, *Lensia lelouveteau*, however, was very regular in its distribution despite its presence in very low numbers. It is unfortunate that the spatial scale of such patchiness cannot be assessed as spectral analyses cannot be applied to sampling procedures such as these where the hauls were not contiguous, as FASHAM (1978a, b) has discussed in detail.

The relative contributions of the polygastic (nectophores) and eudoxid stages to the siphonophore population over the four 48 hr sampling periods are shown in Fig. 2. The '*t*' test

shows that the mean day and night total siphonophore populations (excluding those in the hauls around sunset and sunrise, as indicated in Fig. 1) in the 100 m ($p < 0.1\%$) and 450 m ($p < 1\%$) series were significantly different from each other, while those for the other two series were not ($p > 20\%$). Taking the two stages (nectophores and eudoxids) separately it was found that whereas the means for both stages in the 100 m series remained significantly different ($p = 0.2$ and 1% respectively), the difference in the day/night means at 450 m was caused by the variations in the large numbers of eudoxids present. Thus the means for the eudoxid stage are significantly different ($p < 1\%$), while those for the nectophores are not ($p > 60\%$). The eudoxids of *Chuniphyes multidentata* predominated in the catches from this depth and the reasons for the day/night differences are discussed in the section on that species.

3.2. *The distribution of the individual siphonophore species during the four 48 hr series*

A total of 35 species of siphonophores was found in the 97 samples examined, and these species are listed in Table 1, together with their mean numbers per 10^4 m^3 (assuming 100% filtration efficiency and no loss of material) by day and by night at each depth sampled. These mean values differ from those in the figures as all the data have been used; the sunset/sunrise hauls being considered, somewhat arbitrarily, as either day or night ones according to in whichever period the fishing time was greater. The number of species found in each haul is plotted in Fig. 2. Relatively few species, from two to eight, were present in any one haul in the 100 m series, with a total of 17 species being found over the whole sampling period at that depth. Proportionally more species per haul were present in the deeper 48 hr series with the greatest number in the 600 m one, with an average of 14.05 ± 2.01 species per haul from a total of 24. Of the 35 species of siphonophores identified eight were found in only one or two hauls at a single depth; namely, *Nanomia cara*, *Halistemma striata*, *Praya dubia* and *Lensia fowleri* were found in the 100 m series; *P. reticulata* and *L. meteori* at 250 m; *L. panikkari* at 450 m; and *Amphicaryon acaule* at 600 m; while *Heteropyramis maculata* at 450 m and *Maresearsia praeclara* and *L. lelouveteau* at 600 m were found infrequently. In addition, *Prayoides intermedia* occurred once in both the 250 and 600 m series (Table 1).

Before presenting the data for the more abundant species, those for two physonect species will be considered briefly as they are symptomatic of the difficulties involved in estimating siphonophore population abundances, as discussed in Appendix 1. Nectophores of *Halistemma rubrum* were present at all of the four depths sampled, but most abundant in the 100 m series. At that depth 236 nectophores were identified, with 203 of these in the hauls at or on either side of sunset or sunrise, although 103 occurred in a single haul (St. 8507#49). It might be construed from this that there was some crepuscular vertical migration through this 100 m depth zone, but it must be remembered that for physonect siphonophores the presence of 103 nectophores in a haul might mean that only two or three specimens were present. On the other hand catches which contained only single nectophores must indicate the presence of that species, although the specimen originally could have preserved up to 40 or more nectophores, and exemplify the fragility of these animals. Thus it is difficult to make quantitative estimates of the abundance of such physonect species. Similarly, nectophores of another physonect species, *Bargmannia elongata*, were most abundant in the 250 m 48 hr series, especially during the crepuscular periods. They also were found in the 100 m series, all in the hauls around sunset or during the night. Again these data could be interpreted as demonstrating a diel vertical migration from below 250 m during the day to ca. 100 m at night, but such an interpretation must be treated with great caution.

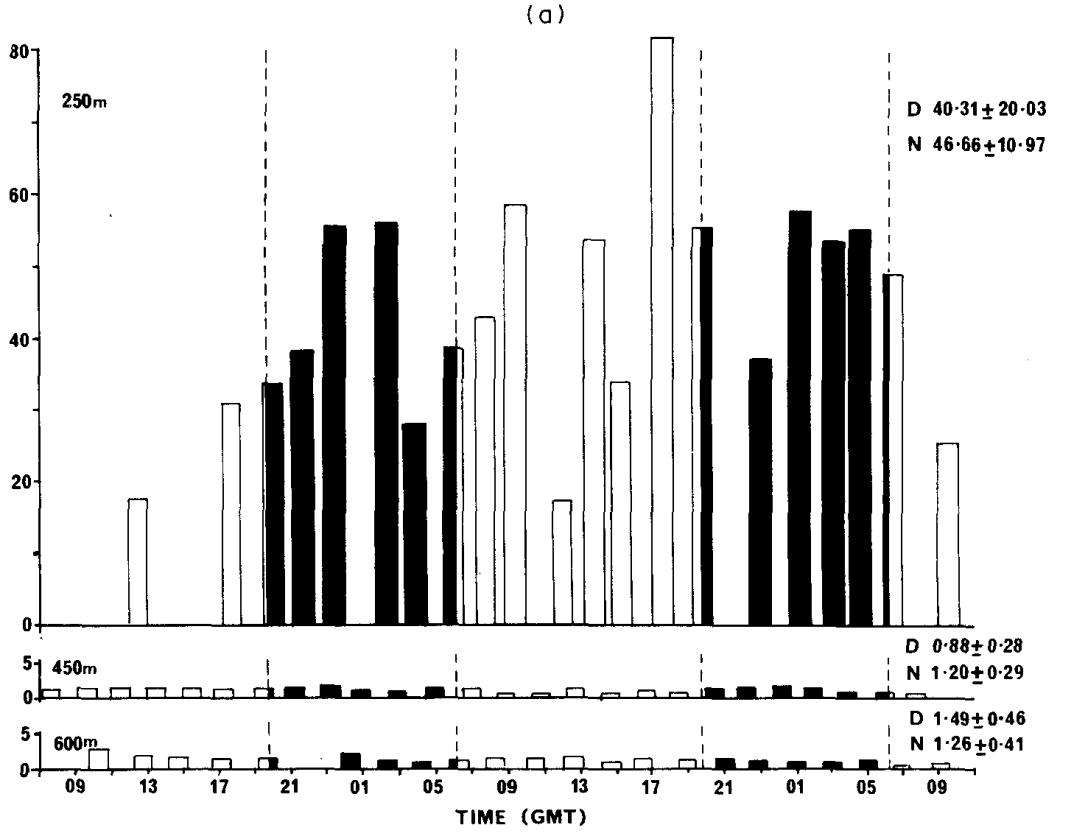

FIG. 3(a). The temporal distribution of *Chuniphyes multidentata* anterior nectophores in three of the 48 hr series, with the mean day and night numbers per 1,000 m^3 and their standard deviations. See also legend to Fig. 1.

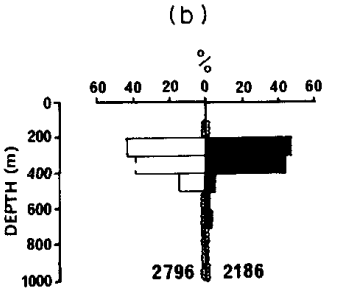

FIG. 3(b). The day and night (black) depth distribution of the polygastric stage of *C. multidentata* shown as percentages of the total numbers found in the top, 1000 m of the water column, by day and by night. These totals are given. The data are derived from the "Miniseries" samples. ~~~ denotes less than 2%.

The commoner species in the four 48 hr series are dealt with in the following sections according to their ranked order of abundance (Table 1). The data for certain species will be considered a little more fully than others in order to illustrate some of the difficulties inherent in interpreting such data.

3.2.1. Chuniphyes multidentata (*Figs 3 and 4*). This was by far the most abundant species collected in the four 48 hr series and comprised 61.2% of the total siphonophore numbers,

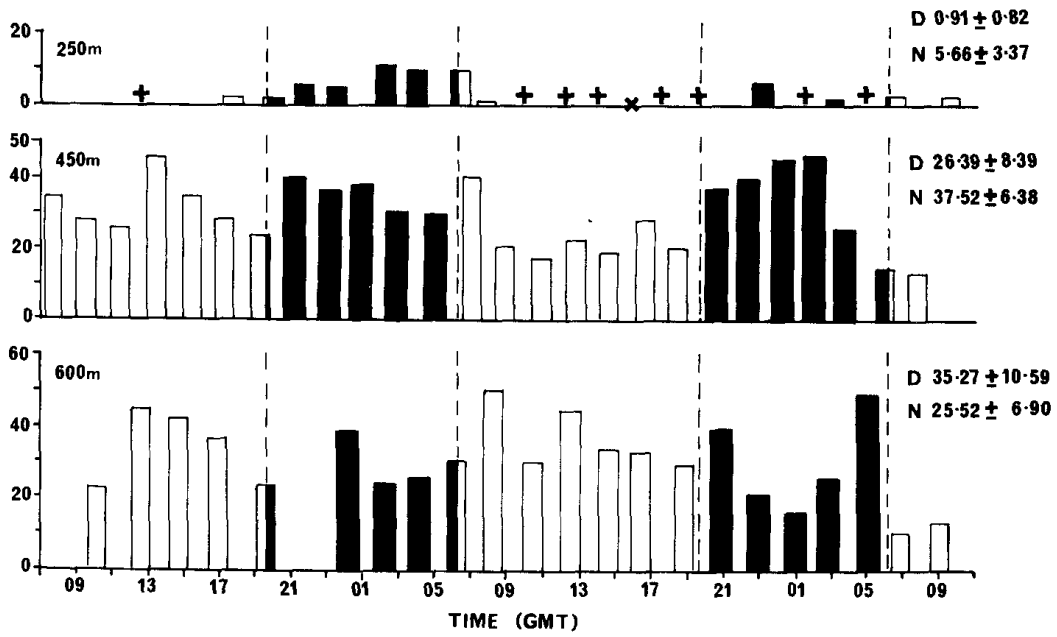

FIG. 4. The distribution of *Chuniphyes multidentata* eudoxid gonophores in three of the 48 hr series, with the mean day and night numbers per 1,000 m^3 and their standard deviations. X denotes absence; + presence at less than 1/1,000 m^3. See also legend to Fig. 1.

with 23.4% being polygastric stage individuals and 37.8% eudoxids. Neither stage, however, was present in any numbers in the 100 m series and those data are not presented in the figures. At 250 m, the polygastric stage was the more important contributor to the population, represented by 55% of the total siphonophore numbers compared with only 3.7% for the eudoxids, while in the deeper two series the eudoxids predominated. The nectophores at 250 m show an erratic distribution [Fig. 3(a)] during the 48 hr period of sampling and although the mean nighttime numbers were greater than the daytime ones, there is no significant difference between them ($p > 40\%$). LLOYD's (1967) 'patchiness' coefficient obtained using the whole data set, has a value of 1.124 ± 0.041, so that, within 99% confidence limits, the population is between 1.00 and 1.25 times more 'crowded' than if it were randomly distributed. Thus, there is a slight indication of spatial heterogeneity in the distribution of the nectophores at this depth although, as discussed earlier, no spatial scale can be calculated for this patchiness.

In the 450 and 600 m series the nectophores of *Chuniphyes multidentata* contributed only 2.7 and 2.8% of their respective total siphonophore populations. There was a significant difference ($p = 4\%$) between the day and night mean populations at 450 m, although this is difficult to see in Fig. 3(a) because of the comparatively low numbers. Further, if the mean numbers for the individual days and nights are considered, the second day ($\bar{x} = 0.69 \pm 0.27$ per 10^3 m^3) is significantly different ($p = 1$–2%) from both the first day ($\bar{x} = 1.08 \pm 0.12$ per 10^3 m^3) and the second night ($\bar{x} = 1.33 \pm 0.23$ per 10^3 m^3), but does not differ ($p > 10\%$) from the first night ($\bar{x} = 1.07 \pm 0.29$ per 10^3 m^3). The 'patchiness' coefficient, C, has a value of 1.061 ± 0.026, which indicates 'crowding' only within the 95% confidence limits, which, because of the small number of samples, may not be a sufficient criterion for attributing patchiness to the data. None the less, the smaller population present on Day 2 in comparison with the remainder of the sampling period cannot be attributed to any diel vertical migration and again probably indicates a spatial heterogeneity in the distribution of the nectophores at this depth. In the 600 m series

the nectophore numbers again were relatively low and there were no significant differences between the day and night means.

The "Miniseries" data [Fig. 3(b)] show a close similarity in the day and night depth distribution of the nectophores of *Chuniphyes multidentata*, with between 80 and 90% of the population occurring in the 200–400 m depth range. A possible indication of a small-scale diel vertical migration of the deeper living part of the population is shown by the reduction in numbers in the 400–500 m depth range at night. However, this is contrary to the results from the 450 m 48 hr series where numbers were higher at night.

The eudoxid stage was comparatively rare in the 250 m 48 hr series (Fig. 4), but there was a significant difference ($p < 1\%$) between the day and night mean numbers, with considerably more eudoxids being present at night. This difference mainly was caused by the large numbers of eudoxids present during the first night ($\bar{x} = 7.57 \pm 2.53$ per 10^3 m^3), whereas the second night mean was not significantly different ($p > 75\%$) from the second day mean. The data might be interpreted as demonstrating a diel vertical migration, but probably spatial heterogeneity of the population is playing a greater part.

In the 450 m 48 hr series, the eudoxids of *Chuniphyes multidentata* numerically dominated and contributed 83.7% to the total siphonophore numbers. The eudoxids appeared to be fairly evenly distributed over the sampling period but there was a significant difference ($p < 1\%$) between the day and night mean numbers as mentioned earlier and the 'patchiness' quotient, C, has a value of 1.177 ± 0.053. However, the day/night difference can be attributed to the reduced number of eudoxids found during Day 2, such that their mean value is significantly different from both the Day 1 mean ($p = 1$–2%) and the two night means ($p < 1\%$). This reduction in the Day 2 population also was noted for the nectophores and is apparent with other species, e.g., *Dimophyes arctica.*

The numbers of eudoxids present in the 600 m 48 hr series were similar to those in the 450 m series, but their percentage contribution (63.6%) to the total siphonophore population was reduced due to the presence of large numbers of nectophores of *Clausophyes ovata.* In this series there were more eudoxids present during the day although the difference between the day and night means is not significant ($p > 5\%$). Overall one might interpret the data as indicating a diel vertical migration of part of the population from 600 m to 450 m or less, and the weighted mean calculation indicates a diel migration from ca. 550 m by day to ca. 480 m at night, although there are many inherent problems in such calculations as is discussed in regard to the distribution of *Vogtia glabra.* However, the eudoxid stage probably is too small to undergo such a migration and spatial heterogeneity in the population probably is the main contributor to the observed variability.

3.2.2. Rosacea plicata (*Fig. 5*). This species was the second most abundant siphonophore and its nectophores contributed 15.4% to the total numbers (Table 1). However, 93% of these nectophores occurred in the 250 m samples and at this depth it represented 32% of the total numbers. The histograms [Fig. 5(a)] indicate no apparent temporal change in the population resulting from a synchronous diel vertical migration at any of the depths sampled. There are no significant differences ($p > 25\%$) between the day and night mean numbers in all four series. The 'patchiness' quotient, C, for the 250 m series has a value of 1.076 ± 0.025 which would be consistent with some spatial heterogeneity in the distribution of this species.

The results of the "Miniseries" [Fig. 5(b)] show that 95 and 92% of the population of *Rosacea plicata* occurred in the 200–400 m depth range by day and by night respectively. There is, perhaps, a slight indication of a diel vertical migration by part of the population as

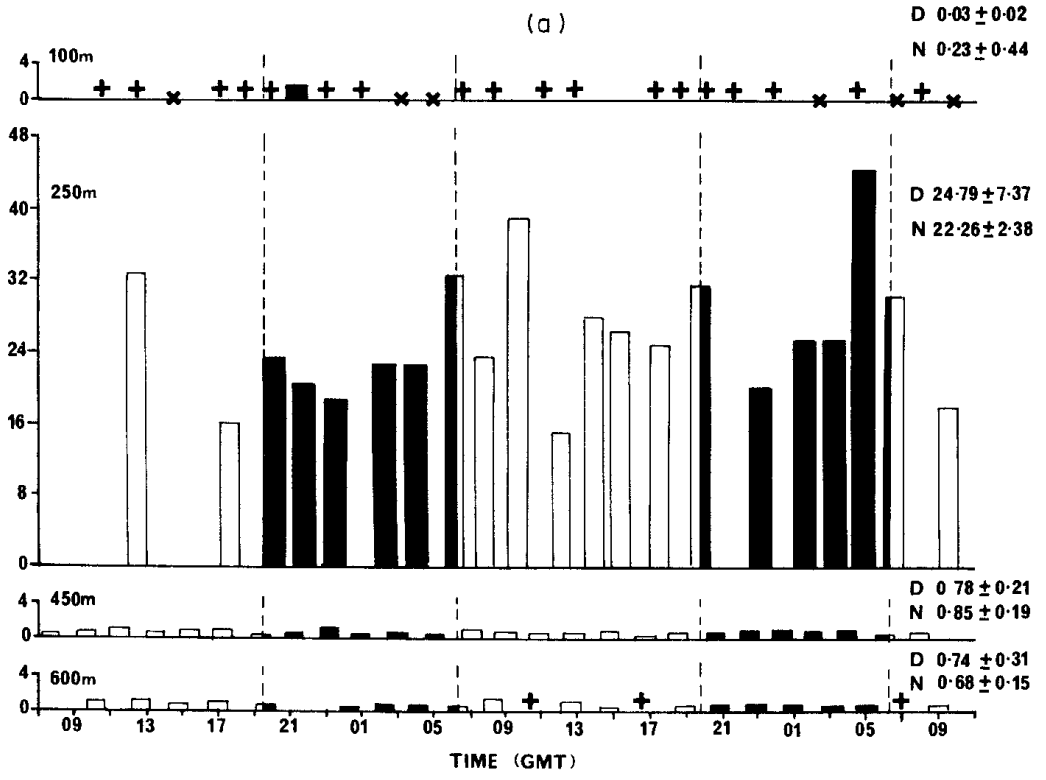

FIG. 5(a). The distribution of *Rosacea plicata* nectophores in the four 48 hr series, with the mean day and night numbers per 1,000 m^3 and their standard deviations. Left ordinate:– numbers per 1,000 m^3 of water filtered. × denotes absence of specimens in that haul. + denotes the presence of specimens but in densities less than 0.4/1,000 m^3.

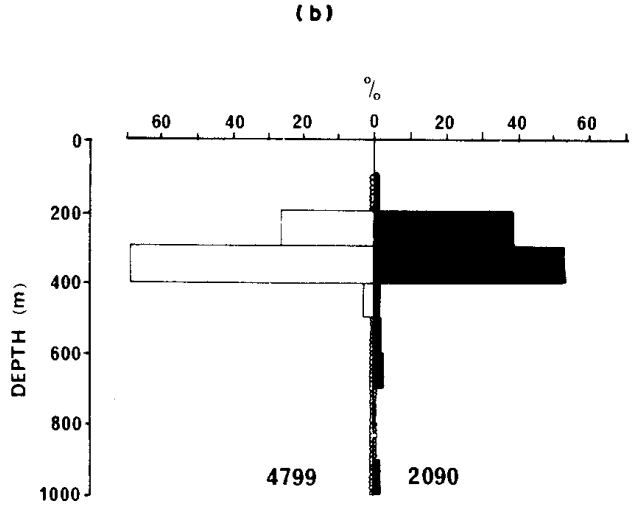

FIG. 5(b). The day and night (black) depth distribution of *R. plicata*. See legend to Fig. 3.

an increased percentage of nectophores was found in the 200–300 m depth band at night, but the total number of nectophores taken at night was considerably lower than in the day hauls. However, a greater influence on these particular "Miniseries" hauls may be derived from the probability that they were fished on either side of a frontal region (see Discussion), which

possibly gives rise to the mesoscale variability mentioned by ANGEL (1977). It is unfortunate that the depth intervals between the individual 48 hr series are too great to investigate any possibilities of small-scale diel vertical migrations.

The "Repeat" series of hauls, in the 300 to 600 m depth range at 44°N 13°W, showed that there was considerable variability in the depth distribution of this and other siphonophore species, even within the initial six week period when these depth horizons were sampled seven times. These depth changes are not necessarily attributable to ontogenetic or seasonal migrations but appear to be associated with the population dynamics of the plankton community as a whole. The most obvious example of this was when enormous numbers of the ctenophore, *Pleurobrachia* sp., appeared in the 300–400 m depth horizon, during June 1974, and caused a reduction in the population of both *Rosacea plicata* and *Chuniphyes multidentata*, in comparison with earlier hauls, and an increase in the concentration of these latter species at deeper depths. Thus any study of a single taxon *per se* could lead to erroneous conclusions unless it is related to the population dynamics of the whole community at that depth.

3.2.3. Lensia conoidea (*Fig. 6*). This species ranked third overall, but appeared in any numbers only in 100 m 48 hr series where it dominated the siphonophore catches, making up

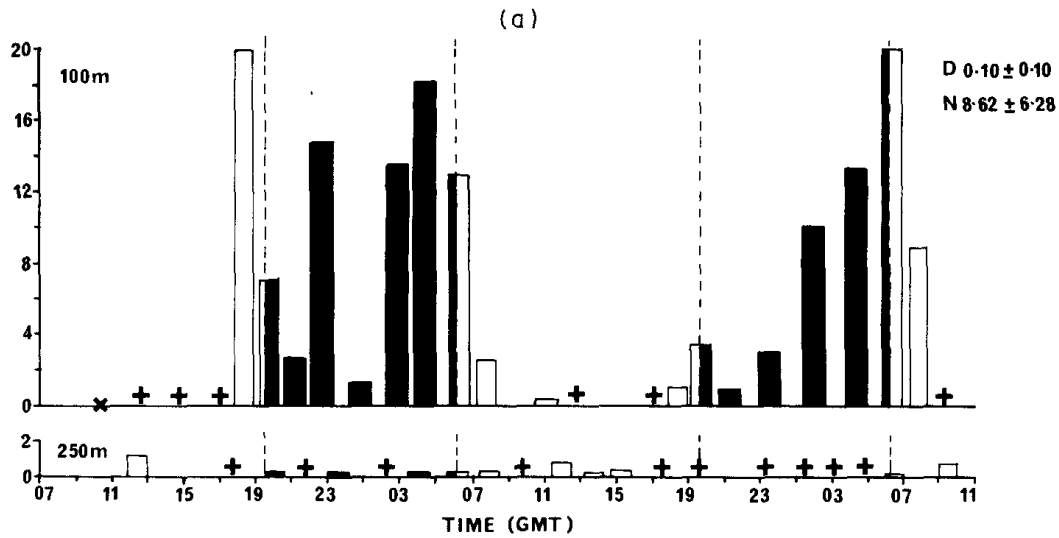

FIG. 6(a). The distribution of *Lensia conoidea* anterior nectophores in the 100 and 250 m 48 hr series with the mean day and night numbers, at 100 m, per 1,000 m^3 and the standard deviation. × denotes absence; + denotes less than 0.2/1,000 m^3.

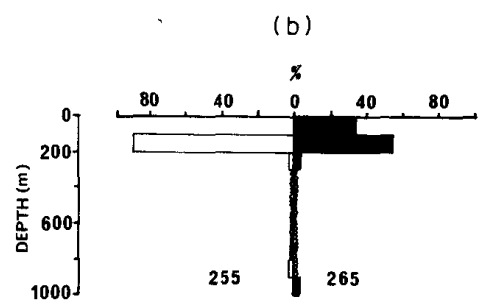

FIG. 6(b) The day and night (black) depth distributions of *L. conoidea*. See legend to Fig. 3.

89.2% of the total (Table 1). Its appearance in the other 48 hr series was erratic, with no significant features. There is evidence, from the "Repeat" series of hauls, that a deeper population of this species appeared later on in the year, but it is uncertain whether this represents a seasonal migration as only the 300–600 m depth range was sampled. However, BIGELOW and SEARS (1937) suggested that such a seasonal migration did occur in the Mediterranean population of this species.

In the 100 m series there was a clear indication of a diel vertical migration [Fig. 6(a)] through the depth zone. The species was virtually absent by day, reached peak numbers at sunset and sunrise, and there was a nocturnal decrease in numbers presumably as the animals migrated to shallower depths. The "Miniseries" data [Fig. 6(b)] showed that almost the entire population of *Lensia conoidea* occurred in the 100–200 m depth range by day, whilst part of this population migrated into the top 100 m by night. In comparison with the 100 m 48 hr series, the numbers of nectophores found were low, e.g. at night the numbers in the 0–100 and 100–200 m depth ranges were 2.73 and 4.14/10^3 m^3 respectively, as compared with a maximum of ca. 20/10^3 m^3 in the 48 hr series. This might indicate that the population of *Lensia conoidea* occupies a relatively narrow depth band.

3.2.4. Clausophyes ovata (*Fig. 7*). Although this overall fourth ranked species was found in all the 48 hr series, it made a substantial contribution to the siphonophore population only in

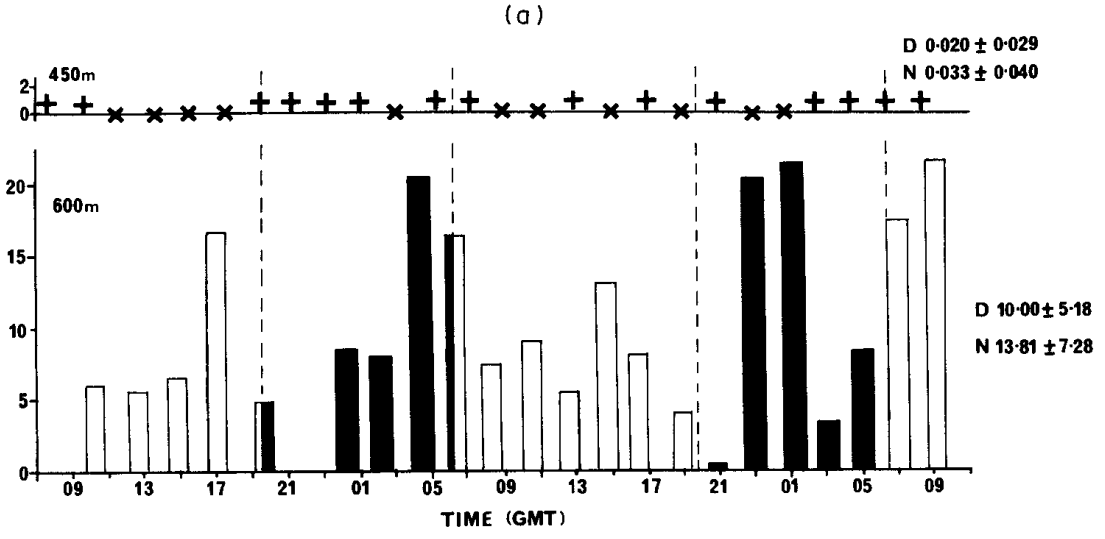

FIG. 7(a). The distribution of *Clausophyes ovata* anterior nectophores in the 450 and 600 m 48 hr series with the mean day and night numbers per 1,000 m^3. See also legend to Fig. 1.

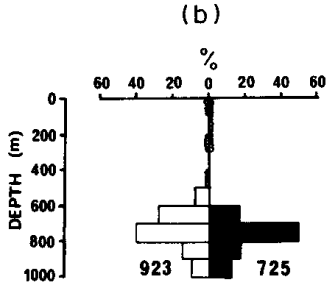

FIG. 7(b). The day and night (black) depth distribution of *C. ovata*. See legend to Fig. 3.

the 600 m one, where it was ranked second contributing 21.7% to the total population (Table 1). Its temporal distribution at this depth was somewhat erratic [Fig. 7(a)] and the day and night mean numbers are not significantly different ($p > 20\%$). The 'patchiness' quotient, C, has a value of 1.361 ± 0.128 indicating a $> 95\%$ probability of some 'crowding' of the population and, since there are no obvious signs of a diel vertical migration a heterogeneity in the spatial distribution of the species. The "Miniseries" data [Fig. 7(b)] indicate that 600 m was at the upper depth limit of the population, with peak numbers in the 700–800 m depth range.

A related species, *Clausophyes massiliana* also was found in the 600 m 48 hr series. Although it was present only in small numbers its distribution appeared to be random. There is very little information on this recently described species, but in the *Discovery* collection from the N.E. Atlantic occasional specimens are found, at depths usually greater than 500 m, particularly at temperate latitudes.

3.2.5. Vogtia serrata (*Fig. 8*). This species was present in all four 48 hr series, although only present as individual nectophores in five of the 100 m series hauls. Although fifth ranked in abundance it contributed only 2.1% to the total population (Table 1) and, as it is a hippopodiid species, the number of individuals may have been overestimated, as discussed in Appendix 1. In the 250 m series [Fig. 8(a)] the greatest number of nectophores appeared during the first night (N1) and, more especially, in the samples taken around the first sunset and sunrise. Thus, despite the significant difference ($p = 1$–2%) between the mean day and night population, there was a similar difference between the mean catches on the two nights ($N1 = 1.47 \pm 0.30$ per $10^3\ m^3$; $N2 = 0.59 \pm 0.31$ per $10^3\ m^3$). The reason for these nocturnal differences is not clear, but overall the 48 hr period the data appear to point to the possibility of a diel vertical migration into and above the 250 m zone at night.

The majority of nectophores of *Vogtia serrata* were found in the 450 m 48 hr series, where it was the second most abundant species. The mean day and night populations are very similar [Fig. 8(a)], and their coefficients of variability are relatively low, although the 'patchiness' quotient, C, (1.095 ± 0.032) indicates a very slight 'crowding', significant at the 5% level. However, the means for the two nighttime populations are significantly different ($p = 5\%$), but this difference cannot be related directly to the similar difference found in the 250 m series as the sampling periods are not the same. In the 600 m 48 hr series the numbers of nectophores showed no obvious temporal changes but there may have been some spatial heterogeneity in the population ($C = 1.202 \pm 0.082$; $p < 5\%$).

The data would seem to indicate that the population of *Vogtia serrata* was spread over a wide depth range, but mainly found in the region of 450 m. The shallower part, at least, of this population appeared to have migrated into and above the 250 m depth zone at night, but it is uncertain whether the apparently temporally stable population at 450 m can be related to an absence of diel migration or to a balanced loss and recruitment of specimens from and to that depth zone during such a migration. The "Miniseries" data [Fig. 5(b)] offer no evidence for either conjecture and, indeed, as themselves somewhat confusing. By day the majority of specimens occurred in the 300–400 m depth range, while at night the population was fairly evenly spread between 300 and 600 m giving the impression of a reversal diel migration. However, there was a great disparity in the numbers of specimens caught by day and by night and it is likely that the factors discussed in relation to the depth distribution of *Rosacea plicata* also are relevant here. With slow swimming species such as this, whose diel vertical migration may describe a sinusoidal pattern of depth change, the time at which any depth zone is sampled obviously will be critical and, then, the data obtained for its day/night depth distribution, as in

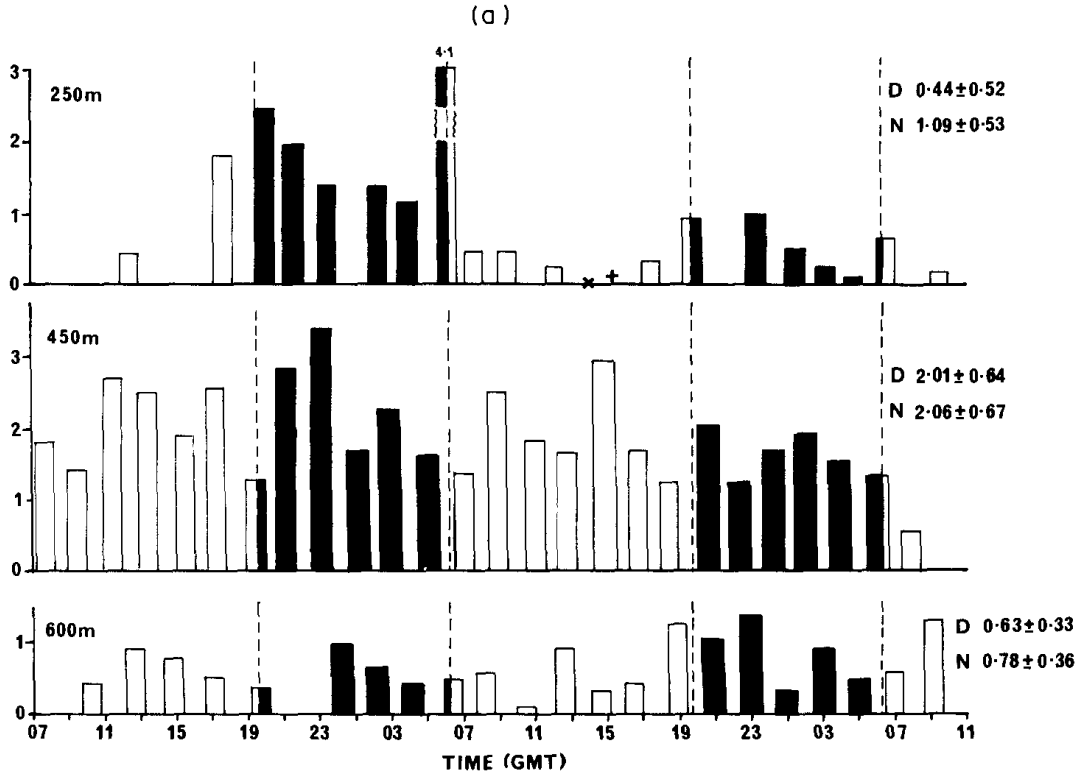

FIG. 8(a) The distribution of *Vogtia serrata* nectophores in three of the 48 hr series with the mean day and night numbers per 1,000 m^3 and their standard deviations. + denotes less than 0.1 nectophore per 1,000 m^3. See also legend to Fig. 1.

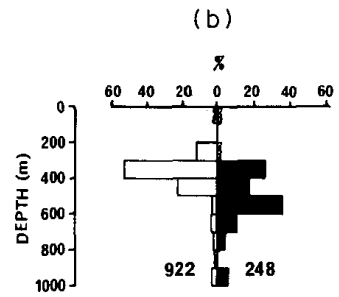

FIG. 8(b). The day and night (black) depth distribution of *V. serrata*. See legend to Fig. 3.

the "Miniseries", may be misleading. However, since such data represent the integrated population density over 100 m depth bands, this problem probably is minimized.

3.2.6. Lensia multicristata (*Fig. 9*). This species was totally absent from the 100 m series and present only in very small numbers in the 450 m series. It ranked fourth, both by day and by night, in the 250 m series despite the smaller daytime population and the significant difference, at the 1–2% level, between the day and night mean numbers [Fig. 9(a)]. Apart from the high numbers in the first day haul, the results indicate a diel vertical migration into the 250 m depth zone before sunset, with a stable or equilibrium population during the night and a post-dawn migration from the zone, presumably downward, although neither the 48 hr series

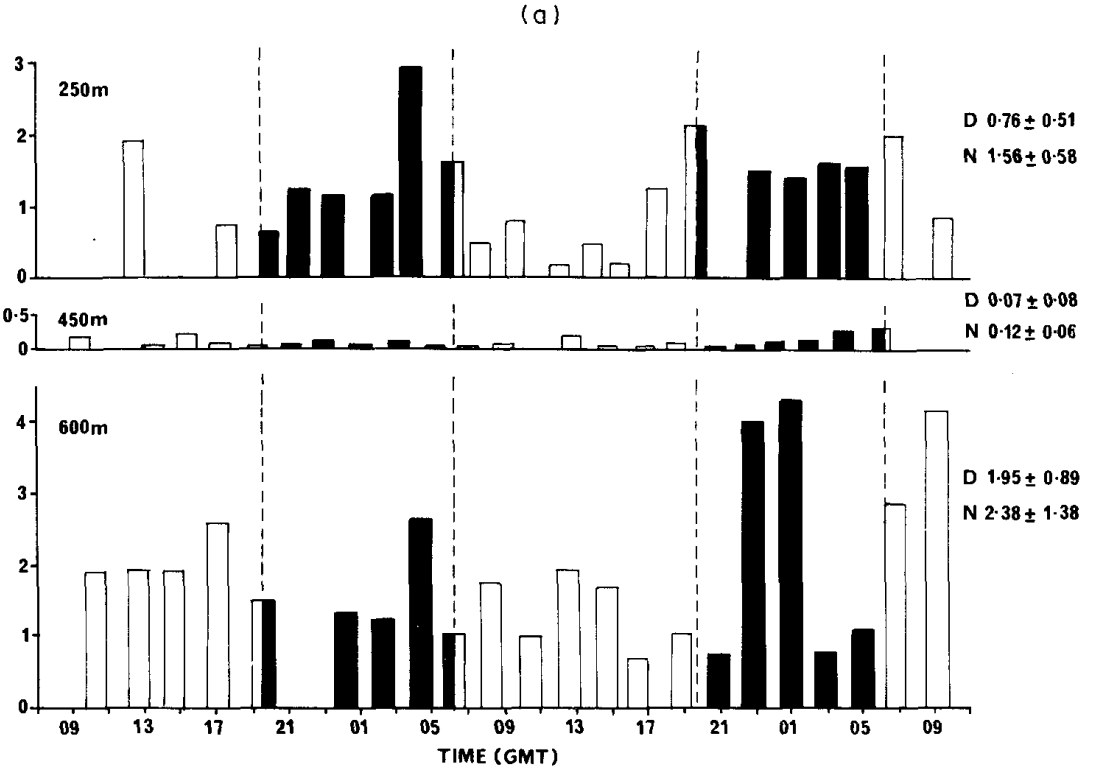

FIG. 9(a). The distribution of *Lensia multicristata* anterior nectophores in three of the 48 hr series with the mean day and night numbers per 1,000 m^3 and their standard deviations. See also legend to Fig. 1.

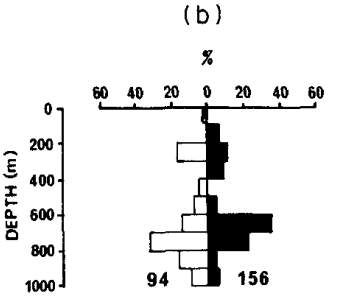

FIG. 9(b). The day and night (black) depth distribution of *L. multicristata.* See legend to Fig. 3.

data nor the "Miniseries" data [Fig. 9(b)] provide confirmation of this. At 600 m *Lensia multicristata* was the third ranked species with a somewhat erratic distribution, although there were no significant differences between the day and night mean numbers. The 'patchiness' quotient ($C = 1.300 \pm 0.109$) could indicate some spatial heterogeneity in the population. This sort of variability is reminiscent of that found in the earlier 24 hr series at 250 m (PUGH, 1977) where the species was considered to be a non-migrant.

The virtual absence of any nectophores of *Lensia multicristata* in the 450 m series means that its depth distribution appears to be bimodal and this is borne out by the data from the "Miniseries". A similar bimodal distribution was noted at the 24 hr series site, i.e. 30°N 23°W, (PUGH, unpublished data) but here the shallower population was the larger. In more temperate

waters the distribution pattern for this species appears to be unimodal. PEARRE (1979) discusses a hypothetical means by which a bimodal depth distribution of a population might arise. This requires that the animals within the population are vertically migrating but in an asynchronous manner. The relative length of "transit time" in comparison with "stationary time" determines the degree of the bimodality in the depth distribution. The resultant bimodal distribution would be a constant temporal feature and thus would appear to suggest, erroneously, that no vertical migration was occurring. Although the present data can neither prove nor disprove such a hypothesis, intuitively it is not thought likely to be happening as no siphonophore is known to migrate over a depth range of 350 m or more. Moreover a diel vertical migration pattern is apparent in the 250 m series samples which is not reflected in the 600 m series.

3.2.7. Dimophyes arctica (*Fig. 10*). This species was common in the 450 and 600 m series and present in the other two series, ranking seventh overall (Table 1). In the 100 m series nectophores were found in only six hauls and so its distribution at this depth is not shown in Fig. 10. At 250 m the day and night mean numbers indicate that over twice as many nectophores were present during the night in comparison with the day. However, the standard deviation are large and there is no significant difference ($p > 20\%$) between the two means. Much of the variability in the daytime population can be attributed to the unusually large number of nectophores found in the very first sample and if this is ignored then the day/night mean population are significantly different ($p = 4\%$). None the less, since the numbers are very low it would be presumptive to consider the above as possible evidence for a diel vertical migration.

In the 450 m 48 hr series *Dimophyes arctica* was the third most abundant species, although contributing only 2.85% to the total numbers of siphonophores present at that depth. The overall day and night mean numbers are very similar, and the coefficients of variability relatively low, which might indicate a temporally or spatially homogeneous population. However,

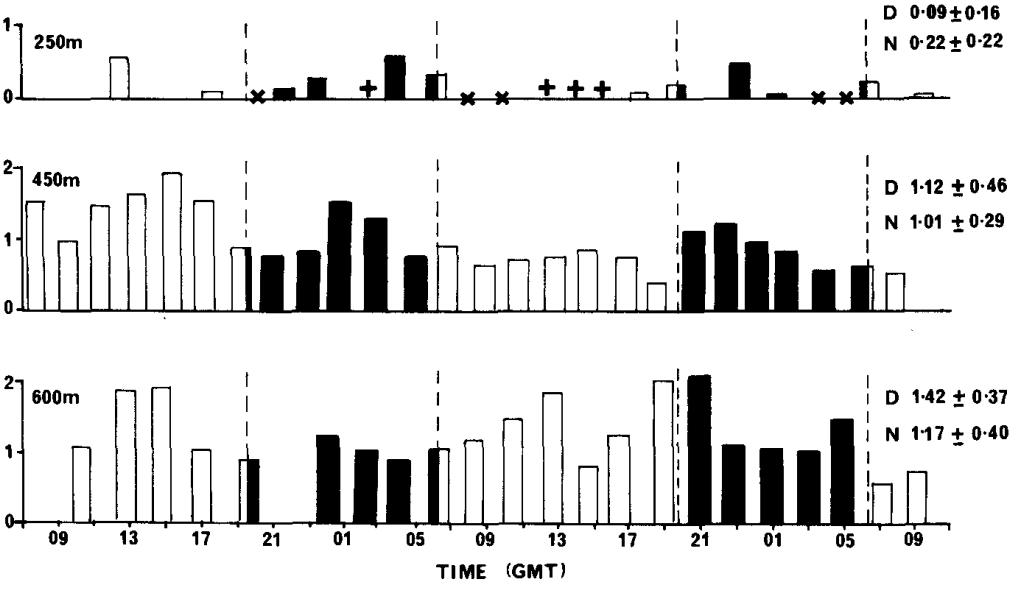

FIG. 10. The distribution of *Dimophyes arctica* anterior nectophores in three of the 48 hr series with the mean day and night numbers per 1,000 m^3 and their standard deviations. X denotes absence; + presence at less than 0.05/1,000 m^3. See also legend to Fig. 1.

a glance at the data shows that there are more nectophores present during the first day than during the second. If the data are split up into separate days and nights, then significant differences between the means appear, in that not only are the two daytime means very significantly different ($p < 0.1\%$), but also the D1 mean differs ($p = 3\%$) from that of the first night. These differences cannot be interpreted as indicating any diel vertical migration of the species at this depth but probably are the result of some spatial patchiness, although the 'patchiness' quotient ($C = 1.121 \pm 0.046$) suggests that this only is slight. Such differences in the 450 m 48 hr series, between the two daytime mean populations also were noted in the case of *Chuniphyes multidentata*, but not for, for instance, *Vogtia serrata*. The reason for these differences is not clear but it is thought unlikely that the difference in the light regime on the two days (see ROE *et al.*, 1984) could be a cause since there is no evidence for any diel vertical migration. In general, this species is considered to be a non-migrant and PUGH (1977) has commented on the erratic but permanent presence of this species during the 24 hr series at 250 m.

Dimophyes arctica usually is found at depths shallower than 500 m (PUGH, unpublished data) and so its presence in greatest numbers in the 600 m 48 hr series is somewhat unusual. At this depth, there were a few more nectophores present during the daytime than at night, but the means were not significantly different ($p > 20\%$), and there does not appear to be any indication of a diel vertical migration.

3.2.8. Vogtia spinosa (*Fig. 11*). This species was the eighth most abundant siphonophore overall, but it appeared mainly in the 250 m series where it made up 16.9% of the total population (Table 1), although it should be noted that this is a hippopodiid species (see Appendix 1). It was more abundant by day (Fig. 7) ($p = 5\%$) which might indicate a small-scale diel vertical migration, although the data are not conclusive. The "Miniseries" data also indicate such a migration for although about 89% of the population was found in the 200–300 m both by day and by night, a small part of the population appeared in the 100–200 m band at night. The possibility of a more pronounced diel vertical migration was noted in the results from the 24 hr series at 30°N 23°W. There the species was present at 250 m only at sunset and in three of the

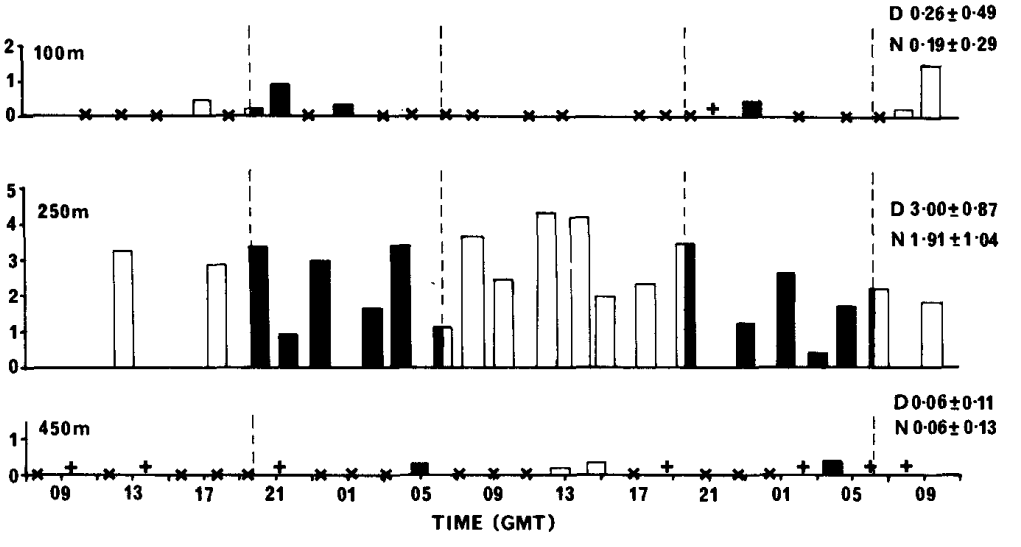

FIG. 11. The distribution of *Vogtia spinosa* nectophores in three of the 48 hr series with the mean day and night numbers per 1,000 m^3 and their standard deviation. + denotes less than 0.01/1,000 m^3, X denotes absence from that haul. See also legend to Fig. 1.

nighttime hauls, being absent from the one around midnight, indicating a slow migration into and above this depth zone during the night. The deeper depth distribution of this species in the warner waters at this latter station is consistent with other data, e.g. for *Vogtia serrata.*

3.2.9. Vogtia glabra (*Fig. 12*). This species ranked ninth overall, although it was mainly confined to the 250 and 450 m 48 hr series, and was absent from the 100 m one (Table 1). The data [Fig. 12(a)] appear to indicate a clear-cut diel vertical migration from about 450 m, during the middle part of the day, to shallower than 250 m at night. At 250 m the largest numbers of nectophores usually were found in the sunset and sunrise hauls, the second sunset haul being

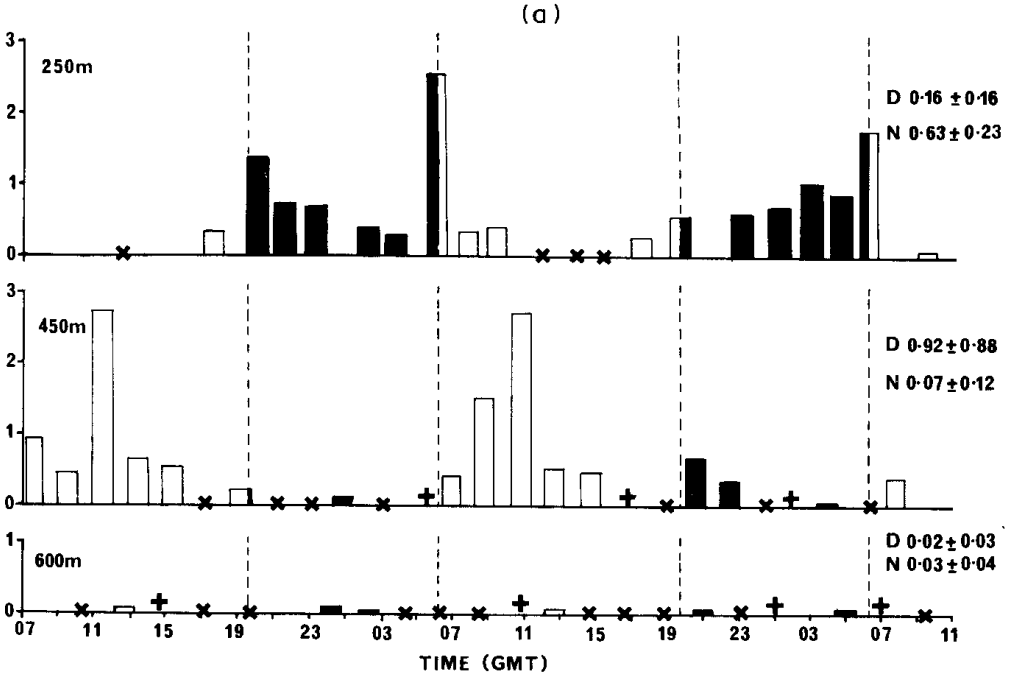

FIG. 12(a). The distribution of *Vogtia glabra* nectophores in three of the 48 hr series, with the mean day and night numbers per 1,000 m^3 and their standard deviations. + denotes less than 0.05 nectophores per 1,000 m^3. See also legend to Fig. 1.

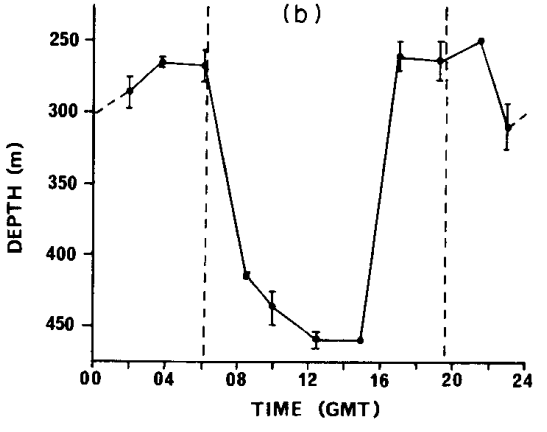

FIG. 12(b). The distribution of the weighted mean depths for *V. serrata.* See text for details.

the exception, and there was a decrease in numbers during the night, presumably indicating that the population migrated above this zone. No nectophores were found at this depth during the middle part of the day and there was a highly significant difference ($p < 0.1\%$) between the day and night mean despite the obviously slow, sinusoidal pattern of the diel migration at this depth, which could have masked such differences.

In the 450 m series, *Vogtia glabra* reached peak numbers shortly before noon on both days, had virtually disappeared before sunset and was largely absent during the night. The day and night means were significantly different ($p = 2\%$) despite the high standard deviations, which reflect the sinusoidal nature of the diel migration pattern. Since a pattern of diel vertical migration appears in two of the 48 hr series, despite the 200 m depth interval between them, then *V. glabra* is one of the few siphonophore species where an attempt can be made to visualize such a pattern of migration using the concept of weighted means, as discussed by ROE *et al.* (1984). In general the depth intervals between the zones sampled are too coarse to take account of siphonophore vertical migrations and are better related to more active migrants such as euphausiids or decapods. Moreover, it should be remembered that the four 48 hr periods of sampling were not carried out concurrently but consecutively. In Fig. 12(b) the calculated depth for each specified time (see ROE *et al.*, 1984) is the mean for the two 24 hr periods, with range bars. The results raise two interesting points. Firstly, since specimens of *V. glabra* did not reach the 100 m zone at night, then the weighted means generate a misleading effect in that it appears that the population sinks down during the middle of the night whereas it is more likely that some of the population migrated above the 250 m depth zone during this time. Secondly, there appeared to be a rapid vertical migration from the daytime maximum depth of 460 m to 260 m, this depth being reached over 2 hr before sunset. This feature is not necessarily the result of the necessity to move some of the data in order to fit in with a standard time regime (see ROE *et al.*, 1984), but more likely due to the low numbers of nectophores present at both 250 m and 450 m at that particular time of day. The weighted mean calculation does not take account of the fluctuations in population numbers and, in this case, the chance presence or absence of only a few nectophores at one depth would lead to a bias in the calculations. Thus, at about 1700 hr it is more likely that the majority of the population is migrating between 450 and 250 m, rather than the majority having reached the 250 m depth zone already, as the calculations imply.

The remaining species were present only in very low numbers and showed no obvious diel vertical migrations, except perhaps for *Lensia grimaldi* which was more abundant, at 600 m, during the day than at night, but there was no significant difference ($p = 20\%$) between the two means.

4. DISCUSSION

As has been mentioned in some other papers in this issue, the choice of the position (44°N 13°W) at which the sampling programme was carried out was not ideal as it lay in the transitional region between subtropical and temperate waters in the N.E. Atlantic Ocean. It is not easy to set limits on the boundary between these water masses although it is usual to speak of the region between the permanently thermally stratified waters to the south and the more northerly temperate regions where the seasonal thermocline is broken down during the winter and the water becomes mixed down to at least 400 m of depth. However, the extent to which this thermocline is eroded varies with the latitude. The hydrography of this region in the N.E. Atlantic is little understood, although it is undergoing increasing scrutiny. Recent data

(R. POLLARD, *pers. commun.*) indicate that, in Spring at least, two frontal regions are present which, in the region of 15°W, lie at about 41.5° and 44°N, with the southerly one appearing as the major feature. The physical properties of these fronts are different, but there are insufficient data as yet to say what temporal changes might occur in their positioning or their hydrography. However, the northerly front appears to be present in the region of 44°N 13°W during the time at which the present series of samples was taken. Some of the temperature–salinity curves derived from the STD data taken during that cruise have been illustrated elsewhere (ANGEL, 1977; ROE *et al.*, 1984). Comment was made in the latter paper on the possibility of mesoscale activity and the effects of presence of Mediterranean water at 600 m during the time that the 48 hr series was made. It was suggested that because of this the 600 m series data might not be directly comparable with those from the shallower series, although there was no biological evidence to this effect. ANGEL (1977) also commented on the presence of mesoscale activity in the area, but considered that such activity was unlikely to affect the distributional pattern of the animals.

A detailed study of the STD data obtained during the cruise shows that the hydrographical structure of the water differs from station to station. As an example, the temperature–depth structure at three stations (*Discovery* St. 8506#97, 8508#30 and #35) are shown in Fig. 13(a). The positions of the stations (represented by the series numbers 97, 30 and 35) are shown in Fig. 1 of ANGEL (1977) or Fig. 5 of ROE *et al.* (1984). STD cast #97 was made $3\frac{1}{2}$ days before #30, followed 12 hr later by #35. The *T/S* relationships at these three stations are shown in Fig. 13(b). It can be seen that there are marked differences between the stations corresponding to a transition between waters typically of more northerly origin in the temperate waters of the N.E. Atlantic Ocean (#30), through to those warmer waters which have a more southerly origin and in which there is a greater mixing with Mediterranean water, resulting in a higher salinity maximum at ca. 930–950 m (#97). In addition, at the latter station the salinity minimum is shallower, ca. 510 m, as compared with ca. 630 m for the more northerly waters, at which depth these waters are some 0.3 to 0.4°C colder than the others. These differences are exemplified by marked changes in the depth of the 10.8°C isotherm, ranging from 830 m in the more northerly waters to 570 m in the more southerly ones [Fig. 13(a)].

Taking all the STD casts into account (see aforementioned figures) one finds the more northerly waters at #8, 30 and 72, while intermediate waters are found at #22 and 35. The more southerly waters are present at all of the remaining stations figured. Since these STD casts were taken over a period of 23 days one might assume that the frontal feature is fairly stable in its position. However, some STD casts taken on later cruises indicate a shift in the front's position. Nonetheless the presence of this front could help to explain the anomalous depth distributions of ostracods which ANGEL (1977) reported, since the relevant hauls were made on both sides of the frontal region. From the point of view of the 48 hr series of hauls however, it transpires that the area within which they were taken is, according to the STD casts, entirely in the region of the more southerly waters, with the frontal region lying to the north-west. Thus, it is considered that there was no great change in the water column during any of the 48 hr series and it was unlikely that any mesoscale activity affected the results from the 600 m series.

Although relatively few of the siphonophore species collected during the four 48 hr series appear to undergo obvious diel vertical migrations one should note, as discussed by PEARRE (1979), that the lack of any synchronous migration pattern by an individual species does not preclude any asynchronous one. However, the nature of the present sampling programme does not allow any conclusions to be reached on this matter. There are a few other studies on the

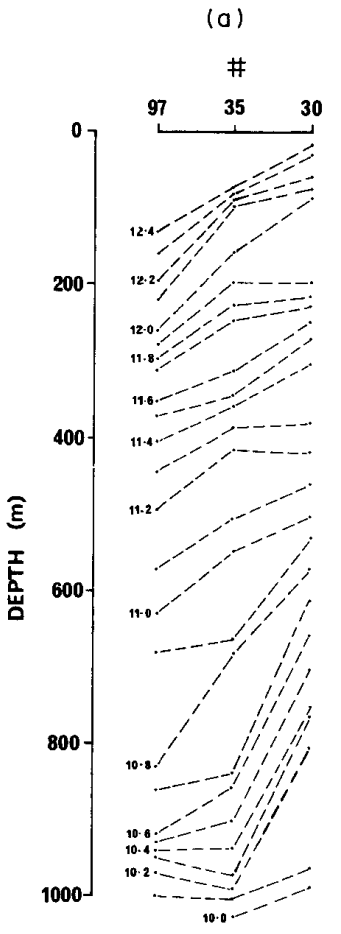

FIG. 13(a). The temperature structure of the top, 1,000 m of the water column at three stations in the vicinity of 44° N 13° W. See text for details.

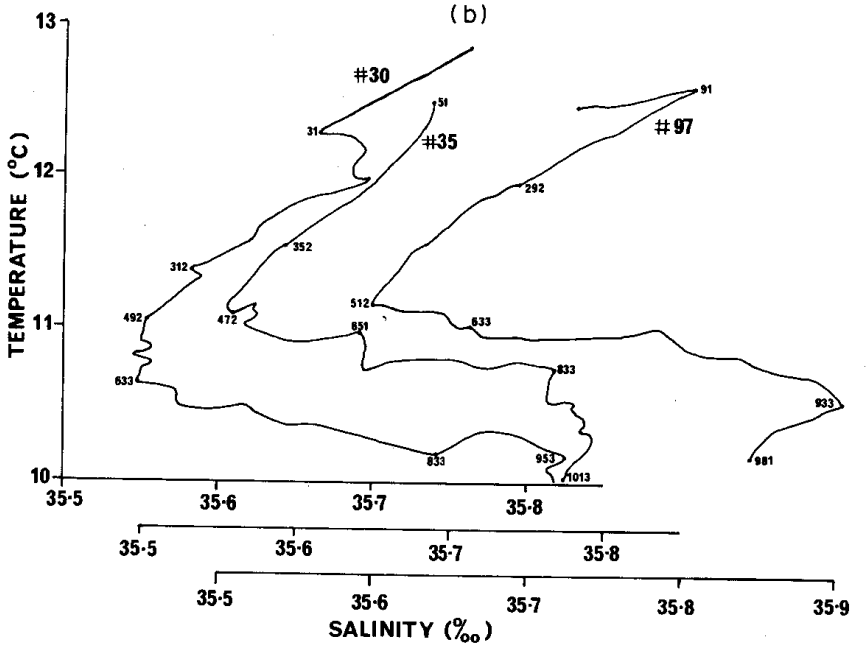

FIG. 13(b). *T/S* curves for the same stations.

diel vertical migration of siphonophores, e.g. MOORE (1949), MUSAYEVA (1976), but comparisons often are difficult to make. Thus, MUSAYEVA (1976) found that differences in the hydrological conditions in the Indian Ocean had a great effect both on the actual vertical distribution of siphonophore species in general and on the intensity and range of their diel vertical migrations. Similarly, the depth ranges for diel vertical migration in the 24 hr series of hauls at 250 m at 30°N 23°W (PUGH, 1977) were greater than at the present site. However, in the case of the siphonophore it is not clear whether there is a latitudinal change in the percentage number of migrant species, as ANGEL (1977) found for the ostracods. The number of siphonophore species in the top 2,000 m of the water column is greatest, in the North Atlantic Ocean, at 18°N (PUGH, 1977) and there is a progressive decrease northwards. This decline in numbers is mainly due to the disappearance of the near-surface living, warm-water species such as the abylids and *Sulculeolaria* species, but it is likely that the decrease in potential diel migrants is commensurate with the overall decrease in numbers. For instance, the decrease in the siphonophore population results in the absence, at 44°N 13°W, of the rapidly migrating abylid, *Ceratocymba sagittata* (QUOY and GAIMARD, 1827) which passed rapidly through the 250 m depth zone at dawn and dusk in the 24 hr series at 30°N 23°W. The more northerly siphonophore populations tend to be dominated by those species which have a poor swimming ability e.g. *Rosacea plicata* and the hippopodiid species, and the more streamlined forms are less common, with the notable exception of *Lensia conoidea*.

The diel vertical migration of those siphonophore species, where it was apparent, appeared to be correlated with the diel light cycle. As PUGH (1977) has discussed, the reasons for such a correlation are not clear since it is not obvious how siphonophores are able to sense light, although they undoubtedly can. MACKIE (1964) showed that the stem region is sensitive to flashes of light, and PURCELL (1981a, b) has demonstrated that certain siphonophores feed only during periods of darkness or light, irrespective of the time of day at which these occur. None the less it seems unlikely that siphonophores are able to distinguish relatively small changes in light intensity, although MOORE (1949) has correlated the surface abundance at night of certain species with the phase of the moon. Probably these animals are sensitive to orders of magnitude change in light intensity which may then initiate a vertical migration. However, even if light is the proximal stimulus for vertical migration, it is thought not to control the depth limits of that migration. Temperature probably is one of the controlling factors here particularly with regard to the daytime depth distribution, for MOORE (1949) noted that the daytime depth distribution for several siphonophore species was correlated with the depth of the 15°C isotherm, and MUSAYEVA (1976) has made many further observations. However, this may not be the case at the present site under consideration for there is very little temperature structure in the water column (Fig. 13), but on the other hand this could be associated with the more diffuse and widespread depth distributions noted for some species. Thus, MUSAYEVA (1976) commented that the deeper a siphonophore species lived the greater was the depth range over which it was spread.

The possibility that light intensity was affecting the depth distribution of some siphonophore species in the present 48 hr series of hauls was considered earlier, but interestingly enough the anomalous distributions mainly were found with those species which were considered to be non-migrants e.g. *Dimophyes arctica*. The significant differences between the mean numbers of animals present on the two successive days were, however, not though to be caused by the differences in light intensity. Indeed significant differences often were found between the two night mean numbers, which would seem to indicate the influence of other factors. However, the possible effects of differences in the daily isolation are discussed with

relation to the other groups of animals, e.g. ROE *et al.* (1984) and ANGEL (1984), where the diel vertical migration patterns are more pronounced.

Because of the narrow depth ranges over which some of the siphonophores were migrating or, conversely, the broad intervals between the depth zones sampled in these 48 hr series, it is difficult to make any estimates of migration rates. In most cases the diel migration resembles a sinusoidal wave-pattern, although probably with some "stationary time" (PEARRE, 1979) at the extremes of its depth range, particularly for those species with a diel feeding behaviour. PUGH (1977) pointed out that the weakly-swimming siphonophore species, such as *Rosacea plicata* or *Vogtia* spp., might accomplish their observed vertical migrations only if they swam, vertically, almost continuously, allowing little time for any feeding, since the fishing and swimming cycles usually are distinct (BIGGS, 1977). However, there is probably some ionic or biochemical control of buoyancy which may facilitate such vertical migrations (JACOBS, 1937). Indeed, BIDIGARE and BIGGS (1980) have shown that there is active exclusion of heavy sulphate ions in siphonophores which would aid in buoyancy control.

The part which siphonophores play in the planktonic food chain is of particular importance in the area under study where these and other gelatinous organisms totally dominate the macroplankton–micronekton size group of animals. PURCELL (1980, 1981a, b, 1983) has shown that siphonophores are by no means unselective predators, but that they have often complex feeding strategies. For example, PURCELL (1981b) found that *Hippopodius hippopus* (FORSKÅL, 1976) fed exclusively on ostracods. It would be interesting if one could extrapolate this dietary requirement to all the hippopodiid species e.g. those of the genus *Vogtia*. PUGH (1974) commented on the possible niche positionining in these species, noting relatively little overlap in their day time depth distribution. This is not so clear cut in the present data sets, although *V. spinosa* was found mainly at 250 m, while *V. glabra* occurred down to 450 + m by day migrating to a minimum of 250 m by night. *V. serrata* was generally a little deeper although part of its population reached 250 m at night. About 90% of the overall ostracod population was found in the 450 and 600 m 48 hr series (ANGEL, 1984), which would appear to be too deep for some of the *Vogtia* species, but there was a considerable migration of ostracods into the 250 m depth zone by night, and 18.6% of the nocturnal population was found at that depth. One could speculate in addition that the absence of the near-surface dwelling species, *H. hippopus*, in more temperate waters was related to the relatively low number of ostracods to be found at these depths in such waters (cf. ANGEL, 1977).

The interaction of siphonophore species in the concept of niche partitioning thus need not come only from different feeding strategies, so that co-occurring species are not in direct competition, but could come also from a depth stratification of closely related species. However, siphonophores are not the only predators and animals of other taxa are competing for the same food source. In addition there are the species specific relationships, ranging from phoresis to parasitism, which many amphipod species have with gelatinous organisms (HARBISON, BIGGS and MADIN, 1977). Thus, one should not consider the population dynamics of a single taxon of planktonic organisms without regard to all the other taxa with which those organisms interact, but such a concept cannot be covered in this paper.

5. SUMMARY

Siphonophores are by far the dominant macroplanktonic–micronektonic taxon of animals present in the 48 hr series of samples as a whole. A total of 35 species were identified, with four of these making up over 90% of the total numbers. Details of how the siphonophore population

was estimated are discussed, but few species underwent clear cut diel vertical migration although there was considerable variability in their distributions over the sampling periods. The hydrography of the sampling area was investigated in relation to its possible effects on the faunal assemblages, and the important role of siphonophores as carnivores in the planktonic food chain was discussed.

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APPENDIX 1

A1.1. *Method for the estimation of siphonophore population abundance*

There are several problems associated with the estimation of the total number of specimens of siphonophores present in any net sample, but we will deal here only with that arising from the general morphology of the individual specimens, i.e. how many pieces make a whole. Siphonophores come in three basic forms depending on the presence or absence of a pneumatophore (gas-filled float) and/or nectophores (swimming bells). The first type, the cystonects, have a pneumatophore but no swimming bells *per se*. These species are generally robust and their presence in a sample would be indicated by a typical float and stem. None were found in the present samples. The assessment of the numbers of individuals of the second type, the physonects with both float and nectophores, is more difficult. Although each individual bears a single float, this float is usually small and is rarely found in net samples, but the presence of nectophores and other components indicates that a specimen has been captured. However, it is difficult to make quantitative estimates from the number of nectophores present for despite their loss through the netting as the specimen disintegrates, the number of nectophores per specimen is not only specifically variable but also increases with the age of the specimen, although probably reaching a maximum after a certain time. Notwithstanding this, the physonect siphonophores play only a minor role in the present series of samples, except for a few in the 100 m series. Thereby the errors involved in considering the total number of nectophores to represent the total number of physonect individuals are negligible. This is exemplified by considering the percentage contribution of the physonect nectophores to the total number of siphonophores, thus:–

	% Physonects	
48 hr Series	Day	Night
100 m	13.7	3.6
250 m	0.5	1.1
450 m	0.1	0.1
600 m	0.2	0.09

The calycophoran siphonophores, those without pneumatophores, present further problems when attempts are made to assess their population numbers. Most prominent of these is due to the typically hydroid alternation of generations between the asexual, polygastric stage and the similarly free-swimming sexual or eudoxid stage, both of which stages being countable as individuals in the present analysis. This is not a problem in itself but the eudoxid stages develop on the stem of the other (polygastric) stage and are detached only when fully mature. Further, it is not possible, in most cases, to distinguish between the more fully developed components which are still attached to the stem and the free-swimming eudoxids, so that, by counting all the apparent eudoxids, this latter number of individuals may be overestimated. However, the only species in the present series where the eudoxid stage components were present in any significant numbers was *Chuniphyes multidentata*, and the results show that the proportion of polygastric to eudoxid stages was not a constant for the former stage dominated the 250 m 48 hr series while the latter likewise in the 450 and 600 m series. Thus it was reasonable to assume that the eudoxid stage components represented separate 'individuals' from the polygastric stage nectophores. In the case of *Ch. multidentata* eudoxids it was the gonophores which were counted, the eudoxid bracts being minute and easily lost. It is assumed, and there are no observations to contradict it, that only one gonophore was associated with each eudoxid bract.

In the majority of calycophoran species belonging to the families Diphyidae, Clausophyidae and Abylidae, the polygastric stage includes only two dissimilar nectophores, called anterior and posterior. The number of anterior nectophores in each sample usually were taken to represent the number of individuals present. In these cases there should have been no overestimation of the population, rather an underestimate due to net losses. In the family Prayidae, the Nectopyramidinae develop a single definitive nectophore only, while the Amphicaryoninae develop two different ones. Of the prayine species, *Rosacea plicata* was the only one present in any significant numbers. Two, sometimes more, similar nectophores are developed but, due to the uncertainties of net losses and developmental stage, the total number of nectophores was taken to represent the number of polygastric individuals present. This assumption would have a significant effect only on the 250 m 48 hr series, as the percentage contribution of individual *R. plicata* nectophores to the total estimated numbers shows:–

#m	Day	Night
100	0.9	1.7
250	34.4	30.9
450	2.8	2.0
600	1.6	1.3

Finally, in the family Hippopodiidae, the total number of nectophores again is used to assess the population density, even though up to fifteen, in some species, nectophores may be present in a polygastric individual. Once again net losses are assumed to play a considerable role here, but nonetheless the percentage contribution of *Vogtia* spp. to the whole is low, namely:–

#m	Day	Night
100	5.9	1.5
250	6.0	6.0
450	8.5	5.5
600	1.4	1.6

To assess the possible differences to the estimation of siphonophore population numbers if the above correction had been made, let us divide the physonect and hippopodiid numbers by ten, the prayine ones by two and take the rest as is. This would result in the population numbers having to be reduced from the present estimates to the following percentages:–

m	Day	Night
100	81.8	94.5
250	76.9	78.2
450	90.9	94.0
600	97.7	97.8

Such alterations are considered not to make any great difference to the conclusions which are drawn and discussed in this paper.